

José H. Cattânio · Eric A. Davidson
Daniel C. Nepstad · Louis V. Verchot · Ilse L. Ackerman

Unexpected results of a pilot throughfall exclusion experiment on soil emissions of CO₂, CH₄, N₂O, and NO in eastern Amazonia

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Abstract The eastern Amazon Basin may become drier as a result of less regional recirculation of water in a largely deforested landscape and because of increased frequency and intensity of El Niño events induced by global warming. Drier conditions may affect several plant and soil microbial processes, including soil emissions of CO₂, CH₄, NO, and N₂O. We report here unanticipated results of a pilot study that was initiated to test the feasibility of a larger-scale throughfall exclusion experiment. In particular, soil drying caused a switch from net consumption of atmospheric CH₄ by soils in the control plot to net CH₄ emission from soils in the experimentally dried plot. This result is surprising because production of CH₄ requires anaerobic microsites, which are uncommon in dry soil. A plausible explanation for increased CH₄ emissions in the dried plot is that dry soil conditions favor termite activity and increased coarse root mortality provides them with a substrate. Another surprise was that both NO and N₂O fluxes were elevated several years after initiation of the drying experiment. Apparently, a pulse of N availability caused by experimental drying persisted for at least 3 years. As expected, CO₂ emissions were lower in the dried plots, which is consistent with lower rates of root growth observed in

root in-growth cores placed in the dried plots. More work is needed to test these explanations and to confirm these phenomena, but these results demonstrate that changes in climate could have unanticipated effects on biogeochemical processes in soils that we do not adequately understand.

Keywords Carbon dioxide · Methane · Nitric oxide · Nitrous oxide · Termites

Introduction

Land-use change in the Amazon region is predicted to result in drier conditions because of less regional recirculation of water between the deforested biosphere and the atmosphere (Costa and Foley 2000; Nobre et al. 1991; Shukla et al. 1990). Global warming may also increase the frequency and intensity of El Niño events (Timmermann et al. 1999; Trenberth and Hoar 1997), which cause severe drought in the eastern Amazon Basin (Nepstad et al. 1999). Reduced precipitation in the Amazon Basin may have important feedback effects on climate change by altering soil emissions of carbon dioxide (CO₂), methane (CH₄), nitrous oxide (N₂O), and nitric oxide (NO), which are strongly dependent on soil water content (Firestone and Davidson 1989; Linn and Doran 1984; Whalen and Reeburgh 1996). The direct effects of land-use change in the Amazon region on soil emissions of these gases have been studied (Davidson et al. 2000a; Fearnside 1996; Matson et al. 1990; Steudler et al. 1996; Verchot et al. 1999, 2000), but the possible effects of changes in precipitation have not been addressed.

We report here the results of a pilot study conducted in the eastern Amazon region, where throughfall was excluded from a 10×10-m plot by a subcanopy roof for 4 years. We hypothesized that throughfall exclusion would cause root mortality, a decrease in root production, and, therefore, a decrease in soil emissions of CO₂. We hypothesized that drier soil conditions would favor NO production over N₂O production (Firestone and

J.H. Cattânio
Instituto de Pesquisa Ambiental da Amazônia, Av. Nazaré,
669 Belém, PA 66035–170, Brazil

E.A. Davidson (✉) · D.C. Nepstad
The Woods Hole Research Center, P.O. Box 296, Woods Hole,
MA 02543, USA
e-mail: edavidson@whrc.org
Fax: +1-508-5409700

L.V. Verchot
International Centre for Research in Agroforestry, Nairobi, Kenya

I.L. Ackerman
Department of Crop and Soil Sciences, Cornell University, Ithaca,
NY 14853, USA

Present address:

J.H. Cattânio, Institute for Crop Production in the Tropics,
Grisebachstrasse 6, 37077 Goettingen, Germany

Davidson 1989) and would facilitate increased diffusion of atmospheric CH_4 into the soils, because water often limits rates of CH_4 consumption (Dörr et al. 1993; Striegl 1993). Although this was a pilot study designed to test a concept as a basis for a larger study that is now underway (Nepstad et al., in press), the surprising results merit consideration because they challenge, in part, our understanding of factors that control emissions of these gases from soils.

Materials and methods

Site description

The study was conducted in an old growth forest stand at Fazenda Vitória, located 6.5 km northwest of the town of Paragominas, Pará, Brazil, in eastern Amazonia (2°59' S, 47°31' W), an area of extensive land-use change since the 1960s (Nepstad et al. 1991). Average annual rainfall is 1,800 mm and is highly seasonal, with <250 mm falling from July to November (Jipp et al. 1998). The forest maintains an evergreen canopy throughout the dry season by extracting water from deep in the soil profile, where roots have been observed at 18-m depth (Nepstad et al. 1994; Jipp et al. 1998). The soils were classified by Sombroek (1966) as Kaolinitic Yellow Latosols (Haplustox, according to USDA Soil Taxonomy). Soil temperature at 10-cm depth under the forest canopy only varies between 22°C and 25°C both seasonally and diurnally (Davidson et al. 2000a).

Throughfall exclusion

This experiment was begun in 1993 as a pilot study to test the feasibility of conducting a similar experiment on a larger scale. A 10×10-m plot containing mature trees was trenched to 0.5-m depth around the perimeter. A sub-canopy cover was constructed of sheets of asbestos roofing, 2×0.5 m, placed in rows at about a 2-m height in the center of the plot and draining into wooden gutters at the plot edges. All four sides were open, allowing good ventilation. Because of the dense forest canopy cover, only transient sunflecks hit the roof, and no heating was observed. Soil temperature below the enclosure did not differ from soil temperature outside the enclosure. Openings were also made in the roofing to permit tree trunks to penetrate. Stem flow collectors made of rubber were placed around the tree trunks and the water was emptied onto the roof. Gutters carried the captured throughfall off of the plot to an 80-l barrel at a distance of 4.0 m from the plot. Litter that fell on top of the roof was routinely collected and spread onto the ground beneath the roof. Measurements of canopy water stress were begun immediately, but these data will not be reported here. Taking advantage of this pilot experiment already in progress, root and soil gas studies were initiated in 1995. A similar area was identified 10 m away from the throughfall exclusion plot to serve as the control plot. Most of the canopy cover and basal area of the two plots was from two mature individuals of *Lecythis idatimon* within each plot that were part of the canopy overstory.

Instrumentation and measurements in soil pits

In February of 1995 a soil pit (1.3×0.6 m) was dug to a depth of 4 m within each plot. All coarse roots (>2 mm diameter) were retained during excavation, using sampling depth increments of 0–20, 20–50, 50–100, 100–150, 150–200, 200–250, 250–300, and 300–400 cm. At these same depths, a 10-cm-long increment borer was used to collect three samples for fine roots (<2 mm diameter). These fine root samples were washed, and a sub-sample of root material was separated manually using a dissecting microscope into live and dead root fractions (Nepstad 1989).

Root in-growth bags were prepared by placing mixed subsoil into nylon mesh (2 mm) bags. Four bags of about 1.5 l volume (dry weight =38.2±0.1 g) were placed at two depths, 20 cm and 350 cm, in the walls of the pits of both control and treatment plots. An auger hole of the same diameter as the in-growth bags was used to make a 40-cm-long hole in the sides of the pit walls. The bags were inserted at the ends of the holes in April 1995, and the holes were backfilled. The bags were retrieved in February 1996. The material was washed and sieved (0.4 mm mesh). Live and dead roots were separated manually under a dissecting microscope, samples were dried at 65°C for 72 h and weighed.

In March 1995, the walls of the soil pits were instrumented with time domain reflectometry (TDR) probes at 30-, 50-, 100-, 200-, and 300-cm depth, following the methodology of Jipp et al. (1998). Auger holes were made 1.4 m horizontally into the side of the pit walls, the 30-cm-long, two-prong TDR probes were pushed into the end of these holes, and the holes were backfilled. Two probes were installed at each depth on opposite sides of the soil pit, and were averaged to estimate soil water content. The TDR readings were converted to volumetric water content using the calibration curve for these soils derived by Jipp et al. (1998).

Stainless steel gas sampling tubes (3 mm diameter) were installed into the pit walls of the throughfall exclusion and control plots at depths of 20, 30, 50, 100, 150, 200, 300, and 400 cm, following the methodology of Davidson and Trumbore (1995). The tubes were placed into 1.5-m-long horizontal auger holes that were then backfilled. Gas samples of 20 ml were withdrawn from each tube through a septum and fitting on the exposed end in the soil pit using a nylon syringe. The N_2O and CH_4 analyses by gas chromatography are described below. For CO_2 , the method of Davidson and Trumbore (1995) was used, in which syringe samples were injected into a stream of CO_2 -free air flowing through a LiCor CO_2 analyzer. Profiles of NO concentrations were not measured.

Flux measurements

Fluxes of gases at the soil surface were made using chambers consisting of a polyvinyl chloride (PVC) ring (20-cm diameter × 10-cm height) and a vented PVC cover made from an end-cap of a 20-cm-diameter PVC pipe. In June 1995, PVC rings were pushed into the soil to a depth of 2–3 cm to make the base of the chamber and were left in place for the duration of the study. Eight rings were placed in the throughfall exclusion plot and eight more in the control area.

Fluxes of NO and CO_2 were measured using a dynamic chamber technique described in detail by Verchot et al. (1999) and Davidson et al. (2000a). Air drawn from the chamber was circulated through a Nafion gas sample dryer, a Scintrex LMA-3 NO_2 analyzer, and a LiCor infrared gas analyzer, and then back to the chamber, using Teflon tubing and a battery operated pump, at a flow rate of 0.5 l min^{-1} . Varying the flow rate from 0.4 to 1.2 l min^{-1} had no detectable effect on measured flux rates. NO is converted to NO_2 by a CrO_3 converter, and the NO_2 is detected by chemiluminescent reaction with Luminol. Fluxes were calculated from the rate of increase of NO and CO_2 concentrations, recorded by a datalogger at 12-s intervals between 1 and 3 min after placing the cover over the ring. The instruments were calibrated twice daily in the field.

Fluxes of N_2O and CH_4 were measured using a static chamber technique (Matson et al. 1990) on the same chamber bases as those described above. Both dynamic and static chamber flux measurements were made on the same day and, in most cases, within 90 min of each other. Syringe samples removed from the chamber headspace at 30 s, 10 min, 20 min, and 30 min were analyzed in the laboratory by gas chromatography within 24 h, using an electron capture detector for N_2O analysis and a flame ionization detector for CH_4 analysis (Verchot et al. 1999, 2000). Fluxes were calculated from the rate of concentration change, determined by linear regression.

Eight chamber flux measurements were made in the control plot and eight measurements in the treatment plot on one day in each month from June 1995 to April 1996. Diel effects have been found to be minor in this forest, and sources of spatial and temporal

variation using this sampling scheme have been addressed in other publications (Davidson et al. 2000a; Verchot et al. 1999, 2000).

Small throughfall exclusions with replication

Because the 10×10-m throughfall exclusion plot was not replicated, our statistical comparisons of data from the treatment and control plots compare within-plot variance among subsamples to differences between the treatment (plot) means. In order to provide replication, we established five blocks of small throughfall exclusion plots between trees within the forest in February 1995. Each block consisted of a pair of 2×2-m plots with inclined plastic sheeting placed over the top of a wooden frame at about 0.5 m above the soil surface. Throughfall from the plastic was captured in PVC gutters and carried away from the plot. Five throughfall collectors were also installed in the experimental area so that the amount of throughfall could be quantified. A quantity of throughfall water equivalent to the mean rate of throughfall was added back with a sprinkling can to one plot within each block on approximately a weekly basis during the wet season and a monthly basis during the dry season. The throughfall water was obtained from the barrel in the larger throughfall exclusion plot. Hence one plot within each block of small plots had complete throughfall exclusion and the other had throughfall excluded, but then an equivalent amount of water added back onto the plot. If there was an effect of the plastic on microclimate or on the quality of light penetrating to the forest floor, both treatment and control plots were equally affected. Gravimetric water content of soil cores (0–10 cm) destructively sampled from these small plots at the end of the experiment in November 1995 was measured by drying at 105°C.

A PVC ring was inserted into the soil in the middle of each plot for trace gas measurements. Fluxes of the four gases were measured monthly between June and December 1995. A split-plot design was used to partition variance into main effects of the blocks, treatments, months, and month-treatment interactions.

Results and discussion

Soil water content

The throughfall exclusion was effective in reducing soil water content (Fig. 1). The largest difference was apparent in April, near the end of the wet season, when the soil under the throughfall exclusion was drier at all depths. Although effective, the exclusion was not 100%, as it appears that some recharge took place during the wet season in the soil of the exclusion plot. Lateral movement of water below the level of trenching is also possible.

Because there was very little rain during the dry season months of July to November (Fig. 2a), the soils dried out in the control plot. Plant uptake of water stored in the deep soils maintains an evergreen canopy in this region (Jipp et al. 1998; Nepstad et al. 1994). At the end of the dry season in November, the top 30 cm of soil was still drier under the throughfall exclusion, but differences had disappeared at other depths (Fig. 1).

Root biomass and growth

Coarse and fine live root biomass, determined in the soil pits dug 2 years after the throughfall exclusion began, varied among depths, and no consistent difference between

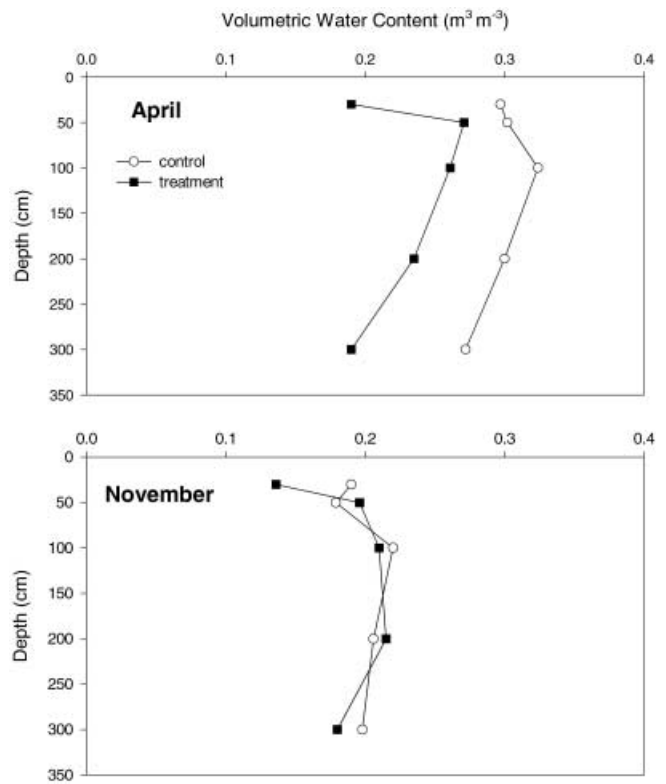


Fig. 1 Profiles of volumetric water content in soil pits in control and throughfall exclusion plots in the wet season (April) and dry season (November) 1995

control and throughfall exclusion plots was observed (Table 1). Fine dead root biomass was the same for the two treatments when summed over the entire profile, but there were significant differences in dead fine roots in the top 100 cm of soil, with higher values in the exclusion plot than the control plot. Coarse dead root biomass was greater in the pit dug in the throughfall exclusion plot than in the soil pit of the control plot. Either trenching around the perimeter of the throughfall exclusion plot (about 5 m from the central soil pit) or drought stress experienced within the plot could have caused root mortality.

Root growth during the 10 months that the in-growth bags were in place was significantly lower under the throughfall exclusion [71 ± 16 and 26 ± 5 g m⁻³ (mean \pm standard error of four in-growth cores) at 20- and 350-cm depth, respectively] than in the control plot (156 ± 20 and 145 ± 46 g m⁻³ at 20- and 350-cm depth, respectively). The difference between treatments was significant at both depths (*t*-test; $P < 0.01$). The root in-growth bags provide an index of the ability of the roots to grow into newly mixed soil, which was clearly inhibited by the dry conditions of the throughfall exclusion plot.

Gas fluxes

Emissions of CO₂ were higher in the wet season than in the dry season in the control plot (Fig. 2b), which is con-

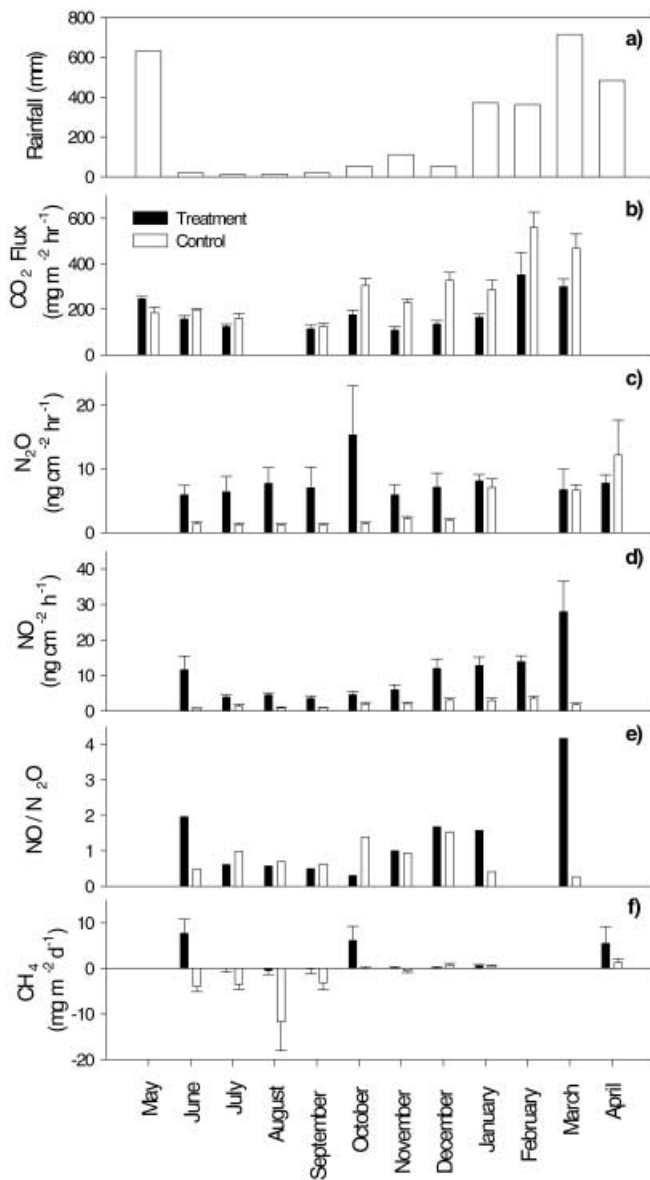


Fig. 2a–f Throughfall and trace gas emissions from May 1995 to April 1996. Some months of missing data for trace gas emissions were due to equipment failure. Each *bar* represents the mean and each *error bar* represents the standard error of eight chamber measurements per site and date

sistent with previous results at this ranch (Davidson et al. 2000a). Emissions in the throughfall exclusion plot were lower for CO_2 (Fig. 2b) compared to the control plot for most months. Lower CO_2 fluxes from the soil in the throughfall exclusion plot indicate that lower soil water content during the wet season caused reduced rates of root respiration or soil microbial respiration or both. This result is consistent with reduced root growth into the in-growth bags. The effect appears to have persisted into the dry season.

Emissions of N_2O and NO were higher in the wet season than in the dry season in the control plot (Fig. 2c, d), which is also consistent with previous results (Verchot et al. 1999). Emissions in the throughfall exclusion plot

were higher for N_2O (Fig. 2c) and NO (Fig. 2d) compared to the control plot for most months. The ratio of $\text{NO}:\text{N}_2\text{O}$ flux was similar in the two treatments during the dry season, but was higher in the throughfall exclusion plot than in the control plot during the wet season (Fig. 2e). Higher fluxes of NO in the throughfall exclusion plot (Fig. 2d) can be explained by drier conditions favoring the more oxidized form of N – NO – over the more reduced form – N_2O – resulting from either nitrification or denitrification (Davidson et al. 2000b; Firestone and Davidson 1989). Nitrification and chemodenitrification can also be favored over denitrification in dry soils (Davidson 1992), which would usually result in an increase in NO emissions relative to N_2O emissions.

In addition to an effect on the ratio of $\text{NO}:\text{N}_2\text{O}$, the sum of $\text{NO} + \text{N}_2\text{O}$ emissions also increased as a result of throughfall exclusion, because both NO and N_2O emissions were often higher in the exclusion plot than in the control plot (Fig. 2c, d). The increase in total emissions of the two N oxide gases could result from less reduction of these gases to N_2 via denitrification. Another explanation is that root mortality and reduced root uptake of N due to drought stress would increase the availability of NH_4^+ to nitrifying bacteria and NO_3^- to denitrifying bacteria, thus promoting greater bacterial production of nitrogen oxide gases.

If the enhanced NO and N_2O emissions are the result of a pulse of N availability due to root mortality and to reduced plant uptake of N, then the emissions of these gases might also eventually decline once that pulse of available N is spent and a new equilibrium is established in an ecosystem adapted to drier conditions. These results do not provide an estimate of how long it might take to establish a new equilibrium in the soil cycles of C and N as a result of changes in precipitation, although the disturbance effect was still readily apparent 3 years after the initiation of the throughfall exclusion experiment.

Also as previously observed in this forest (Verchot et al. 2000), the soil of the control plot consumed atmospheric CH_4 during the dry season and had zero net flux (consumption equaled production of CH_4 in the soil) or was a modest net source of CH_4 during the wet season (Fig. 2f). In contrast, the throughfall exclusion plot had about zero net flux for most months of the dry season and had a positive flux from the soil to the atmosphere (net production) during two of the dry season months (June and October) and one month during the wet season (April).

Diffusion of atmospheric CH_4 into the soil is often the dominant factor constraining the rate of CH_4 oxidation within soil (Davidson and Schimel 1995; Dörr et al. 1993; Striegl 1993; Verchot et al. 2000). Hence, we expected that dry soils would have higher rates of CH_4 consumption than the control soils (i.e. larger negative values in Fig. 2f). To the contrary, we observed that fluxes of CH_4 were either zero (production equaled consumption) or positive (production exceeded consumption). The soil of the throughfall exclusion plot was a net source of atmospheric CH_4 .

Table 1 Root mass by soil volume (g dry roots m⁻³ soil) for each sampling depth increment in soil pits of the throughfall exclusion and control plots. For fine roots (<2 mm diameter), means ± standard errors of three samples per depth increment are given. Student's *t*-tests (*P* = 0.05) for each depth showed no significant differences between treatments for live fine roots. For fine dead fine

roots, the differences were significant above the 100-cm depth and not significant below 100 cm. For coarse roots (>2 mm diameter), the entire volume of the soil pit was sampled; no statistical tests are possible. The root mass by area (g m⁻²) is summed for the top 4 m of soil

Depth (cm)	Fine roots				Coarse roots			
	Live roots		Dead roots		Live roots		Dead roots	
	Exclusion	Control	Exclusion	Control	Exclusion	Control	Exclusion	Control
	(g m ⁻³)							
0–20	195±51	244±37	652±26	554±27	2,390	6,300	332	168
20–50	99±24	97±31	154±36	82±15	7,670	1,910	498	0
50–100	64±22	28±4	62±15	16±2	410	283	8	4
100–150	12±3	5±4	26±14	4±2	49	28	29	2
150–200	12±7	109±82	7±2	254±116	27	15	9	0
200–250	16±10	5±3	7±2	2±1	22	59	9	0
250–300	7±3	1±1	7±3	1±0	0	29	2	0
300–400	2±1	1±0	1±1	1±0	0	19	0	1
	(g m ⁻²)							
0–400	126	153	232	275	3,033	2,057	244	37

It is possible that water stress reduced the capacity of methane oxidizers in the soil (King 1997), but soil drying should also reduce the incidence of anaerobic microsites where CH₄ production occurs (Davidson and Schimel 1995). Hence, higher rates of CH₄ production in drier soils are difficult to explain if the CH₄ production is by free-living soil methanogens. Another anaerobic microsite where CH₄ is produced is the gut of termites (Seiler et al. 1984), which are common in Amazonia (Martius 1994). The presence of remarkable termite activity in the throughfall exclusion plot was anecdotally noted, but, unfortunately, no faunal measurements to quantify this unexpected result had been planned. Termite activity may have been stimulated by the presence of greater dead coarse root biomass (Table 1) or by the wooden structures holding up the throughfall exclusion panels (although it is difficult to see how this latter explanation would affect CH₄ concentrations at a 2-m soil depth; Fig. 3c). The drier soil conditions created by our throughfall exclusion may have been closer to the optimal soil moisture range preferred by termites for foraging (Hanne 2001).

Termite biomass has been related to CH₄ fluxes in other tropical forests (MacDonald et al. 1998; Martius et al. 1996; Sanderson 1996), and soil termites are the presumed source of net CH₄ emissions measured in savanna ecosystems (Scharffe et al. 1990; Poth et al. 1995). Soil feeding termites have been shown to reduce the net uptake of CH₄ by soils, presumably by partially offsetting bacterial oxidation of CH₄ with termite emissions of CH₄ (MacDonald et al. 1999). In the absence of other plausible explanations, we speculate that the increased production and reduced net consumption of CH₄ as a consequence of throughfall exclusion was due to a more favorable soil environment for termites. If true, this would be an unexpected effect resulting from reduction of precipitation in the Amazon Basin.

Profiles of concentrations of CO₂, N₂O, and CH₄ support the chamber flux measurements. In general, the concentrations of CO₂ were lower (Fig. 3a) and the concentrations of N₂O (Fig. 3b) and CH₄ (Fig. 3c) were higher in the throughfall exclusion soil profiles than in the control soil profile. Increasing CO₂ concentration with depth (Fig. 3a) indicates a significant deep soil source of this gas (Davidson and Trumbore 1995). Irregular patterns of N₂O and CH₄ concentrations with depth (Fig. 3b, c) indicate that there were pockets of production, such as at the 50- to 100-cm depth for N₂O and 200 cm for CH₄. Verchot et al. (1999) showed production of N₂O at a 2-m depth in this same forest soil, and Verchot et al. (2000) showed hot spots of CH₄ production within the soil profile.

Replicated mini-exclusion plots

Because this pilot study of a moderate-sized (100 m²) throughfall exclusion was not replicated, we installed replicated small plots (4 m²). Other differences are that these miniplots were not trenched, that both control and treatment plots received the same level of disturbance and the same artifacts that might be caused by the throughfall exclusion structure, and that the throughfall exclusion was begun in the same year as the measurements (compared to 2 years after initiation of throughfall exclusion for the larger unreplicated plot). At the end of the experiment, gravimetric water content of the top 10 cm soil was slightly but statistically significantly lower in the exclusion miniplots (0.259 g H₂O g⁻¹ dry soil) compared to the control miniplots (0.274 g H₂O g⁻¹ dry soil). As in the larger experiment, the small difference between treatment and control plots in November is probably due to uptake of most of the plant available wa-

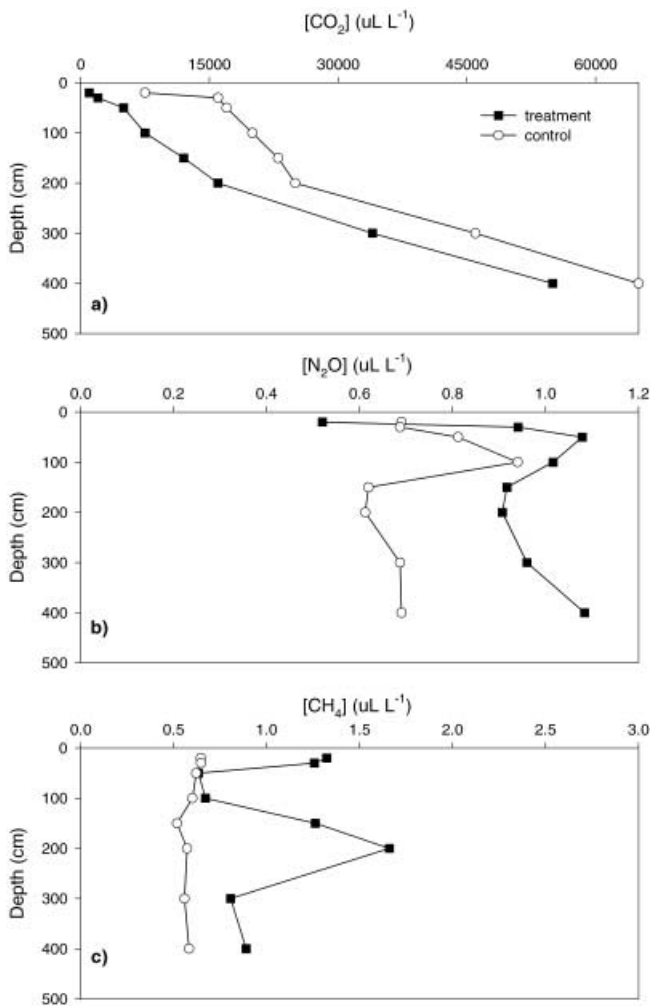


Fig. 3a–c Profiles of concentrations of CO_2 , N_2O , and CH_4 measured in treatment and control soil pits in November 1995

ter by the vegetation in both the treatment and control plot during the long dry season.

Also consistent with the results from the large plot, throughfall exclusion in the miniplots significantly decreased soil emissions of CO_2 and caused a switch from mostly net consumption of atmospheric CH_4 in the con-

trol miniplots to net CH_4 emission from the dried miniplot soils during all of the monthly measurements (Table 2). However, very large variation among replicates of the dried plots (Table 2) precluded a statistically significant treatment effect for CH_4 . The increased variance of CH_4 fluxes under throughfall exclusion suggests production is localized in hotspots. No treatment effect was apparent for NO and N_2O fluxes in the miniplots (Table 2). Hence, the effect of experimental drying was almost immediate for the carbon gases, but did not occur during the first dry season of miniplot treatment for the nitrogen gases. Perhaps respiration responds quickly to changes in soil water content, whereas an increase in N availability due to reduced root uptake of N or due to root mortality and decomposition takes longer to materialize.

Longer term monitoring is needed to address these processes. A new throughfall exclusion experiment has been initiated that will include long-term monitoring, as well as address several of the methodological limitations of this pilot study, such as plot size, depth of trenching, transparency of the throughfall exclusion panels, measures of soil faunal activity, and pre-treatment comparisons of control and treated plots (Nepstad et al., in press).

Conclusion

The results of this pilot study present new questions. In particular, how can soil drying cause a switch from net consumption of atmospheric CH_4 by soil to net CH_4 emission from soils? Apparently, diffusivity of gases in soils is not always the dominant mechanism that controls soil CH_4 fluxes. How quickly do processes in humid tropical soils respond to perturbations? Although decomposition of dead roots and other soil organic matter is presumed to be rapid in humid tropical soils, the pulse of N availability and emissions of NO and N_2O caused by experimental drying persisted for at least 3 years, and probably more. We have offered speculative explanations for these observations, but more work is clearly needed to test these hypotheses. In any case, these results show that expected changes in climate, such as reduced

Table 2 Fluxes from replicated miniplots of throughfall exclusion and control treatments. Means \pm standard errors of five chamber measurements (one in each miniplot) are presented for each month and treatment. The treatment effect was significant by ANOVA (α

$=0.05$) only for CO_2 . For CH_4 , *positive values* indicate net emission from the soil to the atmosphere, and *negative values* indicate net consumption of atmospheric CH_4 by the soil

Month	CO_2 ($\text{mg C m}^{-2} \text{h}^{-1}$)		N_2O ($\text{ng N cm}^{-2} \text{h}^{-1}$)		NO ($\text{ng N cm}^{-2} \text{h}^{-1}$)		CH_4 ($\text{mg CH}_4 \text{m}^{-2} \text{d}^{-1}$)	
	Exclusion	Control	Exclusion	Control	Exclusion	Control	Exclusion	Control
June	149 \pm 14	156 \pm 19	0.87 \pm 0.15	0.80 \pm 0.22	1.68 \pm 0.45	0.84 \pm 0.27	-0.96 \pm 1.77	-5.65 \pm 0.45
July	120 \pm 17	109 \pm 26	0.52 \pm 0.13	1.10 \pm 0.75	1.24 \pm 0.47	1.07 \pm 0.72	1.96 \pm 5.53	-5.62 \pm 0.36
August	83 \pm 8	96 \pm 17	0.43 \pm 0.06	0.48 \pm 0.22	1.02 \pm 0.28	0.52 \pm 0.14	5.74 \pm 7.67	-5.59 \pm 0.80
September	79 \pm 11	86 \pm 2	0.63 \pm 0.10	0.69 \pm 0.18	1.15 \pm 0.10	1.46 \pm 0.24	2.21 \pm 1.88	-1.23 \pm 0.25
October	100 \pm 16	170 \pm 35	0.51 \pm 0.09	1.02 \pm 0.18	1.46 \pm 0.42	5.33 \pm 2.32	3.50 \pm 2.54	-1.03 \pm 0.12
November	97 \pm 20	121 \pm 11	0.56 \pm 0.11	0.89 \pm 0.24	1.79 \pm 0.35	2.99 \pm 1.69	3.49 \pm 1.62	-1.35 \pm 0.22
December	102 \pm 23	135 \pm 34	0.52 \pm 0.19	0.36 \pm 0.03	3.58 \pm 0.35	3.86 \pm 1.61	-0.43 \pm 1.59	-1.22 \pm 0.29

precipitation in the eastern Amazon Basin, could have unanticipated biogeochemical effects in soils, and that we do not fully understand all of the underlying processes.

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