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Nitrous oxide emissions from soil of an African rain forest in Ghana

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Abstract

Most recently atmospheric studies have evidenced the imprint of large N_2O sources in tropical/subtropical lands. This source might be attributed to agricultural areas as well as to natural humid ecosystems. The uncertainty related to both sources is very high, due to the paucity of data and small frequency of sampling in tropical studies. This is particularly relevant for the African continent. The principal objective of this work was to quantify the annual budget of N_2O emissions in an African tropical rain forest. Soil N_2O emissions were measured over 19 months in Ghana, National Park of Ankasa, in upland and lowland areas, for a total of 119 days of observation. The calculated annual average emission was $2.33 \pm 0.20\,kg\,N - N_2O\,ha^{-1}\,yr^{-1}$, taking into account the proportion of upland vs. lowland, as the two areas showed significantly different fluxes, the lowland being characterized by lower N_2O emissions. N_2O fluxes peaked between June and August and were significantly correlated with soil respiration on a daily and monthly basis. No clear correlation was found in the upland areas between N_2O fluxes and soil water content or rain whereas in the lowland soil water content concurred with soil respiration in determining N_2O flux variability. The N_2O source strength calculated in this study, very close to those reported for the other two available studies in African rain forests and to the estimated mean derived from worldwide studies in humid tropical forests ($2.96 \pm 2.0\,kg\,N - N_2O\,ha^{-1}\,yr^{-1}$), supports the concept that tropical humid forests represent the strongest natural source of N_2O emissions, most probably the strongest source of N_2O in the African continent.

1 Introduction

Tropical forests are a key ecosystem for terrestrial carbon cycling, being the most productive ecosystems on Earth (Grace et al., 2001) and accounting for 59 % of the global carbon pool in forests (Dixon et al., 1994). Recent evidence indicates that these ecosystems might have a key role not only in the C cycle but also in the global

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atmospheric balance of the greenhouse gas nitrous oxide (N_2O). Kort et al. (2011) measurements of vertical atmospheric profiles (from surface to 14 km altitude) between 67° S to 85° N latitude have shown significant sources of N_2O in tropical areas with high temporal variability. The available data to support these atmospheric observations are still quite limited in terms of geographical coverage, length of sampling campaign, significance of spatial replication. Most of the available data come from Brasil (Keller et al., 1983, 1988, 2005; Verchot et al., 1999; Maddock et al., 2001; Melillo et al., 2001; Davidson et al., 2004; Sousa Neto et al., 2011) and Central America (Matson and Vitousek, 1987; Keller et al., 1993; Keller and Reiners, 1994; Weitz et al., 1998). Only very recently some data from tropical ecosystems in Asia have been published (Verchot et al., 2006; Werner et al., 2006; Yan et al., 2008). Few observations are available for Oceania (Breuer et al., 2000; Kiese and Butterbach-Bahl, 2002; Kiese et al., 2003) and just two studies are available for tropical rain forests in the African continent (Serca et al., 1994; Werner et al., 2007a). Moreover, most of the available studies in remote tropical areas are often based on short campaigns of few days of measurements, which make the annual estimate highly uncertain. Given the wide surface covered by tropical forests there is a clear need to have a sufficient number of studies to improve our estimates and to help to validate theoretical estimates and downscaling quantifications (Potter et al., 1996; Stehfest and Bouwman, 2006; Werner et al., 2007b). Africa is, in this respect, the least investigated continent.

The principal objective of this work was to quantify the annual budget of N_2O emissions in an African tropical rain forest. N_2O fluxes were sampled monthly, with a frequency of 6 days per month, for 19 months. To better understand the dynamics of N_2O production, soil CO_2 emissions, soil temperature and soil water content were also monitored and their variability related to N_2O flux variability.

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2 Materials and method

2.1 The study site

The study site (05° 16′ 11″ N, 02° 41′ 41″ W) located in Ankasa Wildlife Protected Area, is an ancient rainforest with the highest biodiversity in Ghana. The forest has an area of about 500 km^2 and in 1976 became a wildlife protected area, to preserve the forests from cutting, slash and burn, conversion to agro-ecosystems. A core area of about 343 km^2 represents the only rain forest protected area, in almost pristine state, in Ghana. The mean annual temperature is about 25 °C and the mean annual precipitation is between 1500–2000 mm, depending on the year, mainly concentrated from March to mid-July and from September to November, with a relative humidity ranging from 75 % to 90 %. A relatively dry period generally occurs between December and February (Hall and Swaine, 1981). The landscape is characterized by the presence of hills with an average elevation of 90 m a.s.l., alternating with steep valleys. Soils are deeply weathered and highly acidic and are classified as Oxisols (Ahn, 1961). Soil, developed on coherent biotite-rich granites of the Cape Coast complex, forms the Ankasa association, consisting of "Abenia" series, the most widespread series on top of the hills, which alternates to the "Ankasa" series, along the slopes. Alluvial soils occupy the bottom of the fluvial valleys. The main characteristics of the soil sampled in upland and lowland study areas are presented in Table 1. Surface litter C in the hill top area is 15 ± 9 mg C ha^{-1}, and a preliminary estimate of the aboveground biomass, including live and dead wood, is 138–170 mg C ha^{-1} (Chiti et al., 2010).

2.2 Experimental set up

Soil N_2O and CO_2 flux measurements were carried out during years 2009 and 2010. Sampling started in 2009 in an upland area where a tower for eddy covariance measurements is located. The micrometeorological station was identified as the centre of 4 quadrants (north-east, east-south, south-west, west-north) and 2 chambers were

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positioned at a minimum distance of 50 m from the tower, in each quadrant (8 replicates in all). A second plot of about one hectare was set in 2010 at the bottom of the valley, where soil conditions are expected to change significantly, in particular soil humidity. Also in this case 8 replicates were used. Chamber position was changed every day to improve the coverage of spatial variability, taking care to insert the chamber base in the ground about 3 h before starting the measurements so as to avoid false fluxes caused by soil pressure changes and by root mortality and decomposition (Keller et al., 2000), and keeping the replicates at a minimum distance of 10 m one from the other. Within each plot, monthly campaigns of soil-atmosphere gas exchange were carried out, over six consecutive days. Sampling in the upland area started in April 2009 while in the lowland area sampling started in May 2010, data are reported up to November 2010. The initial experimental set-up included soil temperature and water content measurements undertaken by local micrometeorological station. However, a failure of sensors due to lightning hampered the quality of data. Therefore, from May 2010, soil temperature (HI93510 thermometer, Hanna Instruments Canada Inc., Laval, Quebec) and volumetric soil water content (ThetaProbe ML2, Delta-T Device Ltd, Cambridge, UK) were hand-measured close by each chamber (0–5 cm depth), 5 cm from the chamber edge, at each sampling date. Gas sampling was generally done between 10:00 and 12:00 a.m. Soil temperature has an annual average maximal daily variation of about 0.5 °C at 5 cm depth and 0.1 °C at 10 cm depth (meteorological station at site, 2008–2009 data). Soil water content was expressed as water filled pore space % (WFPS) equal to $100 \times \theta_v / \varepsilon$, where θ_v is the volumetric water content and ε is the total porosity ($\varepsilon = 1 -$ bulk density/particle density).

2.3 Gas flux determination

Gas fluxes were measured using closed static chambers (Hutchinson and Mosier, 1981; Smith et al., 1995) made of PVC collars (7 cm high with a diameter of 15 cm), inserted in the soil to about 5 cm depth, and chamber lids (20 cm high with a diameter of 15 cm). To determine gas fluxes, gas (30 ml) was sampled, using gas-tight

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syringes, from the chamber headspace at 0, 30 and 60 min after closure; it was immediately stored in pre-evacuated gas-tight vials (20 ml), slightly overpressure, which were sealed with thermal glue and shipped for gas chromatographic analysis. N_2O flux rates were determined by linear regression of the three sampling points (0, 20, 60 min) for each chamber and by applying a temperature and pressure correction. The analytical precision of the GC for standards at ambient concentration was approximately 3 %, using one standard deviation as a measure of mean error. The analytical set up (Loftfield et al., 1997) allowed both N_2O and CO_2 fluxes to be measured from the same chamber. Gas was loaded on a 2 ml loop connected to a 10-ports valve (Valco Europe, Switzerland). A pre-column of 1 m (O.D. 1/8″, 0.08″ I.D.), filled with Porapak 80–100 Q and maintained at 60 °C, was connected to the 10-port valve in order to operate front-flush and back-flush. From the pre-column, the gas passed into the main column (T Porapak 80–100 Q, O.D. 1/8″, 0.08″ I.D., 2 m length), also held at 60 °C and was then directed to an electron capture detector (ECD) held at 280 °C for the determination of CO_2 and N_2O concentration. Pure nitrogen was used as carrier gas at a flow rate of 40 $cm^3 min^{-1}$. Four concentrations of calibrated standards were used and were injected in duplicate every 20 samples to allow for instrumental drifting. The CO_2 fluxes determined using this approach can be used for comparative analysis between sites and to identify trends in soil respiration (Yan et al., 2009; Mapanda et al., 2010; Liu et al., 2011) rather than to quantify annual soil CO_2 efflux site budgets. For this latter goal CO_2 efflux are usually determined by infrared gas analyzer (IRGA) using dynamic closed or open chambers (Rayment and Jarvis, 1997; Heinemeyer and McNamara, 2010). For this reason no attempt was made in this study to quantify the annual budget of soil CO_2 emissions but seasonal variations of soil respiration were used to interpret variations of N_2O emissions.

2.4 Statistics

A two-way analysis of variance was used to compare gas fluxes, soil temperature and water filled pore space measured in the lowland and upland plots. A normality test

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(Kolmogorov-Smirnov, with Lilliefors correction, Sigma Stat, Jandel Scientific) was performed before running parametric tests (Sigma Stat, Jandel Scientific). When the difference was significant ($P < 0.05$) an "all pair wise" comparison was carried out using the "Student Newman–Keul test". When normality tests failed, a Kruskal–Wallis ANOVA on ranks was performed. Simple linear regressions, multiple linear regression and non-linear regression analysis were performed to find the relationship between independent and dependent variables (Sigma Stat, Jandel Scientific). Significant differences were at the $P < 0.05$ level.

3 Results

3.1 Spatial and temporal variability of N_2O fluxes

Single chamber N_2O fluxes varied between −0.15 and 29.13 $mg N_2O m^{-2} d^{-1}$ in the upland and −0.53 and 16.62 $mg N_2O m^{-2} d^{-1}$ in the lowland. The daily spatial variability (range CV% 33–288) was on 46 % of sampling days higher than the annual temporal flux variability calculated on daily averages (CV% 110). N_2O flux showed a marked seasonal variability (Fig. 1a), with daily average fluxes ranging from 0.04 to 8.04 $mg N_2O m^{-2} d^{-1}$ in the upland and from 0.06 to 2.84 $mg N_2O m^{-2} d^{-1}$ in the lowland (Fig. 1a). In both environments, the distribution of daily mean values was log-normal. Referring to the period when both environments were monitored, the average daily N_2O emission in the lowland (0.62 $mg N_2O m^{-2} d^{-1}$) was significantly lower ($P = 0.001$) than in the upland (1.76 $mg N_2O m^{-2} d^{-1}$). The maximum seasonal peak of N_2O emissions was between June and August in both 2009 and 2010 (Fig. 1a). The total annual N_2O budget was calculated by summing daily means of measured fluxes. The flux of periods in between measured fluxes was calculated as the area delimited by two successive couples of x, y values (x Julian day, y corresponding N_2O flux). In the upland area fluxes were measured from April 2009 to November 2010, so we calculated the cumulative flux for two periods of twelve months,

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April 2009–March 2010 and October 2009–November 2010. The calculated annual fluxes were 2.54 and 2.72 kg N – N_2O ha^{-1} yr^{-1}, respectively, and the average was 2.63 ± 0.23 kg N – N_2O ha^{-1} yr^{-1}. The error associated to the mean value was calculated as $\sqrt{\delta^2 \cdot 365}$, where δ is the daily average standard deviation derived from all the analyzed days of sampling (0.012 kg N – N_2O ha^{-1} d^{-1}. Comparing the lowland and upland N_2O cumulative fluxes over the same period of observation (May to November 2010), the total lowland N_2O emission was only 44 % of the emission measured in the upland. The surface covered by lowland in the Ankasa National Park was estimated to be about 20 %, derived by SRTM DEM at 90 m resolution (CGIAR-CSI free source). The calculated weighted annual emission per hectare, taking into account the upland/lowland ratio, was 2.33 ± 0.20 kg N – N_2O ha^{-1} yr^{-1}, a value which is within the error estimate of the calculated flux for upland areas.

3.2 Relationship between environmental drivers and N_2O fluxes

The potential drivers of N_2O fluxes measured at site were soil temperature, soil water content, expressed as soil water filled pore space%, soil CO_2 fluxes, monthly rainfall and monthly air temperature, calculated as the average of data from the two weather station closest to Ankasa site (TRMM database). The seasonal trend of N_2O emissions was similar to that of soil respiration (Fig. 1a, b). On a daily basis, higher fluxes of N_2O emissions corresponded to higher soil respiration rates (Fig. 2). On monthly basis, the match between temporal trends of the two gases was particularly clear (Fig. 3a, b). The wider seasonal variations of N_2O emissions, compared with soil respiration, most probably reflected the complex interplay of environmental factors which concurred in N_2O production and emission. Mean monthly trends values of N_2O and CO_2 emissions did not correspond with trends of average air temperature and total rainfall (Fig. 3c). On a daily basis, variability of N_2O and CO_2 fluxes were related to variations of soil water filled pore space and soil temperature. For the upland area, a lognormal relationship was found between both average daily N_2O emissions and soil respiration and

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WFPS% (Fig. 4a), with a gas flux peak between 30 and 35 WFPS%, slightly shifted towards higher WFPS values for N_2O compared to CO_2 fluxes (Fig. 4a, b). In the lowland area no significant trend was found between N_2O or CO_2 fluxes and WFPS, although both gases showed a tendency to increase for WFPS values above 50 %. However, a significant relationship was found between N_2O and a linear combination of CO_2 fluxes and WFPS% in the lowland ([N_2O flux ($mg\,m^{-2}\,d^{-1}$) = $-0.907 + 0.24\times$ CO_2 flux ($g\,m^{-2}\,d^{-1}$) $+0.02\times$ WFPS%], $R^2 = 0.13$, $P < 0.05$, $N = 227$). Average daily N_2O and CO_2 fluxes significantly increased in a range of soil temperatures comprised between 22.5 and 25 °C, the increase being smoother for CO_2 fluxes (Fig. 5). The narrow range of temperatures in which a sharp increase of N_2O flux was observed corresponded to intermediate values of soil WFPS (Fig. 4a). Multilinear regression analysis did not evidence any other significant relationship between analysed variables and N_2O emissions.

4 Discussion

The annual budget calculated for the Ankasa rain forest ($2.33 \pm 0.20\,kg\,N-N_2O\,ha^{-1}\,yr^{-1}$) is very close to the annual N_2O emission estimates reported by Serca et al. (1994) for a primary rain forest of the Mayombe region in Congo ($2.9\,kg\,N-N_2O\,ha^{-1}\,yr^{-1}$) and by Werner et al. (2007a) for a mountain rainforest in the Kakamega forest national park in Kenya ($2.6\,kg\,N-N_2O\,ha^{-1}\,yr^{-1}$). The three African sites, including Ankasa, have similar rain regime and acidic soil; Ankasa is characterized by a higher percentage of sand in the soil texture, compared with the other two sites, the Kenya mountain forest has a highest content of soil C (about twice Ankasa values, in the top 5 cm), whereas Ghana and Congo soil C contents are comparable. Although the observed differences of soil C and texture might be expected to influence N_2O emissions rates (Kiese et al., 2005; Werner et al., 2007b), the observed small difference of annual N_2O emissions among sites indicate that the effect of such influence most probably was within the uncertainty associated

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to the annual N_2O emission estimate. On the other end, the comparable annual N_2O fluxes in the three African sites indicate that key driving mechanisms of N_2O production are similar in the three tropical rain forests. Both Serca et al. (1994) and Werner et al. (2007a) have evidenced the link between magnitude of N_2O emissions and the magnitude of N mineralization activity, indicating the high rates of the latter in rain forests, in spite of acid soil pH, as one of the key factors which supports high N_2O emission rates. Werner et al. (2007a) also pointed out that while short-term variations of N_2O might be associated to significant changes in soil moisture, hence to isolated rain events, seasonal N_2O emission patterns and the annual budget mainly depend on decomposition rates which control N availability. These observations are in accordance with our results, which indicated a very similar pattern of N_2O emissions and soil respiration on a monthly average basis and a good correlation between the two variables at daily time step. In the well drained upland site, where WFPS never exceeded 50 %, soil respiration was the independent factor, the variability of which best predicted the variability of N_2O emissions. Soil CO_2 emission, namely soil respiration, is the result of combined rates of autotrophic and heterotrophic respiration. The partitioning of these two components in the overall CO_2 soil efflux is variable depending on site characteristics, time of the year and of the day (Sotta et al., 2004). Both these components tend to increase with increasing soil temperature and moisture, although in tropics soil CO_2 efflux has been reported to be depressed by strong rain events due to both the limiting of gas diffusion and the decrease of soil temperature (Sotta et al., 2004). Although we could not distinguish between autotrophic and heterotropic sources of soil CO_2 emissions, we might expect that both processes would have influenced N_2O production positively. High respiration rates, no matter which organism is involved, tend to decrease soil oxygen content and favour the development of anaerobic hotspots of N_2O production within aerobic soils (Smith et al., 1990). Higher heterotrophic respiration rates can be expected to coincide with peaks of fresh organic matter input (litterfall), which also represent a source of N for microbes. In rain forests, peaks of litterfall have been reported to occur mostly at the

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onset of the rainy season (Muoghalu et al., 1993; De Moraes et al., 1999). Considering that air humidity inside the close and shaded canopy of a rain forest is always quite high, humidity and temperature conditions can generally be considered not limiting for decomposition in the humid tropics, compared with temperate and boreal forest ecosystems, so that a flow of N which supports nitrification and denitrification processes and N_2O emissions (Firestone and Davidson, 1989) is assured during the whole year. An increase of decomposition rates and mineralization can be expected to coincide with peaks of litter fall and in the first weeks following the onset of heavy precipitation events if they are close to peaks of litter fall (Werner et al., 2007a). The lower fluxes measured in the lowland area, which coincided with much higher WFPS (37 %–78 %) compared with upland, might in part be explained by lower soil respiration rates but also by a predominance of reducing conditions during part of the year, leading to further reduction of produced N_2O to N_2 in soil hotspots where WFPS is close to saturation. The occurrence of such hotspots of anaerobic microbial activity is also confirmed by measured CH_4 fluxes which showed high emission rates only in the lowland (Castaldi et al., data not published).

The average annual N_2O emission estimate derived from the three available studies in African rain forests (Ghana, Kenya, Congo), 2.6± 0.3 kg $N-N_2O$ ha^{-1} yr^{-1}, is quite close to the global average calculated for tropical humid forests from different continents, 2.96 ± 2.0 kg $N-N_2O$ ha^{-1} yr^{-1} (Table 2), excluding studies where estimates are based on sampling campaigns carried out only in one season (dry or wet). Of the studies reported in Table 2, which represent the most cited literature for humid tropical forests for which a tentative site assessment of N_2O emission strength is made, about 50 % are characterized by medium to high uncertainty, in particular concerning the temporal frequency of sampling. Only nine of the 40 presented studies show an average sampling frequency higher than 4 samples per month. Within the group of sites characterized by medium/low uncertainty the range of observed fluxes varies from 0.94 to 7.45 kg $N-N_2O$ ha^{-1} yr^{-1}. All the sites which show fluxes higher than 3 kg $N-N_2O$ ha^{-1} yr^{-1} are characterized by annual total rainfall higher than 2000 mm,

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with the sole exception of Kauri Creek site in Australia (Table 2), hence higher than rainfall at Ankasa site. Rainfall represents both a proximal and distal factor which exert a positive control (stimulation) on N_2O emission, because it influences soil water filled pore space, NPP, and decomposition rates. Moreover, at increasing rainfall rates there is a progressive reduction of the length of periods with clear dry conditions, which are less favourable for N_2O production.

5 Conclusion

Results showed that the rain forest in Ghana has annual emission rates very close to other rain forest sites of Central Africa characterized by similar rainfall conditions. Fluxes were characterized by high temporal variability, which supported the extremely importance of adequate sampling frequency in this natural environment. Moreover, the study also showed the importance of spatial coverage, with valley area having statistically different fluxes from upland area. This is a common feature of many tropical landscapes which need to be taken into account when scaling up. Overall the observed N_2O emission rates support the concept that tropical humid forests are key sources of N_2O emissions, most probably the strongest source of N_2O in the African continent.

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Table 1. Main chemico-physical characteristics (±1 stdev, n = 6) of the soil sampled in the study areas.

Site	Dept	Horizon	Sand[a]	Silt[a]	Clay[a]	BD[b]	pH[c]	C[d]	N[d]
	cm		($g\,kg^{-1}$)	($g\,kg^{-1}$)	($g\,kg^{-1}$)	($Mg\,m^{-3}$)		($g\,kg^{-1}$)	($g\,kg^{-1}$)
Upland	0–5		665 ± 21	185 ± 12	150 ± 15	1.32 ± 0.12	3.6 ± 0.3	9.8 ± 1.12	0.66 ± 0.21
	5–15	Bo	580 ± 20	191 ± 12	229 ± 31	1.36 ± 0.04	4.2 ± 0.2	1.15 ± 0.5	0.13 ± 0.07
	15–3	Bo	574 ± 63	171 ± 20	255 ± 78	1.35 ± 0.09	4.5 ± 0.2	0.86 ± 0.2	0.11 ± 0.05
	30–5	Bo	572 ± 21	170 ± 26	258 ± 27	1.36 ± 0.13	4.2 ± 0.2	0.78 ± 0.1	0.09 ± 0.04
Lowland	0–5		734 ± 19	152 ± 15	114 ± 19	1.3 ± 0.09	4.3 ± 0.2	2.74 ± 0.6	0.22 ± 0.01
	5–15	A1	725 ± 32	170 ± 32	105 ± 23	1.34 ± 0.11	4.3 ± 0.2	2.44 ± 0.0	0.22 ± 0.02
	15–3	Bo	668 ± 25	190 ± 17	142 ± 34	1.32 ± 0.15	4.8 ± 0.3	2.32 ± 0.1	0.18 ± 0.01
	30–5	Bo	598 ± 17	186 ± 21	216 ± 26	1.38 ± 0.18	5.0 ± 0.2	1.10 ± 0.0	0.10 ± 0.02

[a] Determined using the pipette method after destruction of the organic cement using sodium hypochlorite at pH 9 (Mikutta et al., 2005).
[b] Bulk density determined with the core method (Blake and Hartge, 1986).
[c] Measured in deionised water with a sure-flow electrode, using a ratio soil-solution of 1 : 2.5 (w/w).
[d] Measured by dry combustion (ThermoFinnigan Flash EA112 CHN).

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Table 2. Annual or seasonal rates (bold) of N_2O emission ($kg\,N\,ha^{-1}\,yr^{-1}$) as reported by authors or calculated (where indicated) from literature studies in humid tropical forests. Reported campaigns occurred only in dry (D) or wet (W) seasons; over a whole year (Y); during periods longer than one year (months are indicated). Arbitrary uncertainty levels are given (explained in Table notes) not as an absolute level of uncertainty but as a comparative indication among studies.

Reference	Country	Site	Sampling period	N_2O emission $kg\,N\,ha^{-1}\,yr^{-1}$	N° chambers/days of sampling	Uncertainty spatial/temporal[a]
Breuer et al. (2000)	Australia	Kauri Creek	W-D	5.36	5/2084	M/L
Breuer et al. (2000)	Australia	Lake Eacham	W	1.15	5/1137	M/L
Breuer et al. (2000)	Australia	Massey Creek	D-W	3.75	5/1637	M/L
Castaldi et al. (2012)	Ghana	Ankasa National Park	19 months	2.33	8-16/114	M-L/L
Davidson et al. (2004)	Brasil	Tapajos National Forest	D-W, 5 yr	1.4	18/20	M/H
Keller and Rainers (1994)	Costa Rica	La Selva, prim for.	Y	5.86[b]	8/12	M/M
Kellers and Reiners (1994)	Costa Rica	La Selva, second. for.	Y	3.74[b]	8/12	M/M
Keller et al. (1983)	Brazil	Terra firme	W	**1.90**[b]	2/6	H/H
Keller et al. (1993)	Costa Rica	La Selva	Y	6	8/12	M/M
Keller et al. (2005)	Brasil	Tapajos Forest Ultisol	2Ys	1.4	8/31	M/M
Keller et al. (2005)	Brasil	Tapajos Forest Oxisol	2Ys	6.5	8/31	M/M
Kiese,Butterbach-Ball (2002)	Australia	Kauri Creek	D-W	4.36	5/400	M/L
Kiese,Butterbach-Ball (2002)	Australia	Bellender Ker	D-W	7.45	5/351	M/L
Kiese,Butterbach-Ball (2002)	Australia	Pin Gin Hill	D-W	6.89	5/451	M/L
Kiese et al. (2003)	Australia	Bellender Ker	Y	0.97	5/52	M/L
Livingston et al. (1988)	Brazil	Manaus, clay	D	**0.48**[b]	4/2	H/H
Livingston et al. (1988)	Brazil	Manaus, sandy	D	**0.43**[b]	4/2	H/H
Luizao et al. (1989)	Brazil	Terra Firme	Y	1.9[c]	8/11	M/H
Maddock et al. (2001)	Brasil	Tinguà biol. Res	Y	3.14[c]	5/21	M/M
Matson et al. (1990)	Brazil	Manaus, Oxisol	W	**0.86**[c]	8/10	M/M
Matson et al. (1990)	Brazil	Manaus, Ultisol	W	**0.19**[c]	8/4	M/H
Matson et al. (1990)	Brazil	Manaus, Spodsol	W	**0.07**[c]	8/2	M/H

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Table 2. Continued.

Reference	Country	Site	Sampling period	N_2O emission kg N ha^{-1} yr^{-1}	No. chambers/days of sampling	Uncertainty spatial/temporal[a]
Matson and Vitousek (1987)	Costa Rica	La Selva	W	**1.2**[c]	8/2	M/H
Matson and Vitousek (1987)	Costa Rica	La Selva	W	**1.66**[c]	8/2	M/H
Matson and Vitousek (1987)	Costa Rica	Turialba	W	**1.14**[c]	10/1	M/H
Melillo et al. (2001)	Brazil	Rondonia	Y	1.94	3/11	H/H
Nepstad et al. (2002)[d]	Brasil	Tapajos National Forest	34 months	2.3	18/13	L/H
Sousa Neto et al. (2011)	Brasil	Picinguaba	Y	**2.2**	4/12	H/M
Sousa Neto et al. (2011)	Brasil	Santa Virginia	Y	**0.9**[c]	4/12	H/M
Sousa Neto et al. (2011)	Brasil	Serra do Mar	Y	**0.7**[c]	4/12	H/M
Serca et al. 1994	Congo	Mayombe region	W-D	2.9	6-8/15	M/M
Verchot et al. (1999)	Brazil	East Amazon, primary	Y	2.43	8/16	M/M
Verchot et al. (1999)	Brazil	East Amazon, secondary	Y	0.94	8/16	M/M
Verchot et al. (1999)	Brazil	Parà	D	**0.09**[b]	8/1	M/H
Verchot et al. (2006)	Indonesia	Sumatra, forest	9 months	1.2	8/4	M/H
Verchot et al. (2006)	Indonesia	Sumatra, wet forest	9 months	1.3	8/4	M/H
Yan et al. (2008)	China	Xishuangbanna	Y	2.7	3/50	H/L
Weitz et al. (1998)	Costa Rica	La Selva, sec for, dystrop	13 months	**1.42**e	8/20	M/M
Weitz et al. (1998)	Costa Rica	La Selva, sec for, eutrop	14 months	**1.28**e	8/22	M/M
Werner et al. (2007)	Kenya	Kakamega forest	D-W	2.6	6/347	M/L

[a] Spatial uncertainty classified as high (H) when no. Chambers < 5, medium (M) when 5 < no. ch < 10, low (L) when no. ch > 10; temporal uncertainty classified as high (H) when only one season is sampled or when over the year we have less than 1 measurement per month, medium (M) when sampling frequency is between 1 and 4 days per month, low (L) when sampling frequency is higher than 4 days per month.

[b] Extrapolated from mean estimates for the sampling period.

[c] Extrapolated from monthly measurements.

[d] Same site of Davidson et al. (2004).

[e] Calculated from annual average.

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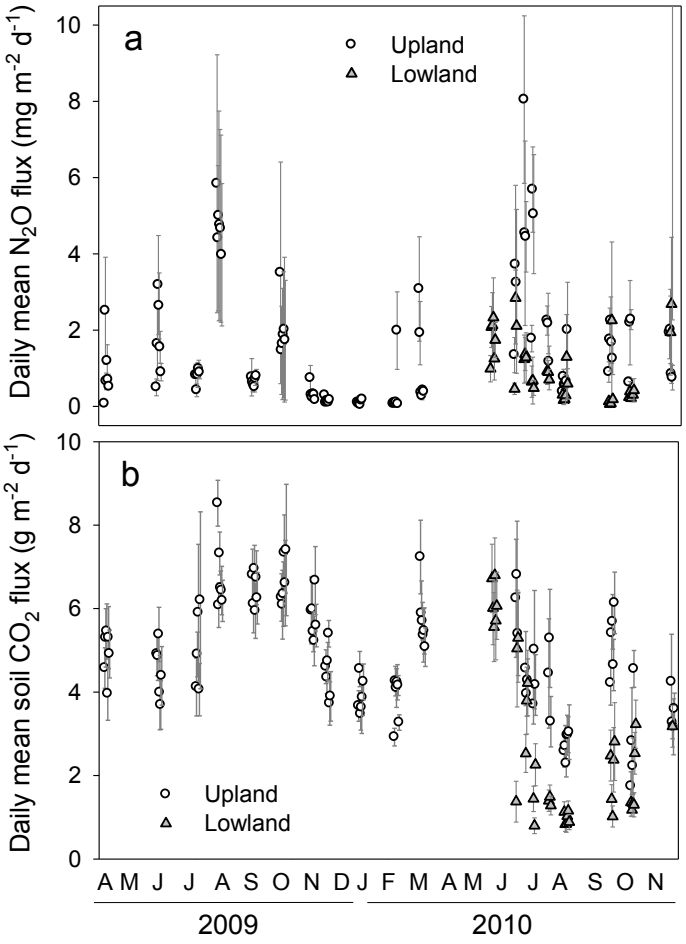

Fig. 1. Daily mean values (± one st dev) of N_2O fluxes **(a)** and soil respiration **(b)** measured in the upland and lowland areas in 2009 and 2010.

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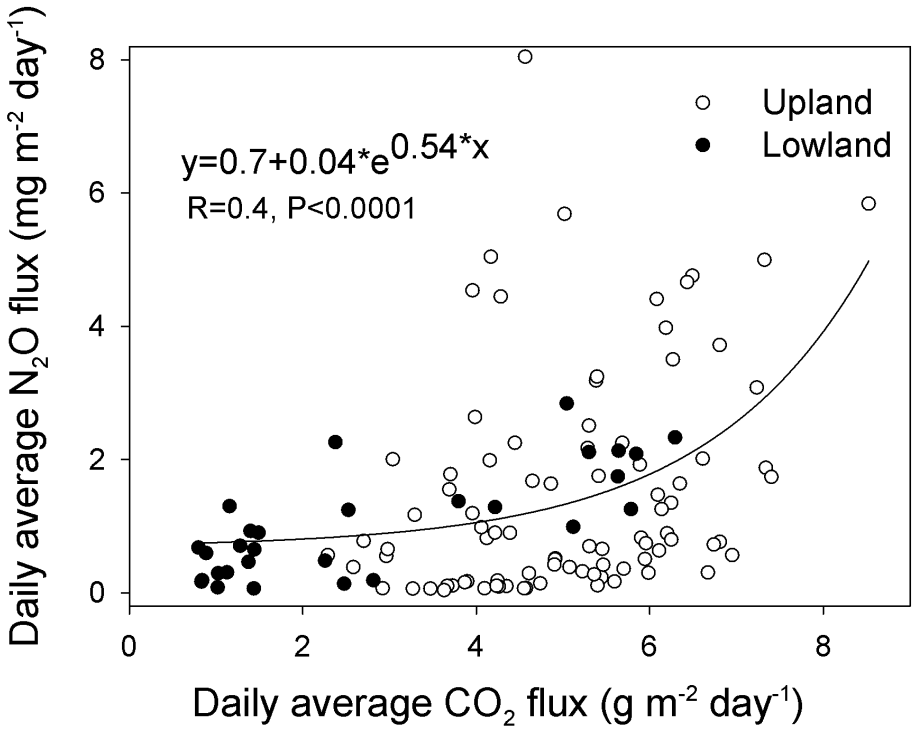

Fig. 2. N_2O daily average fluxes plotted versus daily average CO_2 fluxes measured in the upland and lowland sites. Plain line is the fit of data (R^2 = 0.57, P < 0.0001, DF = 58).

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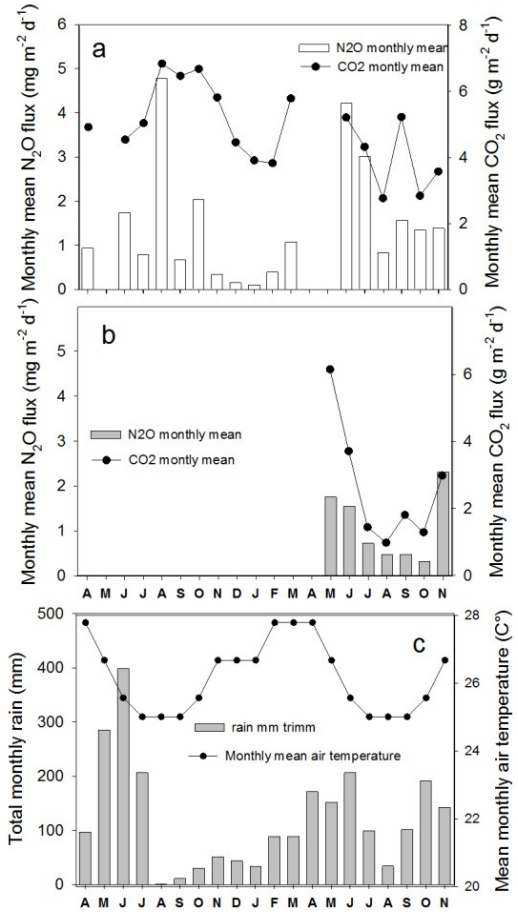

Fig. 3. Monthly mean N_2O flux (bars) and soil CO_2 flux (black dots) calculated for the upland **(a)** and lowland **(b)** area; total monthly rainfall and mean air temperature from TRMM dataset **(c)**.

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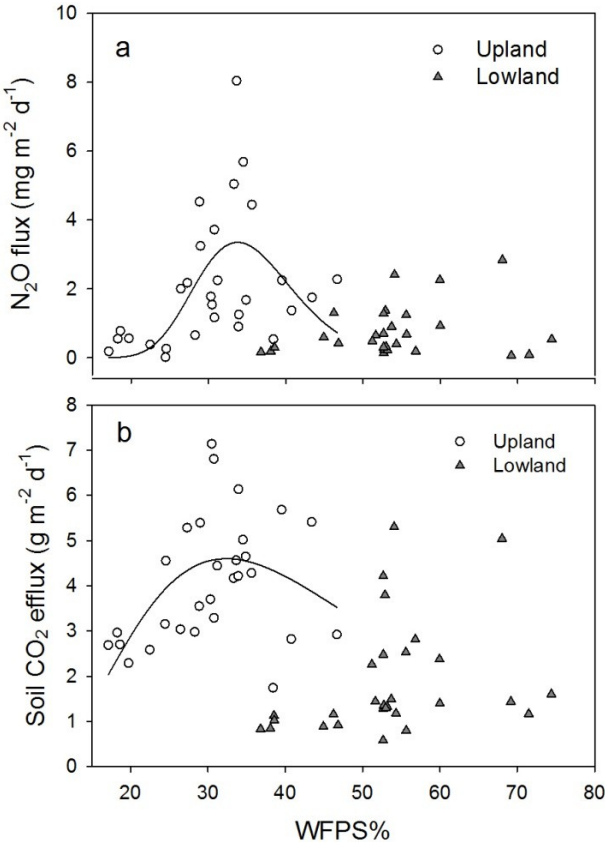

Fig. 4. N_2O and CO_2 daily average fluxes plotted versus values of soil WFPS% . The regression lines are lognormal fits of upland data set of N_2O (**a**: $R^2 = 0.31$, $P = 0.007$, DF = 29) and CO_2 (**b**: $R^2 = 0.26$, $P = 0.02$, DF = 29) fluxes.

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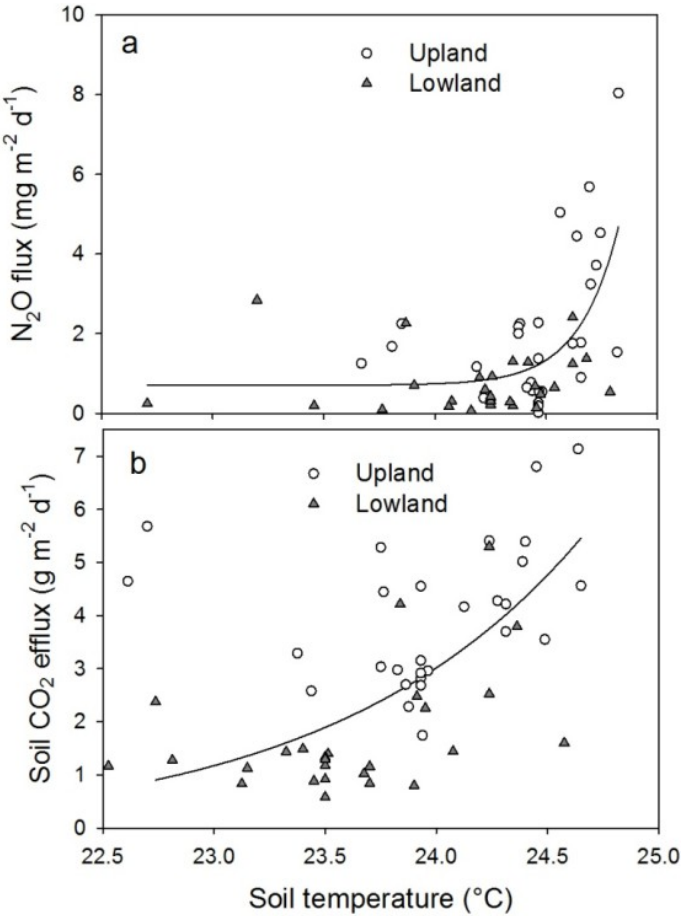

Fig. 5. N_2O and CO_2 daily average fluxes plotted versus soil temperature. The regression lines are exponential fit of both upland and lowland data sets. N_2O **(a)** $R^2 = 0.35$, $P < 0.0001$, DF = 57 and CO_2 **(b)** $R^2 = 0.46$, $P < 0.0001$, DF = 51.

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