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Methane uptake responses to nitrogen deposition in three tropical forests in southern China

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[1] Methane (CH_4) uptake responses to simulated nitrogen (N) deposition in a mature forest, a rehabilitated forest and a disturbed forest in tropical China were studied. The experiment was designed with four N treatment levels (three replicates) (0, 50, 100, 150 kg N ha^{-1} a^{-1} for Control, Low-N, Medium-N, and High-N treatment, respectively) in the mature forest, but only three levels (Control, Low-N, and Medium-N) in the disturbed and rehabilitated forests. Between October 2005 to September 2006, soil CH_4 flux was measured once a week from April to September and once every other week in the other time using static chamber and gas chromatography techniques. Monthly ammonium-nitrate (NH_4NO_3) application had been applied previously to the plots since July 2003 and continued during the CH_4 flux measurement period. The average CH_4 uptake rates in control plots were -41.1 ± 1.8, -28.6 ± 2.2, and -17.8 ± 1.6 μg CH_4-C m^{-2} h^{-1} in the mature, rehabilitated, and disturbed forest, respectively. For the mature forest, average CH_4 uptake rates decreased by 6, 14, and 32% when compared to the control plots for the Low-N, Medium-N, and High-N plots, respectively. These decreases in soil CH_4 uptake mainly occurred in the fall (October and November). Nitrogen additions had no significant effect on CH_4 uptake in the rehabilitated and disturbed forests. Our results suggest that the response of soil CH_4 uptake to N deposition in tropical forests may vary depending on the soil N status directly, and on land-use history of the forest indirectly.

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1. Introduction

[2] Methane is second only to carbon dioxide (CO_2) as a greenhouse gas and contributes approximately 15% to global warming [*IPCC*, 2002; *Jang et al.*, 2006], with a relative global warming potential 23 times that of CO_2 on a molar basis [*IPCC*, 2002]. The atmospheric concentration of CH_4 had increased 150(±25)% during the 20th century [*Houghton et al.*, 2001]. The major sink for atmospheric CH_4 is its reaction with hydroxyl radicals (OH) in the troposphere [*Crutzen*, 1991; *Schlesinger*, 1997]. Forest soils are an important biological source or sink for atmospheric CH_4 [*Castro et al.*, 1995; *Smith et al.*, 2000; *Jang et al.*, 2006]. A number of soil and environmental factors (e.g., pH values, soil temperature, soil moisture, N status, soil diffusivity, and forest land-use pattern), are considered to limit the consumption of atmospheric CH_4 by forest soils [*Castro et al.*, 1995; *Priemé and Christensen*, 1997; *Gulledge et al.*, 1997; *Brumme and Borken*, 1999; *Davidson et al.*, 2004]. Among the various variables affecting the CH_4 oxidation rate, the effects of N deposition on this biological process have been increasingly concerned [*Butterbach-Bahl et al.*, 1998; *Jang et al.*, 2006].

[3] Over the past century, N deposition (dryfall and rainfall) into terrestrial ecosystems had increased more than threefold, primarily due to anthropogenic activities related to energy production (predominantly fossil fuel consumption) and the production of artificial fertilizer [*Galloway et al.*, 2004]. Increases in inorganic N (ammonium and nitrate) inputs to forest ecosystems have been shown to inhibit methanotrophic bacteria and enzymes involved in CH_4 oxidation [*Butterbach-Bahl et al.*, 1998; *Hütsch*, 1998; *Wang and Ineson*, 2003; *Xu and Inubushi*, 2004; *Jang et al.*, 2006]. Unexpectedly inhibitory effects on CH_4 uptakes have often been observed in forests experiencing high N deposition or treatment with N fertilizer to simulate N deposition [*Mosier et al.*, 1991; *King and Schnell*, 1994; *Schnell and King*, 1994; *Willison et al.*, 1996; *Sitaula et al.*, 2001; *Butterbach-Bahl et al.*, 2002; *Wang and Ineson*, 2003; *Xu and Inubushi*, 2004]. Not all studies support the

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observation that elevated atmospheric N deposition reduces forest soil CH_4 sink strength [*Schnell and King*, 1994; *Bradford et al.*, 2001a]. At high CH_4 concentrations forest stands, adding N can stimulate soil CH_4 uptake [*Bodelier and Laanbroek*, 2004]. Thus studies assessing the potential of N deposition to affect soil CH_4 uptake must carefully take regional diversity into consideration. However, most of these studies have been carried out in temperate/boreal regions, where most forests are naturally N-limited [*Matson et al.*, 2002]. In tropical regions, forests are more typically phosphorus (P) limited than N-limited, and the soils are often highly acidic, with low base cation concentrations [*Hall and Matson*, 2003]. The inhibitory effect of N deposition on soil CH_4 uptake as a result is hypothesized to be more significant in tropical forest than in temperate forest [*Matson et al.*, 2002; *Hall and Matson*, 2003], however more research is required to confirm this.

[4] Current N deposition rates in tropical forests of southern China are high and of the same order in magnitude as in North American and Europe, ranging from 15 to 73 kg N ha^{-1} a^{-1} [*Holland et al.*, 1999; *Ren et al.*, 2000; *Zhou and Yan*, 2001; *Galloway et al.*, 2002; *Mo et al.*, 2006; *Chen and Mulder*, 2007]. Nitrogen deposition in this region has been projected to continue increase in the coming decades, due to the rapid expansion of industrial and agricultural activities [*Galloway et al.*, 2004; *Mo et al.*, 2006, 2007b; *Chen and Mulder*, 2007]. In addition, most of these regional forests have been degraded by human activities for many hundreds of years [*Wang et al.*, 1982; *Mo et al.*, 2003], with the remaining natural forest occupying an area of less than 9% of the total territory in China [*Liu et al.*, 2000]. Over the last few decades, large areas have been reforested with a native species (*Pinus massoniana* Lamb) [*Brown et al.*, 1995; *Mo et al.*, 2004]. Deforestation is usually prohibited, but harvesting of understory and litter is often allowed to satisfy local fuel needs [*Brown et al.*, 1995; *Mo et al.*, 1995, 2003]. The varying management practices within these reforested forests allow us to identify both disturbed forest (understory and litter harvesting are allowed) and rehabilitated forest (no understory and litter harvesting) [*Mo et al.*, 2006, 2007a]. Although forest coverage in China is now 174.91 million hectares or 18.2% of the total territory [*NDRCPRC*, 2007], to date there have been limited research aimed at studying atmospheric CH_4 oxidation in forest soils. Information regarding CH_4 oxidation in response to increased N deposition in forest soils of China is nonexistent. Studying CH_4 uptake in these forest soils in response to human alteration (especially N inputs and forest land-use change) is very important for estimating the contribution of tropical forest soils to the global CH_4 uptake budget and in predicting future uptake trends.

[5] Previously, we reported that the mature forest has been N saturated due to both long-term high N deposition in the region and ecosystem age, and that both the rehabilitated and disturbed forests are still N limited due to previous land-use history [*Mo et al.*, 2006, 2007b]. In this study, we examined the effects of elevated N deposition on soil CH_4 uptake in a mature, a rehabilitated and a disturbed forest in tropical China. We hypothesized that N addition would change the soil N status and inhibit CH_4 uptake in these tropical forests. We also hypothesized that N addition would significantly decrease CH_4 uptake rate in the mature forest due to its high initial soil N status, and have relatively less effect on CH_4 uptake rate in the rehabilitated or disturbed forests due to their low soil N availability resulting from previous human disturbance.

2. Methods

2.1. Site Description

[6] The study was conducted in Dinghushan Biosphere Reserve (DHSBR). The reserve lies in the middle of Guangdong Province in southern China (112°10′E longitude and 23°10′N latitude) and occupies an area of approximately 1200 ha. We have established research sites in a mature (old-growth monsoon evergreen broadleaf) forest, a rehabilitated (mixed pine and broadleaf) forest, and a disturbed (pine) forest within 3–4 km distance of each other. Both the disturbed and rehabilitated forests originated from a 1930s clear-cutting policy and subsequent pine plantation establishment [*Mo et al.*, 2003, 2007a]. The disturbed forest in contrast, underwent continuous human disturbances (generally the harvesting of understory and litter) from 1930s to 1998, with *P. massoniana* remaining as the predominant tree [*Mo et al.*, 2006, 2007a]. Colonization from the natural dispersal of regional broadleaf species in rehabilitated forest has altered its plant community [*Mo et al.*, 2006]. Dominant species in the rehabilitated forest are *Pinus massoniana* Lamb, *S. superba, C. chinensis, Craibiodendron kwangtungense* S. Y. Hu, *Lindera metcalfiana* Allen, and *Cryptocarya concinna* in the tree layer [*Mo et al.*, 2006]. Conversely, the mature forest has been well protected from human impacts for more than 400 years [*Mo et al.*, 2006; *Zhou et al.*, 2006], and is a typical forest in tropical China [*Wang et al.*, 1982; *Mo et al.*, 2003; *Zhou et al.*, 2006]. The major species in the mature forest are *Castanopsis chinensis* Hance, *Schima superba* Chardn. & Champ., *Cryptocarya chinensis* (Hance) Hemsl., *Cryptocarya concinna* Hance, *Machilus chinensis* (Champ. Ex Benth.) Hemsl., *Syzygium rehderianum* Merr. & Perry in the tree layer and *Calamus rhabdicladus* Burret, *Ardisia quinquegona* Bl., and *Hemigramma decurrens* (Hook.) Copel. in the understory layer [*Mo et al.*, 2006].

[7] The reserve has a typical monsoon and humid tropical climate [*Holdridge*, 1967]. The mean annual temperature is 21.0°C, with an average coldest (January) and warmest (July) temperature of 12.6°C and 28.0°C, respectively. The mean annual rainfall of 1927 mm has a distinct seasonal pattern, with 75% of it falling from March to August and only 6% from December to February. Annual mean relative humidity is 80%. Precipitation and air temperature have a distinct seasonal pattern [*Huang and Fan*, 1982]. During the study period, precipitation and temperature (Figure 1c) largely followed the long-term seasonal pattern. Nitrogen deposition in rainfall was 36–38 kg N ha^{-1} a^{-1} in 1990s [*Huang et al.*, 1994; *Zhou and Yan*, 2001], and 34 and 32 kg N ha^{-1} a^{-1} in 2004 and 2005 respectively, with roughly 1:1 NH_4^+ to NO_3^- molar ratio [*Fang et al.*, 2007].

[8] Soil in the preserve is predominantly lateritic red earth formed from sandstone (oxisols) with variable soil depths [*Mo et al.*, 2003, 2006]. In the mature forest, the soil is deeper than 60 cm. In the rehabilitated forest, depth ranges from 30 to 60 cm, and in the disturbed forest the depth is generally less than 30 cm to bedrock [*Mo et al.*, 2006]. Soil

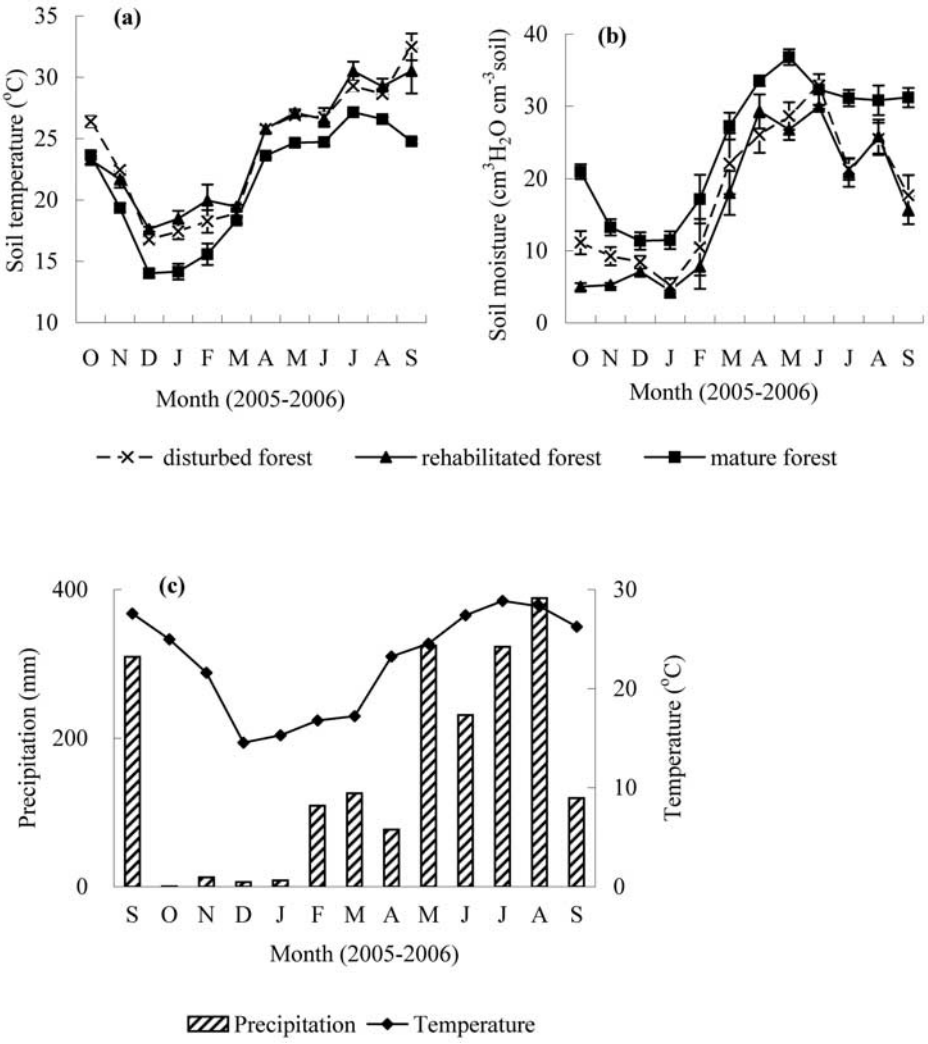

Figure 1. Seasonal patterns of soil temperatures (a) and soil moisture contents (b) in the mature, rehabilitated, and disturbed forests. Monthly precipitation and air temperature (c) of DHSBR from September 2005 to September 2006 (data are from Dinghushan Forest Research Station, Chinese Academy of Science). Error bars represent standard error of means (n = 3).

in the mature forest has a higher total N, total C, and soil moisture content, but a lower pH value, C/N ratio, soil temperature, and soil bulk density than the disturbed and rehabilitated forests. The characteristics of the soils in the study sites are described in Table 1.

2.2. Experimental Design

[9] Four N (NH_4NO_3) addition treatment levels (three replicates) were established in the mature forest: Control (without N addition), Low-N (50 kg N ha^{-1} a^{-1}), Medium-N (100 kg N ha^{-1} a^{-1}), and High-N (150 kg N ha^{-1} a^{-1}), but only three levels (three replicates) were established in both disturbed and rehabilitated forests (Control, Low-N, and Medium-N). A total of 30 plots (20 $\times$ 10 m) were established (12 in the mature, nine in the rehabilitated and nine in the disturbed forest), each surrounded by a 10-m-wide buffer strip. Field plots and treatments were laid out randomly. Monthly NH_4NO_3 application had been applied previously to the plots since July 2003 and continued during the CH_4 flux measurement period. Fertilizer (NH_4NO_3) was weighed, dissolved within 20 L water, and applied to the plots using a backpack sprayer below the canopy. The Control plots received 20 L water without fertilizer addition [*Mo et al.*, 2006].

2.3. Field Sampling and Measurements

[10] Soil CH_4 flux measurements were started 26 months after the initial experimental N applications in October 2005. Gas samples for CH_4 flux measurement were taken once a week from April to September and once every other week at other times using closed static chamber methodology and analyzed using gas chromatography. The static chamber was made of stainless-steel and consisted of two parts, an anchor ring (10 cm height $\times$ 25 cm in diameter) and a removable chamber (35 cm height $\times$ 25 cm diameter) [*Ambus and Robertson*, 2006]. A fan (8 cm diameter) was installed on the top wall of each chamber. Two anchors were installed at each plot in the mature forest, but only one at each plot in the rehabilitated and disturbed forests, therefore sample number is three for each N treatment. Anchors were

Table 1. Soil Properties (0–10 cm Depth) of the Control Plots in the Mature, Rehabilitated and Disturbed Tropical Forests in Southern China

Forest Type	Disturbed Forest	Rehabilitated Forest	Mature Forest
pH value (H_2O)[a]	4.0(0.1)	3.9(0.1)	3.8(0.1)
Total N(mg g^{-1})[a]	1.3(0.1)	1.2(0.1)	2.5(0.2)
Total C(mg g^{-1})[a]	22.7(3.1)	17.3(1.2)	32.1(2.7)
C/N ratio[a]	17.0(1.4)	14.4(1.0)	12.8(2.3)
Available P(mg kg^{-1})[b]	3.6(0.3)	4.2(0.3)	5.0(0.1)
Organic matter(%)[b]	2.7(0.2)	3.5(0.4)	5.4(0.6)
Bulk density(g soil cm^{-3})[b]	1.2(0.1)	1.2(0.1)	1.0(0.1)
Texture[c]	sandy loam	sandy loam	loamy clay
Clay(%)[d]	21.2	28.0	29.2
Sand(%)[d]	54.9	47.8	37.8
Loam(%)[d]	24.9	24.2	33.0

[a]Data are cited from *Fang et al.* [2006].
[b]Data are cited from *Mo et al.* [2006]. Values are means. Standard error in parentheses, n = 3 for all samples, measured in July 2004.
[c]FAO soil textural classes.
[d]Data are cited from *Wang et al.* [1982].

installed at least one month before the first field campaign (15 August 2005). The anchor rings were inserted into the soil to 5 cm depth just below the litter layer and to avoid cutting fine roots. The removable cover chamber was placed on the anchor ring and made airtight during the sampling period using a rubber O-ring seal. Gas samples were collected using plastic syringe (100 ml) at 0, 10, 20, and 30 min after the chamber closure, and were analyzed in the laboratory within 24 h. Prior sampling showed that the decrease in CH_4 concentrations remained linear for up to 2 h following chamber closure. All the coefficients of determination (r^2) of the linear regression were greater than 0.96 ($p < 0.01$). Gas samples were collected during midmorning (9:00–10:00, local time) on each sampling date. Diurnal studies have demonstrated that greenhouse gas fluxes measured during this time period are representative of the daily mean flux in nearby forests [*Tang et al.*, 2006].

[11] A gas chromatograph (Agilent 4890D, Agilent Co. USA) with a flame ionization detector (FID), connected to an automatic sample-injection system was used for CH_4 analysis. The gas chromatography configuration and the method for calculating CH_4 flux were the same as described by *Wang and Wang* [2003]. The oven, injector and detector temperatures were 55, 275, and 330°C, respectively. Nitrogen (99.999%, 30 ml min^{-1}) and hydrogen (99.999%, 30 mL min^{-1}) were used as the carrier and fuel gas, respectively. Dry-clean airflow rate was 60 mL min^{-1}. Calibration gas (CH_4 at 3.13 ppb; No. 71427) was obtained from the Institute of Atmospheric Physics, Chinese Academy of Sciences.

[12] CH_4 flux was calculated from a linear regression of chamber gas concentration versus time according to the following equation [*IAEA*, 1992]:

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

Where F is CH_4 flux (μg CH_4-C m^{-2} h^{-1}), negative value indicates CH_4 uptake by soil. ρ is the density of CH_4 under standard condition (calculated from the molar mixing ratio using the ideal gas law). h, A, and V are the height, the sampling area, and the volume of chamber, respectively. C_t is the concentration of mixed volume ratio of gases inside chamber at t time. P is air pressure of the atmosphere in the plot, and T is air temperature of chamber headspace. T_0 and P_0 are temperature and air pressure under standard conditions, respectively.

[13] Soil temperature (5 cm) and moisture content (10 cm) were monitored at each chamber during gas sample collection. Soil temperature (°C) was measured using a digital thermometer (TES-1310, Ltd., China). Soil moisture content (% WFPS) was measured using an MPKit (ICT, Australia), as described in detail by *Tang et al.* [2006]. Microenvironmental factors, including air temperature of the chamber headspace, air temperature at 1.5 m above ground, as well as atmospheric pressure were measured simultaneously.

[14] Soil samples were collected in September 2005 and August 2006 using a standard soil probe (2.5 cm inside diameter). Four soil cores (10 cm depth) were collected randomly within each plot and mixed, resulting in three sample sizes for each N treatment. Soil moisture contents and pH values (0.01M KCl) were determined initially. Large roots, wood and litter were removed prior to sieving (2 mm). The composite samples were stored at 4°C within 48 h to analysis [*NSBC*, 1987]. Extractable NH_4^+ was determined using the indophenol blue method, followed by colorimetric analysis. NO_3^- was determined after cadmium reduction to nitrite (NO_2^-), followed by sulfanilamide-NAD reaction. Total N was determined with a semimicro-Kjeldahl digestion followed by NH_4^+ detection [*NSBC*, 1987].

2.4. Statistical Analysis

[15] All statistical analyses were performed using SPSS 12.0 (SPSS, Chicago, 2003). Pearson rank correlation was used for determining relations between CH_4 uptake rates and soil temperature or soil moisture content. One-way ANOVA with Tukey's HSD test was used to examine the difference in soil temperature, soil moisture, and NH_4^+ and NO_3^- concentrations among N treatments within the individual forest. Repeated measure ANOVA with Tukey's HSD test was used to examine the difference in CH_4 uptake rates among N treatments for annual mean rates and each month within the individual forest. Statistical significant differences were set with p-values <0.05 unless otherwise stated.

3. Results

3.1. Soil Temperature and Moisture

[16] Soil temperature and moisture (Figures 1a and 1b) exhibited clear seasonal patterns in all treatment plots in the three forests. The soil was warmer and wetter from April to September (growing season) and became cooler and dryer from December to February of next year (winter season). The annual mean soil temperatures were 21.4 ± 0.7, 23.7 ± 0.7, and 23.9 ± 0.5°C for control plots in the mature, rehabilitated, and disturbed forest, respectively. The annual mean soil moisture contents were 24.9 ± 1.4, 17.2 ± 1.6, and 18.4 ± 1.5 (%, cm^3 H_2O cm^{-3} soil) for control plots in the mature, rehabilitated, and disturbed forest, respectively. The averages of soil moisture content and temperature were similar between the disturbed and rehabilitated forests. The

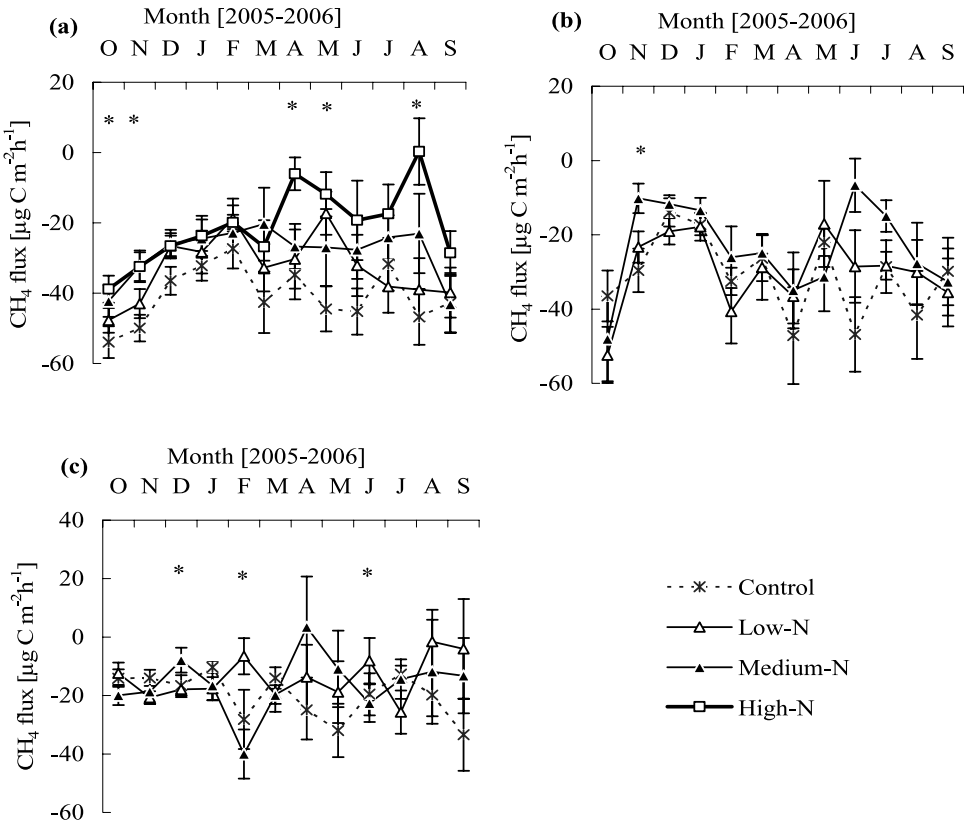

Figure 2. Seasonal variations of CH_4 uptake rates in the mature (a), rehabilitated (b), and disturbed (c) forests. Asterisk indicates significant difference (Tukey's HSD test, $p < 0.05$) among treatments within a forest. Error bars represent standard errors (n = 3).

mature forest showed significantly higher soil moisture content ($p < 0.05$) and lower soil temperature ($p < 0.05$) compared with disturbed and rehabilitated forests (Figures 1a, 1b). There was no treatment effect on soil temperature and soil moisture content in the three forests during the study period.

3.2. CH_4 Uptake in Control Plots

[17] Soil CH_4 uptake rates in the mature forest showed a distinct seasonal pattern with the highest rates observed in the fall and the lowest rates in the summer season ($p < 0.05$) (Figure 2a). In the rehabilitated and disturbed forests, CH_4 uptake rates during the growing season (April to September) were higher than in the cool-dry season (November to February), however this trend was not statistically significant (Figures 2b and 2c ; Table 2). The annual mean rate of CH_4 uptake in the mature forest (-41.1 ± 1.8) was significantly higher than in the rehabilitated (-28.6 ± 2.2) or disturbed forest (-17.8 ± 1.6 μg CH_4-C m^{-2} h^{-1}) ($p < 0.05$, Table 2). Soil CH_4 uptake rates in the three forests were positive linearly correlated with soil temperatures (Figures 3a, 3c, and 3e). The CH_4 uptake rates in the mature forest were negative linearly correlated with soil moisture contents ($p = 0.04$, $r^2 = 0.12$, n = 32) (Figure 3b), but no significant linearly correlated in the disturbed and rehabilitated forests (Figures 3e, 3f).

3.3. Soil N Availability Indices

[18] The concentrations of soil NH_4^+, and NO_3^- in the mature forest were higher than in the disturbed and rehabilitated forests ($p < 0.05$) (Table 3). Nitrogen additions significantly increased contents of soil NH_4^+ and NO_3^- in Medium-N and High-N plots in the mature forest ($p < 0.05$) (Table 3), and in Medium-N plots in the disturbed forest relative to the control plots ($p < 0.05$) (Table 3).

3.4. Effects of N Addition on CH_4 Uptake

[19] CH_4 uptake rates in N treatment plots showed a similar seasonal pattern to that in the control plots (Figures 2a–2c). The effects of N additions on CH_4 uptake varied depending on N addition levels and forest types (Table 2). Repeated measure ANOVA test showed that CH_4 uptake rates in the N treatment plots in the mature forest significantly decreased ($p < 0.05$) following N additions relative to the control plots (Figure 2a). The annual mean rates of CH_4 uptake were decreased by 6, 14, and 32% in the Low-N (-34.4 ± 1.8), Medium-N (-29.4 ± 2.0), and High-N plots (-23.4 ± 2.0), respectively, when compared to the control plots (-41.1 ± 1.8 μg CH_4-C m^{-2} h^{-1}, n = 3). The significant decreases of CH_4 uptake rates in response to N additions were observed during the spring and fall (April to May, September to November, $p < 0.05$, Figure 2a and Table 2), when soil water contents were changing from dry to wet or wet to dry season. CH_4 uptake rates were negative linearly correlated with soil NH_4^+ contents ($r^2 = 0.35$, $p = 0.044$) (Figure 4a) and soil NO_3^- contents ($r^2 = 0.51$, $p =$

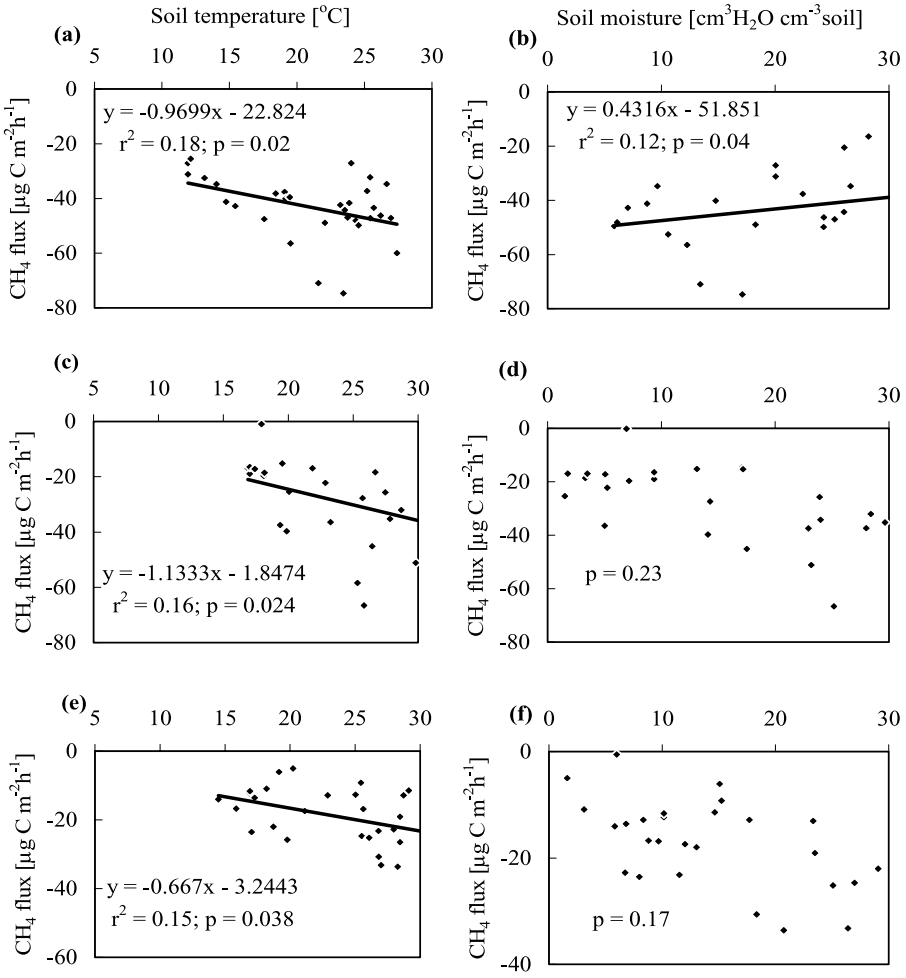

Figure 3. Relationships between CH_4 uptake rates and soil temperature (5 cm) and soil moisture content (0–10 cm) in the control plots of the mature (a, b), rehabilitated (c, d) and disturbed (e, f) forests (n = 3).

0.009) (Figure 4b) in the mature forest. In the rehabilitated and disturbed forests, however, CH_4 uptake rates showed no significant response to N addition.

4. Discussion

4.1. Comparisons With Other Studies

[20] Fluxes of CH_4 in the forest sites were similar to the results reported in the adjacent forests (-38.8 μg CH_4-C $m^{-2}h^{-1}$ [*Tang et al.*, 2006]), and in the Kakamega rain forest in Africa (-56.4 ± 0.8 μg CH_4-C $m^{-2}h^{-1}$ [*Werner et al.*, 2007]). The fluxes of CH_4 uptake rates were within the range reported from other studies in temperate forests in Europe [*Smith et al.*, 2000; *Steinkamp et al.*, 2001; *Bradford et al.*, 2001b; *Borken et al.*, 2003], and in North America [*Castro et al.*, 2000], but lower than fluxes reported in forest studies in Japan (-316.7 μg CH_4-C $m^{-2}h^{-1}$ [*Ishizuka et al.*, 2000]; -245.4 μg CH_4-C $m^{-2}h^{-1}$ [*Tamai et al.*, 2003]) and Russia (-208.8 μg CH_4-C $m^{-2}h^{-1}$ [*Nakano et al.*, 2004]).

4.2. CH_4 Uptake in Three Forest Land-Use Types

[21] The mature forest soil oxidized more CH_4 than that of the rehabilitated and disturbed forests. The same trend was observed by *Tang et al.* [2006] in the adjacent forests. The reason for the phenomenon could be explained by forest age and the status of human disturbances. As previously reported, the mature forest has been protected from human impacts for more than 400 years [*Mo et al.*, 2006, 2007b; *Zhou et al.*, 2006]. The rehabilitated and disturbed forests were planted in 1930s [*Mo et al.*, 1995, 2003]. However, the disturbed forest has been under constant human pressures most of the time since it was planted (generally the harvesting of understory and litter) [*Mo et al.*, 2006, 2007a]. Thus these forests vary both in degree of human impacts as well as stages of succession, site conditions, and species assemblages [*Wang et al.*, 1982; *Mo et al.*, 2003, 2006]. *Priemé and Christensen* [1997] and *Maljanen et al.* [2003] studied CH_4 uptake in different age forests in Europe. They found that the oldest stand was a sink of CH_4, while the younger stands were small sinks or sources of CH_4. Their findings also indicated that when the land use changes from other type to forest again, CH_4 oxidation might increase but very slowly (even need 100–200 years). The trends of CH_4 uptake in the present study also supported the previous studies, which reported that relatively higher CH_4 uptake rates in broadleaf forests

Table 2. Effects of N Additions on the Mean Rates of CH_4 Uptake in the Mature, Rehabilitated and Disturbed Tropical Forests in Southern China

Site-Treatment	CH_4 flux, μg CH_4-C m^{-2} h^{-1}			
	Annual Mean	Warm-Wet Season	Cool-Dry Season	Min-Max
		Mature forest		
Control	−41.1(1.8)a	−33.0(3.9)a	−46.3(2.3)a	−119.9-32.5
Low-N	−34.4(1.8)ab	−32.9(4.1)a	−39.1(2.5)ab	−125.1-27.6
Medium-N	−29.4(2.0)ab	−25.2(4.2)ab	−26.3(2.5)b	−115.4-57.2
High-N	−23.4(2.0)b	−13.1(4.6)b	−25.7(2.3)b	−100.8-73.1
		Rehabilitated forest		
Control	−28.6(2.2)	−33.5(4.4)a	−22.0(2.4)	−100.2-13.7
Low-N	−27.1(2.0)	−26.5(3.7)ab	−23.1(2.5)	−82.0-20.6
Medium-N	−19.9(2.0)	−19.1(3.8)b	−13.8(2.1)	−64.8-26.7
		Disturbed forest		
Control	−17.8(1.6)	−19.3(3.1)	−15.7(2.1)	−92.3-18.1
Low-N	−15.2(1.9)	−16.0(4.6)	−17.0(1.8)	−72.8-42.6
Medium-N	−16.1(1.1)	−14.8(5.1)	−18.1(2.9)	−75.2-62.1

Cool-dry season was from November to February of next year, warm-wet season was from April to September. Gas samples were collected from October 2005 to September 2006. Values are means with SE in parentheses (n = 3). The letters a, b indicate significant different, and "ab" indicates no significant different among treatments within the individual forest (Tukey's HSD test; $p < 0.05$). * Min, minimum value; max, maximum value.

were found than in coniferous forests [*Menyailo and Hungate*, 2002; *Jang et al.*, 2006].

4.3. Effects of Soil Temperature and Soil Moisture Content on CH_4 Uptake

[22] We found a positive correlation between CH_4 uptake rates and soil temperatures in the three forests, and a negative correlation between CH_4 uptake rates and soil moisture only in the mature forest. The results were consistent with the results found in temperate forests in Europe [*Steinkamp et al.*, 2001; *Maljanen et al.*, 2003] and in USA [*Castro et al.*, 1995], where CH_4 consumption increased when the temperature increased from −5 to 10°C, and remained relatively constant at temperatures between 10 and 20°C. *De Visscher et al.* [2007] suggested that the optimum temperature for CH_4 oxidation ranged from 22 to 38°C. *Steinkamp et al.* [2001] also reported that at low soil temperature (<10°C) conditions, temperature was a stronger modulator than soil moisture for CH_4 uptake, but soil moisture was dominant factor controlling CH_4 uptake when soil temperature was >10°C. In the mature forest, average soil temperature was 21.4°C during the study period, being around the optimum temperature for CH_4 oxidation. At the same time, the mean annual rainfall of 1729 mm has a distinct seasonal pattern, with 75% falling from March to August. Thus soil moisture was stronger than soil temperature in the effect on soil CH_4 uptake. The result was consistent with the results found in temperate and tropical forests [*Steudler et al.*, 1996; *Davidson et al.*, 2004]. In the rehabilitated and disturbed forests, the significant seasonal variations of CH_4 uptake rates following soil temperature or soil moisture content change were not observed, although slightly higher CH_4 uptake rates were observed in the growing season. Soil CH_4 uptake could be decreased when soil moisture content exceeds a site-specific value [*Ishizuka et al.*, 2005]. Actually, throughout the study period, soil moisture contents in the rehabilitated and disturbed forests probably did not reach the critical values needed to affect the diffusion for CH_4 uptake.

4.4. Effect of N Addition on CH_4 Uptake

[23] In the mature forest, N additions significantly inhibited soil CH_4 uptake, and the inhibitory effects became stronger with enhanced N treatment level. In the rehabilitated and disturbed forests, however, N additions had no inhibitory effect on CH_4 uptake. The result of the mature forest was consistent with the previous findings that N addition could reduce CH_4 uptake rates in forest soils [*Steudler et al.*, 1989; *Castro et al.*, 1994; *King and Schnell*, 1994; *Hütsch*, 1998; *Wang and Ineson*, 2003; *Xu and Inubushi*, 2004]. Our results in the rehabilitated and disturbed forests were consist with the previous findings in N-limited temperate forests [*Whalen and Reeburgh*, 2000; *Bradford et al.*, 2001a; *Borken et al.*, 2002; *Wang and Ineson*, 2003], which showed that increased N deposition would not reduce soil CH_4 uptake rates. The main explanations for the different response patterns in the three forests can be explained by the followings.

[24] First, NH_4^+ and NO_3^- contents could inhibit the process of CH_4-oxidzing [*King and Schnell*, 1994]. The mature forest soil has high initial soil N status [*Mo et al.*, 2006; *Fang et al.*, 2006]. Nitrogen additions significantly increased soil NH_4^+ and NO_3^- contents. We had measured the lowest CH_4 uptake rates in the plots with the highest NH_4^+ and NO_3^- concentrations. The NH_4^+ inhibition could play an important role as a regulating factor for CH_4 uptake, including a competitive inhibition of the CH_4 monooxygenase enzyme [*Steudler et al.*, 1989; *Nesbit and Breitenbeck*, 1992; *Hütsch*, 1998] and a toxic inhibition by hydroxylamine (NH_2OH) or NO_2^- produced via NH_4^+ oxidation [*Gulledge and Schimel*, 1998]. The NO_3^- might have direct inhibitory effects on CH_4-oxidzing [*Reay and Nedwell*, 2004; *Xu and Inubushi*, 2004]. *Whalen and Reeburgh*

Table 3. Contents of Soil NH_4^+, NO_3^-, pH Values and Exchangeable Al^{3+} in the Mature, Rehabilitated and Disturbed Forests of Tropical China

Site-Treatment	NH_4^+-N	NO_3^--N	C/N	Al^{3+}	pH
		Mature forest			
Control	2.9(0.4)b	5.8(0.5)b	16.1(0.9)	419.7(12.7)b	3.9
Low-N	3.4(0.7)ab	6.7(0.8)b	14.7(0.7)	438.9(13.6)ab	3.8
Medium-N	3.7(0.2)a	8.9(0.9)a	16.1(1.1)	441.8(23.5)ab	3.7
High-N	3.8(0.2)a	10.1(1.3)a	15.1(0.5)	469.9(9.6)a	3.7
		Rehabilitated forest			
Control	2.3(0.4)	3.0(0.2)	21.2(0.4)	337.8(10.3)b	4.0
Low-N	3.5(0.2)	3.3(0.3)	20.0(0.8)	370.7(8.0)a	3.9
Medium-N	3.6(0.6)	3.6(0.1)	19.6(0.5)	368.8(10.5)a	3.9
		Rehabilitated forest			
Control	2.3(0.5)b	3.4(0.9)b	20.1(0.7)	321.2(11.4)	4.1
Low-N	2.8(0.8)b	3.2(0.3)b	21.0(1.0)	335.7(14.9)	4.0
Medium-N	3.5(0.7)a	5.0(0.4)a	20.1(0.8)	303.1(18.6)	4.0

Sampling dates were September 2005 and August 2006. Unit as mg kg^{-1}, means with S.E. in parenthesis, n = 3. Values followed by different letters are significantly different among treatments within a forest (Tukey's HSD test; $P < 0.05$). Data of Al^{3+} are cited from *Lu et al.* [2008].

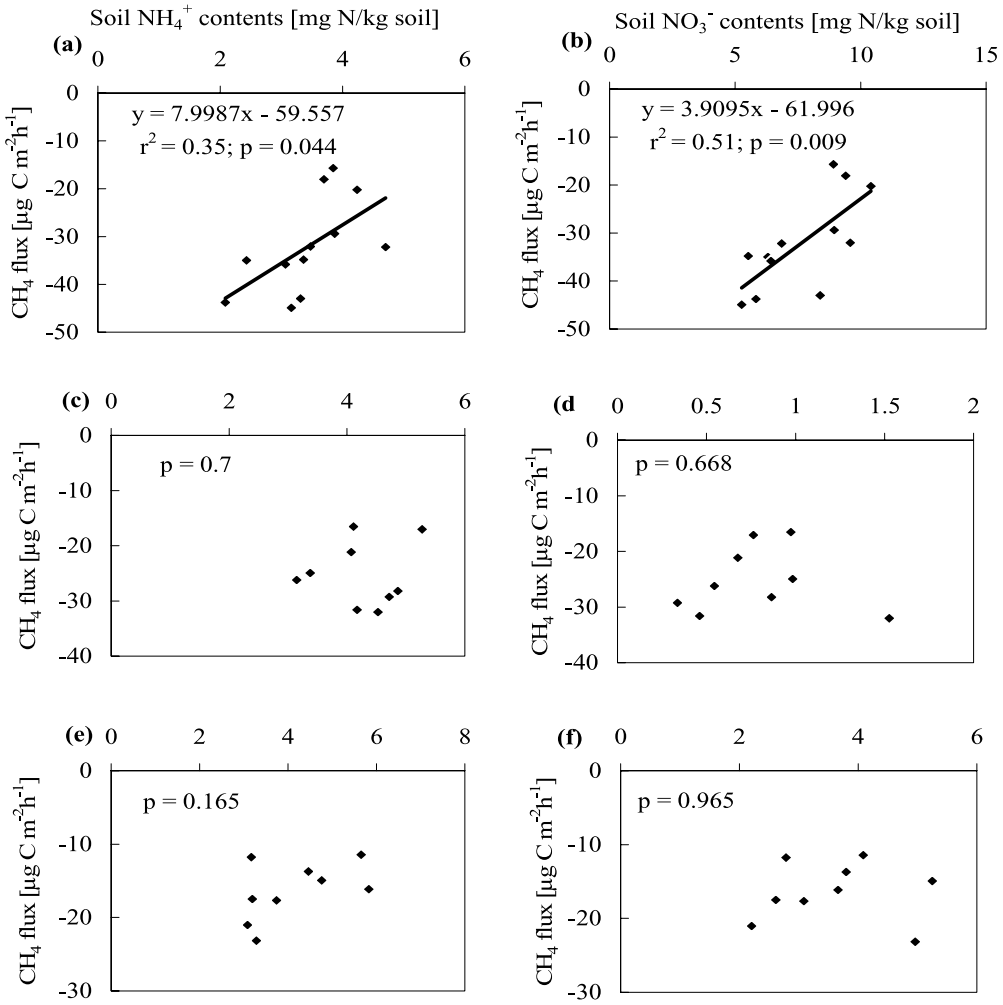

Figure 4. Relationships between CH_4 uptake rates and contents of soil NH_4^+ and NO_3^- in the mature (a, b), rehabilitated (c, d), and disturbed (e, f) forests (n = 3 for soil samples). The CH_4 fluxes were measured in field at the same day of soil sampling (7 August 2006).

[2000] suggested that cations associated with NO_3^- rather than NO_3^- itself were the main factors producing the inhibitory effect on CH_4 uptake. A high level NO_3^-, or NO_2^- produced from the NO_3^- reduction in soil anaerobic microzones, is perhaps toxic to CH_4-oxidizing microbes in forest soils [*Schnell and King*, 1994]. Therefore NH_4^+, NO_3^- or interactions of them were mainly contributed to the inhibitory effect on soil CH_4 uptake in the mature forest.

[25] Second, the mature forest soil has a low pH value, and N additions significantly decreased its pH value. The drop in soil pH might contribute to the decrease in CH_4 uptake rate in the mature forest. *Le Mer and Roger* [2001] reported that the optimal pH for CH_4 oxidizers is 5.0–6.5. *Heyer and Suckow* [1985] suggested that a substantial decrease in CH_4 uptake rates at a pH below 4. *Bradford et al.* [2001b] also observed that the drop in pH in a beech forest in the UK contributed to a decrease in soil CH_4 uptake. The drop in pH might contribute to the decrease in the rates of litter decomposition in Medium-N and High-N treatment plots in the mature forest [*Mo et al.*, 2006; *Fang et al.*, 2007], whereas N additions had no significant effect on litterfall production [*Mo et al.*, 2008], implying that N addition may increase accumulation of floor litter. Litter barriers could reduce substantially the entry of atmospheric CH_4 into the soil.

[26] Third, aluminum (Al^{3+}) toxicity to CH_4-oxidizing bacteria or nitrifiers might be another possible cause of the inhibitory effect [*Nanba and King*, 2000]. The mature forest soil, with a pH of 3.9, was situated in the upper region of the Al^{3+} buffer range (pH 2.8–4.2 [*Ulrich*, 1987]). Al^{3+} was significantly released from cation exchange sites in the soil (Table 3) [*Lu et al.*, 2008], when the NH_4NO_3 treatment caused soil acidification. Therefore the soil of the mature forest, with a low base status and pH, would be particularly sensitive to enhanced N deposition and any acidification might reduce the CH_4 sink strength.

[27] Last, in the rehabilitated and disturbed forests, the reason for little response of CH_4 uptake to N addition might be caused by relatively low initial soil N status resulting from previous human disturbance. Previous results showed that both disturbed and rehabilitated forests are still N-limited [*Mo et al.*, 2006, 2007a; *Fang et al.*, 2006; *Fang et al.*, 2007]. It is well accepted that N-limited forest ecosystems initially retained N due to use in plant growth as well as accumulation in biomass and soil organic matter [*Aber et al.*, 2003], thus plants may be the most important

sinks for NH_4^+ in the rehabilitated and disturbed forests. In addition, sensitivity of atmospheric CH_4 uptake in forest soils to N fertilization may relate to the position of the CH_4 oxidizing community in the soil layer [*Whalen and Reeburgh*, 2000]. Maximum rates of CH_4 oxidation were found 10–20 cm below the soil surface [*Whalen et al.*, 1992]. Hence most of N additions were absorbed by plants before arriving to the active CH_4 oxidizing zone. *Castaldi and Fierro* [2005] found that low soil moisture content in the top 10 cm, as well as high NH_4^+ concentration, did not seem to reduce methanotrophic activity, and suggested that maximal CH_4 oxidation activity might take place deeper in the soil profile. In addition, in the rehabilitated and disturbed forests, where significant soil acidification and Al^{3+} increase were not observed, the mode of Al^{3+} toxicity to CH_4-oxidzing process might not react within these two forests.

5. Conclusions

[28] The mature forest had the highest rate of CH_4 uptake and showed significant response to N addition due to its high initial soil N availability. Both the disturbed and rehabilitated forests, with low initial soil N availability, had relatively lower rates of CH_4 uptake and showed little response to N addition. The decrease of CH_4 uptake could be attributed to the increase in soil inorganic N (NH_4^+, NO_3^-), soil Al^{3+} release and the drop in pH resulted from N addition. Our results suggest that the response of soil CH_4 uptake to N deposition in tropical forests in southern China may vary depending on the soil N status directly, and on land-use history of the forest indirectly.

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References

Aber, J. D., C. L. Goodale, and S. V. Ollinger (2003), Is nitrogen deposition altering the nitrogen status of northeastern forests?, *BioScience*, *53*, 375–389.

Ambus, P., and G. P. Robertson (2006), The effect of increased N deposition on nitrous oxide, methane and carbon dioxide fluxes from unmanaged forest and grassland communities in Michigan, *Biogeochemistry*, *79*, 315–337, doi:10.1007/s10533-005-5313-x.

Bodelier, P. L. E., and H. J. Laanbroek (2004), Nitrogen as a regulatory factor of methane oxidation in soils and sediments, *FEMS Microbiol. Ecol.*, *47*, 265–277.

Borken, W., Y. J. Xu, and F. Beese (2003), Conversion of hardwood forests to spruce and pine plantations strongly reduced soil methane sink in Germany, *Global Change Biol.*, *9*, 956–966.

Borken, W., F. Beese, R. Brumme, and N. Lamersdorf (2002), Long-term reduction in nitrogen and proton inputs did not affect atmospheric methane uptake and nitrous oxide emission from a German spruce forest soil, *Soil Biol. Biochem.*, *34*, 1815–1819.

Bradford, M. A., P. Ineson, P. A. Wookey, and H. M. Lappin-Scott (2001a), The effects of acid nitrogen and acid sulphur deposition on CH_4 oxidation in a forest soil: A laboratory study, *Soil Biol. Biochem.*, *33*, 1695–1702.

Bradford, M. A., P. A. Wookey, P. Ineson, and H. M. Lappin-Scott (2001b), Controlling factors and effects of chronic nitrogen and sulphur deposition on methane oxidation in a temperate forest soil, *Soil Biol. Biochem.*, *33*, 93–102.

Brown, S., M. T. Lenart, and J. M. Mo (1995), Structure and organic matter dynamics of a human-impacted pine forest in a MAB reserve of subtropical China, *Biotropica*, *27*, 276–289.

Brumme, R., and W. Borken (1999), Site variation in methane oxidation as affected by atmospheric deposition and type of temperate forest ecosystem, *Global Biogeochem. Cycles*, *13*, 493–502.

Butterbach-Bahl, K., R. Gasche, C. Huber, K. Kreutzer, and H. Papen (1998), Impact of N-input by wet deposition on N-trace gas fluxes and CH_4-oxidation in spruce forest ecosystems of the temperate zone in Europe, *Atmos. Environ.*, *32*, 559–564.

Butterbach-Bahl, K., L. Breuer, and R. Gasche (2002), Exchange of trace gases between soils and the atmosphere in Scots pine forest ecosystems of the North Eastern German Lowlands. 1. Fluxes of N_2O, NO/NO_2 and CH_4 at forest sites with different N-deposition, *For. Ecol. Manage.*, *167*, 123–134.

Castaldi, S., and A. Fierro (2005), Soil-atmosphere methane exchange in undisturbed and burned Mediterranean shrubland of southern Italy, *Ecosystems*, *8*, 182–190, doi:10.1007/s10021-004-0093-z.

Castro, M. S., W. T. Peterjohn, J. M. Melillo, and P. A. Steudler (1994), Effects of nitrogen on the fluxes of N_2O, CH_4 and CO_2 from soils in a Florida slash pine plantation, *Can. J. For. Res.*, *24*, 9–13.

Castro, M. S., P. A. Steudler, and R. D. Bowden (1995), Factors controlling atmospheric methane consumption by temperate forest soils, *Global Biogeochem. Cycles*, *9*, 1–10.

Castro, M. S., H. L. Gholz, K. L. Clark, and P. A. Steudler (2000), Effects of forest harvesting on soil methane fluxes in Florida slash pine plantations, *Can. J. For. Res.*, *30*, 1534–1542.

Chen, X. Y., and J. Mulder (2007), Indicators for nitrogen status and leaching in subtropical forest ecosystems, South China, *Biogeochemistry*, *82*, 165–180.

NDRCPRC, National Development and Reform Commission of People's Republic of China (2007), China's National Climate Change Programme (available from http://www.sdpc.gov.cn/xwfb/t20070604_139486.htm), Beijing (in Chinese).

Crutzen, P. J. (1991), Methane's sinks and sources, *Nature*, *350*, 380–381.

Davidson, E., F. Ishida, and D. Nepstad (2004), Effects of an experimental drought on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest, *Global Change Biol.*, *10*(5), 718–730.

De Visscher, A., P. Boeckx, and O. Van Cleemput (2007), Artificial methane sinks, in *Greenhouse Gas Sinks*, edited by D. S. Reay et al., pp. 184–200, CABI, New York.

Fang, Y. T., W. X. Zhu, J. M. Mo, G. Y. Zhou, and P. Gundersen (2006), Dynamics of soil inorganic nitrogen and their responses to nitrogen additions in three subtropical forests, South China, *J. Environ. Sci.*, *18*, 752–759.

Fang, H., J. M. Mo, S. L. Peng, Z. A. Li, and H. Wang (2007), Cumulative effects of nitrogen additions on litter decomposition in three tropical forests in southern China, *Plant Soil*, *297*, 233–242, doi:10.1007/s11104-007-9339-9.

Galloway, J. N., E. Cowling, and E. Kessler (2002), Reactive nitrogen, *Ambio*, *31*, 592002.

Galloway, J. N., et al. (2004), Nitrogen Cycles: Past, present, and future, *Biogeochemistry*, *70*, 153–226.

Gulledge, J., and J. P. Schimel (1998), Low-concentration kinetics of atmospheric CH_4 oxidation in soil and mechanisms of NH_4^+ inhibition, *Appl. Environ. Microbiol.*, *64*, 4291–4298.

Gulledge, J., A. P. Doyle, and J. P. Schimel (1997), Different NH_4^+ inhibition patterns of soil CH_4 consumption: A result of distinct CH_4-oxidizer populations across sites?, *Soil Biol. Biochem.*, *29*, 131997.

Hall, S. J., and P. A. Matson (2003), Nutrient status of tropical rain forests influences soil N dynamics after N additions, *Ecol. Monogr.*, *73*, 107–129.

Heyer, J., and R. Suckow (1985), Ökologische untersuchungen der methanoxidation in einem sauren moorsee, *Limnologica*, *16*, 247–266.

Holdridge, L. R. (1967), *Life Zone Ecology*, *Tropical Science Center*, San Jose, Costa Rica.

Holland, E. A., F. J. Dentener, B. H. Braswell, and J. M. Sulzman (1999), Contemporary and pre-industrial global reactive nitrogen budgets, *Biogeochemistry*, *46*, 7–49.

Houghton, J. T., Y. Ding, D. J. Griggs, M. Noguer, P. J. Linden, and D. Xiaosu (2001), Climate change 2001, the scientific basis, in *Contribution of Working Group to the Third Assessment Report of the Intergovernmental Panel on Climatic Change (IPCC)*, p. 944, Cambridge Univ. Press.

Huang, Z. F., and Z. G. Fan (1982), The climate of Dinghushan (in Chinese), in *Tropical and Subtropical Forest Ecosystem*, vol. 1, pp. 11–23, Science Press, Beijing.

Huang, Z. L., M. M. Ding, Z. P. Zhang, and W. M. Yi (1994), The hydrological processes and nitrogen dynamics in a monsoon evergreen broadleafed forest of Dinghushan, *Acta Phytoecol. Sin.*, *18*, 194–199 (in Chinese).

Hütsch, B. W. (1998), Methane oxidation in arable soil as inhibited by ammonium, nitrite, and organic manure with respect to soil pH, *Biol. Fertil. Soils*, *28*, 27–35.

IAEA (1992), Manual on measurements of methane and nitrous oxide emissions from agriculture, International Atomic Energy Agency, Vienna, Austria.

IPCC (Intergovernmental Panel on Climate Change) (2002), *Special Report on Emission Scenarios*, Cambridge Univ. Press, U.K.

Ishizuka, S., T. Sakata, and K. Ishizuka (2000), Methane oxidation in Japanese forest soils, *Soil Biol. Biochem.*, *32*, 769–777.

Ishizuka, S., A. Iswandi, Y. Nakajima, L. Yonemura, S. Sudo, H. Tsuruta, and D. Muriyarso (2005), Spatial patterns of greenhouse gas emission in a tropical rainforest in Indonesia, *Nutr. Cycling Agroecosyst.*, *71*(1), 55–62.

Jang, I., S. Lee, J. H. Hong, and H. Kang (2006), Methane oxidation rates in forest soils and their controlling variables: A review and a case study in Korea, *Ecol. Res.*, *21*, 849–854, doi:10.1007/s11284-006-0041-9.

King, G. M., and S. Schnell (1994), Ammonium and nitrite inhibition of methane oxidation by Methylobacter albus BG8 and Methylosinus trichosporium OB3b at low methane concentrations, *Appl. Environ. Microbiol.*, *60*, 3508–3513.

Le Mer, J., and P. Roger (2001), Production, oxidation, emission and consumption of methane by soils: A review, *Eur. J. Soil*, *37*, 25–50.

Liu, G. H., B. J. Fu, L. D. Chen, and X. D. Guo (2000), Characteristics and distributions of degraded ecological types in China, *Acta Ecol. Sin.*, *20*, 13–19 (in Chinese).

Lu, X. K., J. M. Mo, P. Gundersern, W. X. Zhu, G. Y. Zhou, D. J. Li, and X. Zhang (2008), Effects of simulated N deposition on soil exchangeable cations in three forest land-use types in subtropical China, *Pedosphere*, in press.

Maljanen, M., A. Liikanen, J. Silvola, and P. J. Martikainen (2003), Methane fluxes on agricultural and forested boreal organic soils, *Soil Use Manage.*, *19*, 73–79.

Matson, P. A., K. A. Lohse, and S. J. Hall (2002), The globalization of nitrogen deposition: Consequences for terrestrial ecosystems, *Ambio*, *31*, 113–119.

Menyailo, O. V., and B. A. Hungate (2002), Interactive effects of tree species and soil moisture on methane consumption, *Soil Biol. Biochem.*, *35*, 625–628.

Mo, J. M., S. Brown, M. Lenart, and G. H. Kong (1995), Nutrient dynamics of a human-impacted pine forest in a MAB Reserve of subtropical China, *Biotropica*, *27*, 290–304.

Mo, J. M., S. Brown, and S. L. Peng (2003), Nitrogen availability in disturbed, rehabilitated and mature forests of tropical China, *For. Ecol. Manage.*, *175*, 573–583.

Mo, J. M., S. L. Peng, S. Brown, G. H. Kong, and Y. T. Fang (2004), Nutrient dynamics in response to harvesting practices in a pine forest of subtropical China, *Acta Phytoecol. Sin.*, *28*, 810–822 (in Chinese).

Mo, J. M., S. Brown, and J. H. Xue (2006), Response of litter decomposition to simulated N deposition in disturbed, rehabilitated and mature forests in subtropical China, *Plant Soil*, *282*, 135–151.

Mo, J. M., W. Zhang, W. X. Zhu, Y. T. Fang, D. J. Li, and P. Zhao (2007a), Response of soil respiration to simulated N deposition in a disturbed and a rehabilitated tropical forest in southern China, *Plant Soil*, *296*, 125–135, doi:10.1007/s11104-007-9303-8.

Mo, J. M., S. Brown, J. H. Xue, Y. T. Fang, Z. A. Li, D. J. Li, and S. F. Dong (2007b), Response of nutrient dynamics of decomposing pine (Pinus massoniana) needles to simulated N deposition in a disturbed and a rehabilitated forest in tropical China, *Ecol. Res.*, *22*, 649–658, doi:10.1007/s11284-006-0317-0.

Mo, J. M., W. Zhang, W. X. Zhu, P. Gundersen, Y. T. Fang, D. J. Li, and H. Wang (2008), Nitrogen addition reduces soil respiration in a mature tropical forest in southern China, *Global Change Biol.*, *14*, 412–430.

Mosier, A., D. Schimel, D. Valentine, K. Bronson, and W. Parton (1991), Methane and nitrous oxide fluxes in native, fertilized and cultivated grasslands, *Nature*, *350*, 330–332.

Nakano, T., G. Inoue, and M. Fukuda (2004), Methane consumption and soil respiration by a birch forest soil in West Siberia, *Tellus, Ser. A and Ser. B*, *56B*, 223–229.

Nanba, K., and G. King (2000), Response of atmospheric methane consumption by Maine forest soils to exogenous Aluminum salts, *Appl. Environ. Microbiol.*, *66*(9), 3674–3679.

Nesbit, S. P., and G. A. Breitenbeck (1992), A laboratory study of factors influencing methane uptake by soils, *Agric. Ecosyst. Environ.*, *41*, 39–54.

NSBC (National Standard Bureau of China) (1987), *Analytical Methods for Forest Soils* (in Chinese), National Standard Bureau Press, Beijing.

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

Reay, D. S., and D. B. Nedwell (2004), Methane oxidation in temperate soils: Effects of inorganic N, *Soil Biol. Biochem.*, *36*, 2059–2065.

Ren, R., F. J. Mi, and N. B. Bai (2000), A chemometrics analysis on the data of precipitation chemistry of China, *J. Beijing Polytechnic Univ.*, *26*, 90–95 (in Chinese).

Schlesinger, H. W. (1997), *Biogeochemistry: An Analysis of Global Change*, Academic Press, New York.

Schnell, S., and G. M. King (1994), Mechanistic analysis of ammonium inhibition of atmospheric methane consumption in forest soils, *Appl. Environ. Microbiol.*, *25*, 1415–1421.

Sitaula, B. K., J. I. B. Sitaula, Å. Aakra, and L. R. Bakken (2001), Nitrification and methane oxidation in forest soil: Acid deposition, nitrogen input and plant effects, *Water Air Soil Pollut.*, *130*, 1061–1066.

Smith, K. A., et al. (2000), Oxidation of atmospheric methane is Northern European soils, comparison with other ecosystems, and uncertainties in the global terrestrial sink, *Global Change Biol.*, *6*, 791–803.

Steinkamp, R., K. Butterbach-Bahl, and H. Papen (2001), Methane oxidation by soils of an N limited and N fertilized spruce forest in the Black Forest, Germany, *Soil Biol. Biochem.*, *33*, 145–153, doi:S0038-0717(00)00124-3.

Steudler, P. A., R. D. Bowden, J. M. Mellilo, and J. D. Aber (1989), Influence of nitrogen fertilization on methane uptake in temperate forest soils, *Nature*, *341*, 314–316.

Steudler, P. A., R. D. Jones, M. S. Castro, J. M. Melillo, and D. L. Lewis (1996), Microbial controls of methane oxidation in temperate forest and agricultural soils, in *Microbiology of Atmospheric Trace Gases*, *NATO ASI Series*, edited by J. C. Murrell and D. P. Kelly, *139*, 69–84.

Tamai, N., C. Takenaka, S. Ishizuka, and T. Tezuka (2003), Methane flux and regulatory variables in soils of three equal-aged Japanese cypress (Chamaecyparis obtusa) forests in central Japan, *Soil Biol. Biochem.*, *35*, 633–641.

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

Ulrich, B. (1987), Stability, elasticity and resilience of terrestrial ecosystems with respect to matter balance, in *Potentials and Limitations of Ecosystem Analysis*, *Ecol. Stud.*, vol. 61, edited by E. D. Schulze and H. Zwolfer, pp. 11–49, Springer-Verlag, Berlin, Heidelberg.

Wang, Z. P., and P. Ineson (2003), Methane oxidation in a temperate coniferous forest soil: Effects of inorganic N, *Soil Biol. Biochem.*, *35*, 427–433.

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

Wang, Z., D. He, S. Song, S. Chen, D. Chen, and M. Tu (1982), The vegetation of Dinghushan biosphere reserve, in *Tropical and Subtropical Forest Ecosystem*, vol. 1, pp. 77–141, (in Chinese).

Werner, C., R. Kiese, and K. Butterbach-Bahl (2007), Soil-atmosphere exchange of N_2O, CH_4, and CO_2 and controlling environmental factors for tropical rain forest sites in western Kenya, *J. Geophys. Res.*, *112*, D03308, doi:10.1029/2006JD007388.

Whalen, S. C., and W. S. Reeburgh (2000), Effect of nitrogen fertilization on atmospheric methane oxidation in boreal forest soils, *Chemosphere Global Change Sci.*, *2*, 151–155.

Whalen, S. C., W. S. Reeburgh, and V. A. Barber (1992), Oxidation of methane in boreal forest soils: A comparison of seven measures, *Biogeochemistry*, *16*, 181–211.

Willison, T. W., R. Cook, A. Müller, and D. S. Powlson (1996), CH_4 oxidation in soils fertilized with organic and inorganic-N: Differential effects, *Soil Biol. Biochem.*, *28*, 135–136.

Xu, X. K., and K. Inubushi (2004), Effects of N sources and methane concentrations on methane uptake potential of a typical coniferous forest and its adjacent orchard soil, *Biol. Fertil. Soils*, *40*, 215–221.

Zhou, G. Y., and J. H. Yan (2001), The influence of region atmospheric precipitation characteristics and its element inputs on the existence and development of Dinghushan forest ecosystems, *Acta Ecol. Sin.*, *21*, 2002–2012 (in Chinese).

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

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