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Soil-atmosphere exchange of nitrous oxide, methane and carbon dioxide in a gradient of elevation in the coastal Brazilian Atlantic forest

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Abstract

Soils of tropical forests are important to the global budgets of greenhouse gases. The Brazilian Atlantic Forest is the second largest tropical moist forest area of South America, after the vast Amazonian domain. This study aimed to investigate the emissions of Nitrous Oxide (N_2O) and Carbon Dioxide (CO_2) as well as methane (CH_4) emissions and consumptions along an altitudinal transect and the relation between these fluxes and other climatic, edaphic and biological variables (temperature, fine roots, litterfall, and soil moisture). Annual means of N_2O flux were 2.6 (±0.5), 0.9 (±0.1), and 0.7 (±0.2) ng N cm^{-2} h^{-1} at altitudes 100, 400, and 1000 m, respectively. On an annual basis, soils consumed CH_4 at all altitudes with annual means of −1.0 (±0.2), −1.8 (±0.1), and −1.6 (±0.3) mg m^{-2} d^{-1} at 100 m, 400 m and 1000 m, respectively. Although not sampled in the hottest and wettest portion of the year because of instrument malfunctions, mean fluxes of CO_2 averaged 3.6 (±0.2), 3.5 (±0.3), and 3.1 (±0.3) µmol m^{-2} s^{-1} at altitudes 100, 400 and 1000 m, respectively. N_2O fluxes were significantly influenced by soil moisture and temperature. Soil-atmosphere exchange of methane responded to changes in soil moisture. Carbon dioxide emissions were strongly influenced by soil temperature. While the temperature gradient observed at our sites is only an imperfect proxy for climate warming, our results suggest that increasing temperatures will result in increased in microbial activity with a consequent increase in soil N_2O and CO_2 emissions and soil CH_4 consumption.

1 Introduction

The Brazilian Atlantic Forest is a heterogeneous region that includes a large variety of forest physiognomies and compositions (plant and animal species) and is distributed in different topographic and climatic conditions such as areas of coastal flooded forest (restinga), lowland, submontane and montane forests (Metzger, 2009; Vieira et al., 2008). It originally covered an area of 148.2 million ha, corresponding approximately to

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17.4% of the Brazilian territory, extending for over 3300 km along the eastern Brazilian coast between the latitudes of 3 and 30° S (Metzger, 2009; Ribeiro et al., 2009). The Atlantic forest represents the second largest tropical moist ecosystem of South America, after the vast Amazonian domain (Oliveira-Filho and Fontes, 2000), and it is also considered a hot-spot in terms of biodiversity and endemism (Myers et al., 2000). In spite of that, the Atlantic Forest is among the most threatened tropical forests in the world because its location coincides largely with the most populated areas of Brazil, where the settlement of European pioneer and African slaves started four centuries ago (Oliveira-Filho and Fontes, 2000). Currently the Atlantic Forest is reduced to only 12% of its original cover (Metzger, 2009), and most remnants are both small and disturbed fragments (<50 ha) or wide areas sheltered on steep mountain slopes (Metzger, 2009; Ribeiro et al., 2009).

Despite the importance of the Atlantic Forest biome there are very few data concerning its function (Maddock et al., 2001). Soils of tropical forests are considered as important contributors to the global gas balances as source of atmospheric nitrous oxide (Bouwman et al., 1995; Maddock et al., 2001), and carbon dioxide (Keller et al., 1986), and as sink of methane (Reiners et al., 1994, 1997). Although considerable research has been done for a long time aiming to quantify the main global sources and sinks of the main greenhouse gases (N_2O, CH_4, and CO_2) the uncertainties in the overall balances of these gases remain large in part because of the limited spatial and temporal extent of the sampling in tropical regions (Maddock et al., 2001; Purbopuspito et al., 2006).

The main objective of this paper is to quantify the soil emission rates of N_2O, CH_4 and CO_2 along a gradient of elevation in the Coastal Brazilian Atlantic Forest located in the northern coast of the State of São Paulo, southeast region of Brazil.

We chose to work along a gradient of elevation because of the differences in climatic conditions, species composition and structure (Marrs et al., 1988), nutrient supply (Grubb, 1977) and soil physical and chemical properties (Sollins, 1998; Tanner et al., 1998). Climate and soil properties are well known factors that modulate the

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emission of trace gases by soils (Davidson, 1993; Steudler et al., 1996; Breuer et al., 2000; Davidson et al., 2000; Kiese and Butterbach-Bahl, 2002; Moreira and Siqueira, 2006). Therefore, we expected that soil gas emissions to vary with altitude responding to combinations of the factors described above. Although tropical forest soils are expected to respond to the global warming few studies have investigated soils from forests along a gradient of elevations that might provide some insight into controls on trace gas exchange (Riley and Vitousek, 1995; Purbopuspito et al., 2006) Most studies related to tropical forests soil gas emissions are still strongly biased toward lowland tropical forests (Keller and Reiners, 1994; Davidson et al., 2000; Erickson et al., 2001).

2 Material and methods

2.1 Study area

This study was conducted in the Coastal Brazilian Atlantic Forest, in the northern coast of the São Paulo State, within the *Nucleos* of Picinguaba (lowland, 23°31′ to 23°34′ S and 45°02′ to 45°05 W) and Santa Virginia (montane, 23°17′ to 23°24′ S and 45°03′ to 45°11′ W) of the *Serra do Mar* State Park. Three areas (treatments) were selected at the altitudes 100 m (lowland), 400 m (submontane), and 1000 m (montane) (Alves et al., 2010). According to Köppen classification, climate at the study areas is *Cfa*, characterized as humid subtropical with hot summers, and air temperature that ranges between 8 and 25 °C. According to the meteorological stations of the Department of Water and Energy of São Paulo State (DAEE-SP) the historical annual mean precipitation at the municipality of Ubatuba located at 220 m altitude is 3050 mm and in the municipality of Natividade da Serra, near altitude 1000 m, the annual mean precipitation decreases to approximately 2300 mm. During May through August, the total historical precipitation is 200 mm, about half as much as other months. In this study we considered these four months as *dry season* and the other eight months as *rainy season*.

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Soils of the study sites are mostly sandy, but with higher clay contents at 100 m (Table 1). Soils at the three altitudes have low nutrient contents and the nutritional reserve is concentrated in the upper soil layer (up to 10 cm depth), decreasing with depth. Soil carbon (C) and nitrogen (N) concentrations and stocks progressively increase along the altitudinal gradient (Table 1).

2.2 Soil gas flux

At each altitude four plots (replicates) of 1 ha were delimited (Alves et al., 2010). Gas samples were collected once a month from September 2006 through August 2007, in each plot with a day of collection per altitude, generally between 08:00 and 18:00 LT. Fluxes of nitrous oxide (N_2O), carbon dioxide (CO_2), and methane (CH_4) were measured at random points along 30 m transects that were initiated at randomized seed points in randomized directions each month with eight cylindrical PVC chambers (8 sub-sample chambers per plot) consisting of a pipe that served as a base (0.29 m diameter) and a cap that fit snugly on the base (Keller et al., 2005). For N_2O and CH_4, four samples of 60 ml of the air from the chambers were withdrawn at intervals of 1, 10, 20 and 30 min after closing with 60 ml syringes and then transferred to previously evacuated glass serum vials sealed with gas impermeable, butyl rubber septum stoppers. Samples were analyzed by gas chromatography (SHIMADZU GC-14A Model) within five days of collection. Lab tests showed that N_2O and CH_4 concentrations were unaffected by storage for up to thirty days. Gas concentrations were calculated by comparing peak areas for samples to those of commercially prepared standards (Scott-Marin) that had been calibrated against standards prepared by the National Oceanic and Atmospheric Administration/Climate Monitoring and Diagnostic Laboratory (NOAA/CMDL). Fluxes were calculated from linear regressions of concentration versus time.

A dynamic flow system was used for measurements of CO_2. Air flowed from the soil enclosure through a Teflon-lined polyethylene sample line 5 m in length and then it entered an infrared gas analyzer (Li-Cor 820). Data was stored in a palmtop computer

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and fluxes were calculated from the linear increase of concentration versus time adjusted for the ratio of chamber volume to area and the air density within the chamber (Keller et al., 2005). Because of instrument malfunctions, CO_2 fluxes were not available for several months of the year (see Sect. 3).

2.3 Litterfall and fine roots

Litterfall data were obtained by thirty 80 cm diameter litterfall traps per plot deployed from randomized points in two plots at each elevation and samples were collected every fifteen days, kept in paper bags, labeled, and dried at 60 °C. After drying, samples were weighed. In addition, surface litter layer mass was weighed to assess litterfall stocks simultaneously with litterfall. Thirty surface litter samples were collected from randomly located 0.3×0.3 m plots marked by a rigid frame for two plots at each altitude, every thirty days. Samples were kept in paper bags, dried at 60 °C and weighed to determine stocks of litter on soil surface. Litterfall and surface litter collections started six months after gas sampling (March 2007) and accompanied only six months the gas collection (March through August 2007). Decomposition rates were calculated according to the model proposed by Olson (1963) and decomposition time was determined according to Shanks and Olson (1961).

Five fine root soil cores samples were randomly collected from 0 to 10 cm depth in every plot of each altitude, and treated according to Vogt and Persson (1991). Fine root samples were analyzed for total C and N concentration using a Carlo Erba elemental analyzer at the Laboratory of Isotope Ecology, CENA-USP. For statistical tests, the mean of the five root samples collected at each plot was considered as one of the four replicates per gradient of elevation.

2.4 Soil water filled pore space (WFPS) and N contents

Once a month during one year of collection, and after soil gas collection, the surface litter was removed from each chamber location and a soil core about 5 cm diameter

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and 10 cm deep was collected. After collection, soil samples were transported on ice in an insulated cooler to the Laboratory of Isotope Ecology at CENA-USP and stored at ~4 °C until analysis. Soil samples were sieved (sieve 2 mm mesh) to remove roots and large stones, and a ten grams subsample was oven-dried at 105 °C for 24 h to determine water content gravimetrically and N contents (NH_4^+ and NO_3^-), and N-mineralization and N-nitrification processes as the procedures described by Piccolo et al. (1994). Water filled pore space (WFPS) was obtained from soil core samples collected once a month from each chamber location and calculated according to Carmo et al. (2007). Additionally, we recorded air and soil temperatures (2 cm depth) using electronic thermometers.

2.5 Statistical analysis

All data were first tested for normal distribution and for homoscedasticity by the Kolmogorov-Smirnov test. Due to non-normal distribution of the fluxes for CH_4 and N_2O, these data were log-transformed to homogenize variances. We analyzed gas fluxes and other variables in a 2-way ANOVA design using altitude and month as treatments. Four plots served as replicates at each altitude. Months were considered as treatments because the design of collection points was randomized every month. Tukey's post-hoc analysis was used to make comparisons among gradients. Pearson correlation coefficients between N_2O, CO_2, and CH_4 fluxes, soil N contents, soil temperature, and soil moisture also were calculated by Minitab version 15 software. Statistical analyses were performed by Minitab version 15 software (Minitab Inc., 2006).

3 Results

3.1 Soil temperature and soil chemical-physical properties

As expected, lower soil temperatures ($P<0.05$) were found at higher altitude (1000 m) and soil temperature increased downwards (Fig. 1).

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Soil moisture expressed as WFPS was significantly higher ($P<0.05$) in the plots at 100 m and 400 m than in soils located at 1000 m (Fig. 2). The trends in WFPF reflect in part the soil porosity and packing (Beare et al., 2009). Soil bulk densities at 5 cm depth were greater at the lower elevations (0.98 g m^3 at 100 m and 1.06 g m^3 at 400 m) compared to the montane site (0.8 g m^3 at 1000 m).

There was no difference ($P>0.05$) in annual net mineralization and net nitrification rates among altitudes. However, ammonium (NH_4^+) and nitrate (NO_3^-) concentrations were significantly higher ($P<0.05$) at altitude 1000 m (9.7±0.6 and 19.1±1.0 µg g^{-1}, respectively). No significant correlations were found between soil nitrate or ammonium concentrations and flux of soil gases during the sampling period nor was soil net N, net mineralization and net nitrification rates significantly correlated to soil gas emissions.

3.2 Fine root and litter production

On average total fine root biomass (0–10 cm depth) was greater ($P<0.05$) in the rainy season than in the dry season. During the rainy season fine roots had larger live mass ($P<0.05$) than dead mass and fine root mass (live and dead) was larger ($P<0.05$) at 1000 m (Table 2). In the dry season, there was no significant difference ($P>0.05$) between live and dead mass along the altitudes but greater root mass ($P<0.05$) was again found at 1000 m altitude.

Carbon to nitrogen (C:N) ratio of fine roots (live and dead) collected during the rainy season was significantly higher ($P<0.05$) than in the dry season (Table 3). In both seasons, the C:N ratio of live roots was significantly ($P<0.05$) higher than dead roots. There was no significant difference of C:N ratio of fine roots among altitudes (Table 3).

Although a decrease in litterfall was observed at higher altitudes, there was no significant difference among altitudes (Table 4). Litterfall stocks on soil surface were significantly higher ($P<0.05$) at 1000 m (Table 4). According to Shanks and Olson's model (1961), litter decays decreases as altitude increases ($P<0.05$, Table 4), and litter takes 18 months for 95% loss at 100 m and about 50% more time at 400 and 1000 m.

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3.3 Soil-atmosphere emissions of trace gases

Annual means of soil N_2O flux decreased ($P<0.05$) with the increase of altitude (Table 5). At all altitudes, we observed consumption of soil CH_4 with the smallest consumption ($P<0.05$) observed at 100 m (Table 5). CO_2 fluxes do not correspond to a full year and valid data correspond to the months from March 2007 through August 2007. For these months, soil CO_2 fluxes averaged 3.1 (±0.3) $\mu mol\, m^{-2}\, s^{-1}$ at 1000 m and were significantly lower ($P<0.05$) at than at 400 m and 100 m (3.3 (±0.3) and 3.6 (±0.2) $\mu mol\, m^{-2}\, s^{-1}$ respectively) which were not distinguishable from one another.

3.4 Altitudinal and monthly variations of soil gas fluxes and their dependency on changes in soil temperature and WFPS

At 100 m there was a significant ($P<0.05$) variation in N_2O fluxes during sampling period, with the highest fluxes measured in the rainy months of December 2006 and January 2007 (Fig. 3a). A significant positive correlation ($r^2=0.86$, $P<0.05$) between soil moisture (WFPS) and N_2O flux was observed exclusively at 100 m while there was no correlation between soil temperature and N_2O flux at the same altitude.

Fluxes measured at 400 m showed significant differences along the sampling period, with the largest N_2O emissions ($P<0.05$) measured during the rainy season, between August 2006 and January 2007 (Fig. 3a). At 1000 m there was a weak but significant ($P<0.05$) monthly variation of N_2O fluxes, and the largest emissions were observed between the rainy months of November 2006 and January 2007 (Fig. 3a) whereas significantly ($P<0.05$) lower fluxes were found in the dry months of July and August 2007. A weak but significant correlation ($r^2=0.52$, $P<0.05$) between soil temperature and N_2O fluxes was observed at altitude 1000 m.

At 100 m soil-atmosphere exchange of CH_4 showed only negative fluxes (soil consumption of atmospheric methane) and consumption varied significantly ($P<0.05$) among months. The largest consumption occurred in August 2006 (transition between

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rainy and dry seasons) and in the hot and wet period between February and March 2007 (rainy season). Smaller consumption was measured during the cool and dry months of June, July and August 2007 (Fig. 3b).

Methane consumption varied significantly ($P<0.05$) among months at 400 m altitude. More consumption ($P<0.05$) occurred in the rainy months of September 2006 and March 2007 and less consumption was measured during November 2006 and December 2006 (rainy season) and in the dry month of June 2007 (Fig. 3b). At 1000 m consumption of CH_4 also varied among months ($P<0.05$). The pattern was similar to the pattern at 400 m with less consumption ($P<0.05$) in the rainy months of November and December 006 and more ($P<0.05$) consumption in September 2006, and August 2007 (Fig. 3b).

In general, there was no significant correlation between CH_4 fluxes and soil temperature at any altitude. In contrast, CH_4 correlated weakly ($r^2=0.40$, $P<0.05$) with WFPS at 100 m.

Higher fluxes of CO_2 were observed in all altitudes between February and April, 2007, during the rainy season, and lower fluxes were measured between May and August, 2007, during dry season (Fig. 3c). Carbon dioxide emissions increased with soil temperature ($r^2=0.7$ at 100 m, $r^2=0.9$ at 400 m and 1000 m, respectively, $P<0.05$), but no correlation was observed with WFPS.).

4 Discussion

4.1 Soil-atmosphere emissions of N_2O

In order to understand the decrease in soil N_2O emissions with altitude we compared our data with the hole-in-the-pipe (HIP) model (Firestone and Davidson, 1989; Davidson et al., 2000). According to this model, at a broad scale, N_2O emissions increase with the nitrogen availability in the system. Comparing different tropical regions, Davidson et al. (2000) showed that N_2O emissions increased with the increase of soil nitrate

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concentration, N-mineralization and nitrification, and decreased with the increase of soil ammonium concentration.

Our results present a contrast to this picture. At 1000 m forest site, soil concentrations of ammonium and nitrate were higher and average nitrate concentration was 30% higher than average ammonium concentration. Nonetheless, despite this evidence of greater nitrogen availability, N_2O fluxes were significantly lower than they were in the lowlands. In part, this may be the result of the limitation of denitrification by easy drainage in the sandy soil and good aeration. WFPS was significantly lower at 1000 m than at l00 and 400 m. Also important is the pace of decomposition. High rates of decomposition consume oxygen promoting low-oxygen conditions that promote greater N_2O emissions in tropical forest soils (Keller and Reiners 1994). The data on litter stocks (Table 4) show that the rate of decomposition (promoted by higher temperatures) is nearly twice as great in the lowlands as in the montane sites.

No single factor promotes the greatest N_2O fluxes found in months of December 2006 and January 2007 at elevation 100 m. Rather it is the combination of high temperature, elevated soil WFPS, and high rates of decomposition promoting low-oxygen conditions (note that methane consumption is diminished at the same time) that provoke high fluxes. The association of low oxygen conditions with high N_2O fluxes is corroborated by the correlation between N_2O and WFPS (r^2=0.86; P=0.05) at 100 m (McSwiney et al., 2001). The influence of soil temperature over gas emissions is corroborated by the significant positive relation between N_2O and soil temperature at 1000 m (r^2=0.5, P<0.05).

We compare our N_2O emissions with the survey made by Breuer et al. (2000) adding recent emissions measurements made in tropical forests, mainly in the Amazon region (Garcia-Montiel et al., 2001, 2002; Keller et al., 2005). The median value of all these measurements was approximately 2.0 kg N ha^{-1} yr^{-1}. Emissions measured at 400 m and 1000 m forest sites were lower than these values, and near the lower end of the spectrum of emissions. On the other hand, N_2O emissions at the 100 m forest sites were larger (2.2 kg N ha^{-1} yr^{-1}) than the median value, but approximately half as great

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as the highest observed emissions from tropical forests (6 to 7 kg N ha^{-1} yr^{-1}). N_2O emissions measured at 100 m were similar to the mean fluxes found in the only other study that measured annual N_2O emissions in the coastal Atlantic Forest of Brazil (Tianguá Biological Reserve, Rio de Janeiro, 170 to 300 m a.s.l.) (Maddock et al., 2001).

4.2 Soil-atmosphere exchange of CH_4

Tropical rain forests can function as a significant sink for atmospheric CH_4 and most studies have reported negative fluxes (Verchot et al., 1999; Breuer et al., 2000; Gut et al., 2002; Kiese et al., 2003). In the Atlantic forest, we observed, on average, only negative fluxes (consumption) of CH_4 at all altitudes, and the annual mean fluxes of CH_4 found in this study are similar to fluxes reported by other studies conducted in tropical forests (Keller et al., 2005). Well-drained soils generally consume CH_4 from the atmosphere and soil water content regulates the flux through its control on the diffusion of CH_4 in the soil (Crill, 1991; Born et al., 1990). Butterbach-Bahl et al. (2004) in a study in an Australian tropical rainforests have shown that CH_4 uptake was correlated with WFPS. Although weak, there was a significant ($P<0.05$) positive correlation between WFPS and CH_4 flux at 100 m forest site ($r^2=0.4$, $P<0.05$) there was no correlation between WFPS and CH_4 flux at the higher altitudes. We note that temperature and moisture correlate in these systems and that when soil moisture conditions are optimal for CH_4 consumption in the cooler sites (400 m and 1000 m), low soil temperatures probably limit the microbial activity responsible for CH_4 consumption.

4.3 Soil-atmosphere emissions of CO_2

Because of equipment malfunctions, the temporal CO_2 extent of emissions measured in our study was limited to only about one-half year. We therefore avoid comparisons to annual fluxes measured elsewhere.

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Comparing among altitudes or the period of measurement, carbon dioxide emissions were significantly higher at 100 m (Table 5) as would be expected as a result of the higher temperatures (Fig. 3) and the greater rates of decomposition (Table 4). As noted in most studies, soil CO_2 emissions are tightly related to temperature (Joergensen et al., 1990; Kiese and Butterbach-Bahl, 2002; Davidson and Janssens, 2006; Moreira and Siqueira, 2006). The largest soil CO_2 emissions were observed between February and April 2007 (Fig. 3c) when soil and air temperatures were highest (Fig. 3), reinforcing the evidence for a strong temperature effect.

5 Conclusions

Overall we found that the emissions of N_2O and the uptake of CH_4 by soils of the coastal Atlantic Forest of Brazil are within the range of other tropical forests of the world. We observed that N_2O and CO_2 emissions were lower at higher altitudes, although the nitrogen and carbon stocks were higher at higher altitudes. This contrast may be explained by the greater air and soil temperatures observed at the low altitude forest sites that promotes microbial activity. While the temperature gradient observed at our sites is only an imperfect proxy for climate warming, our results suggest that increasing temperatures will result in increased in microbial activity with a consequent increase in soil N_2O and CO_2 emissions and soil CH_4 consumption.

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Table 1. Physical-Chemical characterization of the soil layers (0.3 m depth) sampled at the studied sites (mean±standard error; n=32 for each altitude and depth). Data source: Martins, 2010.

Depth (cm)	N	C	Sand	Clay	Bulk Density
	($g\,kg^{-1}$)		(%)		($g\,m^{-3}$)
100 m					
0–5	3.4±1.4	45.9±19.4	60.4±9.7	31.5±8.0	0.9±0.1
5–10	2.4±1.1	31.8±15.3	56.5±9.3	35.1±8.6	1.1±0.1
10–20	1.9±0.7	25.9±10.1	56.8±9.9	35.3±9.7	1.3±0.1
20–30	1.2±0.4	16.5±5.9	55.8±9.6	37.4±9.7	1.4±0.1
400 m					
0–5	4.6±1.1	58.9±15.5	66.7±6.6	16.4±3.8	1.0±0.0
5–10	3.6±0.8	45.8±12.7	62.2±3.8	20.5±3.7	1.1±0.1
10–20	2.7±0.5	34.7±8.8	61.4±6.0	22.1±4.5	1.2±0.1
20–30	2.0±0.3	26.0±5.9	59.5±5.9	23.4±4.2	1.3±0.1
1000 m					
0–5	6.8±3.1	91.5±45.3	57.3±12.2	20.3±8.5	0.8±0.2
5–10	4.5±1.5	58.8±21.2	53.9±14.3	22.3±10.8	0.8±0.2
10–20	3.8±1.2	49.6±17.1	54.0±12.2	19.8±10.7	1.0±0.2
20–30	3.1±1.2	44.4±22.5	53.5±12.3	20.6±11.5	1.1±0.2

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Table 2. Fine root biomass (live and dead) at different altitudes in the rainy and in the dry season. Values represent mean and standard error of four replicates per altitude.

Altitude (m)	Rainy season ($g\,m^{-2}$)		Dry season ($g\,m^{-2}$)	
	Live	Dead	Live	Dead
100	204.2 (±28.1)a	82.1 (±16.0)b	433.8 (±119.1)a	275.4 (±131.9)a
400	293.1 (±38.1)a	143.34 (±17.4)b	310.6 (±87.6)a	219.5 (±98.2)a
1000	464.0 (±80.2)a	220.7 (±44.5)b	1098.3 (±89.8)a	896.2 (±82.3)a

Lower case letters indicate difference between columns within seasons.

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Table 3. Concentrations of carbon and nitrogen and C:N ratio of fine roots (<2 mm) at different altitudes in rainy (January, 2007) and dry (August, 2007) months. Values represent mean and standard error (in parenthesis) of four replicates per altitude.

Season	Altitude (m)	Category	C (%)	N (%)	C:N
Rainy	100	Live	42.8 (±1.2)	1.4 (±0.1)	32.6 (±2.7)a,A
		Dead	37.8 (±1.4)	1.5 (±0.1)	26.5 (0.1)b,A
	400	Live	42.9 (±0.3)	1.5 (±0.1)	31.1 (±2.2)a,A
		Dead	38.0 (±2.4)	1.4 (±0.1)	27.1 (±0.5)b,A
	1000	Live	45.4 (±1.0)	1.3 (±0.1)	35.7 (±2.1)a,A
		Dead	44.0 (±1.2)	1.5 (±0.1)	29.9 (±0.9)b,A
Dry	100	Live	41.4 (±1.2)	1.7 (±0.2)	25.6 (±1.8)a,B
		Dead	37.4 (±0.5)	1.7 (±0.1)	22.1 (±1.5)b,B
	400	Live	39.4 (±0.5)	1.6 (±0.1)	26.4 (±1.0)a,B
		Dead	37.2 (±1.0)	1.7 (±0.2)	22.3 (±1.7)b,B
	1000	Live	43.6 (±0.8)	1.7 (±0.1)	27.1 (±1.6)a,B
		Dead	39.6 (±0.9)	1.7 (±0.1)	23.3 (±1.4)b,B

Lower case letters indicate difference between altitudes within seasons and upper case letters indicate difference between seasons.

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Table 4. Litterfall inputs and stocks in different altitudes and litter decomposition rates (k) and time (months) for decay of 50% ($t_{0.5}$) and 95% ($t_{0.05}$). Data represents six months of sampling (March through August 2007). Values represent mean and standard error (in parenthesis). Different letters represent statistically significant differences among altitudes.

Altitude	Litterfall		Forest Floor		
(m)	Inputs ($t\,ha^{-1}\,y^{-1}$)	Stocks ($t\,ha^{-1}$)	DC[1] (k)	$t_{0.5}$	$t_{0.05}$
100	8.4 (±1.5)[a]	4.3 (±0.8)[a]	2[a]	3	18
400	7.4 (±1.8)[a]	4.4 (±0.4)[a]	1.4[b]	5	25
1000	5.5 (±0.9)[a]	4.8 (±0.6)[b]	1.3[b]	5	27

[1]DC=Decomposition coefficient

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Table 5. Annual mean flux of N_2O and CH_4 for different altitudes. Values represent mean and standard error (in parenthesis). Different letters represent statistically significant differences among the altitudes.

Altitude (m)	N_2O $ng\,N\,cm^{-2}\,h^{-1}$	CH_4 $mg\,CH_4\,m^{-2}\,d^{-1}$
100	2.6 (±0.5)[a]	−1.0 (±0.2)[a]
400	1.0 (±0.1)[b]	−1.8 (±0.1)[b]
1000	0.7 (±0.2)[c]	−1.6 (±0.3)[b]

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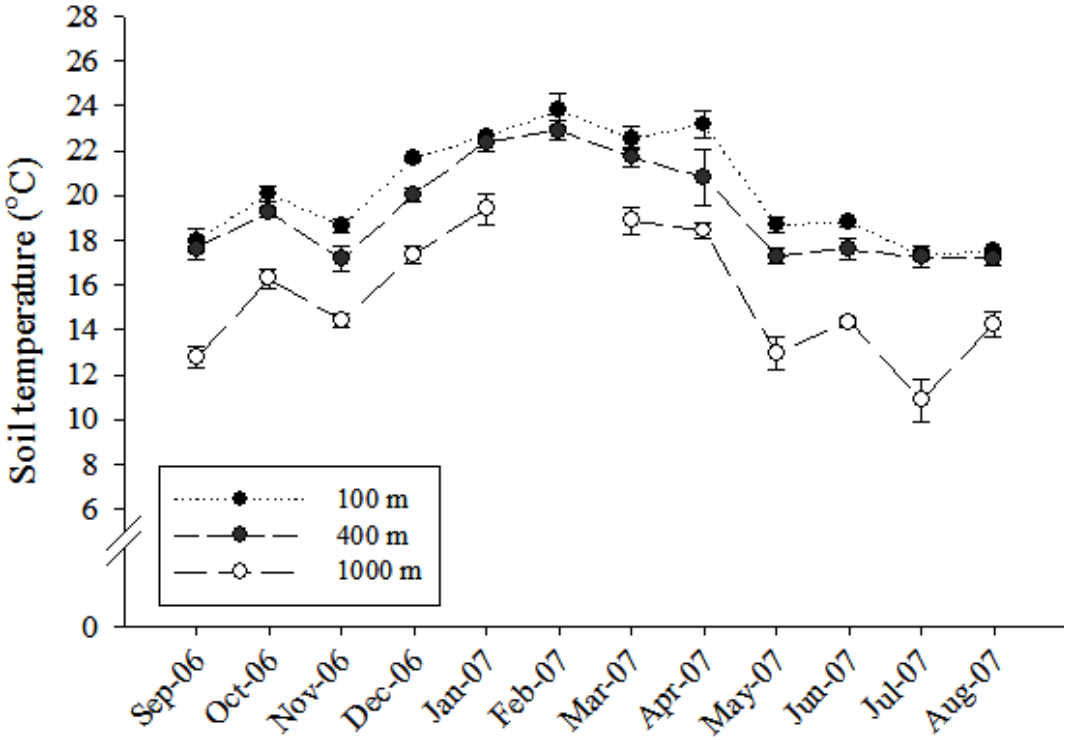

Fig. 1. Monthly soil temperatures (2 cm depth) at the three different elevations. Values represent the mean of four replicate plots per elevation, and error bars represent the standard error. Due to weather conditions it was not possible to collect at altitude 1000 m in February 2007.

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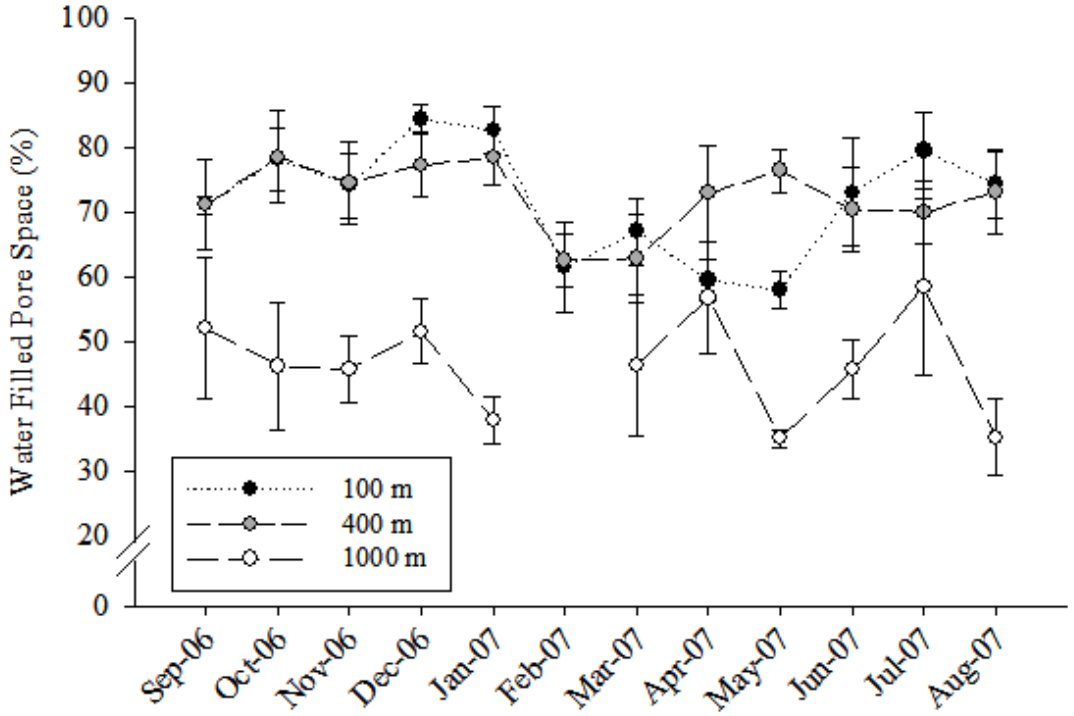

Fig. 2. Monthly variation of Water Filled Pore Space (WFPS) at different elevations. Values represent means of four replicates per elevation and bars represent standard errors. Due to weather conditions it was not possible to collect at altitude 1000 m in February 2007.

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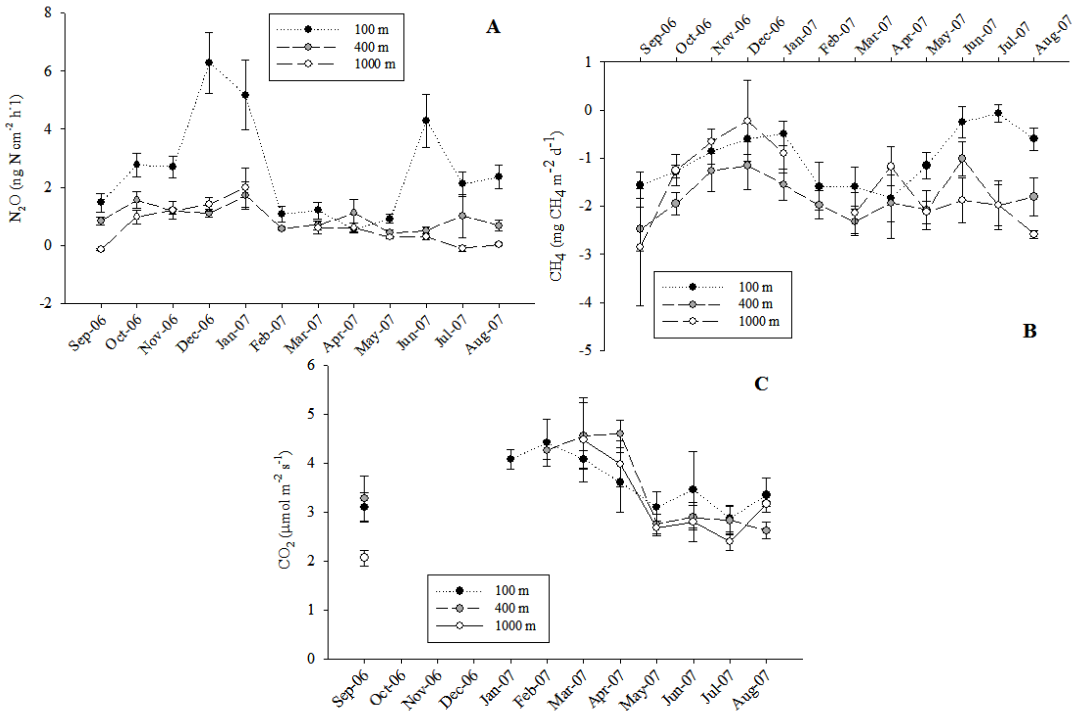

Fig. 3. Monthly soil-atmosphere gas flux of (**A**) nitrous oxide (N_2O), (**B**) methane (CH_4), and (**C**) carbon dioxide (CO_2) at different altitudes. Values represent the mean of four replicates per elevation and bars represent standard errors.

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