Research paper

Effects of canopy gaps on N$_2$O fluxes in a tropical montane rainforest in Hainan of China

Huai Yang$^{a,b}$, Matteo Detto$^c$, Shirong Liu$^b$, Wenping Yuan$^d$, Cheng-I Hsieh$^e$, Xu Wang$^a$, Renli Chen$^a$, Huai Chen$^{f,e}$, Changhui Peng$^{g,h}$, Xinhua Jiang$^f$, Yide Li$^a$, Han Xu$^a$, Wenjie Liu$^{d,i}$, Qiu Yang$^1$

$^a$ Research Institute of Tropical Forestry, Chinese Academy of Forestry, Guangzhou 510520, China
$^b$ Key Laboratory of Forest Ecology and Environment of State Forestry Administration, Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry, Beijing 100091, China
$^c$ Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Balboa, Ancon, Panama
$^d$ State Key Laboratory of Cryospheric Sciences, Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou 730000, China
$^e$ Department of Bioenvironmental Systems Engineering, National Taiwan University, Taipei 10617, China
$^f$ Key Laboratory of Mountain Ecological Restoration and Bioresource Utilization & Ecological Restoration Biodiversity Conservation Key Laboratory of Sichuan Province, Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu 610041, China
$^g$ State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, College of Forestry, Northwest A&F University, Yangling 712100, China
$^h$ Institute of Environment Sciences, Department of Biology Science, University of Quebec at Montreal, Montreal C3P 3P8, Canada
$^i$ Institute of Tropical Agriculture and Forestry, Hainan University, Haikou, Hainan 570228, China

A R T I C L E   I N F O

Article history:
Received 4 November 2016
Received in revised form 20 March 2017
Accepted 27 April 2017
Available online 16 May 2017

Keywords:
Climate change
Tropical forest
Greenhouse gas
Soil moisture
Soil temperature

A B S T R A C T

Background and aims: Tropical montane rainforests play an important role in increasing atmospheric N$_2$O concentration. Although accurate estimations of N$_2$O fluxes in tropical montane rainforests are critical for predicting global climate change, there are still considerable uncertainties about the spatial and temporal variability of the emissions. This study aims to investigate the effects of canopy gap caused by typhoons on N$_2$O emissions, a key factor for understanding the spatial heterogeneity and supporting environmental regulations.

Methods: N$_2$O fluxes were measured monthly using static chambers both inside and outside two large canopy gaps in the tropical montane rainforest of the Jianfengling National Natural Reserve on Hainan Island, south of China, from August 2012 to July 2013.

Results: Mean annual N$_2$O emissions were $2.19 \pm 0.43$ kg N$_2$O-N ha$^{-1}$ yr$^{-1}$ inside canopy gaps, and $1.19 \pm 0.29$ kg N$_2$O-N ha$^{-1}$ yr$^{-1}$ outside canopy gaps, revealing substantial differences in N$_2$O emissions resulting from forest structure. Moreover, N$_2$O emission rates within canopy gaps during the wet season (2.89 kg N$_2$O-N ha$^{-1}$ yr$^{-1}$) were significantly higher than those during the dry season (1.34 kg N$_2$O-N ha$^{-1}$ yr$^{-1}$), suggesting strong regulation of soil moisture and precipitation in controlling soil N dynamics. However, there were significant nonlinear relationships between N$_2$O fluxes and water filled pore space, and soil temperature within canopy gaps, but no significant relationships were found under the closed canopy.

Conclusions: Contribution of canopy gaps should be considered to avoid underestimation of N$_2$O emission rates from disturbed forests. Interestingly, emissions from gaps are more strongly coupled with climate drivers (moisture and temperature), with important implications for climate change projections. Therefore, the further research is needed to study the biogeochemical processes and mechanisms behind such phenomenon.

© 2017 Elsevier B.V. All rights reserved.

1. Introduction

Nitrous oxide (N$_2$O) is a stable and strong greenhouse gas (12 times larger than CH$_4$ and 298 times larger than CO$_2$), accounting for 6% of the total greenhouse effect (Houghton et al., 2001).
Its concentration in the atmosphere has been increasing approxi-
mately 0.25% per year throughout the past decade (IPCC, 2014). Emissions from soil are important sources for N₂O, accounting for about 57% of global atmospheric sources of N₂O (Breuer et al., 2000). Besides oceans and agricultural soils, tropical rain forest soils are the major sources for N₂O emissions contributing 24% or 2.2–3.7 TgN₂O-Nyr⁻¹ to the global atmospheric budget (Prather et al., 2001). Considering the large variability of sources and uncertainties in global N₂O emissions (IPCC, 2014), accurate estimations of soil N₂O fluxes from tropical rainforest could provide important information for both future climate change predictions and simulations (Butterbach-Bahl et al., 2014).

N₂O emissions from tropical forest soils widely vary, with estimations of 0.1–87.7 μgN₂O-N·m⁻²·h⁻¹ in the Neotropics (Keller et al., 1993; Verchot et al., 1999), 1.7–207.0 μgN₂O-N·m⁻²·h⁻¹ in African rainforests (Serca et al., 1994), 11.3–123.4 μgN₂O-N·m⁻²·h⁻¹ for Australian rainforests (Breuer et al., 2000), and 1.5–4.4 μgN₂O-N·m⁻²·h⁻¹ and 1–7.5 μgN₂O-N·m⁻²·h⁻¹, for tropical primary forests in Indonesia (Ishizuka et al., 2002) and in Borneo (Hall et al., 2004) respectively. Although there are many studies of N₂O emissions from tropical forest soils, we still need more data from different regions to give the scientific community a whole picture about soil N₂O emissions in tropical rainforests all over the world.

The emissions of N₂O from the soil into the atmosphere are a result of microbial nitrification and denitrification, i.e. conversion of NH₃ to NO₃⁻ when ammonia is oxidized into nitrate in the presence of oxygen, and the conversion of NO₃⁻ to N₂O or N₂ when nitrites are used as an electron acceptor instead of oxygen (Davidson et al., 2000; Hall et al., 2004). These processes are controlled by many factors, such as oxygen availability, soil temperature, soil water-filled pore space (WFPS) and nutrients availability. Soil temperature and moisture directly control production, consumption and transport of N₂O through effects caused by the metabolic activity of microorganisms, soil aeration and diffusivity (Barneze et al., 2014; Luo et al., 2013). Higher temperatures promote the mineralization of the soil’s organic nitrogen (such as proteins, nucleic acid), increasing input of nutrients (Wu et al., 2014), and thus providing the reaction substrate (mainly NO₃⁻ and NO₂⁻) for soil denitrification, which offers the energy for soil microorganism that take part in this process (Barneze et al., 2014). Nitrification is maximized for WFPS ranging from 50% to 70%, however in wetter conditions denitrification becomes dominant (Mazzetto et al., 2014) and when soil is saturated, diffusion becomes the limiting factor (Li et al., 2000). N₂O fluxes from tropical forests are greater during rainy seasons than during dry seasons, a result generally observed in Amazon (Davidson et al., 2004), in Central Africa (Reeset et al., 2006), and in south China forests (Werner et al., 2006).

Tropical forests located at latitudes between 5° and 20° south or north frequently experience hurricanes or typhoons (Gray, 1979; McDowell, 2011; Zhang et al., 2011). The frequency and intensity of these large scale events are increasing as a consequence of rising sea surface temperatures, oceanic heat content, higher atmospheric temperature and water vapor, all of which can be attributed to global warming (Anthes et al., 2006; Pielke et al., 2005). Consequently, the percentage of canopy gaps will increase with greater frequency of typhoons.

In tropical rainforests, canopy gaps could potentially alter many features of understory microenvironments (Schliemann and Bockheim, 2011). The most obvious effects are on understory light regimes (Everham et al., 1996 Gálhidy et al., 2006). The soil absorbs more solar radiation, which results in higher soil temperatures (Ritter et al., 2005) and alterations of soil moisture regime by changing energy partitioning between sensible and latent heat (Detto et al., 2006; Gálhidy et al., 2006). In addition, the soil nutrient cycle is also altered through dead biomass accumulation. NO₃⁻-N and extractable P concentrations are expected to increase due to the lower uptake by vegetation and the priming effect of leaf and fine root litter associated with tree fall (Davidson et al., 2000; Lodge et al., 1994). However, their effects on magnitude and the temporal variability of soil-atmosphere N₂O exchanges are not completely understood and literature reports mixed results. For example, increased fluxes of N₂O after gap disturbances were reported by Erickson and Ayala (2004) and Steudler et al. (1991). No significant changes were reported by Riley and Vitousek (2000) after Hurricane Iniki. While Bowden et al. (1993) reported a reduction 78% of N₂O emissions after a simulated Hurricane. Canopy gap formation increases local resource heterogeneity, spatial and temporal variability of the fluxes, adding considerable uncertainty in the estimation of regional N₂O emissions. Moreover, knowledge of the temporal and spatial patterns of soil N₂O fluxes and identification of the climatic and environmental controls is important to accurately quantify GHG budgets, upscale GHG fluxes to the regional scale and design sampling strategies.

To investigate the effect of canopy gaps on N₂O emissions we conducted a study in the Jianfengling reserve on Hainan Island (China). Hainan Island is frequently disturbed by tropical typhoons, averaging 8–10 typhoons per year, 3–5 of which directly impact montane rainforests (Chen et al., 2012; Zhang et al., 2011). The proportion of typhoon-induced canopy gaps within Jianfengling tropical mountain rainforest is about 21%. Thus, the effect of gaps may be relevant for estimating the emissions of N₂O. The objectives of this study were (1) to quantify spatial variability as the differences of N₂O fluxes inside and outside recently formed canopy gaps and (2) to understand their temporal variability by revealing the role of soil temperature and moisture as key factors in controlling the seasonal variation of N₂O fluxes.

2. Materials and methods

2.1. Site description

This study was conducted in the Jianfengling National Natural Reserve (JFR) (18°23′N–18°50′N, 108°36′E–109°05′E), located in the southwest region of Hainan Island, South of China. This region has one of the best-protected and most typical old-growth tropical montane rainforests in the northern edge of tropical Asia. JFR comprises 472 km² tropical rainforests and 150 km² tropical montane rainforests. And the tropical rainforests of the world is 1.0 × 10⁶ km² (Newman, 1990). Canopy gaps cover 21.3% of the tropical montane rainforests in the study area (Jianfengling National Natural Research Station of Forest Ecosystems, unpublished data). The region is characterized by a tropical monsoon climate, with distinct wet (from May to October) and dry (from November to April of the following year) seasons. Based on meteorological data collected from 1980 to 2006, the mean annual air temperature is 19.8 °C, ranging from 14.8 (January) to 23.3 °C (June). Mean annual precipitation is 2449 mm, 80–90% of which falls between May and October (Zhou et al., 2013). The study site has a complex topography. Granite is the predominant soil parent material, with montane lateritic red or yellow earth being the most common soil type. The vegetation is dominated by Fagaceae, Myrtaceae, Lauraceae, Rubiaceae, Palmaeae, Euphorbiaceae and one Dipterocarpaceae species, Hapnea hainanensis (Jiang and Lu, 1991). On 29th September of 2011, typhoon Nesat, the strongest typhoon to hit Hainan since 2006 (maximum wind speed 42 m s⁻¹), produced two large canopy gaps within the study site (Fig. 1). The two gaps, approximately elliptical in shape, with length-width of 45 m–20 m and, 38 m–22 m, respectively, were separated by one kilometer.
2.2. Sampling design and gas flux measurements

Meteorological data on the forest canopy were collected from the Jianfengling National Forestry Station. Soil \( \text{N}_2\text{O} \) fluxes were measured monthly from August 2012 to July 2013 (excluding February). Twelve PVC collars were placed inside the canopy gaps (six for each gap) and eight outside (four for each gap) as depicted in Fig. 1. The number of samples and measuring interval were comparable to most \( \text{N}_2\text{O} \) emissions studies from other tropical and subtropical forests (Table 2). The collars were 20 cm, internal diameter, 15 cm high and were inserted in the soil at a depth of 6–7 cm. The top chamber was 40 cm high and equipped with a thermometer and air connection pipe for gas sampling. There were no plants inside the collars.

Gas samples were collected from 8:30 to 12:30 p.m., with 10 mL disposable vacuum blood tubes at 10-min intervals over a 30 min period after closing the chamber. Simultaneously, soil temperature was measured at depths of both 5 and 10 cm within 5 cm of each chamber using a handheld digital thermometer (SP-E-17 thermometer, Jinzhengmao Instruments China Inc., Beijing). Air temperature inside the chamber was also recorded. \( \text{N}_2\text{O} \) concentrations in the samples were measured by a gas chromatograph (7890A, Agilent Co., USA) equipped with an electron capture detector (ECD), which operated at 350 °C. The column temperature was maintained at 60 °C, and the carrier gas was pure nitrogen at a flow rate of 20 mL min\(^{-1}\). The flux of \( \text{N}_2\text{O} \) \( (F) \) was calculated as:

\[
F = \frac{dC_t}{dt} = \frac{P}{P_0} \times \frac{M}{V_0} \times \frac{T_0}{T} \times H
\]

where \( C_t \) is concentration of mixed volume ratios of gases in chamber at time \( t \), in ppm; \( P \) is the ambient atmospheric pressure (hPa); \( M \) is the molar mass of \( \text{N}_2\text{O} \) (g mol\(^{-1}\)); \( T \) is the absolute temperature inside the chamber (K); \( V_0 \), \( P_0 \), and \( T_0 \) are the molar volume (\( 22.41 \times 10^{-3} \text{ m}^3 \)), atmospheric pressure (1013.25 hPa), and absolute temperature (273.15 K), respectively, under standard conditions; and \( H \) is the chamber height over the soil surface (m). Fluxes are given in unit of mg \( \text{N}_2\text{O} \) m\(^{-2}\) h\(^{-1}\).

Annual budgets were computed as averages of the 12 monthly measurements (the month of February being linearly interpolated) inside and outside canopy gaps multiplied by 24 h and by 365 d and given in unit of kg \( \text{N}_2\text{O-N} \) ha\(^{-1}\) yr\(^{-1}\). The weighted average of the \( \text{N}_2\text{O} \) emission rate was computed according to the areal percentage of canopy gaps (accounted for 21.3% of total areas) and closed canopy.

2.3. Soil samples collection and analysis

Five soil samples were collected at a distance of 30 cm from each chamber every three months, from August 2012 to May 2013 at depths of 0–10 cm. Soil samples were mixed together, sealed in plastic bags and placed in a cooling box before being transported to the laboratory, where each mixed sample was divided into two parts. One part was immediately sieved through a 2 mm mesh to remove stones, coarse roots, and earthworms and stored at 4 °C and used for \( \text{NH}_4^+ \)-N and \( \text{NO}_3^-\)-N analyses. The soil \( \text{NH}_4^+\)-N and \( \text{NO}_3^-\)-N contents were extracted using 2 M KCl on an orbital shaker for 1 h under ambient temperature and then the suspension was filtered. The extracts were analyzed by a continuous flow analytical system (SKALAR San++, SKALAR Co., Netherlands). The remaining soil samples were air-dried in the laboratory and hand-sieved through a 2 mm screen. Soil pH value was measured in soil-water suspensions (1:2.5 soil: water) (ISSCAS, 1978). Soil samples were further ground to pass through a 0.25 mm sieve and analyzed for soil organic carbon (SOC), total nitrogen (N), total phosphorus (P) and easily oxidized organic carbon (EOOC). SOC and total N contents were determined by the K\(_2\text{Cr}_2\text{O}_7\)-\( \text{H}_2\text{SO}_4 \) oxidation method and Kjeldahl procedure, respectively, while total P was determined by the ammonium molybdate spectrophotometric method with a UV-1601 spectrophotometer (Shimadzu Co. Ltd, Kyoto, Japan), after \( \text{H}_2\text{SO}_4\)-\( \text{HClO}_4 \) digestion (ISSCAS, 1978), EOOC is the fraction of SOC that can be oxidized by 0.333 Mol L\(^{-1}\) KMnO\(_4\) (Blair et al., 1995; Cao et al., 2012).

Two additional soil samples were taken at depths of 0–10 cm using a cutting ring with a volume of 100 cm\(^3\) for measuring soil bulk density (SBD) and volumetric water content (Vol). Water filled pore space (WFPS) was calculated from Vol and SBD with the following equation:

\[
\text{WFPS} = \text{Vol} / (1 - \text{SBD}/\text{QD})
\]
where Vol is expressed in percent, SBD in g cm\(^{-3}\), and QD is the density of quartz, equals to 2.65 g cm\(^{-3}\) \cite{Zhang2012}.

### 2.4. Statistical analyses

Statistical outliers were eliminated according to the Grubbs outlier test. One-way analysis of variance (ANOVA) was used to compare \(\text{N}_2\text{O}\) fluxes inside and outside canopy gaps and to examine the differences in soil properties. Regression analysis was used to describe the relationship between soil temperature, moisture and \(\text{N}_2\text{O}\) fluxes. Best polynomial regression was chosen based on an \(F\)-test for nested models. A \(t\)-test was used to find significant differences between the two treatments (inside and outside canopy gaps). All statistical analyses were conducted with SPSS software (version 11.5).

### 3. Results

#### 3.1. Environmental differences between gaps and canopy

The climate of this region has distinct wet and dry seasons, the former occurring from May to October and the latter from November to April of the following year (Fig. 2). Soil temperature at depths of 5 (\(T_5\)) and 10 cm (\(T_{10}\)), and WFPS, exhibited a clear seasonal patterns, both inside and outside canopy gaps (Fig. 3). Soil temperature was the highest in July and lowest in January. The mean ( \(\pm SE\)) soil temperature at the 5 cm inside the gap was slightly warmer than outside, 20.0 \(\pm 0.7^\circ\text{C}\) and 19.6 \(\pm 0.7^\circ\text{C}\) respectively, but the differences were not significant (\(P > 0.05\)).

WFPS (\(P < 0.01\)), total P (\(P < 0.05\)), \(\text{NO}_3^-\cdot\text{N}\) (\(P > 0.05\)) and SBD (\(P < 0.05\)) were higher inside the canopy gaps, while pH (\(P < 0.05\)), EOOC (\(P < 0.05\)), SOC (\(P > 0.05\)), \(\text{NH}_4^+\cdot\text{N}\) (\(P < 0.05\)), and total N (\(P < 0.01\)) were higher outside the canopy gap (Table 1).

#### 3.2. Variations of \(\text{N}_2\text{O}\) fluxes inside and outside canopy gaps

There were no significant differences of \(\text{N}_2\text{O}\) fluxes in the inside (or outside) gap between the two sites (\(t\)-test, \(P > 0.05\)). However, there were significant differences between the inside and outside canopy gaps for each site (\(P < 0.05\)). The mean \(\text{N}_2\text{O}\) emissions (\(\pm SD\)) from inside and outside canopy gaps were 0.0393 \(\pm 0.0257\) mg \(\text{N}_2\text{O}\) m\(^{-2}\) h\(^{-1}\), 0.0213 \(\pm 0.0172\) mg \(\text{N}_2\text{O}\) m\(^{-2}\) h\(^{-1}\), respectively, with significantly higher emission in the wet season and lower emission in the dry season (\(P < 0.05\)) (Fig. 4). The coefficients of variation (CV) were 66.01%, 29.56%, for the inside and outside canopy gaps,
respectively. These significant differences were consistent during both wet and dry seasons (*P*<0.05, Fig. 4).

N$_2$O fluxes showed a clear seasonal variability during our study period. The trend of temporal variability were similar inside and outside the canopy gaps, but the differences in the magnitude of the fluxes between the gap inside and the gap outside was large, especially in the wet season (Fig. 5). N$_2$O uptake peaks were recorded in November 2012 (−0.0058 ± 0.0348 mg N$_2$O m$^{-2}$ h$^{-1}$, −0.0122 ± 0.0327 mg N$_2$O m$^{-2}$ h$^{-1}$), and the highest N$_2$O emission rate occurred in August 2012 (0.0986 ± 0.0471 mg N$_2$O m$^{-2}$ h$^{-1}$, 0.0609 ± 0.0277 mg N$_2$O m$^{-2}$ h$^{-1}$).

### 3.3. Drivers of N$_2$O emissions

Inside canopy gaps, a significant correlation between the average N$_2$O emission and soil temperature at both 5 and 10 cm depths was found (Fig. 6A and C). On the contrary, there was no significant regulation of soil temperature to N$_2$O emission outside the canopy gaps (Fig. 6B and D). Similarly, inside the canopy gaps, a significant relationship was observed between N$_2$O fluxes and water filled pore space (WFPS) (Fig. 6E) but no significant relationship in outside the canopy gaps (Fig. 6F). Inside the canopy gaps, maximum N$_2$O emission rates occurred when WFPS was above 80%. N$_2$O emissions showed a tendency to increase when the WFPS were above 65%. No significant relationships were found between N$_2$O fluxes and several soil properties (pH, EOOC, SOC, Total P, NO$_3$$^-$-N, NH$_4^+$-N, Total N, Soil bulk density).

### 4. Discussion

#### 4.1. N$_2$O emissions in comparison with other studies

The weighted annual budget for this study was estimated to be 1.40 ± 0.32 kg N$_2$O-N·ha$^{-1}$·yr$^{-1}$. This number was broadly consistent with the range reported for other forest ecosystems, as summarized in Table 2, but relatively lower than other rainforests, such as in the Amazon (2.0 kg N$_2$O-N·ha$^{-1}$·yr$^{-1}$) (Davidson et al., 2001), Costa Rica (5.78 kg N$_2$O-N·ha$^{-1}$·yr$^{-1}$) (Liu et al., 2000) and Kenya (3.76 kg N$_2$O-N·ha$^{-1}$·yr$^{-1}$) (Werner et al., 2007). The relatively low emission rate can be partially explained by the strong seasonality of rainfall at our site, which has a pronounced dry season of almost six months. The seasonal variability of N$_2$O emissions found in this study was in agreement with previous N$_2$O emissions reports from tropical rain forest soils worldwide, with significantly higher fluxes during the wet season (Davidson et al., 2004; Liu et al., 2000) and lower emission or even consumption during dry seasons (Bai et al., 2014). Prolonged dry season promotes nitrification processes and inhibits denitrification processes, which lead to NH$_4^+$ or NO$_3^-$ cannot be converted to N$_2$O, and in fact several negative emissions during dry periods were recorded (Butterbach-Bahl et al., 1998; Goossens et al., 2001; Klemedtsson et al., 1997; Ryden, 1981). Furthermore, wet nitrogen deposition was relatively

---

**Table 1**

Soil properties (at depths of 0–10 cm) and soil temperature (at depths of 5 cm and 10 cm) inside and outside canopy gaps. Values are the annual means ± standard error. * and ** indicate significant differences (*t*-test, *P*<0.05 and **P*<0.01).

| Soil properties | Inside of canopy gap (n = 48) | Outside of canopy gap (n = 32) |
|-----------------|-------------------------------|-------------------------------|
| pH*             | 4.36 ± 0.11 *                 | 4.57 ± 0.07                  |
| WFPS**          | 73.04 ± 2.49 **               | 59.87 ± 3.53                 |
| T$_s$ (°C)      | 19.97 ± 0.70                  | 19.56 ± 0.66                 |
| T$_v$ (°C)      | 20.13 ± 0.71                  | 19.73 ± 0.65                 |
| EOOC (mg kg$^{-1}$)* | 9.62 ± 1.10 *               | 14.05 ± 1.60                 |
| SOC (mg kg$^{-1}$) | 2.06 ± 0.09                  | 2.31 ± 0.11                  |
| Total P (mg kg$^{-1}$) | 0.17 ± 0.01                  | 0.15 ± 0.01                  |
| NO$_3$$^-$-N (mg kg$^{-1}$) | 12.55 ± 2.01                 | 11.61 ± 2.41                 |
| NH$_4^+$-N (mg kg$^{-1}$)* | 12.90 ± 1.14 *              | 17.08 ± 1.86                 |
| Total N (mg kg$^{-1}$)** | 1.33 ± 0.04 **              | 1.58 ± 0.06                  |
| Soil bulk density (mg kg$^{-1}$)* | 1.15 ± 0.02 *               | 1.06 ± 0.03                  |
Table 2
The rates of N₂O emissions (kg N₂O-N ha⁻¹ yr⁻¹) in different tropical and subtropical forests around the world.

| Region | Country | Forest type | Location | N₂O emission | Sampling period | Samples No. | Sample interval | Area | Reference |
|--------|---------|-------------|----------|---------------|-----------------|-------------|----------------|------|-----------|
| Tropical | China | tropical montane rainforest | Jianfengling Nature Park (18°23′N, 109°05′E) | 1.40 | one year | 20 (10 per site) | Monthly | this study |
| Tropical | China | tropical seasonal rainforest | Xishuangbanna (21°56′N, 101°16′E) | 2.70 | one year | 9 (3 per treatments) | weekly | 1 ha | Yan et al. (2008) |
| Tropical | Brazil | tropical moist forest | Serra do Mar State Park (23°17′–23°34′S, 45°02′–45°11′W) | 0.79–3.42 | one year | 24 (8 per site) | monthly | 3 ha | Sousa Neto et al. (2011) |
| Tropical | Brazil | humid tropical forest | Paragominas (2°59′S, 47°31′W) | 2.43 | one year | 8 per site | Monthly-seasonal | Verchot et al. (1999) |
| Tropical | Brazil | humid tropical forest | Fazenda Nova Vida (10°10′S, 62°49′W) | 1.91 | one year | 3 forest and 9 pasture | Bimonthly-monthly | Melillo et al. (2001) |
| Tropical | Australia | tropical rainforest | Atherton Tablelands, Queensland (17°09′–17°37′S, 145°25′–145°45′E) | 3.42 | two years | 15 (5 per site) | 2–3 month | Breuer et al. (2000) |
| Tropical | Australia | lowland rainforest | village of Bellenden Ker, Queensland (17°16′S, 145°54′E) | 2.24 | three months | 5 | 1-h | Butterbach-Bahl et al. (2004) |
| Tropical | Ghana, Africa | tropical rainforest | Ankasa (0°5′16′N, 02°42′W) | 2.33 | 19 months | 16 (8 per site) | monthly | Castaldi et al. (2013) |
| Tropical | Congo, Africa | tropical rainforest | Dimonika natural park (4°30′S, 12°32′E) | 2.90 | one year | 8 | 3 campaigns | Serca et al. (1994) |
| Tropical | Kenya, Africa | tropical rainforest | Kakamega Forest National Park (00°8′–00°23′N, 34°46′–34°58′E) | 3.76 | Three months | 6 | hourly | 0.3 ha | Werner et al. (2007) |
| Tropical | Amazon, Brazil | mature Amazonian forests | Amazon regions | 1.4–2.4 | | | | Davidson et al. (2001) |
| Subtropical | China | pine plantation (20 years) | Heshan Hilly Land Interdisciplinary Experimental Station (22°41′N, 112°34′E) | 3.03 | two years | 12 (6 per site) | 2/every week | Liu et al. (2008) |
| Subtropical | China | monsoon evergreen broadleaf forests | DHS Nature Reserve (23°09′–23°11′N, 112°30′–112°33′E) | 2.57 | one year | 30 (3 per treatments) | Monthly | 6000 (6000 per treatment) | Zhang et al. (2008) |
| Subtropical | Brazil | subtropical forest | Tiangua Biological Reserve (22°28′–22°39′S, 43°13′–43°34′W) | 4.20 | Over one year | 8 (4 per site) | 2–3 week | 5000 (2500 per site) | Maddock et al. (2001) |
lower at Jianfengling (6.10 kg N ha\(^{-1}\) yr\(^{-1}\)) (Bai et al., 2014) compared to other Chinese forests in the Xishuangbanna tropical forest (9.00 kg N ha\(^{-1}\) yr\(^{-1}\)) (Sha et al., 2001) and the Dinghushan subtropical forest (38.00 kg N ha\(^{-1}\) yr\(^{-1}\)) (Wang et al., 2009), which further indicated a slight lower N\(_2\)O production (Matson et al., 2002).

4.2. Influence of gap on N\(_2\)O fluxes

This study demonstrates the importance of canopy structure contribution in accurately quantifying regional N\(_2\)O emission. In the Jianfengling tropical mountain rainforest, the proportion of typhoon-induced gaps was approximately 21%. Consequently, with an 84% higher N\(_2\)O emission at these gaps, approximately 18% of N\(_2\)O emissions would be underestimated in this region if gaps were not taken into account. The result that N\(_2\)O fluxes inside canopy gaps was significantly higher (about 74%, \(P<0.05\)) than outside canopy gaps which can be explained by several factors. Firstly, the soil moisture was higher at the canopy gaps (WFPS was 73.04 ± 2.49% and 59.87 ± 3.53%, inside and outside canopy gaps, respectively, \(P<0.05\)) because of reduced transpiration after tree
removal. The wetter soil moisture of inside canopy gaps was easy to form the anaerobic environment, which would promote soil denitrification processes, which lead to higher N₂O emission in inside canopy gaps (Kiese et al., 2008).

Secondly, rain can directly reach the soil without being intercepted by vegetation inside a gap. The total amount of water infiltrating the soil influences both, soil moisture availability and wet atmospheric nitrogen deposition, and providing additional active substrate for the denitrification bacteria (Hietz et al., 2011; Matson et al., 2014).

Thirdly, a recently formed gap contains a large amount of dead organic matter which can be mineralized and be available for denitrification (Keller et al., 2005). This is consistent with the higher value of available nutrients in canopy gaps, especially for NO₃−N, which is the most important substrate for the denitrification process (Table 1). Generally, a positive relationship is expected between inorganic N and N₂O (Cardenas et al., 2010; Hoben et al., 2011). However, such relationship did not emerge in our study. This can be attributed to the fast dynamics of soil denitrification or leaking driven by higher temperature and frequent rainfall (Robertson, 1989; Robertson and Tiedje, 1988). While our soil samples, collected every 3 months, could largely explain seasonal variation, higher sampling frequency may be required to reveal the effects of the inorganic nitrogen on N₂O fluxes.

The trend in temporal variability (Fig. 5) was similar between gap and closed forest. However an in depth inspection revealed that the differences were maximal in August and negligible in April. This suggests that rainfall effects are more important in open areas of the forest and that the influence of canopy structure reduces after a period of prolonged drought.

4.3. Confounding effects of soil temperature and WFSP

The different environmental regulation of N₂O emission by both, soil moisture and temperature, between gaps and canopy was an unexpected and critical aspect of this study. Most studies in tropical forests showed that N₂O emissions increase with rising soil temperatures (Castaldi et al., 2013). In general, temperature regulates the metabolism of microbial communities, including decomposers which provide mineralized nitrogen (Barneze et al., 2014). Smith (2003) attributed the temperature dependence of N₂O to an increase in the anaerobic volume fraction, caused by an increased respiratory sink for O₂.

Our results suggest that the role of temperature is mediated by the presence of trees and the microorganisms that live in the rhizosphere. Soil temperatures were only marginally higher in gaps; however, the fluxes were significantly coupled with temperature and moisture inside the gaps, but not outside. An increase in soil moisture caused an increase in N₂O emission rates inside the gap (Fig. 6E), while outside the increase in soil moisture can generate opposite reaction (Fig. 6F). The reasons were that: (1) Soil bulk density was significant lower outside the gap (Table 1), meaning higher soil porosity and gas diffusivity. With higher diffusivity supply of O₂ is rarely limited, thereby preventing the soil anaerobic environment favorable to N₂O production (Wolf and Russow, 2000). (2) There was a negative relationship between soil temperature and soil moisture outside the gap (Fig. 7), consistent with a previous study showing that the soil temperature was high when soil moisture was low, and vice versa (Davidson et al., 1998). High soil moisture limited gas diffusion in the soil. (3) The spatial variability of the environment outside the gap larger than inside due to a high competition for below-ground resources in closed canopy (Ritter et al., 2005). The lack of response to soil moisture outside the gap (Fig. 6F) may be attributed to confounding factors such as NH₄⁺-N, Total N, pH, Soil bulk density.

Inside the gaps, the relationships between N₂O fluxes and soil temperature and moisture were both cubic, possibly reflecting the tight connection between these two drivers; in this ecosystem, climate is characterized by dry and relatively cool seasons followed by wet and warm seasons. This makes it difficult to disentangle the role of these two drivers in many of soil’s biological processes (Davidson et al., 1998). However, these results reflect the different roles of environmental drivers in regulating N₂O fluxes in different habitats, stimulating further research that can work to clarify the underlying mechanisms. Though microbial processes, such as nitrification and denitrification, are sensitive to changes in environmental conditions, soil moisture and temperature seem to have both synergistic and antagonistic effects which should be investigated with ad hoc manipulative experiments.

5. Conclusions

This study presented the differences magnitude and the temporal variability of N₂O emissions from two contrasting canopy structure conditions within a tropical montane forest. The results indicated that significantly higher N₂O fluxes from within canopy gaps. Temporal variability was also altered in these gaps, especially during the wet season when emission rates were generally higher. The alteration of the seasonal cycle was attributed to the different impact of the environmental drivers, soil temperature and WFPS, which were nonlinearly correlated with N₂O emissions inside the gaps but not outside the gaps. We did not find an effect of other soil
properties, such as pH, EOOC, SOC, Total P, N03•-N, NH4•-N, Total N, and soil bulk density, on N2O emissions. This study demonstrates the importance of canopy structure in accurately quantifying regional N2O emission. In the Jianfengling tropical mountain rainforest, the proportion of typhoon-induced gaps was approximately 21%. Approximately 18% of N2O emissions would be underestimated in this region if gaps were not taken into account.

We recommend that regional studies account for forest structure with a rational stratification of the sampling design, for example, estimating the distribution of the forest gap by satellite or aircraft images, and accurate calculations of regional emissions using weighted averages. Due to the intensity of tropical storms and the proportion of typhoon-induced gaps, which are projected to increase with climate change, N2O emission rates from tropical forests in typhoon-disturbed regions may accelerate. We suggest that further studies be conducted that test the generality of these patterns and disentangle the mechanisms that regulate soil N2O processes inside and outside canopy gaps.

Funding

This study is jointly supported by the National Natural Science Foundation of China (41663010); the National Natural Science Foundation of China (41201061); the Fundamental Research Funds for the Central Non-profit Research Institute of Chinese Academy of Forestry (CAFYBB2014Q010); the Fundamental Research Funds for the Central Non-profit Research Institute of Tropical Forestry, Chinese Academy of Forestry (RITFWXZ2012-02); China Qianren Project; the Lecture and Study Program for Outstanding Scholars from Home and Abroad (CAFYBB2011007); the Forest GEO, Smithsonian Institute.

Acknowledgment

We are grateful to Jianfengling National Key Field Research Station for their help with field work.

References

Anthes, R.A., Corell, R.W., Holland, G., Hurrell, J.W., MacCracken, M.C., Trenberth, K.E., 2006. Hurricanes and global warming–potential linkages and consequences. Bull. Am. Meteorol. Soc. 87, 623–628.

Bai, Z., Yang, G., Chen, H., Zhou, Q., Chen, D., Li, Y., Wang, X., Wu, Z., Zhou, G., Peng, C., 2014. Nitrous oxide fluxes from three forest types of the tropical mountain rainforests on Hainan Island, China. Atmos. Environ. 92, 469–477.

Barneze, A.S., Mazzetto, A.M., Zani, C.F., Neto, M.S., Cerri, C.C., 2014. N2O emission from rice in the soil in the beef production in Southeast Brazil: soil moisture content and temperature effects. EGU Gen. Assem. 16.

Blair, G.J., Lefroy, R.D., Lisle, L., 1995. Soil carbon fractions based on their degree of oxidation, and the development of a carbon management index for agricultural systems. Aust. J. Agric. Res. 46, 1459–1466.

Bowden, R.D., Castro, M.S., Mello, J.M., Studerl, P.A., Aber, J.D., 1993. Fluxes of greenhouse gases between soils and the atmosphere in a temperate forest following a simulated hurricane blowdown. Biochemistry 21, 61–71.

Breuer, L., Papen, H., Butterbach-Bahl, K., 2000. N2O emission from tropical forest soils of Australia. J. Geophys. Res.: Atmos. 105, 26353–26367.

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

Butterbach-Bahl, K., Diaz-Pines, E., Dannenmann, M., 2014. Soil trace gas emissions and climate change. Glob. Change Biol. 1, 325–334.

Cao, L.-H., Liu, H.-M., Zhao, S.-W., 2012. Relationship between carbon and nitrogen in degraded alpine meadow soil. Afl. Agric. Res. 7, 3945–3951.

Cardon, L., Torn, M., Capo, Y., Bubier, J., Patterson, M., Goldhaber, M., Klemedtsson, L., 2008. The global budget of nitrogen deposition: consequences for terrestrial ecosystems. AMBIO: J. Hum. Environ. 31, 113–119.

Cardon, L., Torn, M., Capo, Y., Bubier, J., Patterson, M., Goldhaber, M., Klemedtsson, L., 2008. The global budget of nitrogen deposition: consequences for terrestrial ecosystems. AMBIO: J. Hum. Environ. 31, 113–119.

Cardon, L., Torn, M., Capo, Y., Bubier, J., Patterson, M., Goldhaber, M., Klemedtsson, L., 2008. The global budget of nitrogen deposition: consequences for terrestrial ecosystems. AMBIO: J. Hum. Environ. 31, 113–119.

Cardon, L., Torn, M., Capo, Y., Bubier, J., Patterson, M., Goldhaber, M., Klemedtsson, L., 2008. The global budget of nitrogen deposition: consequences for terrestrial ecosystems. AMBIO: J. Hum. Environ. 31, 113–119.

Cardon, L., Torn, M., Capo, Y., Bubier, J., Patterson, M., Goldhaber, M., Klemedtsson, L., 2008. The global budget of nitrogen deposition: consequences for terrestrial ecosystems. AMBIO: J. Hum. Environ. 31, 113–119.

Cardon, L., Torn, M., Capo, Y., Bubier, J., Patterson, M., Goldhaber, M., Klemedtsson, L., 2008. The global budget of nitrogen deposition: consequences for terrestrial ecosystems. AMBIO: J. Hum. Environ. 31, 113–119.

Cardon, L., Torn, M., Capo, Y., Bubier, J., Patterson, M., Goldhaber, M., Klemedtsson, L., 2008. The global budget of nitrogen deposition: consequences for terrestrial ecosystems. AMBIO: J. Hum. Environ. 31, 113–119.

Cardon, L., Torn, M., Capo, Y., Bubier, J., Patterson, M., Goldhaber, M., Klemedtsson, L., 2008. The global budget of nitrogen deposition: consequences for terrestrial ecosystems. AMBIO: J. Hum. Environ. 31, 113–119.

Cardon, L., Torn, M., Capo, Y., Bubier, J., Patterson, M., Goldhaber, M., Klemedtsson, L., 2008. The global budget of nitrogen deposition: consequences for terrestrial ecosystems. AMBIO: J. Hum. Environ. 31, 113–119.

Cardon, L., Torn, M., Capo, Y., Bubier, J., Patterson, M., Goldhaber, M., Klemedtsson, L., 2008. The global budget of nitrogen deposition: consequences for terrestrial ecosystems. AMBIO: J. Hum. Environ. 31, 113–119.

Cardon, L., Torn, M., Capo, Y., Bubier, J., Patterson, M., Goldhaber, M., Klemedtsson, L., 2008. The global budget of nitrogen deposition: consequences for terrestrial ecosystems. AMBIO: J. Hum. Environ. 31, 113–119.

Cardon, L., Torn, M., Capo, Y., Bubier, J., Patterson, M., Goldhaber, M., Klemedtsson, L., 2008. The global budget of nitrogen deposition: consequences for terrestrial ecosystems. AMBIO: J. Hum. Environ. 31, 113–119.

Cardon, L., Torn, M., Capo, Y., Bubier, J., Patterson, M., Goldhaber, M., Klemedtsson, L., 2008. The global budget of nitrogen deposition: consequences for terrestrial ecosystems. AMBIO: J. Hum. Environ. 31, 113–119.

Cardon, L., Torn, M., Capo, Y., Bubier, J., Patterson, M., Goldhaber, M., Klemedtsson, L., 2008. The global budget of nitrogen deposition: consequences for terrestrial ecosystems. AMBIO: J. Hum. Environ. 31, 113–119.
McDowell, W.H., 2011. Impacts of hurricanes on forest hydrology and biogeochemistry. In: Forest Hydrobiogeochem. Springer.

Newman, A., 1990. Tropical Forest: Facts On File, Inc.

Pielke Jr., R.A., Landsea, C., Mayfield, M., Laver, J., Pasch, R., 2005. Hurricanes and global warming. Bull. Am. Meteorol. Soc. 86, 1571–1575.

Prather, M., Ehhalt, D., Dentener, F., Derwent, R., Dlugokencky, E., Holland, E., Isaksen, I., Katima, J., Kirchhoff, V., Matson, P., 2001. Atmospheric Chemistry and Greenhouse Gases.

Rees, R.M., Wuta, M., Furley, P.A., Li, C., 2006. Nitrous oxide fluxes from savanna (miombo) woodlands in Zimbabwe. J. Biogeogr. 33, 424–437.

Riley, R.H., Vitousek, P.M., 2000. Hurricane effects on nitrogen trace gas emissions in Hawaiian Montane rain forest 1. Biotropica 32, 751–756.

Ritter, E., Dalgaard, L., Einhorn, K.S., 2005. Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark. For. Ecol. Manage. 206, 15–33.

Robertson, G.P., Tiedje, J.M., 1988. Deforestation alters denitrification in a lowland tropical rain forest. Nature 336, 756–759.

Robertson, G., 1989. Nitrification and denitrification in humid tropical ecosystems: potential controls on nitrogen retention. Miner. Nutr. Trop. For. Savanna Ecosyst. 9, 55–69.

Ryden, J., 1981. N2O exchange between a grassland soil and the atmosphere. Nature 292, 235–237.

Schlenmann, S.A., Bockheim, J.G., 2011. Methods for studying treefall gaps: a review. For. Ecol. Manage. 263, 1143–1151.

Serca, D., Delmas, R., Jambert, C., Labrous, L., 1994. Emissions of nitrogen oxides from equatorial rain forest in central Africa. Tellus B 46, 243–254.

Sha, L., Zheng, Z., Feng, Z., Liu, Y., Liu, W., Meng, Y., Li, M., 2001. Biogeochemical cycling of nitrogen at a tropical seasonal rain forest in Xishuangbanna, SW China. Acta Phytocel. Sin. 26, 689–694.

Steupler, P., Melillo, J., Bowden, R., Castro, M., Lugo, A., 1991. The effects of natural and human disturbances on soil nitrogen dynamics and trace gas fluxes in a Puerto Rican wet forest. Biotropica, 356–363.

Verchot, L.V., Davidson, E.A., Cattáneo, H., Ackerman, I.L., Erickson, H.E., Keller, M., 1999. Land use change and biogeochemical controls of nitrogen oxide emissions from soils in eastern Amazonia. Glob. Biogeochem. Cycles 13, 31–46.

Wang, H., Mo, J., Lu, X., Xue, J., Li, J., Fang, Y., 2009. Effects of elevated nitrogen deposition on soil microbial biomass carbon in major subtropical forests of southern China. Front. For. China 4, 21–27.

Werner, C., Zheng, X., Tang, J., Xie, B., Liu, C., Kiese, R., Butterbach-Bahl, K., 2006. N2O, CH4 and CO2 emissions from seasonal tropical rainforests and a rubber plantation in Southwest China. Plant Soil 289, 335–353.

Werner, C., Kiese, R., Butterbach-Bahl, K., 2007. Soil-atmosphere exchange of N2O, CH4, and CO2 and controlling environmental factors for tropical rain forest sites in western Kenya. J. Geophys. Res. 112, D03308.

Wolf, I., Russew, R., 2000. Different pathways of formation of N2O, N2 and NO in black earth soil. Soil Biol. Biochem. 32, 229–239.

Wu, C., Zhang, Y., Xu, X., Sha, L., You, G., Liu, Y., Xie, Y., 2014. Influence of interactions between litter decomposition and rhizosphere activity on soil respiration and on the temperature sensitivity in a subtropical montane forest in SW China. Plant Soil 381, 215–224.

Zhang, Z.-W., Zhang, J.-H., Zhao, Z.-Z., Liu, S.-J., Xie, R.-H., Fan, N., 2011. Analysis of risks in Hainan Island typhoon hazard factor based on GIS. Meteorol. Environ. Res. 2, 31–34.

Zhang, W., Zhu, X., Liu, L., Fu, S., Chen, H., Huang, J., Lu, X., Liu, Z., Mo, J., 2012. Large difference of inhibitive effect of nitrogen deposition on soil methane oxidation between plantations with N-fixing tree species and non-N-fixing tree species. J. Geophys. Res. G: Biogeosci. 117.

Zhou, Z., Jiang, L., Du, E., Hu, H., Li, Y., Chen, D., Fang, J., 2013. Temperature and substrate availability regulate soil respiration in the tropical mountain rainforests, Hainan Island, China. J. Plant Ecol. 6, 325–334.