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Responses of CH_4 uptake to the experimental N and P additions in an old-growth tropical forest, Southern China

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Abstract

It is well established that tropical forest ecosystems are often limited by phosphorus (P) availability, and elevated atmospheric nitrogen (N) deposition may further enhance such P limitation. However, it is uncertain whether P availability would affect soil fluxes of greenhouse gases, such as methane (CH_4) uptake, and how P interacts with N deposition. We examine the effects of N and P additions on soil CH_4 uptake in an N saturated old-growth tropical forest in Southern China to test the following hypotheses: (1) P addition would increase CH_4 uptake; (2) N addition would decrease CH_4 uptake; and (3) P addition would mitigate the inhibitive effect of N addition on soil CH_4 uptake. Four treatments were conducted at the following levels from February 2007 to October 2009: control, N-addition ($15\,g\,N\,m^{-2}\,yr^{-1}$), P-addition ($15\,g\,P\,m^{-2}\,yr^{-1}$), and NP-addition ($15\,g\,N\,m^{-2}\,yr^{-1}$ plus $15\,g\,P\,m^{-2}\,yr^{-1}$). Static chamber and gas chromatography techniques were used to quantify soil CH_4 uptake every month throughout the study period. Average CH_4 uptake rate was $31.2 \pm 1.1\,\mu g\,CH_4\text{-}C\,m^{-2}\,h^{-1}$ in the control plots. The mean CH_4 uptake rate in the N-addition plots was $23.6 \pm 0.9\,\mu g\,CH_4\text{-}C\,m^{-2}\,h^{-1}$, significantly lower than that in the controls. P-addition however, significantly increased CH_4 uptake by 24 % ($38.8 \pm 1.3\,\mu g\,CH_4\text{-}C\,m^{-2}\,h^{-1}$), whereas NP-addition ($33.6 \pm 1.0\,\mu g\,CH_4\text{-}C\,m^{-2}\,h^{-1}$) was not statistically different from the control. Our results suggest that increased P availability may enhance soil mathanotrophic activity and potentially mitigate the inhibitive effect of N deposition on CH_4 uptake in tropical forests. Phosphorus and nitrogen treatments also significantly changed the fluxes of greenhouse gases N_2O and CO_2, altering the net global warming potential (GWP) of this tropical forest located in a high-N deposition zone of Southern China.

1 Introduction

Methane (CH_4) is considered the second most important greenhouse gas after carbon dioxide (IPCC, 2001). Despite its low concentration (global average 1.7 ppm)

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and short residence time in the atmosphere (about 12 yr), its high ability to absorb infrared radiation makes CH_4 20 times more efficient compare to carbon dioxide (CO_2) (Blake and Rowland, 1988; Rodhe, 1990; IPCC, 2007). The global atmospheric concentration of CH_4 has increased from a pre-industrial value of about 0.715 ppm to 1.732 ppm in the early 1990s, and 1.803 ppm in 2009 (IPCC, 2007; WMO, 2010), due primarily to the anthropogenic emissions from energy production, rice cultivation, ruminant animals, biomass burning, and landfills (IPCC, 2007). Major CH_4 sinks include tropospheric oxidation ($\sim 500\,Tg\,yr^{-1}$) and stratospheric loss ($\sim 40\,Tg\,yr^{-1}$) (Hein et al., 1997; Lelieveld et al., 1998). Soil is another major sink of atmospheric CH_4, which consumes CH_4 through the activity of methanotrophs under aerobic conditions ($\sim 30\,Tg\,CH_4\,yr^{-1}$) (Lelieveld et al., 1998).

Soils as biological sinks of CH_4 are subjected to many abiotic and biotic controls, including temperature and moisture (Steudler et al., 1989; Davidson and Nepstad, 2004), acidity (Saari et al., 2004; Xu and Inubushi, 2009), gas diffusivity in relation to soil bulk density and texture (Tate et al., 2007), vegetation and land-use (Menyailo et al., 2008; Pendall et al., 2010), as well as soil fauna (Bignell et al., 1997). Furthermore, nutrient availability, such as ammonium, nitrate, and phosphorus (P), could affect microbial activities and methane-mono-oxygenase (MMO) activity in soil and, consequently, CH_4 flux from the soil (Le Mer and Roger, 2001). Among these factors, the effects of nitrogen (N) deposition on CH_4 oxidation have received increasing attention (Steudler et al., 1989; Bodelier and Laanbroek, 2004; Tate et al., 2007). Nitrogen addition alters the fluxes of greenhouse gases (GHGs, including CH_4) through regulating plant and microbial activities that are directly associated with GHGs production and consumption (Liu and Greaver, 2009). Steudler et al. (1989) first reported in a temperate forest that nitrogen (N) fertilization reduced soil CH_4 uptake by 33 %. Extensive research has been conducted to investigate the relationship between CH_4 consumption and N input and it has been generally accepted that CH_4 uptake is inhibited by nitrogenous fertilization (Bodelier and Laanbroek, 2004; Chan et al., 2005; Zhang et al., 2008). Competition of MMO sites between nitrification and methane oxidation is generally

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considered the major cause of methanotroph inhibition (King and Schnell, 1994; Dunfield and Knowles, 1995; Steinkamp et al., 2001). Aluminium toxicity after extensive N input may also inhibit soil CH_4 uptake (Bradford et al., 2001; Zhang et al., 2008). On the other hand, positive effects of increased nitrogen availability on CH_4 uptake rates were found in severely N-limited forests (Börjesson and Nohrstedt, 2000; Steinkamp et al., 2001). Soil available phosphorus also affects CH_4 flux by regulating changes in soil physico-chemical properties, plant root activities, and soil microbial activities that are directly involved in CH_4 consumption and emission. Furthermore, phosphorus availability could affect litter-decomposing fauna in tropical forests (McGlynn et al., 2007), which may influence CH_4 flux.

While N is often the primary limiting nutrient in temperate and boreal forests, P usually limits ecological processes in tropical and subtropical forests (Vitousek and Sanford, 1986; Cleveland et al., 2002; Vitousek et al., 2010). P-limited forests growing on highly weathered soils (where N cycles quickly) may respond differently to N deposition than N-limited forests (Hall and Matson, 2003). For example, chronic N deposition could lead to soil acidification and then the acidic soils, rich in iron and aluminum oxides, react with labile inorganic P, fixing P into insoluble forms (Matson et al., 1999). Furthermore, P deficiency is likely to result in less carbon (C) fixation and storage in soil, and less microbial growth (Matson et al., 1999). Low P availability would therefore affect the fluxes of major GHGs including CH_4 through the change of soil microbial activity.

We studied the relationships between soil P availability and CH_4 flux in an old-growth tropical forest located in Southern China where elevated N deposition has been well documented (Mo et al., 2006; Fang et al., 2009, 2011). Previous studies have shown this old-growth forest is N saturated due to long-term atmospheric N input and age (Mo et al., 2006). Studying forest CH_4 uptake and its relationship with soil available P and elevated N deposition is very important for evaluating the contribution of tropical forests to global climate change. Due to limited research in tropical forests, it is not clear how P availability would affect soil CH_4 uptake, and how P addition may interact

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with N deposition. This 33 months study experimentally tested the effects of P and N availabilities on soil CH_4 uptake. We hypothesized that: (a) P addition would increase CH_4 uptake; (b) N addition would decrease CH_4 uptake; and (c) P addition would mitigate the inhibitive effect of N addition on soil CH_4 uptake.

2 Materials and methods

2.1 Site description

This study was conducted in the 1200 ha Dinghushan Biosphere Reserve (DHSBR), which is located in the middle of Guangdong Province, Southern China (112°10′ E, 23°10′ N). There are three major forest types in the reserve, a pine forest, a mixed pine and broadleaf forest (mixed forest), and an old-growth evergreen broadleaf forest (mature forest) (Zhou et al., 1986). The average annual precipitation of 1927 mm in the reserve has a distinct seasonal pattern, with 75 % falling from March to August and only 6 % falling from December to February (Huang and Fan, 1982). The mean annual temperature is 21 °C with the January mean temperature of 12.6 °C and July mean temperature of 28.0 °C (Huang and Fan, 1982). Annual mean relative humidity is 80 % (Huang and Fan, 1982). The wet N deposition was 36–38 kg N ha^{-1} in the 1990s (Zhou and Yan, 2001). In the year of 2004 and 2005, N deposition was measured as 34 kg N ha^{-1} and 32 kg N ha^{-1}, respectively (Fang et al., 2006), with roughly 1 : 1 NH_4^+ to NO_3^- molar ratio (Fang et al., 2007). Monthly precipitation and temperature during the study period are displayed in Fig. 1.

The old-growth mature forest has been well protected from human activities for more than 400 yr (Wang et al., 1982; Mo et al., 2003; Tang et al., 2006). Major species in the old-growth forest are *Castanopsis chinensis* Hance, *Schima superba* Chardn. and Champ., *Cryptocarya chinensis* (Hance) Hemsl., *Cryptocarya concinna* Hance, *Machilus chinensis* (Champ. Ex Benth.) Hemsl., *Syzygium rehderianum* Merr. and Perry in the tree layer and *Calamus rhabdicladus* Burret, *Ardisia quinquegona*

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Bl. and *Hemigramma decurrens* (Hook.) Copel. in the understory layer (Wang et al., 1982). The mean annual litter biomass production was 8.3 Mg ha^{-1} yr^{-1} (Zhang et al., 2000). Stem density, tree height and mean diameter at breast height are summarized in Table 1.

Soil in the reserve is oxisols from shale formation (Wu et al., 1982). The soil depth in the old-growth forest is more than 60 cm to the top of the C horizon (Mo et al., 2003). The forest in this experiment is situated on mountain slopes about 30°–35°. General soil properties are listed in Table 2.

2.2 Experimental treatment

Four treatments were established (each with five replicates) in 2007: control, N-addition (15 g N m^{-2} yr^{-1}), P-addition (15 g P m^{-2} yr^{-1}), and NP-addition (15 g N m^{-2} yr^{-1} plus 15 g P m^{-2} yr^{-1}). A total of 20 plots of 5 m × 5 m were established and each plot was surrounded by a 5-m-wide buffer strip. Plots size and fertilizer level were referenced to the experiment in Costa Rica by Cleveland and Townsend (2006). Field plots and treatments were laid out randomly. NH_4NO_3 and NaH_2PO_4 solutions were sprayed once every other month to the forest floor with a backpack sprayer starting from February 2007 and continued through October 2009. Fertilizer was weighed and mixed with 5 l of water for each plot. Each control plot received 5 l of water without fertilizer.

2.3 Field sampling and measurements

CH_4, CO_2 and nitrous oxide (N_2O) flux were measured from January 2007 before the first fertilizer application. Static chambers were installed in each plot in November 2006, two months before the gas sampling. Gas fluxes were monitored once every month using the static chamber and a gas chromatograph (Agilent 4890D). The static chamber was a 25-cm-diameter by 16-cm-tall PVC pipe permanently anchored 8 cm into the soil. During gas collection, a 30-cm-tall removable cover chamber was attached tightly to the anchor ring with a rubber band. Gas samples were collected from

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each chamber from 09:00–10:00 LT. Diurnal studies in the adjacent forests found that greenhouse gas fluxes measured during the mid-morning (09:00–10:00 LT) were closer to the daily means (Tang et al., 2006). The GHG concentrations remained linear for up to 100 min after the chamber was closed in our study. Gas samples were taken with a 60 ml plastic syringe at 0 and 30 min after the chamber closure. Before each sampling, syringes were flushed three times with chamber gas to mix the headspace. Laboratory tests showed that chambers and syringes were inert to N_2O, CO_2, and CH_4 (Steudler et al., 1989; Bowden et al., 1990). Gas samples were analyzed within 12 h in a gas chromatograph (Agilent 4890D) fitted with a flame ionization detector (FID) for CH_4 and CO_2, and an electron capture detector (ECD) for N_2O. CO_2 was transformed into CH_4 via (Ni)H_2 before the FID analysis. Calibration gases (CH_4 at 1.87 ppm, CO_2 at 418 ppm, N_2O at 0.321 ppm, bottle's No. 070811) were obtained from the Institute of Atmospheric Physics, Chinese Academy of Sciences.

The calculation of GHG flux followed that described in Zhang et al. (2008), based on a linear regression of chamber gas concentration versus time (IAEA, 1992; Holland et al., 1999). Atmospheric pressure was measured at the sampling site using an air pressure gauge (Model THOMMEN 2000, Switzerland). Air temperature (enclosure), soil temperature (at 5 cm depth) and moisture (0–10 cm depth) were measured during each sampling. Soil moisture content was detected using a TDR-probe (Time Domain Reflectometry, Model Top TZS-I, China). Soil moisture (0–10 cm depth) values were converted to WFPS (Water Filled Pore Space) according to the following formula:

$$\text{WFPS}\,[\%] = \text{Vol}\,[\%]/(1 - \text{SBD}\,[\text{g cm}^{-3}]/2.65\,[\text{g cm}^{-3}]) \quad (1)$$

Where SBD is soil bulk density, Vol is volumetric water moisture and 2.65 is the density of quartz.

Soil samples were collected in February 2007 (before the first fertilizer application) and February 2009 (after two years of fertilization) for the quantification of soil chemistry and biology. Five soil cores (2.5 cm inner diameter) were collected randomly from each of the 20 plots at 0–10 cm soil depths and combined to one composite sample.

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The litter layer was carefully removed before the soil sampling. The pH of the soil sample was measured in a 1 : 2.5 soil/water suspension. Soil microbial biomass carbon (MBC) was estimated by the chloroform fumigation-extraction method (Vance et al., 1987). Soil organic carbon (SOC) was determined by dchromate oxidation and titration with ferrous ammonium sulfate. Dissolved organic carbon (DOC) was extracted with 0.5 M K_2SO_4 and analyzed using a total carbon analyzer (Shimadzu model TOC-500, Kyoto, Japan). Total N concentration was determined by the micro-Kjeldahl digestion followed by the analysis of ammonium on a Wescan ammonia analyzer, while total P concentration was analyzed colorimetrically after acidified ammonium persulfate digestion (Anderson and Ingram, 1989). Available P was extracted with 0.03 M ammonium fluoride and 0.025 M hydrochloric acid and analyzed colorimetrically.

2.4 Statistical analysis

Repeated measures Analysis of Variance (ANOVA, PROC MIXED with AR(1) from SAS (SAS Institute Inc., Cary NC, USA)) was used to examine the effect of fertilizer treatments on soil GHG fluxes from February 2007 to October 2009. Two-way ANOVA (PROC GLM from SAS) was used to examine the effects of N and P addition. One-way ANOVA was used to examine the difference in soil pH, NH_4^+, NO_3^-, and available P among treatments. Linear regression analysis was performed by Origin 8.0 (OriginLab Corporation, Northampton, MA USA) to examine the relationship between CH_4 fluxes and soil WFPS contents and soil temperature. Out of 680 observations three were identified as outliers, which were probably caused by chamber leaks, abnormally high WFPS, and other unknown factors, and were removed from the data analyses. Statistical significant differences were set at p values < 0.05 unless otherwise stated. Mean values ±1 standard error are given in the text.

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3 Results

3.1 Climate and soil microclimate in the 33 months study period

Our study site located in Southern China has a distinct dry-wet climate, with warm-wet seasons of spring (April to June) and summer (July to September) and cool-dry seasons of fall (October to December) and winter (January to March) (Fig. 1). Annual precipitation from 2007 to 2009 averaged 1947.7 mm, close to the long-term mean of 1927 mm (Wu et al., 1982). Total precipitation in 2007 (1382.4 mm) was 28.3 % lower while precipitation in 2008 (2639.7 mm) and 2009 (1821.0 mm) was 37.0 % and 5.3 % higher compared to the long-term average. Precipitation in the growing season (April to September) was 84.5 % of the yearly total in 2007, 79.7 % in 2008, and 76.9 % in 2009. Monthly air temperature averaged 22.5 °C from 2007 to 2009, with a mean January temperature of 13.0 °C and a mean July temperature of 29.3 °C. No difference in air temperature was observed ($p = 0.64$) between years (Fig. 1).

Soil temperature (at 5 cm depth) followed the air temperature in all plots, with temperatures increased from spring to summer and decreased from fall to winter (Fig. 2a). There was no treatment effect on soil temperature during the study period. Soil WFPS (0–10 cm depth) rose following the increased precipitation from dry winters to wet springs but decreased in summer, possibly due to plant uptake and higher evaporation, despite the high amount of precipitation in summer (Fig. 2b). Repeated measurement ANOVA showed that soil WFPS was significantly lower in the P-addition and NP-addition plots ($p = 0.011$ and $p = 0.018$, respectively) whereas N-addition had no effect ($p = 0.165$).

3.2 Other soil properties

Nitrogen and P treatments significantly changed soil nutrient conditions (Table 3). After 24 months of the treatment, a six fold of soil available P was observed in P-addition plots ($p = 0.0003$) and four fold in NP-addition plots ($p = 0.012$), compared to the

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controls. Furthermore, total P was significant lower in N-addition plots compared to control plots ($p = 0.001$). Soil NH_4^+ concentrations did not show any significant change in any treatment plots (N-addition, P-addition and NP-addition) compared to the controls ($p = 0.163$, 0.152 and 0.368, respectively). However, soil NO_3^- concentrations were significantly lower in P-addition and NP-addition plots ($p = 0.0031$ and 0.0029, respectively) while no change in N-addition plots ($p = 0.339$). Soil pH increased significantly in P-addition plots ($p = 0.021$) and was a little higher in NP-addition plots ($p = 0.062$) while no change in N-addition plots ($p = 0.933$). On the other hand, MBC, SOC, DOC, and total N were not affected by any treatments.

3.3 Soil CH_4 fluxes

Pre-treatment gas measurement (January 2007) showed no difference in different treatment plots compared to control plots ($p = 0.807$, 0.559 and 0.961, respectively in N, P, NP treatment plots). After fertilization treatment, repeated measurement ANOVA showed that P addition significantly increased soil CH_4 uptake while N addition significantly decreased CH_4 uptake (Fig. 3). The mean soil CH_4 uptake rate was $31.2 \pm 1.1\,\mu g\,CH_4\text{-}C\,m^{-2}\,h^{-1}$ in the control plots during the 33 months study period. Soil CH_4 uptake in the P-addition plots was significantly higher (mean CH_4 uptake rate was $38.8 \pm 1.3\,\mu g\,CH_4\text{-}C\,m^{-2}\,h^{-1}$, $p = 0.0068$). On the contrary, N-addition significantly inhibited soil CH_4 uptake (mean CH_4 uptake rate was $23.6 \pm 0.9\,\mu g\,CH_4\text{-}C\,m^{-2}\,h^{-1}$, $p = 0.007$). No significant difference was observed between NP-addition plots ($33.6 \pm 1.0\,\mu g\,CH_4\text{-}C\,m^{-2}\,h^{-1}$) and the controls ($p = 0.177$).

CH_4 uptake was higher in summer and fall (when the soil was low in water content) and was lower in spring (when the soil was wet) and winter (when the soil was cold). Two-way ANOVA showed a significant positive P effect on CH_4 uptake in the summers of 2007, 2008, and 2009, fall 2007, and the springs of 2008 and 2009 (Fig. 4), and a negative N effect in the springs of 2008 and 2009, and summer 2009 (Fig. 4). In summer 2007, CH_4 uptake in the P-addition and NP-addition plots was 26.6 % and

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27.3 % higher than in the control plots ($p = 0.049$ and 0.051, respectively). CH_4 uptake in N-addition plots was reduced by 30.3 % in fall 2007 ($p = 0.052$), 39.1 % in spring 2008 ($p = 0.034$) and 36.7 % in spring 2009 ($p = 0.027$). In addition, CH_4 uptake was increased by 30.6 % in P-addition plots in summer 2009 ($p = 0.038$).

CH_4 fluxes and soil WFPS were positively correlated in both the control plots and N and P addition plots (Fig. 7). Under similar WFPS conditions, CH_4 uptake was the highest in P-addition plots and lowest in N-addition plots. CH_4 flux was not correlated to soil temperature.

3.4 N_2O and CO_2 fluxes

Nitrogen and P additions also significantly altered N_2O and CO_2 fluxes from forest soils, but fluxes of N_2O and CO_2 had very different seasonal patterns (and when treatments had significant effects) compared to the CH_4 flux (Figs. 3–6). The mean soil N_2O flux was $14.0 \pm 0.7\,\mu g\,N_2O\text{-}N\,m^{-2}\,h^{-1}$ in the control plots over the 33 months study period. Repeated measurement ANOVA showed that N-addition significantly increased N_2O emission ($p = 0.030$) while P-additions had no effect (Fig. 3). The mean soil N_2O flux were 17.4 ± 1.1, 14.0 ± 0.8 and $15.9 \pm 0.9\,\mu g\,N_2O\text{-}N\,m^{-2}\,h^{-1}$ in the N-addition, P-addition and NP-addition plots, respectively. Soil N_2O fluxes were the highest in spring and summer (when the soil was wet and warm) and the lowest in winter (when the soil was cold and dry) (Fig. 5). Two-way ANOVA showed a significant positive N effect in spring 2007 and a positive P effect in summer 2009. Interactive effect of N and P was detected in winter 2008.

The mean soil CO_2 flux in the control plots was $71.2 \pm 2.8\,mg\,CO_2\text{-}C\,m^{-2}\,h^{-1}$ over the 33 months study period. Repeated measurement ANOVA showed no significant negative effect from N addition (mean soil CO_2 flux was $69.9 \pm 2.9\,mg\,CO_2\text{-}C\,m^{-2}\,h^{-1}$, $p = 0.808$). However, soil CO_2 flux was significantly increased by both P addition (mean CO_2 flux was $88.4 \pm 4.1\,mg\,CO_2\text{-}C\,m^{-2}\,h^{-1}$, $p = 0.033$) and N plus P addition (mean CO_2 flux was $86.5 \pm 3.5\,mg\,CO_2\text{-}C\,m^{-2}\,h^{-1}$, $p = 0.048$) (Fig. 3). Soil CO_2 fluxes were

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the highest in spring and summer (when soil was warm and wet) and the lowest in fall and winter (when soil was cold and dry) (Fig. 6). Two-way ANOVA showed a significant positive P effect on CO_2 flux in the summers of 2007, 2009 and spring 2009 (Fig. 6), while no N effect was detected.

Net GWP from CH_4 and N_2O were altered by fertilizer application. Compared to the controls, net GWP of P-addition plots decreased by 4.6 % while N-addition plots increased by 34.0 %, over the 33 months of measurements. The combined N plus P addition increased net GWP by 15 %, mainly due to increased N_2O emission.

4 Discussion

The annual CH_4 uptake rates in our old-growth tropical forest site in Southern China ranged from 2.3 to 3.4 kg CH_4-C ha^{-1} yr^{-1} (11 months in 2007, 12 months in 2008, 10 month in 2009), and were higher in the dry year (2007) than in the wet year (2008). The CH_4 fluxes quantified in this study are similar to the previous reported CH_4 fluxes measured at an adjacent forest (Tang et al., 2006; Zhang et al., 2008) and other parts of tropical Southwest China (Werner et al., 2006; Yan et al., 2008; Wang et al., 2010). The rates of CH_4 uptake in other tropical forests are also similar, ranging from 0.8 to 4.73 kg CH_4-C ha^{-1} yr^{-1} (Steudler et al., 1991; Kiese et al., 2003; Davidson and Nepstad, 2004; Davidson et al., 2008).

Soil CH_4 uptake was negatively correlated with the soil WFPS (a better measurement of soil moisture) in this study (Fig. 7), which was consistent with previous publications (Born et al., 1990; Castro et al., 1995; Kiese et al., 2003). Higher WFPS often lead to lower soil aeration and reduced CH_4 oxidation. Steinkamp et al. (2001) similarly reported that soil moisture was the dominant factor controlling CH_4 uptake when soil temperature was $> 10\,^{\circ}C$. Temperature variation has a minor impact on soil CH_4 uptake in the tropical forest we studied, which is consistent with previous results (Tang et al., 2006). In temperate or boreal regions, in contrast, soil CH_4 oxidation was generally positively correlated with soil temperature (Crill, 1991; King, 1997). Castro et al. (1995)

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observed that methanotrophy was affected by soil temperature between −5 and 10 °C, but in our site, almost all of soil temperatures were between 10 and 30 °C (Fig. 2a).

We found P addition significantly increased CH_4 uptake, N addition decreased CH_4 uptake, and P addition mitigated the negative N effect in this 33 months field experiment, as hypothesized. The treatment effects were particularly strong in the summers and falls, when soil uptakes of CH_4 were the highest (Fig. 4). We believe this is the first experimental testing of N and P limitation on soil CH_4 flux in tropical and subtropical forests. Since phosphorus is a common limiting nutrient in tropical forests (Herbert et al., 2003; Wardle et al., 2004), microbial usage of soil C could be strongly P limited (Cleveland et al., 2002). Increased soil CH_4 uptake in this study may be due to stimulated methanotroph activities after increased P availability in soil. A companion study we found that microbial biomass carbon was increased significantly by P addition both in dry and wet seasons when adjusted for pre-treatment differences (Liu et al., 2011). Treseder and Allen (2002) observed that biomass of arbuscular mycorrhizal (AM) fungi was increased by P addition in a P-limited Hawaiian rain forest. Increased phosphorus concentration may also increase soil fauna activity (McGlynn et al., 2007). Phosphorus addition could also affect belowground C flow and indirectly regulate soil physico-chemical properties and plant roots activities. Root growth is a significant C source for microbial organisms and renders an additional fraction of soil C available to microbial utilization (Helal and Sauerbeck, 1986), that could positively affect soil microbial processes involved in CH_4 consumption and emission. Low P availability due to strong sorption is often the main constraint on plant growth and primary production on highly weathered tropical soils (Vitousek, 1984). In 4.1 million year-old forests in Hawaii, P-fertilizer leads to a greater belowground net primary productivity and root turnover (Ostertag, 2001). Therefore, microbial activity could be stimulated by the increased belowground carbon flow due to increased available P. That is in line with our observed higher soil CO_2 emission (from soil respiration) after P-addition (Fig. 3). Finally, phosphorus fertilizer may increase the mineralization of organic P (Ofori-Frimpong and Rowell, 1999) and reduce Al^{3+} toxicity. Increased soil P

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level might stabilize soil aluminum and iron through geochemical reaction of adsorption (Frossard et al., 1995). This coupling effect decreased aluminum toxicity to methanotrophs (Nanba and King, 2000). However, in our experiment we found no treatment effect on soil exchangeable Al^{3+} (unpublished data). On the other hand, in this study we did find that P fertilizer decreased soil WFPS (Fig. 2b), which would increase soil aeration and potentially increase CH_4 consumption. This decreasing of soil WFPS was likely due to increased plant water consumption after P addition.

The inhibitive effect of N input on CH_4 uptake has been reported extensively. Zhang et al. (2008) suggested that the response of forest soil CH_4 uptake on N fertilization possibly depends on soil N status. They compared the CH_4 uptake under various N additions in three subtropical forests with very different N conditions and found N addition in N-saturated old-growth forest significantly decreased soil CH_4 uptake while in N-limited young forests, N addition had a limited effect. Singh et al. (1997) observed in a natural gradient of tropical forests, sites with higher soil mineral nitrogen concentrations had lower CH_4 uptake. In a Puerto Rican wet forest, Steudler et al. (1991) found that maximum reduction in CH_4 uptake coincided with the highest soil NH_4^+, suggesting that nitrogen-CH_4 linkage observed in temperate forests (Steudler et al., 1989) may also function in tropical forests.

Nitrogen inhibition on soil CH_4 uptake would be strengthened due to continuous nitrogen deposition and phosphorus limitation in Southern China tropical forests and other parts of the world. However, P addition could reverse such trends by stimulating forest soil CH_4 uptake. In this 33 months field experiment, we showed that increased P availability might mitigate the inhibitive effect of N addition on soil CH_4 uptake in this N-saturated old-growth tropical forest. While average annual consumption of CH_4 was enhanced after P addition and decreased after N addition, there was no difference between the NP-addition plots and the controls (i.e., the negative effect of N addition on CH_4 uptake was reduced by P addition) (Fig. 4). We are not aware of any other study that experimentally tested the P-addition on soil CH_4 uptake in P-limited tropical forests. Given the importance of tropical forests in global terrestrial ecosystems and

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CH_4 as an important greenhouse gas, further studies of N vs. P controls on soil fluxes of GHGs are urgently needed.

Net GWP (from CH_4 uptake and N_2O emission) was decreased by 2.23 CO_2 equivalents ($g\,CO_2\,m^{-2}\,yr^{-1}$) under P addition, and increased by 16.4 CO_2 equivalents under N addition. However, both were minor compared to the net GWP from soil CO_2 emission (548.2 $g\,CO_2\,m^{-2}\,yr^{-1}$). P addition contributed less to the system's net GWP change due to a neutral effect on N_2O, and a limited positive effect on CH_4 uptake. Adding N contributed positively to the system's GWP due to an enhanced N_2O emission.

5 Conclusions

In this 33 months field experiment, we found that P addition significantly increased soil CH_4 uptake and potentially mitigated the inhibitive effect of N deposition on soil CH_4 uptake in an old-growth tropical forest of Southern China. Soil CH_4 uptake was negatively affected by N addition, likely due to increased nitrification, which would compete with CH_4 oxidation for MMO. Increased nitrification and denitrification also contributed to higher N_2O emission, another potent greenhouse gas. In this N-saturated but P-limited forest, P addition likely increased belowground C flow, soil microbial activity, and consequently CH_4 uptake. We believe this is the first field study experimentally testing the N vs. P controls on soil CH_4 uptake. Considering the global increases of CO_2, CH_4, and N_2O and the global alteration of N and P biogeochemistry, the critical role of soil phosphorus under N deposition needs to be taken seriously to assess forest function as sinks and sources of GHGs.

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Table 1. Indices of an old-growth tropical forest at DHSBR (Dinghushan Biosphere Reserve). Survey was conducted at the beginning of February 2007 (before the start of N and P fertilization).

Species	Stem density (tree ha^{-1})	Mean height (m)	Mean diameter at breast height (cm)	Basal area (m^2 ha^{-1})
Castanopsis chinensis	268	9.8	26.0	18.67
Machilus chinensis	131	9.0	14.8	4.03
Schima superba	185	9.9	18.3	6.37
Cryptocarya chinensis	270	8.3	14.3	4.41
Syzygium rehderianum	185	8.5	12.9	1.19
Other plants	1587	4.3	4.4	3.46
Total	2625			38.14

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Table 2. General characteristics of the 0–10 cm mineral soils, measured at the beginning of February 2007, before the initiation of fertilization. Values are means with SE in parentheses (N = 5). Values followed by different letters are significantly different among treatments with $p < 0.05$.

Treatments	Control		N		P		NP	
pH (H_2O)	3.90 (0.02)	a	3.91 (0.02)	a	3.96 (0.01)	a	3.93 (0.03)	a
NH_4^+-N (mg kg^{-1})	24.05 (3.24)	a	23.78 (1.73)	a	26.38 (2.23)	a	27.58 (2.13)	a
NO_3^--N (mg kg^{-1})	4.26 (0.25)	a	3.07 (0.28)	b	3.30 (0.22)	b	3.22 (0.46)	b
Available P (mg kg^{-1})	5.18 (0.65)	a	3.57 (0.87)	a	4.69 (0.50)	a	5.42 (0.66)	a
Microbial biomass C (mg kg^{-1})	0.55 (0.04)	a	0.31 (0.02)	b	0.30 (0.03)	b	0.36 (0.03)	b
Soil organic carbon (%)	4.05 (0.15)	a	4.48 (0.23)	a	4.15 (0.26)	a	4.63 (0.17)	a
Dissolved organic C (mg kg^{-1})	709.2 (33.6)	a	489.7 (28.1)	b	628.3 (5.3)	c	612.4 (8.6)	c
Total N (g kg^{-1})	1.58 (0.11)	ab	1.23 (0.14)	a	1.74 (0.22)	ab	2.16 (0.27)	b
Total P (g kg^{-1})	0.49 (0.03)	a	0.39 (0.02)	b	0.45 (0.02)	ab	0.49 (0.02)	a

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Table 3. Soil properties after 24 months of fertilization treatment, measured in February 2009. Values are means with SE in parentheses (N = 5). Values followed by different letters are significantly different among treatments with $p < 0.05$.

Treatments	Control		N		P		NP	
pH (H_2O)	3.85 (0.03)	a	3.85 (0.03)	a	3.97 (0.05)	b	3.95 (0.03)	ab
NH_4^+-N (mg kg^{-1})	10.06 (0.80)	a	12.40 (1.12)	a	12.46 (1.55)	a	11.54 (0.89)	a
NO_3^--N (mg kg^{-1})	5.43 (0.36)	a	5.01 (0.31)	a	3.94 (0.33)	b	3.92 (0.18)	b
Available P (mg kg^{-1})	2.12 (0.42)	a	6.53 (2.43)	ab	12.56 (1.06)	c	8.61 (1.83)	bc
Microbial biomass C (mg kg^{-1})	0.30 (0.04)	a	0.21 (0.02)	a	0.27 (0.02)	a	0.28 (0.02)	a
Soil organic C (%)	4.32 (0.47)	a	4.50 (0.43)	a	4.57 (0.29)	a	3.98 (0.21)	a
Dissolved organic C (mg kg^{-1})	341.9 (25.2)	a	325.3 (9.9)	a	334.1 (4.0)	a	312.6 (11.9)	a
Total N (g kg^{-1})	3.54 (0.52)	a	3.56 (0.49)	a	3.39 (0.16)	a	2.91 (0.14)	a
Total P (g kg^{-1})	0.47 (0.03)	a	0.38 (0.01)	b	0.49 (0.01)	a	0.45 (0.02)	a

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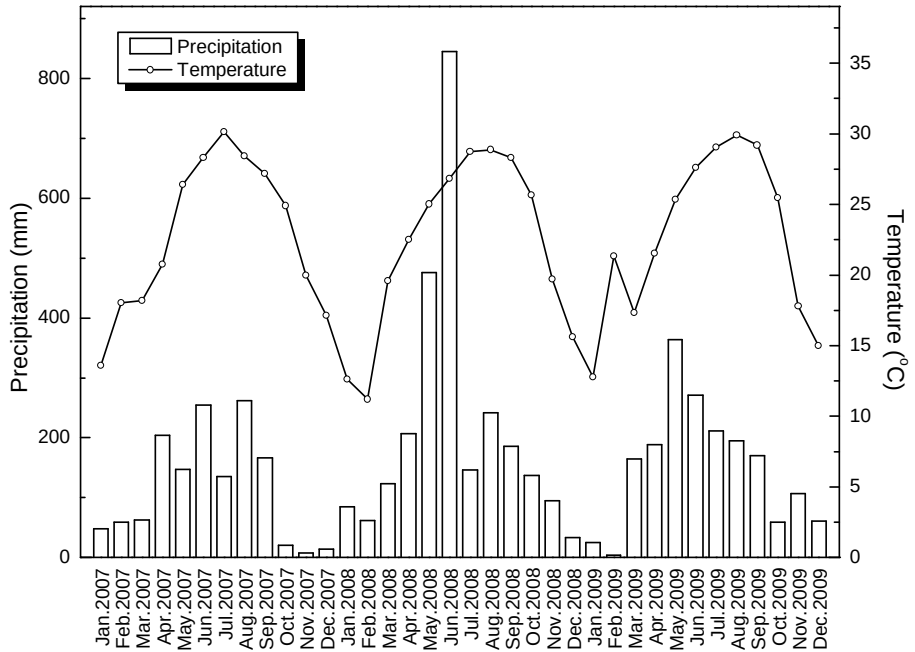

Fig. 1. Monthly precipitation (bar) and average air temperature (line and open circles) of DHSBR (Dinghushan Biosphere Reserve) from 2007 to 2009 (data are from Dinghushan Forest Research Station, Chinese Academy of Sciences).

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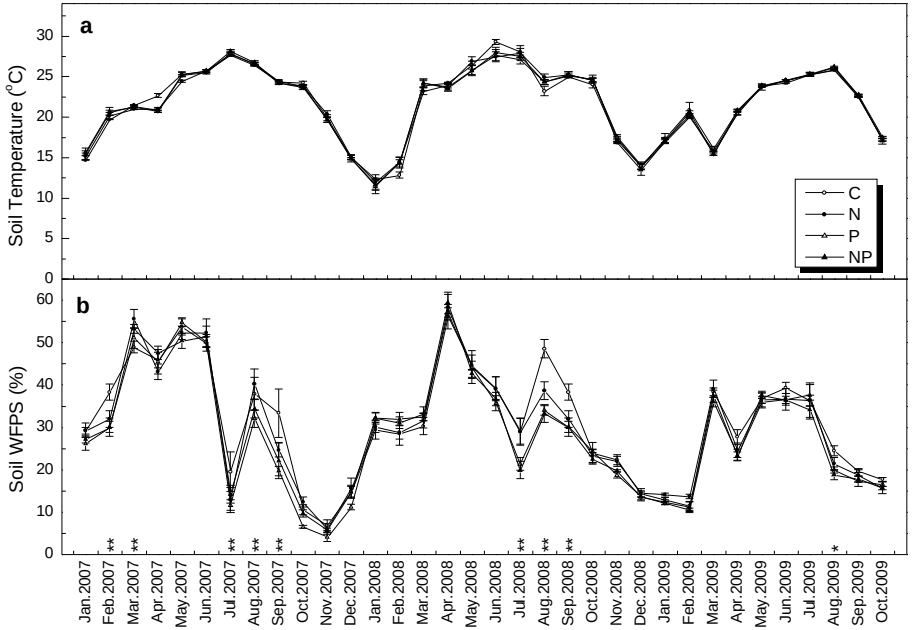

Fig. 2. Soil temperature at 5 cm depth **(a)** and soil WFPS **(b)** during the study period. Error bars represent standard error of means (N = 5). Asterisk (*) and double asterisk (**) indicates significant differences between control and at least one of the experiment treatments at $p < 0.1$ and $p < 0.05$, respectively.

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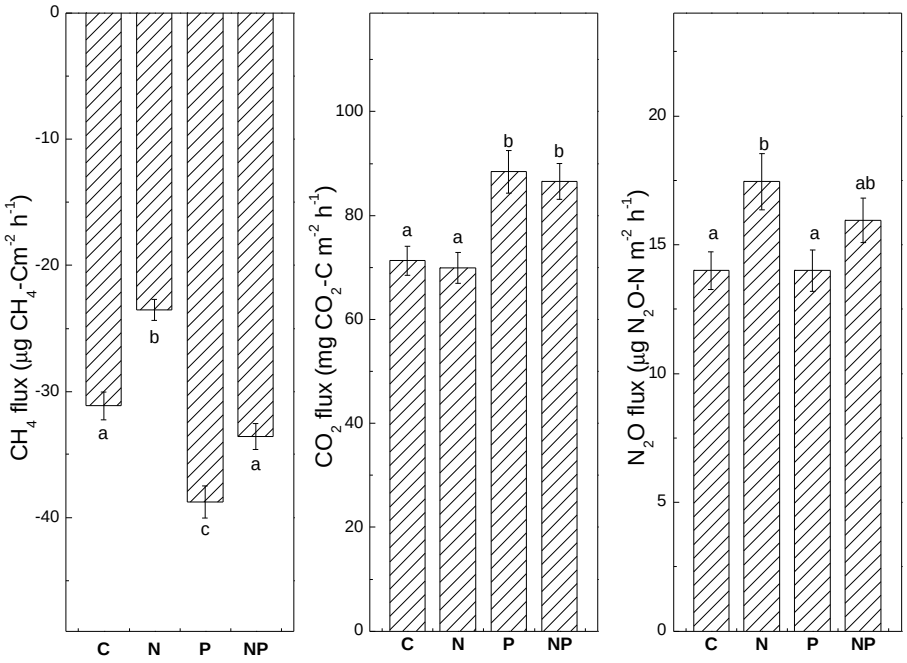

Fig. 3. Comparisons of mean soil GHG fluxes between treatments from 2007 to 2009 after N and P additions. Bars indicate ±1 SE, N = 5. Different letters denote significant difference ($p < 0.05$) between treatments by the Repeated Measurement ANOVA.

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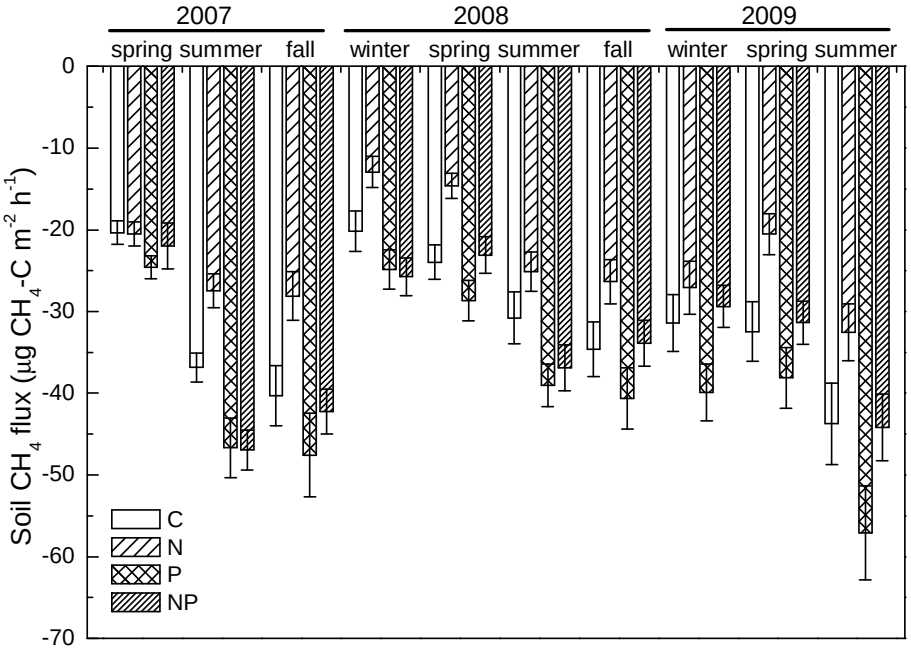

Fig. 4. Seasonal pattern of soil CH_4 uptake (April 2007 to September 2009). Bars indicate ±1 SE, N = 5. Spring form April to June, summer from July to September, fall from October to December and winter from January to March.

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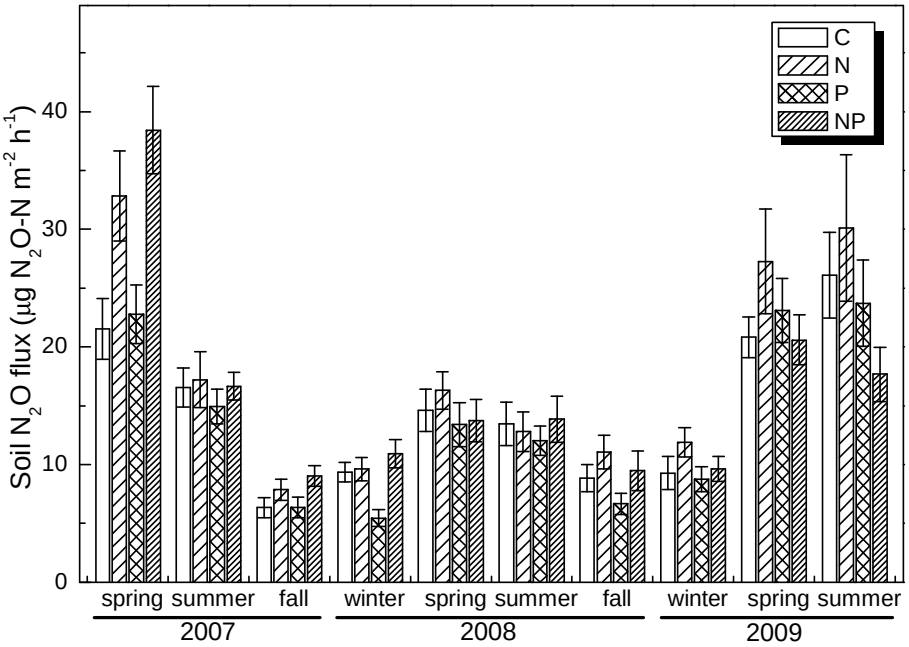

Fig. 5. Seasonal pattern of soil N_2O fluxes (April 2007 to September 2009). Bars indicate ±1 SE, N = 5.

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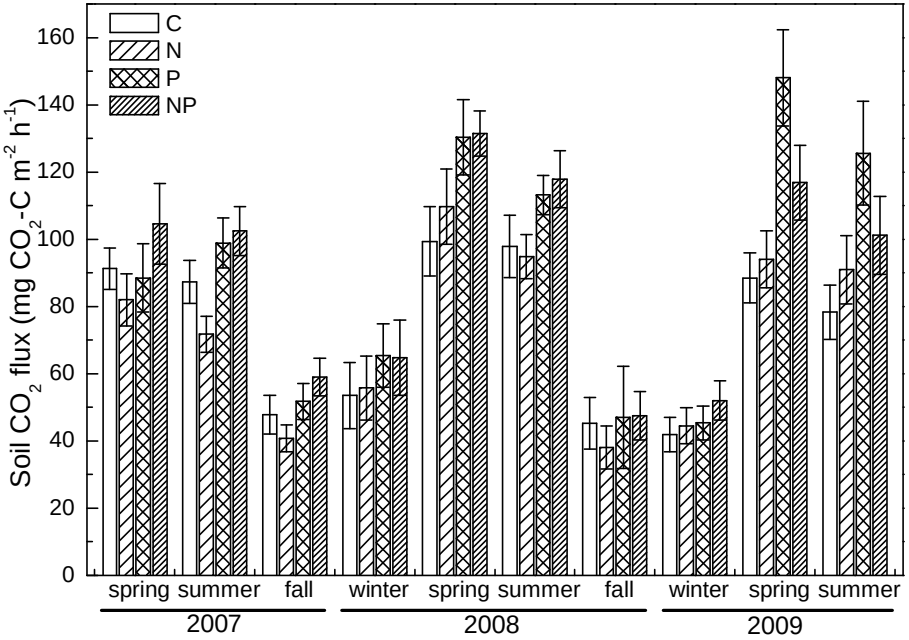

Fig. 6. Seasonal pattern of soil CO_2 fluxes (April 2007 to September 2009). Bars indicate ±1 SE, N = 5.

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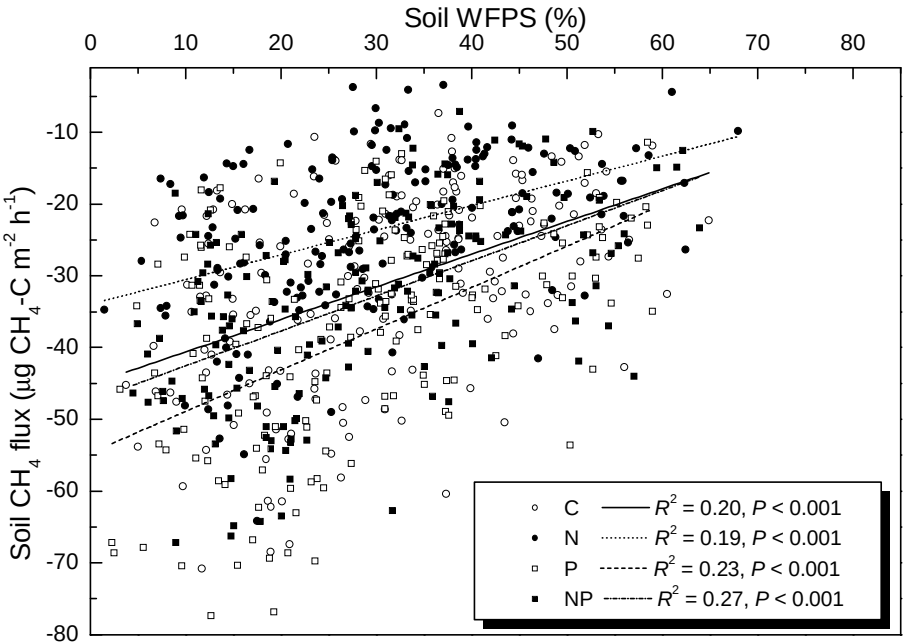

Fig. 7. Correlations between CH_4 flux and soil WFPS under different fertilization treatments. Under similar soil WFPS conditions, CH_4 uptake was higher in P-addition plots and lower in N-addition plots.

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