

Soil-atmosphere exchange of N₂O, CH₄, and CO₂ and controlling environmental factors for tropical rain forest sites in western Kenya

Christian Werner,¹ Ralf Kiese,¹ and Klaus Butterbach-Bahl¹

Received 10 April 2006; revised 6 September 2006; accepted 10 October 2006; published 15 February 2007.

[1] N₂O, CH₄ and CO₂ soil-atmosphere exchange and controlling environmental factors were studied for a 3-month period (dry-wet season transition) at the Kakamega Rain forest, Kenya, Africa, using an automated measurement system. The mean N₂O emission was $42.9 \pm 0.7 \mu\text{g N m}^{-2} \text{ h}^{-1}$ (range: 1.1–324.8 $\mu\text{g N m}^{-2} \text{ h}^{-1}$). Considering the duration of dry and wet season the annual N₂O emission was estimated at $2.6 \pm 1.2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. Large pulse emissions of N₂O were observed after the first rainfall events of the wet season, and the magnitude of N₂O emissions steadily declined thereafter. A comparable trend in soil CO₂ emissions (mean: $71.8 \pm 0.3 \text{ mg C m}^{-2} \text{ h}^{-1}$) indicates that the rapid mineralization of litter accumulated during the dry period produced the high N₂O emissions at the start of the wet season. Manual N₂O emission measurements at four additional rain forest sites were comparable to those measured at the main site, whereas N₂O emissions measured at a regrowth site were significantly lower. Spatial differences in N₂O emissions could be explained by differences in soil texture and topsoil C:N-ratio (CO₂: subsoil C and N concentrations), whereas the temporal variability of N₂O and CO₂ emissions was primarily driven by soil moisture. Soils predominantly acted as sinks for CH₄ ($-56.4 \pm 0.8 \mu\text{g C m}^{-2} \text{ h}^{-1}$). For some chamber positions, episodes of net CH₄ release were observed, which could be due to high WFPS and/or termite activity. CH₄ fluxes were weakly correlated with soil moisture levels but showed no relation to temperature, texture, pH, carbon or nitrogen contents.

Citation: Werner, C., R. Kiese, and K. Butterbach-Bahl (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, doi:10.1029/2006JD007388.

1. Introduction

[2] Following carbon dioxide (CO₂) and methane (CH₄), and despite its low atmospheric concentration of 318.6 ppbv (global mean concentration 12/2004 [World Meteorological Organization (WMO), 2006]), nitrous oxide (N₂O) is the third most important radiatively active greenhouse gas, contributing approximately 6% to the total observed global warming at present [WMO, 2006]. Soils are the major source of N₂O emissions and the contribution of soils to the total atmospheric N₂O budget is estimated at 57% [Mosier et al., 1998]. A major part of these soil-based N₂O emissions originates from tropical rain forest regions, which are also considered to be the largest natural terrestrial source [Mosier et al., 1998; Kroeze et al., 1999]. On the basis of the available field measurements, the global contribution of tropical forest soils to the annual N₂O budget was estimated to range between 14 and 23% [Intergovernmental Panel on Climate Change, 2001; Mosier et al., 1998]. By applying a soil classification system related to substrate availability, the N₂O source strength of moist

tropical forest ecosystems was estimated to be in the range of 2.4–3.5 Tg N₂O-N a⁻¹ [Matson and Vitousek, 1990; Breuer et al., 2000]. However, it has to be stressed that these estimates are based on very simple empirical upscaling approaches.

[3] It is generally accepted that, despite their importance, N₂O emissions from tropical rain forest ecosystems are still poorly characterized [Serca et al., 1994; Breuer et al., 2000; Kiese et al., 2005]. Furthermore, the majority of N₂O measurements have been made in the Amazonian and Central American region [e.g., Matson et al., 1990; Steudler et al., 1991; Keller and Reiners, 1994; Riley and Vitousek, 1995; Verchot et al., 1999] and most of our knowledge is still based on a relatively small number of individual flux measurements (as described by Breuer et al. [2000]). The only data set of N₂O emissions from tropical rain forest soils of the African continent was published by Serca et al. [1994], who worked in the Congo region. To our knowledge, since then, no other attempt has been made to investigate N₂O emissions from tropical rain forest soils in Africa. The same partly applies to the Asian region, for which N₂O emission measurements have been published only in recent years [Ishizuka et al., 2002, 2005a, 2005b; Hadi et al., 2005; Hall et al., 2004; Purbopuspito et al., 2006]. However, the number of investigations is still small compared to the size and heterogeneity of the region. Long-term N₂O flux measurements of high (subdaily-daily)

¹Institute for Meteorology and Climate Research, Atmospheric Environmental Research, Karlsruhe Research Centre, Garmisch-Partenkirchen, Germany.



Figure 1. Location of the Kakamega National Forest Reserve in western Kenya.

temporal resolution have only been obtained from the Australian “wet tropics” [Breuer *et al.*, 2000; Butterbach-Bahl *et al.*, 2004; Kiese and Butterbach-Bahl, 2002; Kiese *et al.*, 2003] and recently from a seasonally dry rain forests of southwest China [Werner *et al.*, 2006].

[4] Advanced techniques, namely computational upscaling approaches, which link detailed geographic information systems (GIS) to mechanistic biochemical models like CASA [Potter *et al.*, 1993], CENTURY [Parton *et al.*, 1988] or PnET-N-DNDC [Li *et al.*, 2000; Stange *et al.*, 2000] to calculate regional or global emission inventories [Kesik *et al.*, 2005; Kiese *et al.*, 2005; Potter *et al.*, 1996] have the potential to further improve our current understanding of the soil contribution to the atmospheric budgets of the environmental important of soil-based emissions of trace gases such as N_2O , CH_4 and CO_2 [e.g., Davidson *et al.*, 1998; Li, 2000; Butterbach-Bahl *et al.*, 2001, 2004]. However, models operating on a daily time step (e.g., PnET-N-DNDC, DayCENT) require trace gas flux measurements of a high temporal resolution and from a variety of sites for adequate model testing [Kiese *et al.*, 2005].

[5] Suitable data sets for model testing are provided by automatic measurement systems that can measure soil-atmosphere greenhouse gas (GHG) fluxes in subdaily resolution. The high resolution and continuity of these flux measurements means that short-term variability in flux rates in response to changing environmental conditions can provide direct insights into the factors governing N_2O emissions from the soil to the atmosphere [Butterbach-Bahl *et al.*, 2004].

[6] In view of the fact that GHG fluxes in tropical rain forest systems of Africa have been poorly studied, we deliberately carried out our study in Kenya. Our main aim was to quantify the magnitude of soil N_2O emissions, but also CO_2 and CH_4 fluxes for sites with different land use histories (primary forest and artificial reforestation) in the defined region of the tropical rain forest of Kakamega, Kenya, during the beginning of the rainy season. Furthermore, we aimed to determine whether the factors governing the temporal and spatial variability of GHG fluxes in earlier studies, i.e., soil properties and soil moisture [e.g., Verchot *et al.*, 1999; Breuer *et al.*, 2000], are of the same importance in Kenya.

2. Methods

2.1. Site Description

[7] The Kakamega Forest National Park is located between $00^{\circ}8'N-00^{\circ}23'N$ and $34^{\circ}46'-34^{\circ}58'E$ at altitudes of 1500–1700 m a.s.l in western Kenya, approximately 70 km north of Kisumu (see Figure 1). It is considered to be the easternmost remnant of the equatorial Guinea-Congo-rain forest, which was isolated by changing climatic conditions, and in more recent times, intense anthropogenic land use conversion [Kokwaro, 1988]. At the beginning of the British colonial occupation, the Kakamega Forest was still a closed forest area covering approximately 25000 ha. However, the forest area diminished quickly from 23777 ha in 1933 to 8600 ha in the present day, with another 3450 ha in isolated forest fragments of Malava, Kisere, Ikuywa and Yala [Brooks *et al.*, 1999].

[8] The average annual precipitation from 1986 to 1997 was 1662 mm (see Figure 2). Most rainfall is concentrated in two distinct wet seasons ranging from March to June and August to October. The average monthly maximum tem-

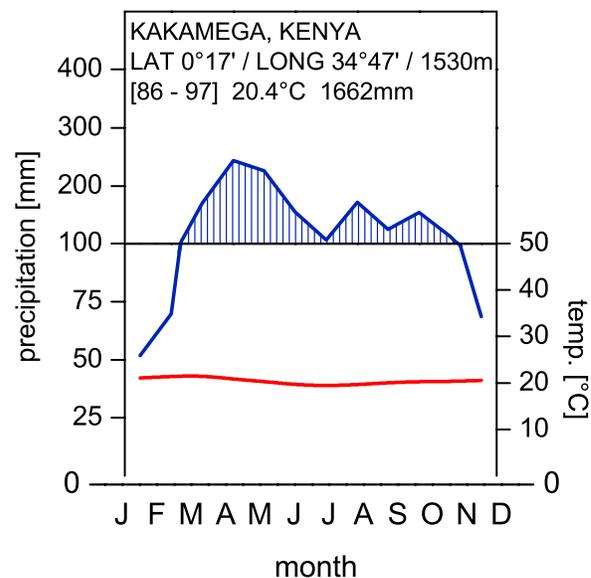


Figure 2. Long-term seasonality of rainfall and temperature at Kakamega climate station ($0^{\circ}17'N$, $34^{\circ}47'E$, 1530 m a.s.l.), Kenya (1986–1997). Hatched areas indicate a surplus of rainfall as compared to potential evapotranspiration.

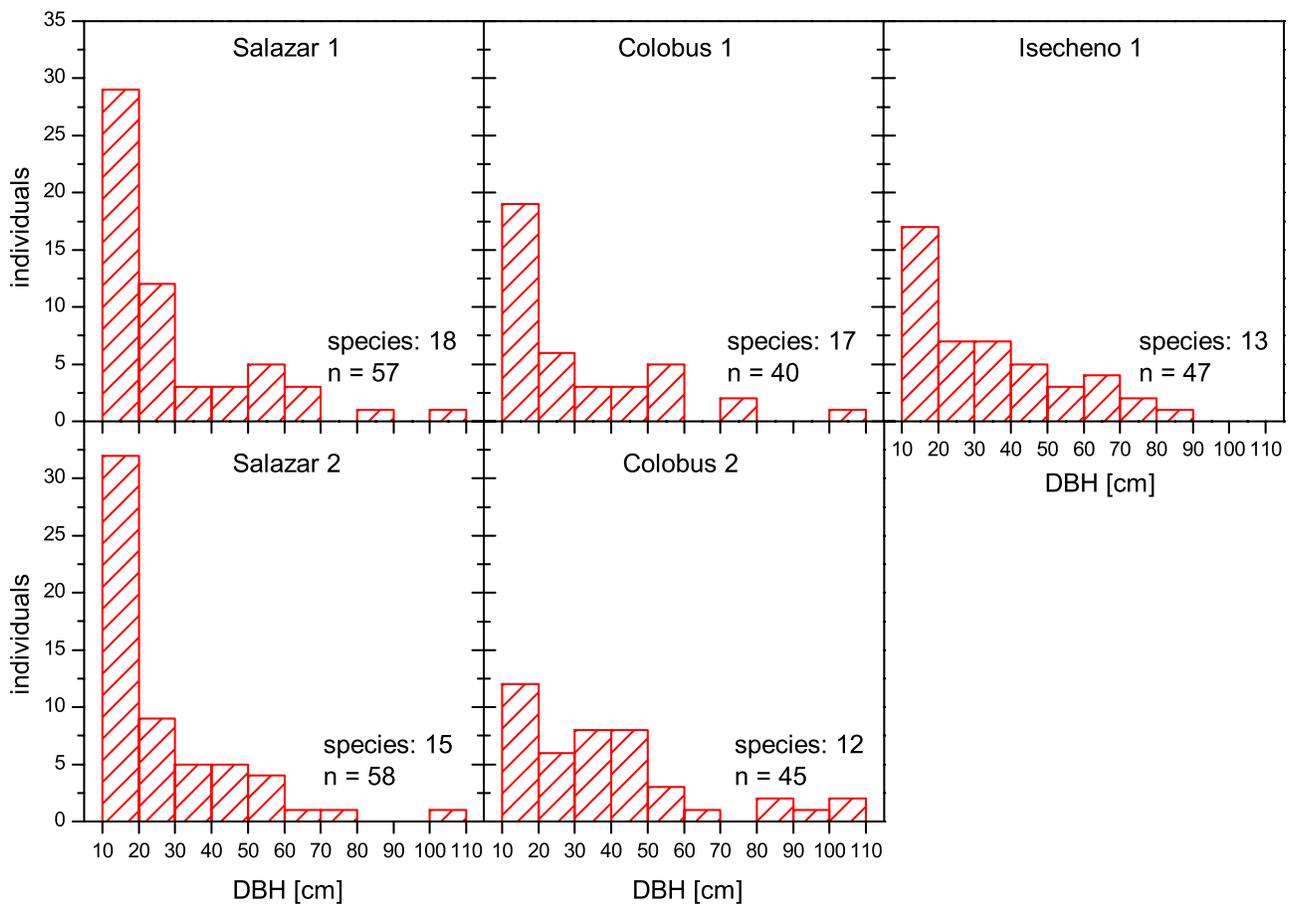


Figure 3. Frequency histograms of stem diameters at breast height (DBH) at the five rain forest plots and the number of tree species encountered (plot size is 25 × 25 m).

perature is 24.9°C, the monthly minimum temperature is 15.4°C. Our field campaign was conducted from 4 April 2004 to 18 June 2004, spanning a transition from dry into wet season. The mean daily air temperature during the campaign was 17.5°C and the mean daily minimum and maximum temperatures were 13.7°C and 23.0°C, respectively. During our field measurements, soil moisture was measured continuously at the site Salazar 1 using three stationary TDR probes (integrating soil depth from 0 to 10 cm). Soil temperatures in the litter layer, at 5 cm and 15 cm depth were recorded. Precipitation at a nearby open site was measured with a rain gauge (0.2 mm tipping bucket rain gauge; Campbell Scientific/USA).

[9] At the study site, deep clay-loamy soils developed from precambrian Gneiss and sedimentary rock formations (especially claystone) can be found [Round-Turner, 1994; Kamoni, 2004]. The most dominant soil types of this area are Luvisols (on alluvial base material), Lixisols (deeply weathered, leached and poor in nutrients), porous Cambisols of fine to medium texture and groundwater table affected Gleysols [Kamoni, 2004].

[10] The forest is structured in four canopy layers (emergent layer, canopy layer, understory layer and herb layer). In general, the canopy is relatively open and the stands reach 45 m in height [Fashing et al., 2004]. Intensive forest use in modern times has altered the structure of the forest dramatically [Kiama and Kiyiapi, 2001]. Because of selective

logging, trees with diameters at breast height (DBH) >100 cm are rare. The southern part of the forest (Isecheno section) has experienced greatest logging operations and exploitation by local communities, while the northern section (Colobus, Salazar) came under the protection of the Kenyan Wildlife Service and has altered less since logging was banned in 1982 [Kiama and Kiyiapi, 2001].

[11] In order to cover differences in forest structure, as well as difference in soil properties, we installed six permanent sampling plots in the Kakamega National Forest. The main measurement site Salazar 1 (S1) was set up in the northern section of the Kakamega Forest, approximately four kilometers southwest of the park entrance. A second site (Salazar 2, S2) was established 250 m away and was sampled manually. In addition, two sites Colobus 1 (C1) and Colobus 2 (C2) near the northern park entrance and two sites Isecheno 1 (I1) and Isecheno 2 (I2) in the southern section of the Kakamega forest were established for manual chamber measurements of N₂O emissions.

[12] Figure 3 illustrates the frequency distribution of stem diameter breast height (DBH) in 25 m × 25 m plots at each measurement site. For the survey, all trees with a DBH >10 cm were registered and classified. Despite the small sample plot area, the differences in tree numbers and their frequency distribution illustrates the differences in vegetation composition between the five rain forest sites. Trees with small stem diameters dominate the forest at the sites S1

Table 1. Measurement Setup and Soil Characteristics of the Measurement Sites (\pm Standard Error)^a

	Salazar 1	Salazar 2	Colobus 1	Colobus 2	Isecheno 1	Isecheno 2
Sampling	automated	manual	manual	manual	manual	manual
Frequency	10–16 d ⁻¹	2–3 week ⁻¹				
Litter layer						
PH	6.8 \pm 0.1 (a,b)	6.6 \pm 0.3 (a,b,c)	7.0 \pm 0.2 (b,d)	6.5 \pm 0.1 (b,c)	7.3 \pm 0.0 (d)	6.3 \pm 0.1 (c)
C:N ratio	20.5 \pm 1.0 (a)	18.0 \pm 1.5 (a,b)	18.3 \pm 1.8 (a,c)	14.9 \pm 0.5 (b,c)	21.0 \pm 0.8 (a)	39.4 \pm 1.8 (d)
Corg, %	42.4 \pm 1.3 (a)	27.2 \pm 5.2 (b)	35.0 \pm 3.4 (c)	23.7 \pm 0.6 (b)	45.4 \pm 0.9 (a)	45.6 \pm 1.3 (a)
Ntotal, %	2.09 \pm 0.07 (a)	1.52 \pm 0.3 (b,c)	1.92 \pm 0.03 (a,b)	1.59 \pm 0.02 (b)	2.17 \pm 0.1 (a)	1.16 \pm 0.05 (c)
Topsoil (Ah; 0–5 cm)						
PH	6.3 \pm 0.1 (a)	5.6 \pm 0.1 (b)	7.2 \pm 0.0 (c)	5.9 \pm 0.1 (b)	6.4 \pm 0.3 (a)	4.7 \pm 0.1 (d)
C:N ratio	11.7 \pm 0.2 (a)	11.9 \pm 0.6 (a)	11.9 \pm 0.2 (a)	11.2 \pm 0.2 (a)	11.0 \pm 0.3 (a)	14.8 \pm 0.3 (b)
Corg, %	11.6 \pm 1.2 (a)	10.0 \pm 2.3 (a)	20.0 \pm 1.3 (b)	10.6 \pm 0.7 (a)	14.1 \pm 1.1 (a)	7.9 \pm 0.4 (c)
Ntotal, %	0.98 \pm 0.09 (a,b)	0.83 \pm 0.15 (b,c)	1.68 \pm 0.12 (d)	0.95 \pm 0.05 (a,b)	1.27 \pm 0.11 (a)	0.53 \pm 0.03 (c)
Subsoil (B; 5–20 cm)						
PH	5.7 \pm 0.1 (a)	4.9 \pm 0.1 (b)	6.7 \pm 0.1 (c)	5.7 \pm 0.1 (a)	6.2 \pm 0.2 (d)	4.7 \pm 0.1 (b)
C:N ratio	10.4 \pm 0.3 (a)	9.4 \pm 0.4 (b)	10.0 \pm 0.2 (a,b)	9.2 \pm 0.1 (b)	9.6 \pm 0.2 (a,b)	12.9 \pm 0.1 (c)
Corg, %	3.5 \pm 0.2 (a)	2.3 \pm 0.3 (b)	6.3 \pm 0.4 (c)	4.0 \pm 0.3 (a)	4.0 \pm 0.3 (a)	3.9 \pm 0.2 (a)
Ntotal, %	0.34 \pm 0.02 (a,b)	0.25 \pm 0.02 (c)	0.63 \pm 0.04 (d)	0.44 \pm 0.03 (e)	0.41 \pm 0.02 (b,e)	0.31 \pm 0.01 (a,c)
Texture	clay loam	clay	clay	clay	clay	clay
Sand, %	43	38	6	19	2	4
Silt, %	23	19	31	25	42	34
Clay, %	34	43	63	56	56	62

^aThe letters in parentheses indicate significant differences between the individual sites (ANOVA analysis; $p < 0.05$).

and S2, while the vegetation structure at the sites C1, C2 and I1 represent more mature forest systems. Species composition is complex at all sites, but the upper canopy is generally dominated by *Ficus sur/thorni*, *Autiaris toxicaria*, *Croton megalocarpus*, *Funtumia africana* and *Strychnos usambarensis*. Since site I2 was reforested in the late 1980s, only two tree species are present, tree height does not exceed seven meters and DBH is generally <10 cm.

[13] At the end of the measuring campaign, all sites and all chamber positions (see below) were sampled for soil and aboveground litter probes ($n = 32$). The total carbon and nitrogen content was determined by measuring the gaseous nitrogen and carbon loss (N_2 , CO_2) from combustion of dry samples at 950°C under high oxygen levels by gas chromatography. Soil texture was classified by wet sieving (sand fraction) and sedimentation (silt and clay fractions) after the destruction of organic components and pH was measured by suspending dried soil samples with 0.01 mol $CaCl_2$ solution. All analyses were conducted by the Agricultural Laboratory Dr. Janssen GmbH (Gillersheim/Germany).

[14] All soils encountered at the manually sampled sites were classified as clay soil (43–63% clay). Only the site S1, with a clay fraction of 34%, was classified as a clay loam (see Table 1). Notably, sites I1, I2 and C1 had very low fractions of sand ($\leq 6\%$). The pH values of topsoil (0–5 cm) and subsoil (5–20 cm) varied considerably between the different sites (Table 1).

[15] The analysis of topsoil samples showed that most acidic conditions are present at site I2 (pH 4.7), while the highest pH values were recorded for site C1 (pH 7.2) (topsoil pH: I2 < S2 \ll C2 \ll S1 < I1 \ll C1; <: smaller; \ll significantly smaller; $p < 0.05$). Maximum subsoil pH values of 6.7 were measured at site C1 and the lowest values of 4.7 and 4.9 were recorded for subsoil samples of I2 and S2, respectively (subsoil pH: I2 < S2 \ll S1, C2 \ll I1 \ll C1; $p < 0.05$). In general, the topsoil pH was 3–14% higher for the secondary and primary forest sites, while no difference between the two soil strata was found at the regrowth site Isecheno 2.

[16] The carbon content in the topsoil was high, and reached 20.0% at site C1. Lowest carbon concentrations were measured at site I2 (7.9%). The concentration of the other topsoil samples ranged between 10.0 and 14.1% (SOC topsoil: I2 \ll S2 < C2 < S1 < I1 \ll C1; $p < 0.05$). Subsoil SOC concentrations were considerably lower, but still ranged from 2.3–6.3% (SOC subsoil: S2 \ll S1 < I2 < C2, I1 \ll C1; $p < 0.05$). Total nitrogen concentrations in both soil strata were significantly higher at site C1 as compared to the other sites (total nitrogen subsoil: S2 < I2 < S1 < I1 < C2 \ll C1; in topsoil: I2 < S2 < C2 < S1 < I1 \ll C1; $p < 0.05$). The nitrogen content in the topsoil (0.53%) at site I2 was less than one third of the richest topsoil at site C1. Surprisingly, the comparison of the carbon-to-nitrogen ratio (C:N-ratio), which can be used as a scalar for soil fertility, did not follow the previous observations. The C:N-ratio of topsoil and subsoil samples, and thus substrate availability, of the nutrient rich site C1 did not differ significantly from the sites S1, S2, C2 and I1 (topsoil: 11.0–11.9; subsoil: 9.2–10.4). However, a significantly wider C:N-ratio was measured for the topsoil (14.8) and subsoil (12.9) at the regrowth site I2 (Table 1). Although the sampling of litter inherits large uncertainties due to its heterogeneous nature and irregular pattern, the analysis of its C:N ratio may allow some conclusions on nutrient turnover dynamics. Table 1 shows that there exists a fundamental difference between the litter properties of the rain forest sites S1, S2, C1, C2 and I1 and the regrowth site I2, which was artificially reforested with hardwood tree species (*grivellia robusta* (exotic), *harungana madagascariensis*). While carbon and nitrogen concentrations in the litter samples of the forest sites vary greatly, their C:N-ratios only range between 14.9 and 21.0. In contrast, the litter C:N-ratio of the regrowth site was approximately double (39.4) that in the other sites.

2.2. Measurements of Soil N_2O , CH_4 , and CO_2

[17] In order to continuously measure trace gas emissions, a fully automated gas sampling system was installed at the main field site (Salazar 1). The static chamber technique

as described by, e.g., *Breuer et al.* [2000] was applied in this field campaign. Six sampling chambers (four $50 \times 50 \times 15$ cm chambers and two $30 \times 30 \times 15$ cm chambers) were installed at randomized positions in a radius of approximately 30 m around the automated sampling system. The chambers were connected to the system by $1/8''$ Teflon tubes and mounted on top of stainless steel frames which were driven approximately 10 cm into the soil. The lids of the chambers were opened and closed automatically by pneumatic cylinders [see, e.g., *Breuer et al.*, 2000].

[18] The sampling system, which included a pump, valves and mass flow rate regulators, allowed us to sample the chambers alternately in an automated cycle. Sampled air from the individual chambers was injected automatically on a GC system (Texas Instruments SRI 8610C, Torrance/United States). We used a ^{63}Ni electron capture detector (ECD) for N_2O detection, whereas CH_4 was measured by a flame ionization detector (FID). CO_2 fluxes were recorded with an infrared CO_2 detector (BUSE Guardian II, Buse Anlagenbau/Germany). Details of the sampling system are given by *Breuer et al.* [2000] and *Kiese and Butterbach-Bahl* [2002]. The detection signals of the analytical devices as well as the readings of soil moisture probes, temperature probes and a rainfall gauge were stored on a laptop computer which also controlled the automated sampling system. The equipment electrical power was supplied by two portable generators. The analytical system was recalibrated on a hourly basis by injecting standard gases (Messers Griesheim/Germany).

[19] The six chambers were sampled in two blocks allowing for the ventilation of three chambers while the other three chambers were sampled. Gas concentration measurements were obtained every nine minutes for each chamber. Flux rates were calculated from the linear increase or decrease of gas concentrations ($n = 4$) of each chamber. The chambers were moved every week to a nearby alternative position to minimize a possible moisture and litter deficit inside the chambers due to the shading by closed lids [see also *Kiese et al.*, 2003]. To avoid soil compaction and its effect on trace gas exchange, all twelve chamber sites and a surrounding safety area were marked and entry was not permitted. The automated system potentially allowed us to record 16 fluxes for each chamber in one day. However, the analysis of manually obtained air samples from the five other sites led to a sampling gap in the late morning hours.

[20] A manual sampling scheme was applied at the sites S2, C1, C2, I1 and I2. We permanently installed four round plastic chambers with a diameter of 36 cm at each of those sites (chamber height 10 cm). The chambers were closed with gas-tight lids prior to the sampling. After five minutes the first 10 mL of chamber air was drawn with a syringe, followed by three more samples taken at ten minute intervals. Sampling took place between 5 and 11 am and the samples were analyzed immediately afterward at site S1. Manual sampling sites were probed at least twice a week (grouping: S2/C1/C2, I1/I2). As for the automated chambers, flux rates were calculated from the linear increase or decrease with time of gas concentrations in the headspace of each chamber.

2.3. Statistical Analysis

[21] The statistical software packages SPSS 8.0 (SPSS Inc., Chicago/United States) and Origin 7.0 (OriginLab Corporation, Northampton/USA) were used for linear correlation analysis, multiple linear regression analysis ("stepwise" approach) and ANOVA testing (LSD method) of N_2O , CH_4 and CO_2 fluxes and the measured environmental parameters.

3. Results

3.1. N_2O Emissions

[22] For each chamber position at site S1, 243 to 347 separate N_2O flux measurements were obtained during the field study. The mean N_2O emission of all 3652 individual flux measurements at this site, covering the period 5 April to 18 June 2004, was $42.9 \pm 0.7 \mu\text{g N m}^{-2} \text{h}^{-1}$. The N_2O emission varied between 1.1 and $324.8 \mu\text{g N m}^{-2} \text{h}^{-1}$, and a distinct temporal gradient was observed (see Figure 4). During the first two weeks of measurements, two N_2O emission pulses were observed (pulse 1: 4–10 April; pulse 2: 12–16 April), driven by the first major rainfalls (pulse 1: $\Sigma 58$ mm; pulse 2: $\Sigma 61$ mm) after the dry season. During this period mean N_2O emissions ranged from 30.1 to $162.0 \mu\text{g N m}^{-2} \text{h}^{-1}$. At chamber positions 2a and 3b fluxes $>310 \mu\text{g N m}^{-2} \text{h}^{-1}$ were measured (Table 2). After these initial peak emission events the mean N_2O emission at site S1 gradually decreased from approximately $70 \mu\text{g N m}^{-2} \text{h}^{-1}$ to $10 \mu\text{g N m}^{-2} \text{h}^{-1}$ toward the end of the measurement period. The spatial heterogeneity (indicated by the size of error bars) of N_2O fluxes at the site S1 also decreased gradually as water filled pore space (WFPS) decreased and the magnitude of N_2O emissions decreased also (see Figure 4).

[23] Figure 4 shows that the temporal variability in the magnitude of N_2O emissions was mainly driven by changes in soil moisture rather than by changes in temperature. However, if we consider only N_2O emissions when the WFPS was in the range of 55–65% WFPS and, thus, under comparable soil moisture conditions, we can demonstrate an exponential decrease in N_2O emission levels over time ($r^2 = 0.66$; Figure 5). This decrease indicates that, with the progression of the rainy season, N_2O emissions become substrate limited. Since the large N_2O emission pulse events at the "break of rains" most likely occurred during a period of rapid litter mineralization (accumulated during the dry season), and therefore non-nitrogen-limiting conditions, we excluded this period from our analysis of the moisture dependencies of N_2O emissions (Figure 6). Using an optimum function (Figure 6), 66% of the variability of the N_2O emissions could be explained by changes in soil moisture. When the WFPS ranged from 40 to 50%, N_2O emissions only slightly increased from approximately 10 to $15 \mu\text{g N m}^{-2} \text{h}^{-1}$, whereas above a 50% WFPS, N_2O emissions strongly increased to a high of $75 \mu\text{g N m}^{-2} \text{h}^{-1}$ at an optimum WFPS of 65%. With further increases in soil moisture N_2O emissions tend to decrease to around 30 to $45 \mu\text{g N m}^{-2} \text{h}^{-1}$.

[24] A multiple nonlinear regression analysis (N_2O emission as function of WFPS and soil temperature) revealed that changes in soil temperature (observed $\Delta T_{5\text{cm}} = 3.1^\circ\text{C}$; $T_{15\text{cm}} = 2.1^\circ\text{C}$) could improve the explanation capacity of the variability of N_2O emissions only by $<1\%$.

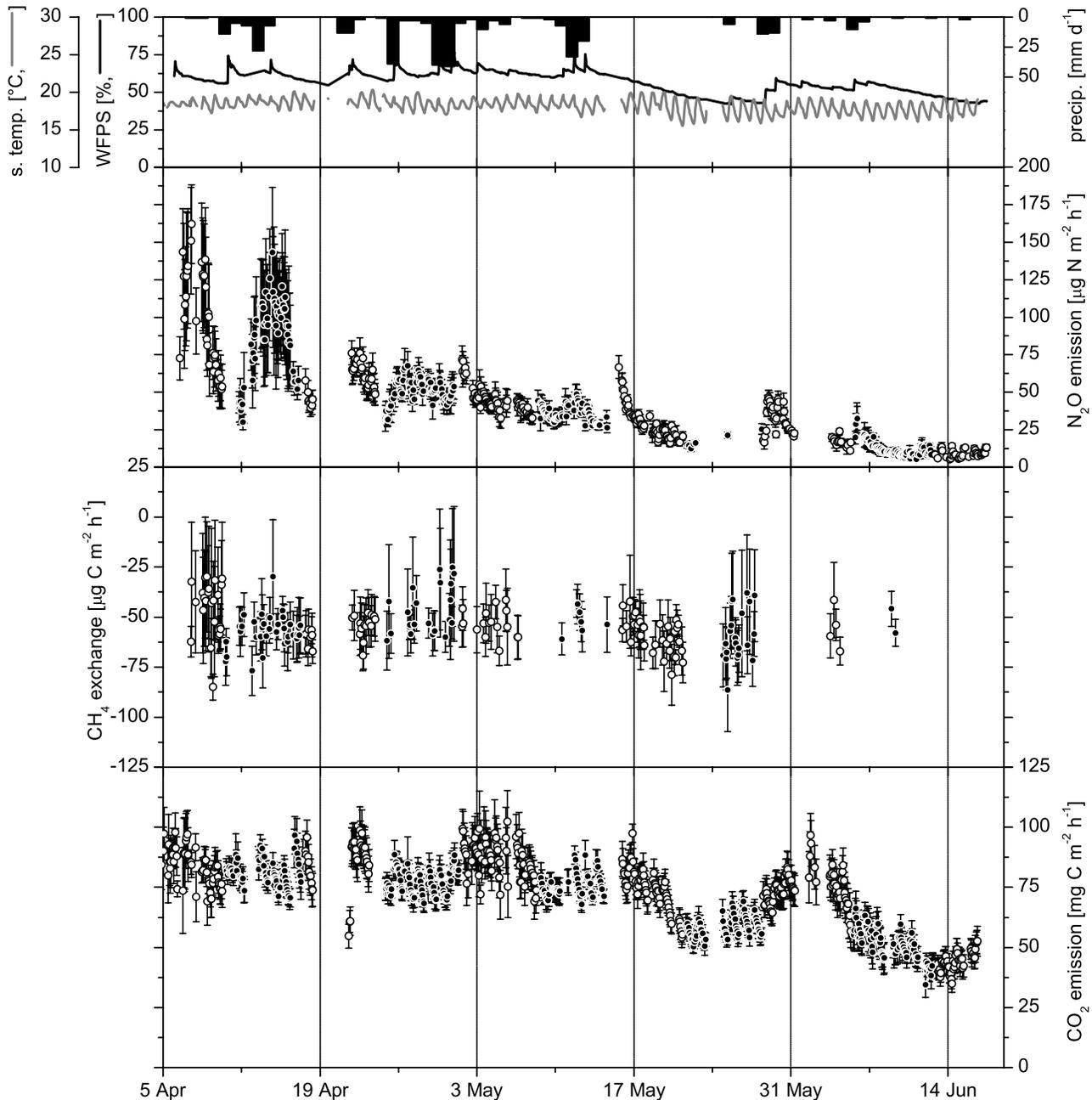


Figure 4. Mean flux rates of N_2O , CH_4 and CO_2 at the Salazar 1 site. Alternating chamber positions are marked by open and solid circles, for positions a and b, respectively. In addition, hourly soil moisture (water filled pore space (WFPS)), hourly soil temperature at 5 cm depth and daily precipitation are given.

Nitrous oxide emissions derived by manual sampling at the other rain forest sites S2, C1, C2 and I1 were comparable with those measured at the main site S1 (see Figure 7). Mean N_2O emissions ranged from 18.7 ± 2.2 to $32.1 \pm 6.5 \mu\text{g N m}^{-2} \text{h}^{-1}$, whereas mean N_2O emission of S1 site was $35.4 \pm 1.0 \mu\text{g N m}^{-2} \text{h}^{-1}$ when calculations are based on matched sampling dates and times (Table 3). Compared to the other four rain forest sites (S1, S2, C2, I1), significantly lower N_2O emissions were recorded at site C1. N_2O fluxes at the regrowth site I2 were, with a mean of $8.8 \pm 2.9 \mu\text{g N m}^{-2} \text{h}^{-1}$, significantly lower than those of all rain forest sites ($p < 0.05$; see Table 3).

Sporadically, we even observed a weak N_2O uptake at site I2 (Table 3). Figure 7 illustrates that manually measured N_2O emissions varied substantially. Notably, for sites S2 and I1 the use of an arithmetic mean may lead to an overestimation of N_2O emissions and the use of the median may be more appropriate for comparing differences in N_2O emissions between different chamber positions at a given site (Figure 7). By analyzing the N_2O emissions of the individual chamber position, a pronounced spatial variability of N_2O emissions can be observed (Figure 7). For example, maximum flux rates at site S1 ranged from 82.2 – $324.8 \mu\text{g N m}^{-2} \text{h}^{-1}$ and significant differences of

Table 2. Minimum, Maximum, and Average N₂O, CH₄ and CO₂ Flux Rates Recorded Automatically at the Main Sampling Site, Salazar 1^a

Chamber	Position	Minimum	Maximum	Mean ± SE	<i>n</i>	<i>c_v</i> , %
<i>N₂O Emission, μg N m⁻² h⁻¹</i>						
1	a	4.7	104.8	34.9 ± 1.0 (a)	331	54.0
1	b	7.5	113.7	37.2 ± 1.1 (a)	346	52.8
2	a	1.2	311.3	34.7 ± 3.0 (a)	291	147.9
2	b	1.2	82.2	26.5 ± 1.0 (b)	264	61.3
3	a	1.1	288.9	52.5 ± 2.8 (c)	340	99.6
3	b	3.8	324.8	67.0 ± 3.9 (d)	333	106.0
4	a	3.8	187.6	51.3 ± 2.0 (c)	297	65.6
4	b	3.8	93.4	37.2 ± 1.3 (a)	243	53.6
5	a	1.8	138.7	38.1 ± 1.4 (a)	281	61.9
5	b	3.1	241.1	56.7 ± 3.0 (c)	297	92.1
6	a	2.5	181.7	38.7 ± 1.4 (a)	324	66.2
6	b	1.5	90.9	34.3 ± 1.2 (a)	290	59.7
Total		1.1	324.8	42.9 ± 0.7	3637	93.8
<i>CH₄ Exchange, μg C m⁻² h⁻¹</i>						
1	a	-102.0	-15.0	-46.6 ± 1.4 (a)	94	29.0
1	b	-102.4	-21.8	-46.5 ± 1.0 (a)	89	20.5
2	a	-89.7	-15.6	-42.0 ± 1.2 (b)	154	35.3
2	b	-69.4	-12.2	-38.9 ± 0.9 (b)	143	26.5
3	a	-87.8	99.7	-2.6 ± 6.1 (c)	60	1855.4
3	b	-42.5	86.7	24.9 ± 5.8 (d)	30	127.6
4	a	-146.9	-26.4	-87.4 ± 1.1 (e)	194	17.8
4	b	-135.8	-45.3	-88.1 ± 1.1 (e)	173	16.0
5	a	-126.5	36.4	-58.2 ± 1.5 (f)	135	30.9
5	b	-127.1	-20.0	-61.5 ± 1.3 (f)	144	25.0
6	a	-107.1	-32.6	-57.5 ± 1.0 (f)	140	20.4
6	b	-103.6	-25.5	-51.9 ± 1.0 (a)	102	20.1
Total		-146.9	99.7	-56.4 ± 0.8	1458	52.1
<i>CO₂ Emission, mg C m⁻² h⁻¹</i>						
1	a	25.9	85.9	58.7 ± 0.5 (a)	412	16.2
1	b	39.7	94.7	64.1 ± 0.5 (b)	400	16.3
2	a	n.d.	n.d.	n.d.	n.d.	n.d.
2	b	n.d.	n.d.	n.d.	n.d.	n.d.
3	a	26.9	155.0	86.4 ± 1.1 (c)	418	26.7
3	b	31.1	126.6	82.7 ± 0.7 (d)	408	17.8
4	a	32.9	129.2	88.1 ± 1.0 (c)	340	20.2
4	b	22.3	114.8	60.6 ± 0.8 (a)	376	26.3
5	a	39.8	114.3	78.8 ± 0.8 (e)	365	20.1
5	b	38.8	105.4	68.6 ± 0.7 (f)	380	21.3
6	a	26.0	114.3	64.5 ± 0.8 (b)	390	25.3
6	b	28.9	100.6	67.0 ± 0.7 (f)	394	21.1
Total		22.3	155.0	71.8 ± 0.3	3883	26.2

^aThe letters in parentheses indicate significant differences between the individual sites (ANOVA analysis; $p < 0.05$). Because of technical difficulties, no CO₂ emission data (n.d.) could be obtained for the chamber positions 2a and 2b (SE, standard error; *c_v*, coefficient of variation).

mean N₂O emissions between individual chamber positions ($n = 12$; 6 chambers times 2 positions [a and b]) were detected using ANOVA analysis ($p < 0.05$; see superscripts in Table 2). With an average emission of $67.0 \pm 3.9 \mu\text{g N m}^{-2} \text{h}^{-1}$, highest N₂O emissions at site S1 were observed at position 3b. Within the remaining eleven positions of site S1, elevated N₂O emissions were measured at the positions 3a, 4a, and 5b. Lowest N₂O emissions were recorded at position 2b ($26.5 \pm 1.0 \mu\text{g N m}^{-2} \text{h}^{-1}$) and the N₂O emissions of the other positions were on a medium level (Table 2).

[25] In order to explain the observed intra and intersite variability of N₂O emissions (see Figure 7), “stepwise” multiple linear regression models using N₂O emissions (dependant variable), soil texture, total soil carbon, total soil nitrogen, C:N-ratio and pH of litter, topsoil and subsoil (independent variables) were performed. The first model aimed at explaining differences in N₂O emissions between

the individual chamber positions ($n = 31$, chamber 3 of site I2 was excluded because of an insufficient number of flux rate measurements). To avoid an overrepresentation of S1 emission measurements, we restricted the N₂O emission measurements of the automated system at S1 to those dates that matched sampling at the sites S2, C1, C2, I1 and I2. The resulting multiple linear regression model, using sand fraction and the topsoil C:N-ratio, explained 56% of the spatial variability of N₂O emissions across chamber positions and sites ($r^2 = 0.56$; $p < 0.001$, Table 4). Other parameters such as total SOC or pH were excluded from the model because of insignificant contributions. While higher fractions of sand were positively correlated with increased N₂O emissions, topsoil C:N-ratio showed a negative correlation.

[26] The second model was developed to explain differences in mean N₂O emissions between the six sites. For this model only mean values of soil and litter properties

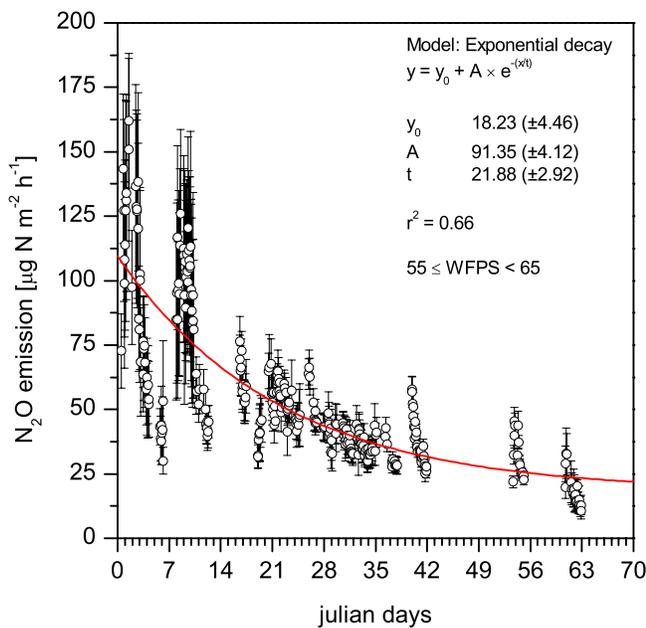


Figure 5. Temporal trend of N_2O emissions during the field campaign using only measurements with a water filled pore space (WFPS) between 55 and 65%. Mean values \pm SE are shown.

were used as independent variables. The resulting model was again a two parameter multiple regression model with soil texture (clay content) and topsoil C:N ratio, both negatively correlated with N_2O emissions, explaining 96% of the site variability in N_2O emissions ($r^2 = 0.96$; $p < 0.01$, Table 4).

3.2. CH_4 Exchange

[27] Soil-atmosphere exchange of CH_4 was only measured at the site S1. At this site, 1458 CH_4 flux measurements were recorded (negative values indicate uptake of atmospheric CH_4 by soils). In general, soil CH_4 uptake was detected for eleven of the twelve chamber positions (Table 2). However, at two chamber positions sporadic net CH_4 emissions were observed (see Table 2). The mean CH_4 exchange rate of the entire measurement campaign ranged from -38.9 to $-88.1 \mu\text{g C m}^{-2} \text{h}^{-1}$, excluding episodes of CH_4 emission. The temporal variation during the entire campaign was low for the individual chamber positions (c_v : 17.8–35.4%). The higher standard errors and coefficients of variation for the chamber positions 3a and 3b are resulting from the fact that these positions temporally switch between being a sink or a source for atmospheric CH_4 . Methane emissions at position 3a were mainly observed from 7–10 April, while CH_4 emissions were detected at position 3b throughout the observation period. Methane uptake was only measured at position 3b during the last weeks of our field campaign.

[28] Mean CH_4 exchange rates showed no clear temporal variability throughout the field campaign (Figure 4). A weak negative correlation between soil moisture and CH_4 uptake rates was observed ($r^2 = 0.18$; $p < 0.01$, data not shown), indicating that CH_4 uptake is higher for lower soil moisture conditions. Soil temperature did not correlate with CH_4

fluxes ($r^2 < 0.05$; $p < 0.01$, data not shown). Using a multiple linear regression of soil temperature and soil moisture to explain the temporal variations in CH_4 fluxes did not result in a significant relationship. Similarly, a multiple linear regression analysis (“stepwise” approach) of mean CH_4 fluxes and soil properties of the individual chambers at site S1 did not return a valid model describing the observed heterogeneous CH_4 gas exchange rates.

3.3. CO_2 Emissions

[29] As for CH_4 fluxes, soil respiration rates were also only recorded at site S1. A total of 3883 soil respiration fluxes were recorded during the measurement period. The maximum soil CO_2 emission was $155.0 \text{ mg C m}^{-2} \text{h}^{-1}$. The mean soil CO_2 emission values for individual chamber positions ranged from 58.7 to $88.1 \text{ mg C m}^{-2} \text{h}^{-1}$ (see Table 2). Figure 4 shows that soil CO_2 emissions decreased during the campaign. The mean soil CO_2 emissions remained relatively stable at emission levels of approximately 70 – $100 \text{ mg C m}^{-2} \text{h}^{-1}$ until the beginning of May. After this period, with decreasing soil moisture levels, soil respiration rates gradually declined. The precipitation events at the end of May stimulated CO_2 emissions again for a few days, but further reductions in soil moisture in the following weeks resulted in decreasing soil respiration values below $50 \text{ mg C m}^{-2} \text{h}^{-1}$ (Figure 4).

[30] However, as indicated by the low c_v -values (16.2–26.7%) of the ten measured chamber positions (for chamber positions 2a and 2b we failed to obtain CO_2 flux measurements for technical reasons), the general temporal variation in CO_2 flux during the campaign was lower than the measured for N_2O . Furthermore, the differences in soil respiration between the chamber positions did not vary

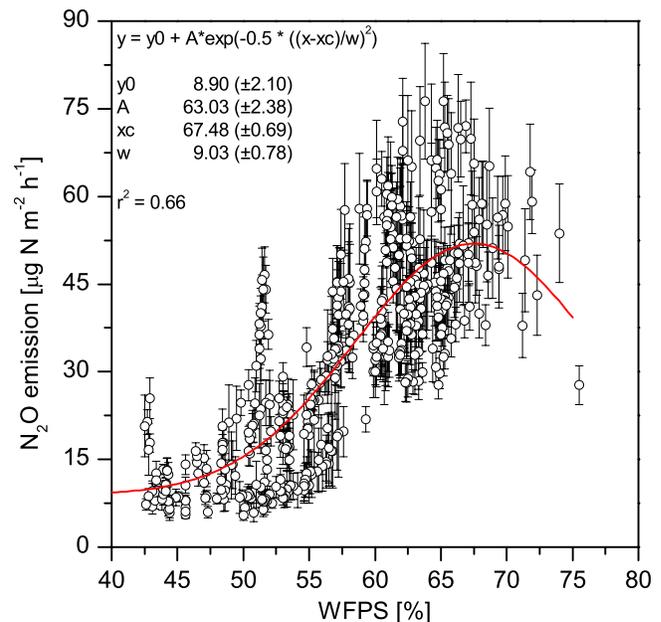


Figure 6. Correlation of water filled pore space (WFPS) and N_2O emissions at the Salazar 1 site (six chamber means; bars indicate standard error). N_2O emissions from 5 to 16 April were excluded as the response of N_2O emissions to the “break of rains” was more pronounced than for these later measurements.

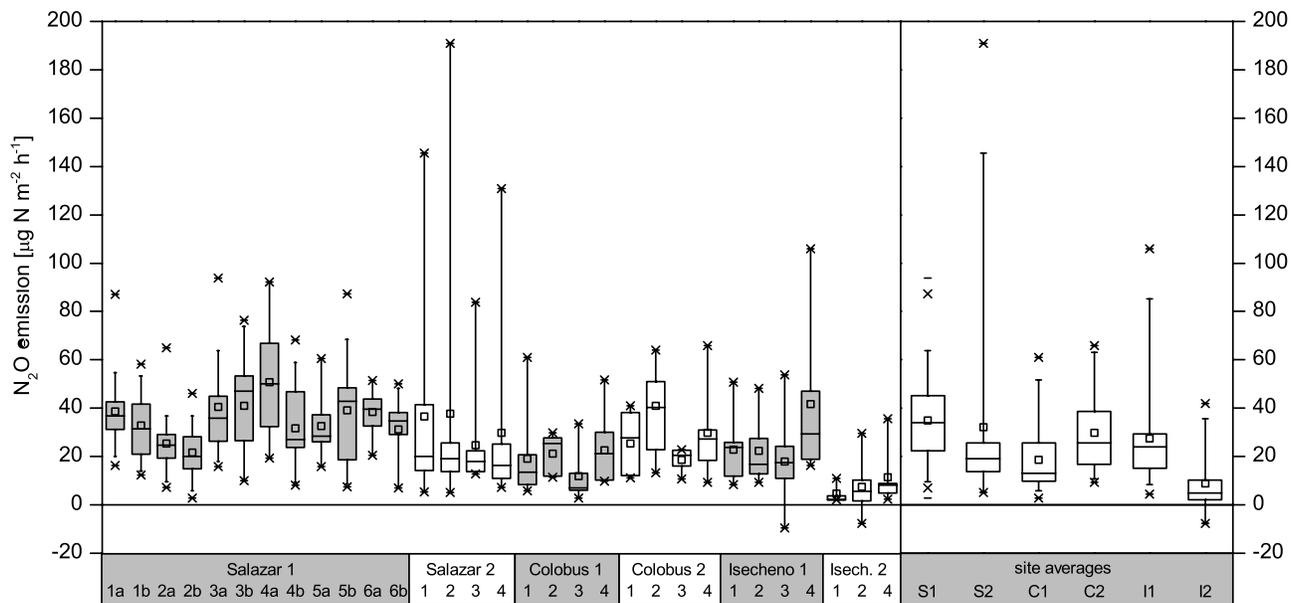


Figure 7. N_2O emissions from the individual chamber positions and mean N_2O emissions for the six sites under investigation. In this analysis we only included those data from the Salazar 1 site that matched the measurement times carried out at the other sites. Because of an insufficient number of valid flux measurements, chamber 3 at site Isecheno 2 was excluded (boxes indicate 25–50–75%, bars indicate 5–95%, crosses indicate 1%/99%, dashes indicate minimum/maximum, and squares indicate mean).

significantly during the entire campaign, as indicated by the relatively constant error bars (standard errors of six-chamber mean; see Figure 4). Like N_2O emissions, CO_2 emissions were also predominantly driven by changes in soil moisture. However, the correlation (Figure 8) was best explained by a linear regression curve ($r^2 = 0.61$), and, thus, was different to the optimum function applied for N_2O emissions. By combining soil temperature at 5 cm depth with soil moisture in a multiple linear regression model we could explain 67% of the temporal variation in measured CO_2 emissions at site S1. This suggests that the inclusion of temperature only improved the capacity of the model to explain variation in CO_2 flux by 6%, only slightly higher than that for N_2O emissions (<1%; soil temperature at 15 cm). Furthermore, at this site we could attribute 89% of the observed spatial variability of mean soil respiration rates to concentrations of carbon and nitrogen in the subsoil (see Table 4), by using the same “stepwise” linear regression model as described above for N_2O emissions.

4. Discussion

[31] To our knowledge, the reported N_2O , CH_4 and CO_2 fluxes obtained from April to June 2004 in the Kakamega

National Forest in western Kenya represent the first high-detail data set of soil-atmosphere trace gas exchange from tropical forest ecosystems on the African continent. We were able to continuously record a total of 3637 N_2O fluxes from twelve chamber positions at the site S1 with the automated measurement system. To characterize the spatial variability of N_2O soil-atmosphere gas exchange, additional manual measurements were conducted at four rain forest plots (S2, C1, C2 and I1) and one artificial regrowth site (I2) by making four replicate chamber measurements at each site on several occasions throughout the field campaign. For these manual samples, a total of 38, 36, 40, 37 and 20 N_2O emissions were recorded for the sites S2, C1, C2, I1 and I2, respectively.

[32] With mean N_2O emissions ranging from 34.3–67.0 $\mu\text{g N m}^{-2} \text{h}^{-1}$ for site Salazar 1, and 18.7–32.1 $\mu\text{g N m}^{-2} \text{h}^{-1}$ for the manually measured rain forest sites, the soils of the Kakamega forest emitted comparable levels of N_2O as reported by *Serca et al.* [1994] for the Mayombe Forest in Congo (mean flux rainy season 1991: 19.6 $\mu\text{g N m}^{-2} \text{h}^{-1}$ [number of flux measurements = 8]; mean flux at the end of a rainy season 1991: 207.0 $\mu\text{g N m}^{-2} \text{h}^{-1}$ [$n = 6$]). While the annual

Table 3. Comparison of N_2O Emissions at All Sites Under Investigation^a

Salazar 1	Salazar 2	Colobus 1	Colobus 2	Isecheno 1	Isecheno 2
35.4 ± 1.0 (a)	32.1 ± 6.5 (a,b)	18.7 ± 2.2 (c)	29.8 ± 2.5 (a,d)	27.6 ± 3.4 (d)	8.8 ± 2.9 (e)
4.3	5.2	2.8	9.3	4.5	−7.6
93.8	191.0	61.1	65.9	106.0	42.0
50.0	104.9	36.8	40.0	55.8	63.7
122	38	36	40	37	20

^aFlux data for the Salazar 1 site were limited to those corresponding to sampling dates at the Salazar 2, Colobus 1/2 and Isecheno 1/2 sites ($\mu\text{g N m}^{-2} \text{h}^{-1}$; SE, standard error; c, coefficient of variation). The letters in parentheses indicate significant differences between the individual sites (ANOVA analysis; $p < 0.05$).

Table 4. Results of Multiple Linear Regression Analysis of Environmental Site Parameters and N₂O and CO₂ Emissions^a

	B	SE	Beta	T	Significance
<i>Nitrous Oxide Emissions</i>					
Individual chamber positions of all sites ($n = 31$) ^b					
Constant	63.62	14.37		4.43	0.000
Sand, %	0.35	0.08	0.55	4.31	0.000
C:N-ratio (topsoil)	-3.69	1.15	0.41	-3.20	0.003
Chamber means of all sites ($n = 6$) ^c					
Constant	104.81	8.66		12.10	0.001
C:N-ratio (topsoil)	-4.40	0.74	-0.62	-5.96	0.009
Clay, %	-0.50	0.89	-0.59	-5.65	0.011
<i>Carbon Dioxide Emissions</i>					
Individual chamber positions at site Salazar 1 ($n = 10$) ^d					
Constant	42.71	5.82		7.34	0.000
Nitrogen (subsoil)	266.87	41.84	2.00	6.38	0.000
Carbon (subsoil)	-17.25	4.05	-1.33	-4.26	0.004

^aSE, standard error. Tested parameters are PH (litter, topsoil, subsoil), total nitrogen (litter, topsoil, and subsoil), soil organic carbon (litter, topsoil, and subsoil), C:N-ratio (litter, topsoil, and subsoil), and texture (sand, silt, and clay).

^bR² = 0.56, corrected R² = 0.53, and SE of predictor is 7.74.

^cR² = 0.96, corrected R² = 0.95, and SE of predictor is 2.16.

^dR² = 0.89, corrected R² = 0.86, and SE of predictor is 4.15.

rainfall amount was comparable (Congo, Mayombe Forest: 1400 mm; Kakamega: 1662 mm), the carbon and nitrogen stocks of the topsoil layer at the Mayombe Forest, Congo, were lower (1.7–4.5% SOC, 0.1–0.3% total N) than those at our sites (7.9–20% SOC, 0.5–1.6% total N), and the C:N-ratio (15:1) approximately 45% greater. However, it has to be noted that the N₂O measurements reported by *Serca et al.* [1994] were done during campaigns lasting 3–7 days each, so that the spatial and temporal dynamics of N₂O fluxes may not be well represented.

[33] In our study, we recorded individual N₂O fluxes of up to 324.8 $\mu\text{g N m}^{-2} \text{h}^{-1}$ (maximum six-chamber average: 163 $\mu\text{g N m}^{-2} \text{h}^{-1}$), which is of a similar magnitude to the reported maximum N₂O emissions of 492.1 $\mu\text{g N m}^{-2} \text{h}^{-1}$ and 570.8 $\mu\text{g N m}^{-2} \text{h}^{-1}$ for Australian rain forest soils by *Breuer et al.* [2000] and *Kiese and Butterbach-Bahl* [2002]. Nitrous oxide emissions were observed to vary on the spatial and temporal scale (see Figures 4 and 7 and Table 2). The mean N₂O emission at the main rain forest site (S1) was 42.9 $\mu\text{g N m}^{-2} \text{h}^{-1}$, which is close to the mean N₂O emission calculated from the data obtained under comparable hygric conditions (literature review by *Breuer et al.* [2000]: min: 1.7, mean: 49.3; max: 123.5 $\mu\text{g N m}^{-2} \text{h}^{-1}$).

[34] It has been shown in various field and laboratory studies of temperate forest soils that a strong positive correlation between temperature and N₂O emissions exists [e.g., *Brumme*, 1995; *Papen and Butterbach-Bahl*, 1999]. However, for tropical rain forest ecosystems it could be demonstrated that such a relationship is weak [*Breuer et al.*, 2000] ($r^2 = 20\%$) or even not existent [*Kiese and Butterbach-Bahl*, 2002], since the daily and seasonal temperature amplitude in tropical climates is small. Our results on the temperature dependency of N₂O emissions, revealed that soil temperature (15 cm) could explain <1% of the N₂O emissions variability, which is in agreement with previous emission studies in the tropics.

[35] Since soil microbial activity is highly affected by soil moisture levels, which in turn also determines soil aeration, microbial based nitrogen emissions in tropical environments are predominantly governed by WFPS [e.g., *Linn and*

Doran, 1984; *Firestone and Davidson*, 1989; *Davidson*, 1991; *Kiese and Butterbach-Bahl*, 2002]. Two main processes, nitrification and denitrification, are involved in N₂O production, consumption and emission. Nitrification, an aerobic process, is optimal at near field capacity conditions, whereas denitrification, an anaerobic process, increases greatly above a WFPS of 80%. However, N₂ instead of N₂O is the main form of N-trace gas production under near, or complete, saturation conditions [*Linn and Doran*, 1984; *Bateman and Baggs*, 2005]. On the basis of these findings, maximum N₂O emissions can be expected at WFPS between 50 to 80% or 60 to 90%, depending on soil physical properties [*Davidson*, 1991; *Bouwman*, 1998; *Bateman and Baggs*, 2005]. This general textbook understanding of N₂O production is also reflected in our detailed measurements at the main rain forest site (S1), where N₂O emissions were

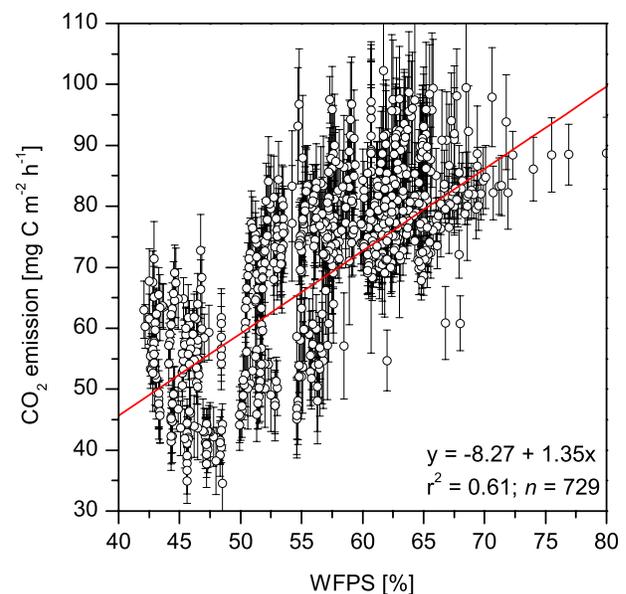


Figure 8. Correlation of water filled pore space (WFPS) and CO₂ emissions at the Salazar 1 site (six chamber mean; bars indicate standard error).

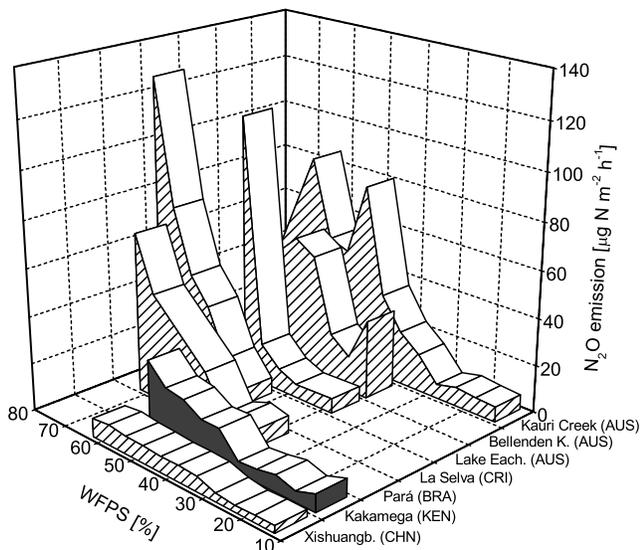


Figure 9. Measured dependency of N_2O emissions on water filled pore space (WFPS) at seven different field sites. N_2O emissions were pooled into 20 WFPS cohorts, ranging from 0 to 100% (Kakamega/Kenya (KEN); Lake Eacham/Australia (AUS) [Breuer *et al.*, 2000]; Bellenden Ker/AUS [Kiese *et al.*, 2003]; Kauri Creek/AUS [Kiese and Butterbach-Bahl, 2002]; Xishuangbanna/China (CHN) [Werner *et al.*, 2006]; La Selva/Costa Rica (CRI) [Keller and Reiners, 1994]; Pará, Brazil (BRA) [Verchot *et al.*, 1999]; see Table 5 for site details).

highest at WFPS levels of 65% and decreased with further increases in soil moisture.

[36] Figure 9 illustrates the N_2O emission response to observed WFPS values for this study, as compared to other studies in rain forests in Australia, Brazil, China and Costa Rica (see Table 5 for site details). Although a quantitative comparison is hampered by differing sampling durations, whole year cycles (Kauri Creek, Bellenden Ker, La Selva, Pará) or single seasons (e.g., transition period, Xishuangbanna, China; end of dry season–early rainy season, Kakamega, Kenya), and different sampling frequencies (subdaily,

daily average, monthly), a universal dependency of N_2O emissions on WFPS levels can be observed (see Table 5 and Figure 9). WFPS above 30–50% led to strong increases of N_2O emissions on all sites, though the absolute level of N_2O emission differs significantly among the sites.

[37] The dependency of N_2O emissions to changes in WFPS were reported to follow a linear as well as exponential relationships in Australian rain forest soils (WFPS levels ranging from 10 to 50% [Breuer *et al.*, 2000; Kiese *et al.*, 2003; Butterbach-Bahl *et al.*, 2004]). For our data set, a peak function (using WFPS) was able to explain 68% of the observed variability in N_2O emissions (note that the first two weeks of N_2O measurements were excluded for this analysis; see Figure 6). Since we did not encounter any WFPS levels above 75% (where a shift in denitrification products from N_2O to N_2 would be expected), our observations may well fit into the broader N_2O :WFPS-emission-dependency models as described by Bouwman [1998], Bateman and Baggs [2005] or Ridolfi *et al.* [2003], and the N_2O emission results from Australian soils reported above. However, as reported by Butterbach-Bahl *et al.* [2004] for the sites in Australia, and by Werner *et al.* [2006] for a seasonally dry rain forest in southwest China, this N_2O emission dependency on WFPS levels is further affected by the availability of substrates for nitrification and denitrification.

[38] Given a sufficient number of flux measurement, the short-term variation in N_2O emission from tropical forest soils was reported to depend mainly on soil moisture, whereas the long-term or seasonal pattern can often be explained by decomposition rates and the resulting changes in available soil nitrogen [e.g., Davidson *et al.*, 1993; Kiese *et al.*, 2003]. Highest N_2O emissions from rain forest soils were found during the transition period from the dry to wet season, and during the wet season [e.g., Breuer *et al.*, 2000; Butterbach-Bahl *et al.*, 2004; Davidson *et al.*, 1993, 2004; Keller and Reiners, 1994; Kiese and Butterbach-Bahl, 2002; Kiese *et al.*, 2003; Vasconcelos *et al.*, 2004]. In the transition period, accumulated litter (above and below ground) is often rapidly mineralized within the first weeks of soil rewetting, leading to large pulse emissions of N_2O , but also NO emissions [Davidson *et al.*, 1993; Butterbach-

Table 5. Comparison of Site Characteristics Used for the Histogram of WFPS Classes and Corresponding N_2O Emission in Figure 9^a

Site	Altitude, m a.s.l.	MAP, mm yr ⁻¹	Soil			SOC, %	C:N-Ratio	Flux Measurements			Source
			Sand	Silt	Clay			Duration	<i>n</i>	N_2O , $\mu\text{g N m}^{-2} \text{h}^{-1}$	
Kakamega Forest (Kenya)	1600	1662	43	23	34	3.50	10.4	Apr–Jun 2004	64 ^b	8.3–130.9	this study
Lake Eacham (Australia)	790	1500	68	11	21	2.34	15.8	May–Jun 1997	177 ^c	0.9–192.0	Breuer <i>et al.</i> [2000]
Kauri Creek (Australia)	790	1594	68	9	23	3.22	14.6	Jan–Dec 2000	44 ^b	5.8–125.8	Kiese and Butterbach-Bahl [2002]
Bellenden Ker (Australia)	80	4395	57	21	22	3.11	12.1	Nov 2001 to Oct 2002	50 ^b	1.2–32.7	Kiese <i>et al.</i> [2003]
Pará (Brazil)	200	1850	n.d.	n.d.	n.d.	2.45	11.1	Feb 1995 to May 1996	14 ^d	6.3–83.0	Verchot <i>et al.</i> [1999]
La Selva (Costa Rica)	100	3962	n.d.	n.d.	n.d.	n.d.	n.d.	Oct 1990 to Nov 1991	10 ^d	6.9–154.3	Keller and Reiners [1994]
Xishuangbanna (China)	770	1490	59	23	18	1.90	10.0	Feb–Apr 2005	53 ^b	2.3–9.0	Werner <i>et al.</i> [2006]

^an.d., no data; SOC, soil organic carbon; MAP, mean annual precipitation.

^bDaily mean flux.

^cIndividual fluxes.

^dMonthly flux.

Bahl et al., 2004]. We also observed marked N₂O emission pulses following precipitation events during the first two weeks of the measurements, i.e., shortly after the start of the rainy season. During this period, the increase in N₂O emissions in response to elevated WFPS was more pronounced than that in the following periods of measurements (see Figures 4 and 5). We therefore assume that in the first weeks of measurements, the high N₂O emissions reflected accelerated mineralization activity which slowed down over time. This interpretation is inline with the observed trend in soil CO₂ emission (Figure 4; N₂O and CO₂ emissions were positively correlated [$r^2 = 0.65$; $P < 0.01$; data not shown]) as well as with the soil moisture corrected trend in N₂O emissions (Figure 5), which shows that for a given WFPS range, N₂O emissions decreased toward the end of the measurements. Both observations can be explained by decreasing availability of mineralized substrate.

[39] While the short-term variability of N₂O emissions is generally controlled by changes of soil temperature, soil moisture, nutrient availability and microbial activity, the general emission potential is predominantly controlled by (1) soil texture which defines the aeration of the soil and thus the environmental conditions for the microbial biomass and processes and (2) carbon and nitrogen stocks in the soil [e.g., *Li et al.*, 2005]. For instance, microbial N biomass and mineralization are positively correlated to soil C and N concentrations and negatively correlated to the C:N-ratio [*Booth et al.*, 2005]. The importance of different soil parameters for explaining the spatial variability of N₂O emissions in our study was assessed with a multiple linear regression analysis. On the level of individual chambers, differences in the magnitude of N₂O emissions could best be explained by differences in the fraction of sand [%] and the C:N-ratio in the organic topsoil (Table 4). Site differences in N₂O emissions between the different rain forest sites and the reforestation site could be explained mainly by differences in the C:N-ratio (negatively correlated) of the organic topsoil and, furthermore by differences in the clay content of the topsoil (negatively correlated) (Table 4). The importance of the C:N-ratio as a scalar to explain site differences in N₂O emissions is in agreement with previous observations by *Breuer et al.* [2000] and *Kiese and Butterbach-Bahl* [2002] for Australian rain forest soils, *Davidson et al.* [2000] for different rain forest sites in Central and South America and by *Klemedtsson et al.* [2005] for forested drained Histosols in northern Europe.

[40] There were striking differences in the soil properties and N₂O emissions of our rain forest plots and those of the artificial regrowth plot, Isecheno 2 (Table 1 and Figure 7). The average N₂O emission of $8.8 \pm 2.9 \mu\text{g N m}^{-2} \text{ h}^{-1}$ at the regrowth site (I2) was significantly (53 to 75%) lower than those observed at all rain forest sites (Table 3). In the topsoil samples, significantly lower carbon concentrations (7.9%) and the lowest nitrogen concentrations (0.53%) were measured at site I2, while the texture was similar to the other sites. The C:N-ratios at the regrowth site (I2) were greater than those of the rain forest sites (topsoil: 24–35%; litter layer: 80–130%). These changes in soil properties and litter quality have obviously altered C- and N-trace gas exchange. If we use the C:N-ratio of the litter as an indicator of nitrogen availability at the site scale as proposed by *Davidson et al.* [2000], the observed reduction in N₂O

emissions can easily be explained by a degradation of the site and a reduction in N cycling.

[41] In summary, one can conclude that the driving factors for N₂O emissions in the rain forest system in Kenya were comparable to those observed in other studies of N₂O emissions from tropical rain forest systems. Also, the weighting of individual factors, i.e., dominance of soil moisture over temperature effects, was comparable to those of earlier studies.

[42] For estimating the annual N₂O emission rate we used a simple approach based on mean N₂O emission representative for different hygric conditions (e.g., applied in most of the cases compiled by *Breuer et al.* [2000]). The annual N₂O emission of a site is calculated by weighting the average N₂O emission of the dry season and the wet season with the respective durations (5 months dry season and 7 months wet season; see Figure 2). We used the average of daily N₂O emissions from 6 April to 10 June ($45.5 \pm 20.1 \mu\text{g N m}^{-2} \text{ hr}^{-1}/10.9 \pm 4.8 \text{ g N ha}^{-1} \text{ day}^{-1}$) as an approximation for the average N₂O emission level under wet season conditions. A representative mean dry season emission ($8.5 \pm 5.0 \mu\text{g N m}^{-2} \text{ hr}^{-1}/2.0 \pm 1.2 \text{ g N ha}^{-1} \text{ day}^{-1}$) was estimated by taking into account only the last seven days of measurements when rainfall and soil moisture levels were lowest. N₂O emissions of around $10 \mu\text{g N m}^{-2} \text{ h}^{-1}$ were reported in several other studies as typical emission level during dry season conditions (e.g., compilation of *Breuer et al.* [2000]). Using this approach, the annual N₂O emission for the main primary rain forest site (S1) can be estimated to be $2.6 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. To give an indication for the level of uncertainty in these calculated annual N₂O emissions, the same weighted calculation was performed using the standard deviation of the calculated mean flux rates for wet and dry season conditions ($1.2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$). The estimated annual N₂O emission for site S1 may therefore range between 1.4 and $3.8 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, which is in the range of annual estimates for other tropical rain forests worldwide (between 1 and $3 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ [e.g., *Riley and Vitousek*, 1995; *Verchot et al.*, 1999; *Breuer et al.*, 2000; *Melillo et al.*, 2001; *Kiese et al.*, 2005]).

[43] The soil-atmosphere exchange of methane is the result of simultaneously occurring production and consumption processes in soils, and is thus controlled by CH₄-producing methanogens operating at anaerobic conditions and CH₄-consuming methanotrophs that depend on oxygen as a terminal electron acceptor [*Topp and Pattey*, 1997]. Activity and population sizes of these microbes are depending on a multitude of soil factors, like aeration of the soil profile, substrate availability, pH, soil moisture and soil temperature [e.g., *Chan and Parkin*, 2001; *Conrad*, 1996; *Khalil and Baggs*, 2005; *Smith et al.*, 2003; *Topp and Pattey*, 1997]. Since methane production usually requires prolonged periods of waterlogging, which is rarely encountered in upland soils, tropical upland forest soils predominantly act as sinks for atmospheric CH₄ [e.g., *Butterbach-Bahl et al.*, 2004; *Delmas et al.*, 1992; *Ishizuka et al.*, 2002; *Keller et al.*, 1986; *Keller and Reinert*, 1994; *Kiese et al.*, 2003; *Weitz et al.*, 1998; *Werner et al.*, 2006].

[44] We observed a mean CH₄ uptake rate of $56.4 \pm 0.8 \mu\text{g C m}^{-2} \text{ h}^{-1}$ ($n = 1458$) and maximum CH₄ uptake rate of $146.9 \mu\text{g C m}^{-2} \text{ h}^{-1}$ at the site S1. The mean

CH₄ uptake rate for the site S1 is higher than previously reported mean CH₄ uptake rates for other tropical rain forest ecosystems of Asia and South and Central America, which are in a range of 29.4–39.4 μg C m⁻² h⁻¹ [e.g., Keller and Reiners, 1994; Kiese et al., 2003; Verchot et al., 2000; Weitz et al., 1998; Werner et al., 2006]. However, this difference may be explained by the seasonality of CH₄ exchange, sampling frequencies, spatial coverage and differences in soil properties such as texture. Atmospheric CH₄-uptake by soils is largely controlled by gas diffusion resistance within the soil. Therefore the structure of the forest floor layer [e.g., Dong et al., 1998; Brumme and Borken, 1999], which is mostly missing or only rudimentary developed in rain forest ecosystems, and the texture of the mineral soil [e.g., Dörr et al., 1993; Boeckx et al., 1997], have a huge effect on the magnitude of CH₄ uptake rates in forest soils. Even though we have not measured the diffusivity of the soil at our study site S1, one can assume that the high sand content of 43% provides sufficient aeration of the topsoil and does not inhibit CH₄ oxidation activity.

[45] Because of its effect on gas diffusion, soil moisture is the dominant factor controlling the seasonality of CH₄ uptake in tropical systems [e.g., Keller and Reiners, 1994; Verchot et al., 2000; Kiese et al., 2003; Werner et al., 2006]. However, in our study the effect of soil moisture changes on CH₄ uptake rates was less pronounced than that in previous studies. Only at the beginning of the measurements, when WFPS values exceeded 60%, was there a pronounced reduction in CH₄ uptake.

[46] Even though our site was generally functioning as a sink for atmospheric CH₄, occasionally when WFPS was great, some chamber positions showed surprisingly strong CH₄ emissions of up to 99.7 μg C m⁻² h⁻¹. Obviously, increased soil moisture and, thus, reduced O₂ penetration into the soil profile, effected the soil at these chamber positions in such a way that the soil switched from an atmospheric CH₄ sink to a source of CH₄. Moreover, while taking soil samples at the end of our measurements, we found a crumbled soil structure in sections of the relevant chamber positions suggesting termite activity. Termite mounds were present 200 m away from our plot at S1. It is well known that termites can produce considerable amounts of CH₄ during their digestion processes [MacDonald et al., 1998; Sanderson, 1996; Bignell et al., 1997]. Therefore the sporadic CH₄ emission activity at some of our measuring positions may also be due to the combined effect of termite activity [Eggleton et al., 1999; MacDonald et al., 1998, 1999] and increased anaerobiosis resulting from elevated soil moisture.

[47] The variation in soil-atmosphere exchange of CH₄ at site S1 did not change significantly during the measurement campaign, even though the number of successful flux measurements, decreased toward the end of our field campaign (Figure 4). We therefore calculated the annual CH₄ soil-atmosphere exchange rate for the main primary rain forest site (S1) by multiplying the average CH₄ exchange rate ($-54.6 \pm 7.9 \mu\text{g C m}^{-2} \text{ h}^{-1}$ / $-13.1 \pm 1.9 \text{ g C ha}^{-1} \text{ day}^{-1}$) by 365 days. Using this approach, the cumulative annual soil-atmosphere exchange of CH₄ at site S1 is $-4.8 \pm 0.7 \text{ kg C ha}^{-1} \text{ yr}^{-1}$.

[48] Previously, Ishizuka et al. [2002], Kiese and Butterbach-Bahl [2002] and Werner et al. [2006]

reported CO₂ emissions of 51.3–93.7 mg C m⁻² h⁻¹, 20.3–247.7 mg C m⁻² h⁻¹ and 18.1–131.6 mg C m⁻² h⁻¹ for primary rain forest soils of Indonesia, Australia and southwest China, respectively. Sotta et al. [2004] described the mean annual CO₂ efflux from soils of the Amazon region to range between 44.6–76.3 mg C m⁻² h⁻¹, while soil CO₂ emissions were considerably lower (20.2–40.4 mg C m⁻² h⁻¹) during the dry season and higher (>85 mg C m⁻² h⁻¹) during the wet season. At the Kakamega Forest of western Kenya we recorded a mean soil respiration rate of 71.8 mg C m⁻² h⁻¹ (range: 22.3–155 mg C m⁻² h⁻¹), which is consistent with previously reported values. Our coefficients of variation of 16.2–26.7% were in good agreement with results from La Scala et al. [2000] and Kiese and Butterbach-Bahl [2002], who reported values of 21.1–31.7% and 11.5–36.7%, respectively. Measurements of soil CO₂ emissions further suggested that most mineralization activity happened at the beginning of the measurements, i.e., at the onset of the rainy season. Toward the end of the measurements, soil CO₂ emissions declined, most likely because of the decreased availability of easily degradable substrate, rather than moisture limitation. Using total carbon and nitrogen concentrations of the subsoil, we were able to explain 89% of the observed variation in CO₂ flux between the ten chamber positions, while the other input parameters were rejected by the multiple linear regression model because of insignificance.

[49] The cumulative CO₂ emission for one year ranges between 4.5 and 6.5 t C ha⁻¹ ($5.5 \pm 1.0 \text{ t C ha}^{-1}$) when the same upscaling approach, as used for N₂O, is applied.

5. Conclusion

[50] The reported data set of N₂O, CH₄ and CO₂ trace gas exchange between tropical rain forest ecosystems and the atmosphere is the first detailed study carried out on the African continent. We found temporal variability of N₂O emissions to be predominantly controlled by changes in soil moisture. Pulse N₂O emissions were only observed in the first weeks of the measurement campaign, which coincided with the start of the wet season. We interpret the observed decrease in N₂O emissions following these pulse events to be an effect of substrate depletion, which is supported by a concurrent decline in CO₂ emissions. The differences in N₂O emitted at the plot and the site level could be explained by differences in soil texture and the C:N-ratio of the topsoil. Furthermore, our study revealed a significantly lower N₂O emission level at an artificial regrowth site. This difference can be explained by the significantly lower C and N stocks as a consequence of clear-cutting and artificial reforestation.

[51] In contrast to N₂O and CO₂ emissions, the CH₄ soil-atmosphere exchange was relatively stable throughout the investigation period, the forest soils generally acting as CH₄ sinks. CH₄ emissions were observed sporadically, as a result of soil anaerobiosis under high water contents and possibly termite activity, but these occasional CH₄ emissions were of minor importance at the site scale. The annual soil-atmosphere exchange of N₂O, CO₂ and CH₄ was calculated using a simple upscaling approach and predicted $2.6 \pm 1.2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (N₂O), $-4.8 \pm 0.7 \text{ kg C ha}^{-1} \text{ yr}^{-1}$ (CH₄) and $5.5 \pm 1.0 \text{ t C (CO}_2\text{)}$, respectively.

[52] **Acknowledgments.** We would like to thank Marcus Walsh and Alex Awiti of ICRAF Kisumu, Kenya, for their generous support during our field measurements and Gertrud Schaab and the members of the BIOTA-East project for providing us access to GIS data.

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K. Butterbach-Bahl, R. Kiese, and C. Werner, Institute for Meteorology and Climate Research, Atmospheric Environmental Research, Karlsruhe Research Centre, Kreuzackbahnstr. 19, D-82467 Garmisch-Partenkirchen, Germany. (klaus.butterbach@imk.fzk.de)