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REGULAR ARTICLE

Emissions of nitrous oxide from three tropical forests in Southern China in response to simulated nitrogen deposition

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Abstract Emissions of nitrous oxide (N_2O) from the soil following simulated nitrogen (N) deposition in a disturbed (pine), a rehabilitated (pine and broadleaf mixed) and a mature (monsoon evergreen broadleaf) tropical forest in southern China were studied. The following hypotheses were tested: (1) addition of N will increase soil N_2O emission in tropical forests; and (2) any observed increase will be more pronounced in the mature forest than in the disturbed or rehabilitated forest due to the relatively high initial soil N concentration in the mature forest. The experiment was designed with four N treatment levels (three replicates; 0, 50, 100, 150 kg N ha^{-1} $year^{-1}$ for C (Control), LN (Low-N), MN (Medium-N), and HN (High-N) treatment, respectively) in the mature forest, but only three levels in the disturbed and rehabilitated forests (C, LN and MN). Between October 2005 to September 2006, soil N_2O flux was measured using static chamber and gas chromatography methodology. Nitrogen had been applied previously to the plots since July 2003 and continued during soil N_2O flux measurement period. The annual mean rates of soil N_2O emission in the C plots were 24.1±1.5, 26.2±1.4, and 29.3±1.6 μg N_2O–N m^{-2} h^{-1} in the disturbed, rehabilitated and mature forest, respectively. There was a significant increase in soil N_2O emission following N additions in the mature forest (38%, 41%, and 58% when compared to the C plots for the LN, MN, and HN plots, respectively). In the disturbed forest a significant increase (35%) was observed in the MN plots, but not in the LN plots. The rehabilitated forest showed no significant response to N additions. Increases in soil N_2O emission occurred primarily in the cool-dry season (November, December and January). Our results suggest that the response of soil N_2O emission to N deposition in tropical forests in southern China may vary depending on the soil N status and land-use history of the forest.

Keywords Anthropogenic disturbances · N_2O emission · N deposition · Tropical forests · China

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Introduction

Nitrous oxide is an important radiatively active greenhouse gas, contributing approximately 6% to total observed global warming (WMO 2006). N_2O is of major concern in the context of climate change due to its atmospheric longevity (about 120 years), global warming potential (310 times that of CO_2 on a per molecule basis over a 100-year period), and its rapid increase in concentration in the atmosphere (0.25% per year, IPCC 2007). In addition, N_2O is involved in the depletion of stratospheric ozone through nitric oxide (NO) production (Crutzen 1970). Although abiological processes (e.g., chemodenitrification) may account for a small portion of total soil derived N_2O, the biological processes of nitrification $\left(NH_4^+ \rightarrow NO_3^-\right)$ and denitrification $\left(NO_3^- \rightarrow N_2\right)$ are believed to be the predominant sources of N_2O production in soils (Williams et al. 1992; Wrage et al. 2001). Forest soils have been acknowledged to represent significant sources of N_2O emission (Papen and Butterbach-Bahl 1999; Butterbach-Bahl et al. 2002; Skiba et al. 2004). The dominant source for N_2O from tropical forest soils was estimated to be in the range of 2.2–3.7 Tg N $year^{-1}$ (24% of the total source strength) to the global atmospheric N_2O budget (Prather and Ehhalt 2001). Soil biological N_2O production is controlled by a set of physical, chemical and biological factors. Soil moisture content, soil temperature and nutrient availability are regarded as key in regulating soil N_2O production in forests (Papen and Butterbach-Bahl 1999; Brumme et al. 1999; Smith et al. 2003). An increase in these factors usually enhances N_2O emission from forest soil. Other studies have also shown that soil N_2O emission depends on forest management and N deposition (Butterbach-Bahl et al. 2002; Horváth et al. 2006).

In the past decades, atmospheric N deposition (dryfall and rainfall) into terrestrial ecosystems has 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). Emissions of N_2O from forest soils have most likely increased in recent decades and will probably further increase in the future due to the anthropogenic perturbation of the global N cycle (Galloway et al. 2004). In a series of recent publications, evidence has been provided that N_2O emissions are positively correlated with N deposition to forest ecosystems (Butterbach-Bahl et al. 1998; Davidson et al. 2000; Zechmeister-Boltenstern et al. 2002; Skiba et al. 2004). However, most of these studies were carried out in temperate regions, where most forests are naturally N-limited (Hall and Matson 1999; 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 (Vitousek and Sanford 1986; Hall and Matson 1999, 2003; Matson et al. 2002). Increases in soil N_2O emission as a result of increased N deposition is hypothesized to have more significant environmental consequences in tropical forest than in temperate forest ecosystems (Matson et al. 2002; Hall and Matson 2003), however more research is required in order to confirm this.

In Asia, the use and emission of reactive N increased from 14 Tg N $year^{-1}$ in 1961 to 68 Tg N $year^{-1}$ in 2000 and is expected to reach 105 Tg N $year^{-1}$ in 2030 (Zheng et al. 2002). This has lead to high (30–73 kg N ha^{-1} $year^{-1}$) atmospheric N deposition of NH_4^+ and NO_3^- in precipitation in some forests of southern China (Ren et al. 2000; Xu et al. 2001; Chen and Mulder 2007). Nitrogen deposition in southern China has been projected to increase in the coming decades, due to the rapid expansion of industrial and agricultural activities (Galloway et al. 2004; Mo et al. 2006, 2007a; Chen and Mulder 2007). In addition, most of the forests in southern China have been degraded by human activities for many hundreds of years (Wang et al. 1982). Deforestation in China is estimated to be on the order of 0.61 million hectare per year, with the remaining virgin forest occupying an area of less than 9% of the total territory in the 1990s (Liu et al. 2000). Over the last few decades, however, large areas have been reforested with a native species (*Pinus massoniana* Lamb) to prevent further degradation of the landscape (Mo et al. 2003, 2007a). Cutting of the trees is usually prohibited, but harvesting of understory and litter is often allowed to satisfy local fuel needs (Brown et al. 1995; Mo et al. 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. 2003, 2007a, b). Although forest coverage in China is now

174.91 million hectares or 18.2% of the total territory (CNCCP 2007), to date there has been limited research aimed at studying N_2O emission from forest soils. Information regarding soil N_2O emission in response to increased atmospheric N deposition in forests of China is non-existent. Studying soil N_2O emissions in these forests 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 N_2O emission budget and in predicting future emission trends. The results will contribute to understanding the effects of increasing N deposition on Asian forest ecosystems.

Previously, we reported that the mature forests have been N-saturated due to both long-term high atmospheric N deposition in the region and ecosystem age, and that both the disturbed and rehabilitated forests are N-limited due to land use history (Mo et al. 1995, 2006, 2007a, b, 2008). In this study, we examined the effects of elevated N deposition on soil N_2O emission in a disturbed, a rehabilitated and a mature tropical forest in southern China. We hypothesized that N addition would alter soil NH_4^+ and NO_3^- concentrations, and increase soil N_2O emissions in these tropical forests. We also hypothesized that any observed increase would be more pronounced in the mature forest than in the disturbed or rehabilitated forest due to the relatively high initial soil N concentration in the mature forest.

Methods

Site description

This 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 1,200 ha. We have established research sites in a disturbed forest (pine), a rehabilitated forest (pine and broadleaf mixed), and a mature (old-growth monsoon evergreen broadleaf) forest within 3–4 km distance of each other (Mo et al. 2006). Both the disturbed and rehabilitated forests originated from a 1930s clear-cutting policy and subsequent pine plantation establishment (Mo et al. 2006, 2007a). The disturbed forest in contrast, underwent continuous human disturbance (generally the harvesting of understory and litter) from the 1930s to 1998, with *Pinus massoniana* remaining as the predominant tree (Mo et al. 2007a). Colonization from the natural dispersal of regional broadleaf species in rehabilitated forest has altered its plant community (Mo et al. 2003, 2007a). Dominant species in the rehabilitated forest are *Pinus massoniana*, *Schima superba*, *Castanopsis 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). 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). Stem density, tree height and mean diameter at breast height in the three forests are given in Table 1.

Litterfall in the studied forests was from the dominant tree species with variations among forest types (Zhang et al. 2000). The mean annual litter biomass production was 8.3, 8.5 and 3.3 Mg ha^{-1} $year^{-1}$, respectively in the mature, rehabilitated and disturbed forests (Zhang et al. 2000). In the mature forest, *Castanopsis chinensis* contributed the greatest amount of litter (40% of total litter), followed by *Cryptocarya chinensis* (12%), *Syzygium rehderianum* (6%) and *Machilus chinensis* (5%). In the rehabilitated forest, *Pinus massoniana* and *Schima superba* contributed 31% and 30%, respectively of the total litter. In the disturbed forest, however, total litter production was predominantly from *Pinus massoniana* (91%; Zhang et al. 2000; Mo et al. 2006, 2007b).

The reserve has a typical monsoon and humid tropical climate (Holdridge 1967). The mean annual temperature is 21.0°C. The average temperature of the coldest (January) and hottest (July) month are 12.6°C and 28.0°C, respectively (Huang and Fan 1982). The mean annual rainfall of 1,927 mm has a distinct seasonal pattern, with 75% of it falling from March to August and only 6% from December to February.

Table 1 Indices[a] of the tree layer in three tropical forests in southern China

Species	Stem density (tree per hectare)	Mean height (m)	MDBH (cm)	Basal area (m^2 ha^{-1})	Relative basal (%)
Disturbed forest					
Pinus massoniana	456	6.9	17.5	13.3	95.1
Other trees	311	4.3	4.4	0.7	4.9
Total	767			14	100
Rehabilitated forest					
Pinus massoniana	133	10.2	22	5.6	41
Schima superba	1,567	5.2	6.4	7.4	53.6
Other trees	233	4.2	5.1	0.8	5.4
Total	1,933			13.8	100
Mature forest					
Castanopsis chinensis	83	12.7	23.5	9.6	37
Machihus chinensis	208	7.1	8.6	4.1	15.8
Schima superbas	183	7.7	10.3	3.8	14.5
Cryptocarya chinensis	113	11.5	20.6	2.3	8.9
Syzygium rehderianum	129	11.1	29.4	1.6	6.2
Other trees	1,013	5.4	5.8	4.6	17.6
Total	1,729			26.0	100

[a] Data are cited from Fang et al. 2006

MDBH, Mean of diameter breast height

Annual average relative humidity is 80% (Huang and Fan 1982). During the study period, monthly precipitation and temperature (Fig. 1c) largely followed this long-term seasonal pattern. The N deposition in rainfall was 36–38 kg N ha^{-1} $year^{-1}$ in 1990s (Huang et al. 1994; Zhou and Yan 2001), and 34 and 32 kg N ha^{-1} $year^{-1}$ in 2004 and 2005, respectively (roughly 1:1 NH_4^+ to NO_3^- molar ratio; Fang et al. 2007).

Soil in the reserve is predominantly lateritic earth formed from sandstone (oxisols) and shale (Wu et al. 1982), with variable depths (from 30 cm in the disturbed/rehabilitated to more than 60 cm in the mature forest; Mo et al. 2003, 2006). Soil in the mature forest has a higher total N, total C, N/P ratio and soil moisture content, but a lower pH value, C/N ratio, soil temperature and soil bulk density than the disturbed and rehabilitated forests (Table 2).

Experimental design

Four N (NH_4NO_3) addition treatment levels (three replicates) were established in the mature forest: C (without N addition), LN (50), MN (100) and HN (150 kg N ha^{-1} $year^{-1}$), but only three levels (three replicates) were established in the disturbed and rehabilitated forests (C, LN and MN treatment; Mo et al. 2006). LN treatment (86–88 kg N ha^{-1} $year^{-1}$, atmospheric deposition plus experimental N input) corresponded to a value similar to the projected N deposition (45–113 kg N ha^{-1} $year^{-1}$) in 2030 in southern China (Zheng et al. 2002). A total of 30 plots (20×10 m) were established (9 in the disturbed, 9 in the rehabilitated and 12 in the mature forest), each surrounded by a 10-m-wide buffer strip. Field plots and treatments were laid out randomly. Fertilizer (NH_4NO_3) was weighed, mixed with 20 l of water, and applied to the plots below the canopy using a backpack sprayer. Two paths were made across each plot to ensure an even distribution of fertilizer. The C plot received 20 l water without fertilizer addition (Mo et al. 2006). The solution was sprayed as 12 equal monthly applications over the entire year, beginning in July 2003 and continuing throughout the study period.

Field sampling and measurements

N_2O flux measurements were started 26 months after the initial N applications in October 2005 (Mo et al. 2008). Gas samples for N_2O flux measurement were taken once a week during the growing season (April–September) and once every other week at other times using closed static chamber methodology and analyzed using gas chromatography (Agilent 4890D, Agilent Co. USA). The static chambers were made of stainless-steel and consisted of two parts, an anchor

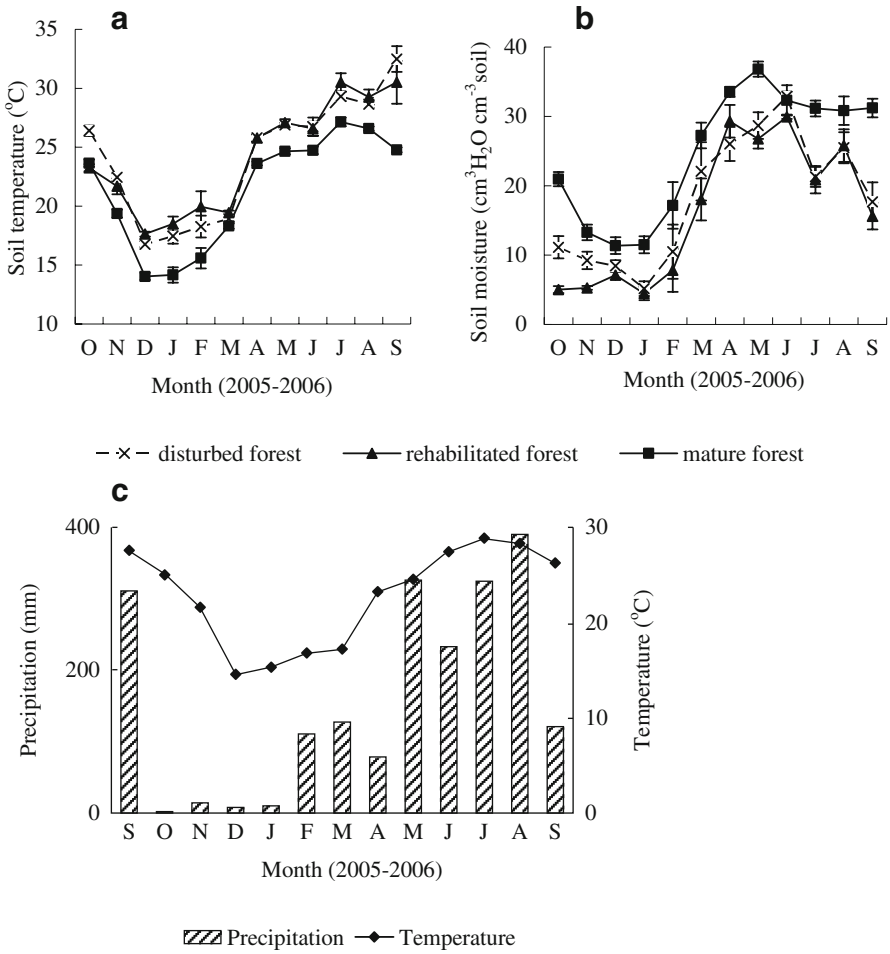

Fig. 1 Seasonal patterns of soil temperatures (**a**) and soil moisture contents (**b**) in the mature, rehabilitated and disturbed forests. Monthly precipitation and air temperature (**c**) of DHSBR from September 2005 to September 2006 (Data are from Dinghushan Forest Research Station, Chinese Academy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

ring (10 cm height and 25 cm diameter) and a removable cover chamber (35 cm height×25 cm diameter). A fan (8 cm diameter, 80 RPM) was installed inside each chamber roof (Mo et al. 2008). 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

Table 2 Soil properties (0–10 cm depth) of the C plots in three tropical forests in Southern China

Forest type	Disturbed forest	Rehabilitated forest	Mature forest
pH value (H2O)[a]	3.93 (0.08)	3.91 (0.03)	3.76 (0.01)
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 (0.28)	4.2 (0.30)	5.0 (0.16)
Total P (mg g^{-1})	0.17 (0.01)	0.18 (0.01)	0.22 (0.01)
N/P ratio	7.7 (0.08)	6.7 (0.09)	11.4 (0.15)
Organic matter (%)[b]	2.7 (0.2)	3.5 (0.4)	5.4 (0.6)
Bulk density (g soil cm^{-3})[b]	1.16 (0.05)	1.22 (0.01)	0.98 (0.06)

Values are means with 1 SE in parentheses, n=3 for all samples; measured in July 2004

[a] Data are cited from Fang et al. 2006

[b] Data are cited from Mo et al. 2006

sampling period using a rubber O-ring seal. Gas samples were taken at 0, 10, 20 and 30 min after chamber closure using 100 ml plastic syringes, and were analyzed in the laboratory within 24 h. Gas samples were collected during mid-morning (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). Gas flux was calculated from the linear regression of concentration versus time using the data points from each chamber to minimize the negative effect of chamber closure on N_2O production (Keller and Reiners 1994; Tang et al. 2006; Mo et al. 2007a, 2008). Prior sampling showed that the increase in N_2O 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 0.98 ($P<0.001$).

Soil temperature (5 cm depth) and moisture content (10 cm depth) were monitored at each chamber during sample collection. Soil temperature (°C) was measured using a digital thermometer (TES-1310, Ltd., China). Soil moisture content (%, cm^3 H_2O cm^{-3} soil) was determined using a MPKit (ICT, Australia), as described in detail by Tang et al. (2006). Micro-environmental factors, including air temperature of the chamber headspace, air temperature at 1.5 m above ground, as well as atmospheric pressure were measured simultaneously.

Soil sampling and analysis

Soil samples were collected in December 2005 and August 2006, for determining soil extractable NH_4^+, NO_3^- and pH values. Two composite samples of four soil cores (10 cm depth) were collected randomly within each plot using a standard soil probe (2.5 cm inside diameter). The composite samples were gently mixed, resulting in three samples for each N treatment. Gravimetric moisture content 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 prior 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 $NO_2^- - N$, followed by sulfanilamide-NAD reaction. Total N was determined with a semimicro-Kjeldahl digestion followed by NH_4^+ detection (NSBC 1987).

Statistical analysis

One-way ANOVA with Tukey's HSD test was used to test the difference in soil NH_4^+, NO_3^- concentration and soil extractable DON among treatments. Repeated measure ANOVA with Tukey's HSD test was performed to examine the difference of the soil N_2O emission rates, soil temperatures and soil moisture contents among treatments for the study period. In order to examine the relationship between soil parameters and the measured N_2O fluxes, multiple linear regression analysis was performed (Tang et al. 2006; Werner et al. 2006; Mo et al. 2008). Gas fluxes and soil parameters were collected at the same day. Mean rate of N_2O emission, soil moisture, and soil temperature were calculated by the average of three replicates for each N-treatment in the three forests. All statistical analyses were performed using SPSS 12.0 (SPSS Inc., Chicago, USA). Statistical significant differences were set with P values <0.05 unless otherwise stated.

Results

Soil temperature and moisture

Soil temperature (5 cm) and moisture (10 cm) exhibited clear seasonal patterns in the three forests (Fig. 1a,b). The soil was warmer and wetter from April to September (growing season) and became cooler and dryer from December to February (winter season). The annual mean soil temperature in the C plots was 23.9±0.5°C, 23.7±0.7°C, and 21.4±0.7°C in the disturbed, rehabilitated and mature forest, respectively. The annual mean soil moisture content in the C plots was 18.4±1.5, 17.2±1.6, and 24.9±1.4 (%, cm^3 H_2O cm^{-3} soil) in the disturbed, rehabilitated and mature forest, respectively. The mean of soil moisture content ($P=0.503$) and soil temperature ($P=0.831$) were similar between the disturbed and rehabilitated forests. The mature forest displayed higher soil moisture content ($P=0.03$) and lower soil temperature ($P=0.02$) compared to the disturbed and

rehabilitated forests (Fig. 1a,b). There was no treatment effect on soil temperature and soil moisture in the three forests during the study period.

Soil N_2O emission in C plots

The annual mean rates of soil N_2O emission were 29.3±1.6, 26.2±1.5 and 24.1±1.5 μg N_2O–N m^{-2} h^{-1} in the mature, rehabilitated and disturbed forest, respectively (Table 3; Fig. 3d). Soil N_2O emission tended to be higher in the mature forest than in the disturbed (P=0.052) or rehabilitated forests (P=0.054). However, no significant difference in N_2O emission was found between the disturbed and the rehabilitated forest (P=0.27). Soil N_2O fluxes were positively and linearly correlated with soil temperature and soil moisture in the three forests (Fig. 2; Table 4). Multiple linear regression models explained up to 54% of variation in N_2O emission in the mature forest through changes in temperature and soil moisture content (Table 4). Soil N_2O emissions in the mature forest exhibited a distinct seasonal pattern, with the highest rates observed in the hot-wet growing season (April–September) and the lowest rates in the winter season (December–February; Fig. 3c; Table 3, P=0.02). In the disturbed and rehabilitated forests, soil N_2O emissions during the growing season (April–September) were higher than in the winter season, however this trend was not statistically significant (Fig. 3a,b; Table 3, P=0.082).

Effects of N addition on soil N_2O emission

Soil N_2O emission in N treatment plots showed a similar seasonal pattern to that in the C plots (Fig. 3a–c). A pulse of N_2O was observed in April in all forest types (Fig. 3a–c). Effect of N addition on soil N_2O emission varied depending on N addition level and forest land-use type (Fig. 3). Repeated measure ANOVA test showed that soil N_2O emission in the N treatment plots in the mature forest (P=0.026, Fig. 3c,d; Table 3) and in MN plots in the disturbed forest (P=0.037, Fig. 3a,d; Table 3) increased significantly following N additions relative to the C plots. In the mature forest, the annual mean rate of soil N_2O emission was increased by 38%, 41% and 58% in the LN (40.3±2.1), MN (41.2±2.1), and HN plots (46.2±2.2), respectively, when compared to the C plots (31.39±1.45 μg N_2O–N m^{-2} h^{-1}, annual mean±SE, n=3). In the disturbed forest, the annual mean rate of soil N_2O emission in the MN plots (33.84±1.9) was 40% higher than that in the C plots

Table 3 Annual mean (±SE), season mean, minima and maxima rates of N_2O emissions and soil available N (NH_4^+ and NO_3^-) in the disturbed, rehabilitated and mature tropical forests

Site-treatment	N_2O emission (μg N m^{-2} h^{-1})				Soil available N	
	Annual mean	Hot-wet	Cool-dry	Min–max	NH_4^+–N	NO_3^-–N
Disturbed forest						
Control	24.1 (1.5) b	22.5 (2.3)	21.7 (2.8) b	0.3–57.3	2.32 (0.5) b	3.36 (0.9) b
Low-N	26.6 (1.6) ab	24.1 (2.1)	22.9 (2.9) b	3.8–69.4	2.37 (0.8) b	3.18 (0.3) b
Medium-N	33.9 (1.9) a	32.5 (2.8)	29.6 (3.5) a	10.1–90.2	3.47 (0.7) a	4.98 (0.4) a
Rehabilitated forest						
Control	26.2 (1.4)	30.0 (2.1)	25.2 (2.8)	7.0–63.9	2.29 (0.4)	3.03 (0.2)
Low-N	27.5 (1.5)	31.8 (2.7)	23.8 (1.7)	6.6–69.9	3.49 (0.2)	3.33 (0.3)
Medium-N	33.4 (1.8)	35.6 (3.2)	27.8 (2.5)	9.1–84.2	3.60 (0.6)	3.64 (0.1)
Mature forest						
Control	29.3 (1.6) b	37.4 (3.2)	15.4 (1.6) b	0.9–114.5	2.87 (0.4) b	5.77 (0.5) b
Low-N	40.3 (2.1) a	56.4 (3.5)	21.8 (2.0) b	2.1–127.3	3.40 (0.7)ab	6.68 (0.8) b
Medium-N	41.2 (2.1) a	57.3 (3.8)	32.8 (4.1) a	4.1–121.6	3.68 (0.2) a	8.89 (0.9) a
High-N	46.2 (2.2)a	56.9 (4.2)	31.9 (3.9) a	2.9–140.7	3.80 (0.2) a	10.14 (1.3) a

Cool-dry season was from December to February, hot-wet season was from April to September. Gas samples were collected from October 2005 to September 2006. Soil available N unit is mg kg^{-1}. Different letter within a single forest indicate significant different among treatments at P value <0.05 level. Values are means with 1 SE in parentheses

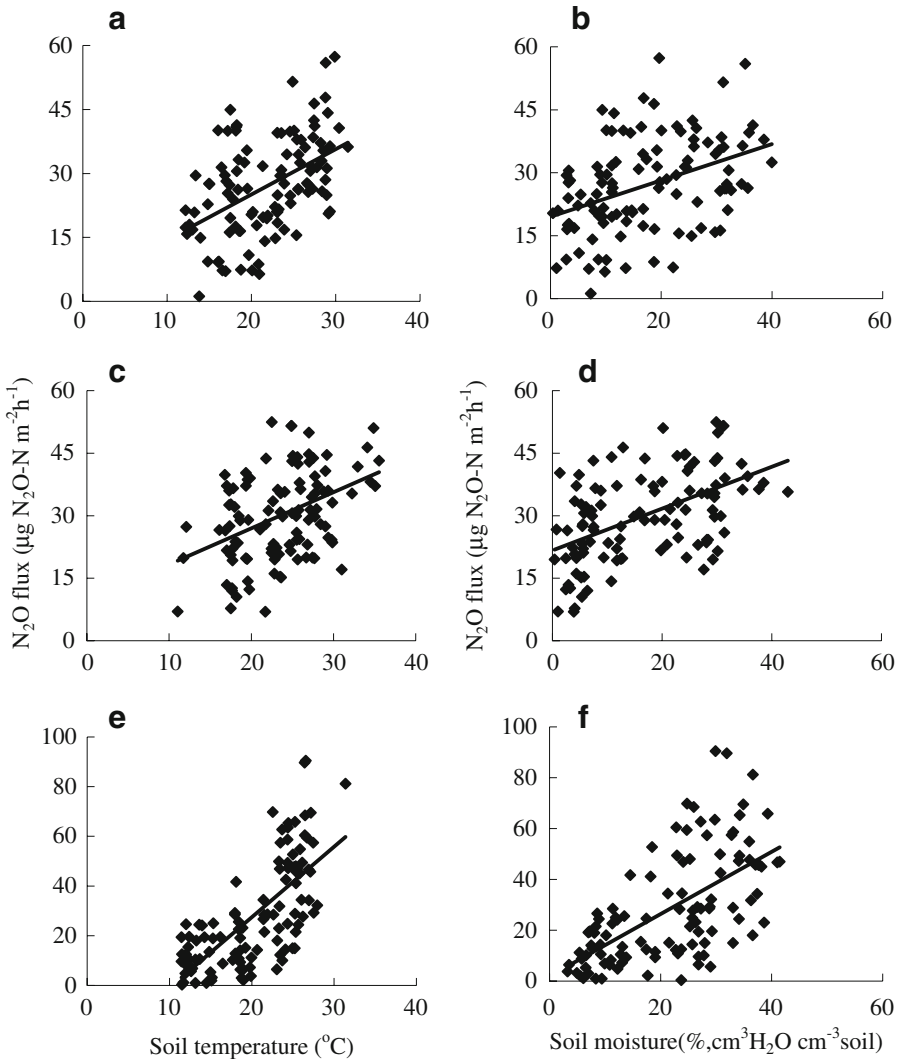

Fig. 2 Relationships between soil N_2O emission rates and soil temperature (5 cm) and soil moisture contents (10 cm) in the C plots of disturbed (**a**, **b**), rehabilitated (**c**, **d**) and mature forest (**e**, **f**; n=108). Gas samples, soil temperature and soil moisture were collected simultaneity

(24.14±1.5 μg N_2O–N m^{-2} h^{-1}, P=0.037, n=3). The significant increases of soil N_2O emission in response to N addition were mostly observed during the winter season (December–February; P<0.05, Fig. 3a,c; Table 3). In the rehabilitated forest, however, there was no significant response of soil N_2O emission to N addition (P=0.19, Fig. 3b,d; Table 3).

Soil N availability indices

In the C plots, the concentrations of soil NH_4^+ and NO_3^- in the mature forest were significantly higher than those in the disturbed or rehabilitated forest (P=0.04, Table 3). Nitrogen addition significantly increased concentrations of soil NH_4^+ and NO_3^- in the MN and HN plots in the mature forest (P<0.05, Table 3), and in MN plots in the disturbed forest (P=0.047 for NH_4^+, P=0.039 for NO_3^-, respectively, Table 3), when compared to the C plots. For all sites, a significant positive correlation existed between N_2O emissions and soil NH_4^+ and NO_3^- concentrations (Table 5; Fig. 4). Changes in soil NH_4^+ concentration explained up to 53% of variation in N_2O emissions in the mature forest, 44% in the disturbed forest, but only 29% in the rehabilitated forest (Table 5). Regression analysis indicated that changes in soil NO_3^- concentration explained 45%, 30% and 27% of variations in N_2O emissions for the mature, rehabilitated and disturbed forest, respectively (Table 5). Multiple linear regression models explained up to 61% of variation in N_2O emissions through changes in soil NH_4^+ and NO_3^- concentrations (Table 5).

Table 4 Regression analysis between mean daily N_2O fluxes and changes in mean daily soil temperature and soil moisture in the C plots

Disturbed forest (n=108)		Rehabilitated forest (n=108)	Mature forest (n=108)	All sites (n=324)
Soil temperature [T (°C)]				
R^2	0.23**	0.17**	0.49**	0.29**
p value	<0.001	<0.001	<0.001	<0.001
$f(T)$	3.744+1.107 T	9.632+0.867 T	−29.339+2.837 T	−5.417+1,547 T
Soil moisture [M (WFPS, %)]				
R^2	0.16**	0.25**	0.38**	0.24**
p value	<0.001	<0.001	<0.001	<0.001
$f(M)$	19.524+0.433 M	21.684+0.501 M	1.923+1.224 M	15.679+0.691 M
Multiple linear regression analysis (soil temperature and soil moisture)				
R^2	0.27**	0.28**	0.54**	0.36**
p value	<0.001	<0.001	<0.001	<0.001
$f(T,M)$	4.512+0.835 T+0.245 M	14.205+0.389 T+0.400 M	−26.371+2.096 T+0.559 M	−4.029+1.122 T+0.425 M

Gas samples, soil temperature and soil moisture were collected simultaneously

*P<0.05; **P<0.01

Discussion

Comparisons with other studies

The observed fluxes of N_2O in our study were similar to the results reported from other studies in the forests of southern China (10.4–59.1 μg N_2O–N m^{-2} h^{-1}, Tang et al. 2006; Chen and Mulder 2007). Our results were higher than those reported for other tropical forests. Werner et al. (2006) reported that soil N_2O emission flux was 6.0±0.7 μg N_2O–N m^{-2} h^{-1} in a primary tropical forest in Xishuangbana, Southwest China. Ishizuka et al. (2002) reported that N_2O fluxes varied from 1.5 to 4.4 μg N_2O–N m^{-2} h^{-1} in tropical forests in Indonesia. Hall et al. (2004) also reported that the fluxes of N_2O were in a range of 1.0 to 7.5 μg N_2O–N m^{-2} h^{-1} in primary tropical forests in Borneo. Our results were also high in comparison with the results for temperate forests in Europe (mean range of 2.3–22.8 μg N_2O–N m^{-2} h^{-1}, Papen and Butterbach-Bahl 1999; Pilegaard et al. 2006; Horváth et al. 2006), North America (<10 μg N_2O–N m^{-2} h^{-1}, Peterjohn et al. 1998; Venterea et al. 2003), and in Japan (0.5–14.1 μg N_2O–N m^{-2} h^{-1}, Oura et al. 2001). However, our results were lower than reported N_2O emissions for rain forests in western Kenya (42.9±0.7 μg N_2O–N m^{-2} h^{-1}, Werner et al. 2007) and in Australian (maximum of 492.1–570.8 μg N_2O–N m^{-2} h^{-1}, Breuer et al. 2000; Kiese and Butterbach-Bahl 2002).

Soil N_2O fluxes in the C plots tended to be higher in the mature forest than in the disturbed or rehabilitated forest. This result indicates that forest land-use type has an effect on soil N_2O emissions. This result is supported by the suggestion that N_2O emissions at the secondary forest site are lower than at the primary forest site (Keller and Reiners 1994; Verchot et al. 1999). The reason for higher soil N_2O emission in the mature forest than in the disturbed or rehabilitated forest can be explained by the difference in forest succession stage and plant composition (Erickson et al. 2002). As mentioned above, the mature forest has been protected from human impacts for more than 400 years and is the representative forest of the tropics in China. However, the original site of both the rehabilitated and the disturbed forests was badly eroded and degraded (Brown et al. 1995; Mo et al. 1995). The previous understory and litter harvesting practice reduced the nutrient content of the soil, resulting in low soil N concentration in the disturbed forest (Mo et al. 1995, 2006). Similarly, the rehabilitated forest originating from a planted pine forest that was naturally invaded and colonized by broadleaf species, also has low soil N availability, having not fully recovered their potential soil nutrient content during the past several decades (Mo et al. 2006). It is likely that soil N availability is one of the major factors limiting N_2O emissions in both the disturbed and rehabilitated forests. Plant composition, soil TOC, soil N/P ratio, soil organic

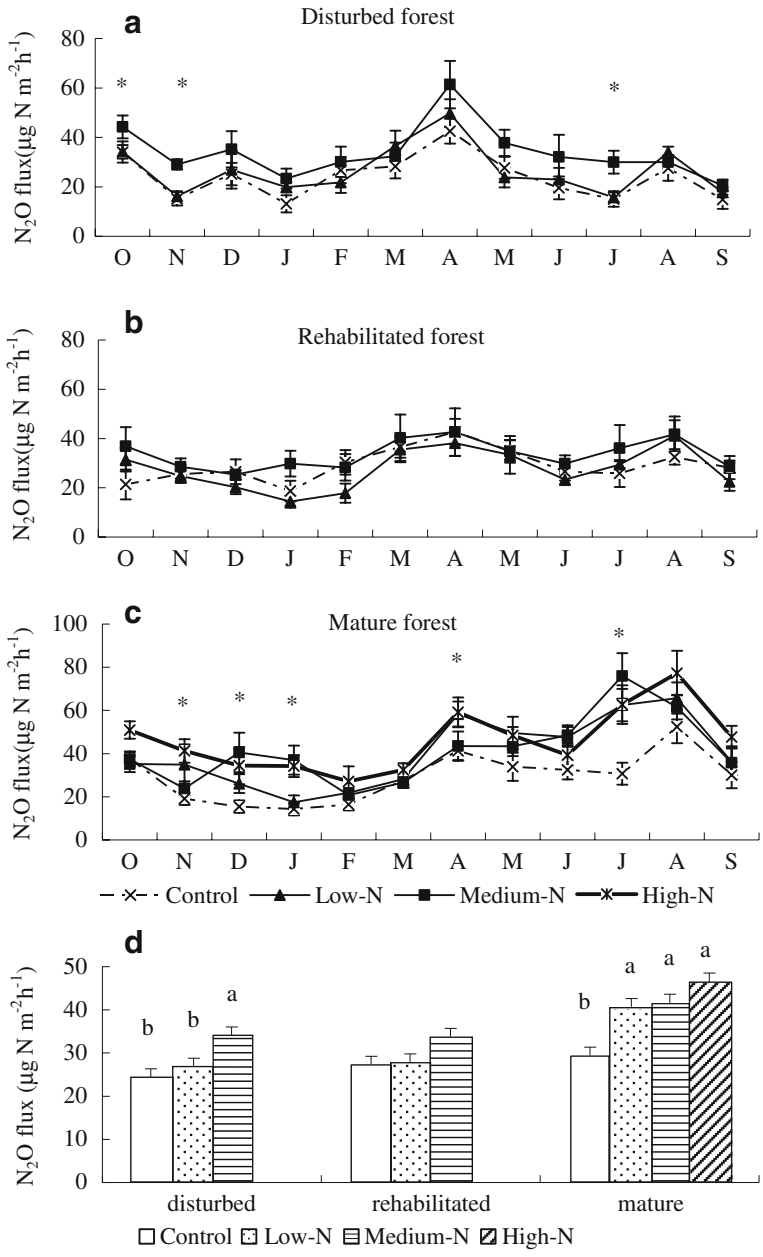

Fig. 3 Seasonal variations of soil N_2O emission rates in experimental plots in disturbed (**a**), rehabilitated (**b**) and mature (**c**) forests during the monitoring period of October 2005 to September 2006. The annual mean soil N_2O emission rates (**d**) in the three forests. *Asterisk* (*) and *different letters* denote significant difference (P value <0.05) between treatment plots within a forest. *Error bars* are standard errors (n=3)

matter content (Table 2), litter production (Zhang et al. 2000) and litter decomposition rate (Mo et al. 2006; Fang et al. 2007) are greater in the mature forest when compared with the disturbed and rehabilitated forests. This indicates that microbial (nitrifying and denitrifying bacteria) activity is likely higher in the mature forest than in the rehabilitated or disturbed forests. Moreover, a study of soil organic C content over two decades in the mature forest indicated an accumulation of soil C (Zhou et al. 2006). Greater carbon can enhance denitrification by stimulating the growth of denitrifying bacteria or by increasing the supply of the electron donor required by this process, and thus, increase soil N_2O emissions (Peterjohn et al. 1998; Li et al. 2005). Soil with lower C/N ratio, but higher N/P ratio generally supports greater N_2O emissions (Erickson et al. 2002; Werner et al. 2006).

Table 5 Regression analysis between N_2O emission fluxes and soil NH_4^+ and NO_3^- concentrations

Disturbed forest (n=18)		Rehabilitated forest (n=18)	Mature forest (n=24)	All sites (n=60)
Ammonium concentration [A (mg kg^{-1})]				
R^2	0.44**	0.29*	0.53**	0.33**
p value	0.003	0.02	<0.001	<0.001
f (A)	18.289+3.491 A	16.565+3.125 A	9.673+8.305 A	15.751+4.870 A
Nitrate concentration [N (mg kg^{-1})]				
R^2	0.27*	0.30*	0.45**	0.35**
p value	0.026	0.018	<0.001	<0.001
f (N)	21.288+2.741 N	19.547+10.3 N	2.167+4.42 N	23.36+1.857 N
Multiple linear regression analysis (NH_4^+ and NO_3^- concentrations)				
R^2	0.44*	0.40*	0.61**	0.54**
p value	0.014	0.023	<0.001	<0.001
f (A,N)	18.321+3.596 A−0.128 N	15.276+2.046 A+6.948 N	−0.22+5.779 A+2.318 N	12.903+3.841 A+1.493 N

Gas fluxes and soil samples were collected on the same day.

*P<0.05; **P<0.01

Effects of soil temperature and moisture content on N_2O emission

In these three forests, we observed a positive linear correlation between soil moisture content and N_2O fluxes (R^2 from 0.15 to 0.38). The result was consistent with previous studies in tropical forests. Butterbach-Bahl et al. (2004) found a linear correlation between soil moisture contents and N_2O emissions for tropical forest soils in Northern Queensland, Australia. Kiese and Butterbach-Bahl (2002) also reported a linear correlation between N_2O emissions and soil moisture contents less than 60%, but noted a decline in N_2O emissions at higher moisture levels, which is most likely due to the increasing formation of N_2 rather than N_2O. Changes in soil moisture ultimately control soil aeration and effect nutrient availability. This would affect nitrification and denitrification processes and associated soil N_2O emissions (Conrad 1996). In water unsaturated soil, high moisture values are generally expected to support higher N_2O emissions.

However, a clear seasonal pattern of N_2O emission was only observed in the mature forest. This might be attributed to the substrate limitations in the disturbed and rehabilitated forests. Previous studies for temperate forests have showed that a strong positive correlation between temperature and N_2O emissions exists (Brumme et al. 1999; Papen and Butterbach-Bahl 1999). Whereas for tropical forests, such a relationship may be weak (Breuer et al. 2000) or non-existent (Kiese and Butterbach-Bahl 2002; Werner et al. 2007), due to small daily and seasonal temperature changes. Our results showed that soil temperature (5 cm) could explain up to 49% of variation in N_2O emissions, potentially due to the monsoon climate with a distinct seasonal pattern in temperature in the study region.

In this study site, soil moisture and temperature increased after rainfall events in early spring (March and April; Fig. 1a,b). Pulses of soil N_2O emission were observed in the three forests in April 2006 (Fig.3a–c). This result was consistent with previous studies that found re-wetting of soils after prolonged dry periods could stimulate pulses of N_2O emission (Davidson et al. 2000; Butterbach-Bahl et al. 2004; Werner et al. 2006). Such N_2O pulse emissions were associated with the rapid microbial consumption of NH_4^+ or NO_3^- accumulated during the dry period (Davidson et al. 2000).

Effects of N addition on soil N_2O emission fluxes

We found that N addition significantly increased the rate of soil N_2O emission in the mature forest. This result was consistent with the hypothesis that N addition can increase soil N_2O emission in N-saturated forests (Peterjohn et al. 1998; Hall and Matson 1999; Butterbach-Bahl et al. 2002; Venterea et al. 2003). In the rehabilitated and disturbed forests,

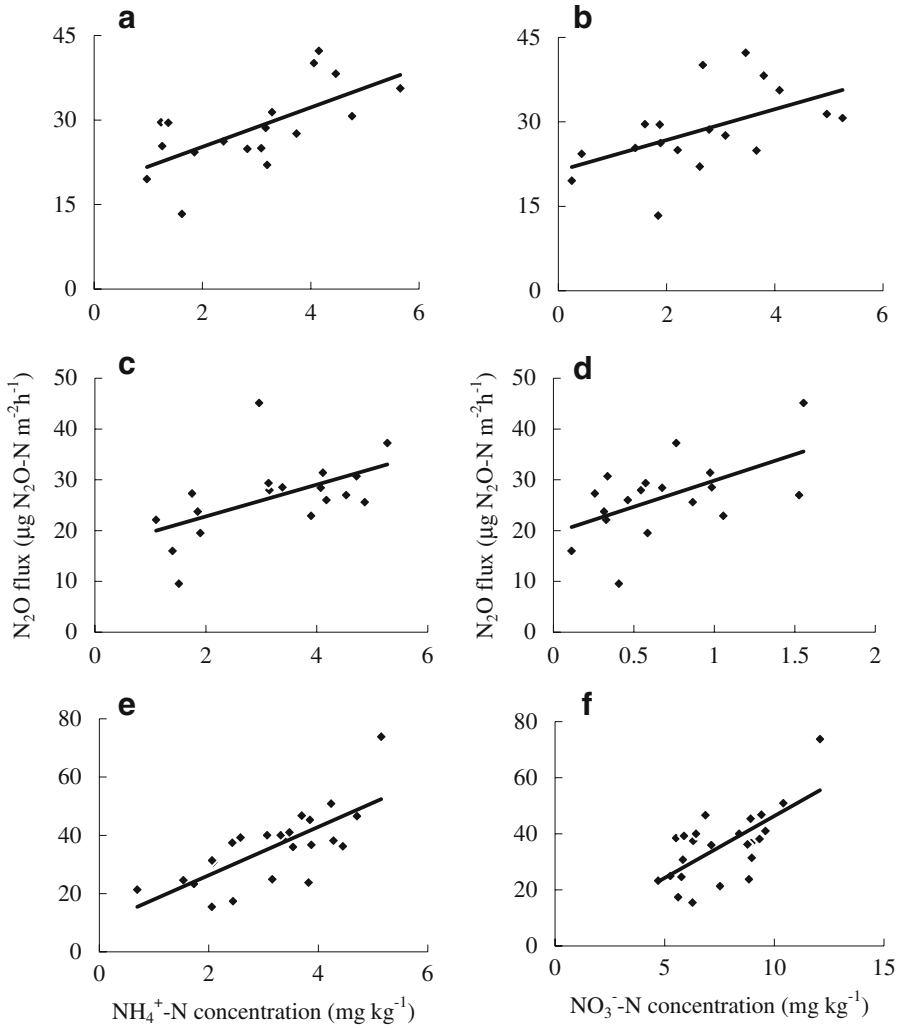

Fig. 4 Relationships between soil N_2O emission rates and NH_4^+ and NO_3^- concentrations in the disturbed (**a**, **b**), rehabilitated (**c**, **d**) and mature forest (**e**, **f**; n=18 for samples in the disturbed and rehabilitated forests, n=24 for samples in the mature forest). Gas fluxes and soil samples were collected on the same day

N addition did not significantly increase soil N_2O emissions, except for the MN treatment plots in the disturbed forest. These results are consistent with previous findings in N-limited temperate forests (Matson et al. 1992; Davidson et al. 2000; Skiba et al. 2004), which showed that N additions did not enhance soil N_2O emissions. Bowden et al. (1991) also reported that heavy N fertilization (270 kg N ha^{-1}) resulted in only small increases in N_2O emissions (0.5–4.1 μg N_2O–N m^{-2} h^{-1}) for a 65-year-old N-limited pine forest at the Harvard Forest. The different N_2O response patterns in the three forests may be explained by the following.

Firstly, the different response of soil N_2O emissions following N addition may be explained by the initial soil N concentration in each of the forests. In N-saturated forest ecosystems, such as the mature forest in this study, N addition increases soil N availability to nitrifying and denitrifying microorganisms (Hall and Matson 1999). If inputs of N exceeded the biotic (and perhaps abiotic) demands for N within the mature forest ecosystem, the ecosystem N retention capacity may be exceeded (Gundersen et al. 1998), with the potential for increased hydrological losses of N as NO_3^- and elevated gaseous losses of N as N_2O (Gundersen et al. 1998; Lohse and Matson 2005). In contrast, the disturbed and rehabilitated forests are not N-saturated (Mo et al. 2006). In general, N deficient forest ecosystems initially retained N due to use in plant and microbial growth

as well as accumulation in biomass and soil organic matter (Aber et al. 1998). Magill et al. (2000) also found that no significant response of soil N_2O emission to N addition was observed until 8-years following N addition in the Harvard Forest. Thus, it is possible that much of N added in our study remained in the soil organic matter, microbial biomass (Lohse and Matson 2005) and vegetation (Harrington et al. 2001) in the disturbed and rehabilitated forests sites. Our result was consistent with Hall and Matson (1999), who suggested that N_2O emissions from P-limited tropical forests (N-saturation) might be especially sensitive to N inputs, in that they might respond to even small initial N additions with larger losses than predicted by models developed for N-limited temperate forests.

Secondly, the contents of NH_4^+ and NO_3^-, demonstrating substantial nitrification and denitrification in the soil (Sitaula et al. 1995), were significantly increased with increasing N additions in the mature forest and MN plots in the disturbed forest. Regression analysis revealed that soil N_2O emissions were positively correlated to soil NH_4^+ and NO_3^- concentrations in the three forests. Increases in soil inorganic N (NH_4^+ and NO_3^-) resulting from N addition are likely a major cause of increased soil N_2O emission in the mature forest and in the MN plots of disturbed forest. Our findings are similar to results found in previous studies (Ambus et al. 2001; Venterea et al. 2003; Wallenstein et al. 2006), Other studies indicating soil inorganic N availability as a key factor controlling N_2O emissions from forest soils have been reported in temperate (Bowden et al. 1991; Sitaula et al. 1995), and tropical (Hall and Matson 1999) Zones. These relationships were consistent with the "hole-in-the-pipe (HIP)" model which describes N_2O emission primarily as a function of N cycling rates and other indices of N availability (Firestone and Davidson 1989).

Thirdly, forest age and forest land-use type likely contributed to the difference in response of soil N_2O emission to N additions. Hall and Matson (1999) found that fertilizer-induced N trace gas fluxes from the oldest forest site were higher after a single N addition than were those from plots at the youngest forest site that had received 12 years of chronic N addition. Unlike the disturbed and rehabilitated forests which experienced delay in their response to N addition, the mature forest responded with a large and immediate increase in N_2O emissions. This was consistent with our hypothesis, as the mature forest: 400-year-old, rich in N and SOC, with a lower C/N ratio (Fang et al. 2006) and higher N/P ratio is likely a "hotspot" for nitrification and denitrification and sensitive in response to increased N deposition. We believe that vegetation sinks for additional N would act as a buffer and provide most of the resistance in preventing N losses and therefore would be saturated fairly quickly in the disturbed and rehabilitated forests. Our results suggest that initial soil N status, which varied with forest land-use types, strongly influenced soil N_2O emission, and significantly affected the response of soil N_2O emission to N deposition in tropical forests in southern China.

Lastly, the difference in response of soil N_2O emission to N addition between the disturbed and rehabilitated forests was likely caused by the varying plant communities in these two forests. Studies in North America (Magill et al. 2000; Venterea et al. 2003) and Europe (Butterbach-Bahl et al. 1998; Merino et al. 2004) demonstrated that coniferous forests have a lower capacity to retain N inputs when compared to other forest types with a similar land-use history. Soil nitrification rates in response to N inputs in the pine forest were faster than in the hardwood forest (Magill et al. 2000). In addition, measurements by Brumme et al. (1999) and Papen and Butterbach-Bahl (1999) showed that vegetation was a key parameter influencing N_2O emission. There are more plants (Table 1), fine roots and microorganisms (Brown et al. 1995; Mo et al. 2003, 2006) in the rehabilitated forest. Their ability to compete with microbes (e.g., nitrifying and denitrifying bacteria) for N could be higher (St. Clair and Lynch 2005), compared to those in the disturbed forest.

Our results suggest that the responses of soil N_2O emission to N deposition in tropical forests in southern China may vary depending on the soil N status and land-use history of the forests. Our results were evaluated for just one site of each forest type and only three replicates for each N treatment, so this study should not be generalized broadly to all forests in tropical China. Further investigations in N addition experiments in other regions or across N deposition gradients are needed to confirm our findings.

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