

Moisture and substrate availability constrain soil trace gas fluxes in an eastern Amazonian regrowth forest

Steel S. Vasconcelos,¹ Daniel J. Zarin,¹ Marinela Capanu,² Ramon Littell,² Eric A. Davidson,³ Francoise Y. Ishida,⁴ Elisana B. Santos,⁴ Maristela M. Araújo,⁵ Débora V. Aragão,⁵ Lívia G. T. Rangel-Vasconcelos,⁶ Francisco de Assis Oliveira,⁷ William H. McDowell,⁸ and Claudio José R. de Carvalho⁹

Received 18 December 2003; revised 29 March 2004; accepted 7 April 2004; published 21 May 2004.

[1] Changes in land-use and climate are likely to alter moisture and substrate availability in tropical forest soils, but quantitative assessment of the role of resource constraints as regulators of soil trace gas fluxes is rather limited. The primary objective of this study was to quantify the effects of moisture and substrate availability on soil trace gas fluxes in an Amazonian regrowth forest. We measured the efflux of carbon dioxide (CO₂), nitric oxide (NO), nitrous oxide (N₂O), and methane (CH₄) from soil in response to two experimental manipulations. In the first, we increased soil moisture availability during the dry season by irrigation; in the second, we decreased substrate availability by continuous removal of aboveground litter. In the absence of irrigation, soil CO₂ efflux decreased during the dry season while irrigation maintained soil CO₂ efflux levels similar to the wet season. Large variations in soil CO₂ efflux consistent with a significant moisture constraint on respiration were observed in response to soil wet-up and dry-down events. Annual soil C efflux for irrigated plots was 27 and 13% higher than for control plots in 2001 and 2002, respectively. Litter removal significantly reduced soil CO₂ efflux; annual soil C efflux in 2002 was 28% lower for litter removal plots compared to control plots. The annual soil C efflux:litterfall C ratio for the control treatment (4.0–5.2) was consistent with previously reported values for regrowth forests that indicate a relatively large belowground C allocation. In general, fluxes of N₂O and CH₄ were higher during the wet season and both fluxes increased during dry-season irrigation. There was no seasonal effect on NO fluxes. Litter removal had no significant impact on N oxide or CH₄ emissions. Net soil nitrification did not respond to dry-season irrigation, but was somewhat reduced by litter removal. Overall, these results demonstrate significant soil moisture and substrate constraints on soil trace gas emissions, particularly for CO₂, and suggest that climate and land-use changes that alter moisture and substrate availability are therefore likely to have an impact on atmosphere chemistry.

INDEX TERMS: 0315

Atmospheric Composition and Structure: Biosphere/atmosphere interactions; 1615 Global Change: Biogeochemical processes (4805); 1866 Hydrology: Soil moisture; 1842 Hydrology: Irrigation; KEYWORDS: Amazon, dry-season irrigation, litter removal, methane, nitrogen oxides, soil respiration

Citation: Vasconcelos, S. S., et al. (2004), Moisture and substrate availability constrain soil trace gas fluxes in an eastern Amazonian regrowth forest, *Global Biogeochem. Cycles*, 18, GB2009, doi:10.1029/2003GB002210.

1. Introduction

[2] Tropical forests represent an important source of atmospheric greenhouse gases including carbon dioxide

(CO₂), nitrous oxide (N₂O), and methane (CH₄), along with nitric oxide (NO), a precursor to the photochemical production of tropospheric ozone [Vitousek and Matson, 1992]. The production and consumption of these gases are strongly linked to the availability of both soil moisture and decom-

¹School of Forest Resources and Conservation, University of Florida, Gainesville, Florida, USA.

²Department of Statistics, University of Florida, Gainesville, Florida, USA.

³Woods Hole Research Center, Woods Hole, Massachusetts, USA.

⁴Instituto de Pesquisa Ambiental da Amazônia, Belém, Brazil.

⁵Departamento de Ciências Florestais, Universidade Federal Rural da Amazônia, Belém, Brazil.

⁶Soil and Water Science Department, University of Florida, Gainesville, Florida, USA.

⁷Departamento de Ciências do Solo, Universidade Federal Rural da Amazônia, Belém, Brazil.

⁸Department of Natural Resources, University of New Hampshire, Durham, New Hampshire, USA.

⁹Embrapa Amazônia Oriental, Belém, Brazil.

posable substrate. However, seasonal cycles of precipitation, litterfall, and decomposition are often confounded in ways that limit our ability to quantify the relative importance of these interacting factors from seasonal observations of gaseous fluxes.

[3] Observational studies in tropical forests have shown that higher soil moisture availability during the wet season usually increases soil CO₂ and N₂O effluxes, decreases NO efflux, and decreases CH₄ consumption rates [Verchot *et al.*, 1999; Davidson *et al.*, 2000; Verchot *et al.*, 2000; Garcia-Montiel *et al.*, 2001; Fernandes *et al.*, 2002; Kiese and Butterbach-Bahl, 2002; Kiese *et al.*, 2003]. Fewer studies have evaluated the response of soil trace gas fluxes to experimental manipulation of soil moisture availability in tropical forests. In a throughfall exclusion experiment in the Tapajós National Forest, Brazil, emissions of N₂O and CH₄ were reduced by the exclusion of about 50% of annual throughfall, but no treatment effect was observed for NO or CO₂ emissions [Nepstad *et al.*, 2002]. Addition of water to dry soil in short-term, small-scale field studies has resulted in increased emissions of CO₂, NO, and N₂O in wet [Nobre *et al.*, 2001; Garcia-Montiel *et al.*, 2003b] and seasonally dry [Davidson *et al.*, 1993] tropical forest soils.

[4] To our knowledge, there are no reports of field studies that assess emissions of soil trace gases in response to the manipulation of substrate availability in tropical forests. In temperate forests, reduction of substrate availability through litter removal resulted in decreased soil CO₂ efflux [Bowden *et al.*, 1993; Jandl and Sollins, 1997; Rey *et al.*, 2002], but we encountered no published reports of litter removal effects on NO, N₂O, and CH₄.

[5] Measurements of soil CO₂ efflux and non-woody litterfall can be used to estimate total belowground carbon allocation (TBCA) in forests [Raich and Nadelhoffer, 1989]. For mature forests, TBCA is about 2 times aboveground litterfall, while for regrowth forests, TBCA is about 3 times aboveground litterfall [Raich and Nadelhoffer, 1989; Davidson *et al.*, 2002], indicating that regrowth forests allocate a relatively larger proportion of C to belowground structures than mature forests [Davidson *et al.*, 2002]. Although TBCA represents the single largest flux of C in forest ecosystems aside from canopy C assimilation [Davidson *et al.*, 2002], little is known about this flux of C in tropical forests.

[6] A better understanding of how trace gas emissions from tropical forest soils are affected by moisture and substrate availability can help to improve current biogeochemical models that predict impacts of changes in climate and land-use practices on the atmospheric concentrations of these gases [Potter and Klooster, 1998]. Such data, together with more estimates of total belowground C allocation in tropical forests, are also needed to better understand carbon dynamics in regrowth forests [Johnson *et al.*, 2000]. Few such data are available for Amazonian regrowth forests, a significant and dynamic component of forest landscapes in this region [Fearnside, 1996; Zarin *et al.*, 2001].

[7] Our primary objective in this study was to quantify the effects of moisture and substrate availability on soil trace gas emissions in an Amazonian regrowth forest stand. In

one experiment, dry-season moisture limitation was reduced by irrigation. In the other experiment, substrate limitation was provoked by litter removal.

2. Study Site

[8] This study was conducted at a field station belonging to the Federal Rural University of Amazonia (Universidade Federal Rural da Amazônia (UFRA)), Brazil, near the city of Castanhal (1°19'S, 47°57'W). Mean ± SE annual rainfall received from 1993 to 2002 in this area was 2539 ± 280 mm, most of which falls between January and June (Figure 1a); total rainfall was 2399 mm in 2000, 3179 mm in 2001, and 2301 mm in 2002. Mean daily temperatures fluctuate between 24° and 27°C. The soils are classified as Distrophic Yellow Latosol Stony Phase I [Tenório *et al.*, 1999] in the Brazilian Classification, corresponding to Sombriustox in U.S. Soil Taxonomy. Soil granulometric composition in the first 20 cm is 20% clay, 74% sand, and 6% silt. In the surface soil (0–10 cm), pH is 5.0, organic C is 2.2%, organic C stock is 2.9 kg m⁻², total N is 0.15%, C:N is 14.4, and Mehlich-1 extractable phosphorus is 1.58 mg kg⁻¹ [Rangel-Vasconcelos, 2002].

[9] Regrowth forests, annual crops, and active and degraded pastures characterize the landscape surrounding the field station. The stand under study was last abandoned in 1987 following multiple cycles of shifting cultivation, beginning in the 1940s when the old-growth forest was first cleared. Each cycle included cultivation of corn, manioc, and beans, for 1 to 2 years followed by fallow. Typical shifting cultivation cycles lasted 7 to 10 years (G. Silva e Souza and O.L. Oliveira, personal communication, 2002). The four most abundant overstory species are *Lacistema pubescens* Mart., *Myrcia sylvatica* (G. Mey) DC, *Vismia guianensis* (Aubl.) Choisy, and *Cupania scrobiculata* Rich., representing 71% of all stems in the stand. In November 1999, stem density was 213 ± 19.7 individuals per 100 m², basal area was 13 ± 6 m² ha⁻¹, and height was 4.9 ± 0.4 m for the stand [Coelho *et al.*, 2004].

3. Experimental Design

[10] Plots were established in 1999, when the regrowth forest was 12 years old. Each plot was 20 × 20 m with a centrally nested 10 × 10 m measurement subplot. There were four replicate plots for the irrigation treatment, four plots for the litter removal treatment, and four plots left untreated as controls.

[11] Irrigation was applied at a rate of 5 mm day⁻¹, for about 30 min, during the dry seasons of 2001 (from 10 August to 16 January) and 2002 (from 16 August to 20 January) in the late afternoon. Total irrigation amount was 665 and 790 mm in 2001 and 2002, respectively. The amount of daily irrigation applied corresponds to regional estimates of daily evapotranspiration [Shuttleworth *et al.*, 1984; Lean *et al.*, 1996; Jipp *et al.*, 1998]. Irrigation water was distributed through tapes with microholes every 15 cm. In 2001, irrigation tapes were spaced 4 m from each other. In 2002 we reduced the distance between tapes to 2 m to facilitate more even distribution of water.

[12] We used rainfall and soil suction data to define approximate boundaries for the dry and wet seasons. The start of the dry season was defined by total rainfall less than 150 mm in the previous 30 days and soil suction more negative than -0.010 MPa; the end of the dry season was defined by total rainfall greater than 150 mm in the previous 30 days and soil suction less negative than -0.010 MPa. Since the soil suction data were obtained on a weekly basis, we estimate that the error in the location of seasonal boundaries is about 7 days.

[13] In the litter removal plots, leaf and branch fall were removed from the forest with plastic rakes every 2 weeks, beginning in August 2001 with the removal of the pretreatment litter layer ($538 \pm 35 \text{ g m}^{-2}$, $n = 4$); C and N stocks of the pretreatment litter layer were 222.9 ± 14.6 and $7.3 \pm 0.5 \text{ g m}^{-2}$, respectively ($n = 8$). Total new non-woody litterfall removed during the treatment period was $1309 \pm 68 \text{ g m}^{-2}$ ($n = 4$) with C and N concentrations of 47.9 ± 0.2 and $1.2 \pm 0.02\%$, respectively, and C:N ratio of 40 ± 0.7 ($n = 12$).

[14] Measurements of gravitational soil moisture content in the first 10 cm of soil for one date during the 2001 dry season indicated that irrigated plots had about twice as much moisture as control plots ($22 \pm 2\%$ versus $10 \pm 2\%$); in the litter removal plots soil moisture was $11 \pm 2\%$. For one date during the 2001 wet season, gravitational soil moisture content was $27 \pm 2\%$ for control and irrigated plots, and $31 \pm 2\%$ for litter removal plots [Rangel-Vasconcelos, 2002]. The difference in soil moisture status between control and irrigated plots was reflected in dry-season differences in pre-dawn leaf water potential for an understory species (*Miconia ciliata*); in November 2001, pre-dawn leaf water potential for control plants was about -1.2 MPa while irrigated plants were about 1 MPa less negative [Fortini et al., 2003].

4. Material and Methods

4.1. Field Measurements

[15] Since July 2001, daily rainfall has been measured 500 m away from the experimental area using a standard rain gauge. Prior to July 2001, rainfall data reported here are from the National Agency of Electrical Energy (ANEEL) network meteorological station at Castanhal ($01^{\circ}17'53''\text{S}$, $47^{\circ}56'56''\text{W}$), which is no longer in operation and that was about 3 km away from our site.

[16] One tensiometer (Jet Fill Tensiometers, Soilmoisture Equipment Corp., Santa Barbara, California) was installed at a depth of 10 cm in each plot, and soil suction was recorded on a weekly basis in the morning. The number of actual replicates per treatment varied due to loss of water column tension during the dry season.

[17] Soil CO_2 efflux was generally measured bi-weekly, beginning in March 2000, with an LI-6400 portable photosynthesis system fitted with an LI-6400-09 soil CO_2 flux chamber (LI-COR Inc., Lincoln, Nebraska). The chamber was fit into circular polyvinyl chloride (PVC) collars (115 mm internal diameter \times 55 mm deep), which were installed approximately 20 mm into the soil. Each plot contained three soil collars, spaced at least 1 m apart, totaling 12 collars per treatment and

sampling date. No live vegetation was contained within the collars. Measurements were taken between 0630 and 1100 hours.

[18] To better understand the results of CO_2 flux analyses within the context of stand-level C dynamics, we also collected data on litterfall. Three 1×1 m screen litter traps were installed in the 10×10 m measurement subplots. Each week, we collected all material present in each trap, and air-dried the material in the lab to remove excess moisture before storage. At 4-week intervals, we composited material from the same collector and then separated it into woody and non-woody fractions (includes leaves and their petioles, foliar rachises, and reproductive parts). We weighed woody and non-woody litterfall after drying at 60° – 70°C until constant weight. We estimated that non-woody litterfall was 48% C based on the monthly non-woody litterfall C concentration ($47.9 \pm 0.2\%$) during the period of October 1999 to March 2001. Non-woody litterfall was 80 to 90% of total litterfall. Woody litterfall data are not reported here because of its much smaller impact on short-term trace gas emissions due to its slow turnover rate.

[19] Two additional PVC collars with 20 cm diameter and 10 cm height were installed within each plot (total of eight collars per treatment and sampling date) and inserted approximately 2–3 cm into the soil for measurement of soil NO , N_2O , and CH_4 gas fluxes. During the measurements, a vented PVC cover made from the end cap of a 20-cm-diameter PVC pipe was fit into the collars. On average, NO , N_2O , and CH_4 flux measurements were made every 2 months, beginning in August 1999. The flux measurement technique for NO used a chemiluminescence detector (Scintrex LMA-3, Scintrex Limited, Concord, Ontario, Canada) as described by Verchot et al. [1999]. N_2O and CH_4 fluxes were measured by gas chromatography analyses of four syringe samples extracted from the same chambers at 10-min intervals [Verchot et al., 1999, 2000]. The PVC collars used for soil trace gas measurements were left in place throughout the course of the experiments.

[20] To augment our understanding of the N gas fluxes (NO and N_2O), we also include here results of potential soil nitrification determined with a variation of the aerobic incubation method [Hart et al., 1994]. Nitrification is the precursor to the denitrification process, and both processes produce NO and N_2O [Firestone and Davidson, 1989]. For each plot, we analyzed one composite sample made of four samples collected at a depth of 10 cm in October 2001. We estimated net N nitrification from changes in nitrate concentrations during 7-day incubation of soil. We corrected soil gravimetric moisture to 75% field capacity before sample incubation at about 28°C in an incubator (Isuku FR24BS, Isuku Seisakusho Ltd., Tokyo, Japan). We did extractions of samples in 2 M potassium chloride (KCl) 3 days after collection in the field and in incubated samples. We kept samples under refrigeration (4°C) prior to the initial extraction. We filtered extracts through Whatman Number 42 filter paper before analysis of nitrite/nitrate using a flow-injection system on a Lachat Quik-Chem AE autoanalyzer (Lachat Instruments, Milwaukee, Wisconsin). Prior to the extractions, we dried subsamples

of soil for 24 hours at 105°C to determine actual moisture content.

4.2. Statistical Analyses

[21] We used the SAS System version 9.00 to run the statistical analyses. We analyzed with PROC MIXED the effects of treatment, date, and treatment-by-date interaction on the variables trace gas flux, soil suction, and non-woody litterfall using a repeated measures analysis with compound symmetric covariance structure. This structure assumes constant variance at all dates and equal correlations between all pairs of measures on the same experimental unit, i.e., collar, tensiometer, or trap for the soil trace gases, soil suction, and litterfall variables, respectively. We ran separate tests to compare each of the treatments with the control. Within this analysis, significant treatment effects would have indicated temporally consistent differences between treatment and control measurements both pre- and post-treatment and across seasons (none were observed), significant date effects were generally indicative of seasonal trends that affected both treatment and control measurements, and treatment-by-date effects indicated a significant difference between treatment and control measurements that occurred after the treatment was initiated. We used CONTRAST statements to explicitly test whether the measured variables differed between seasons and between treatments within each season (wet and dry). We used the TTEST procedure to compare treatments and control means for soil nitrification.

[22] When necessary, we performed log and square root transformations to meet the model assumptions of normality, based on the criteria of $P > 0.05$ in the Kolmogorov-Smirnov test, and equal variances, based on the absence of a pattern of heteroscedasticity in the plots of residual versus predicted values. Means and standard errors were calculated on the basis of untransformed data. All results are reported as significant when $P \leq 0.05$; we report marginal significance when $0.05 < P < 0.10$.

[23] We estimated annual soil C efflux by linear interpolation between sampling dates using the EXPAND procedure. To estimate annual soil C efflux, we assumed that the variation in soil CO₂ efflux with time of day was minimal as previously reported by Davidson *et al.* [2000] for an eastern Amazonian primary forest. We tested for interannual and between-treatment differences in annual soil C efflux and annual litterfall C values for control and irrigated plots in 2001 and 2002 using the PROC MIXED procedure. For the litter removal versus control plot comparison of annual soil C efflux and annual litterfall C, we used the TTEST procedure for 2002 data only; we did not include the 2001 data in the litter removal versus control comparison because the treatment regime was not initiated until August 2001. We estimated the relative contribution of above-ground litter to soil respiration by subtracting litter removal soil CO₂ efflux from control soil CO₂ efflux.

5. Results

5.1. Irrigation Experiment

[24] Rainfall declined from mid-July to early January (dry season) during each year of the study (Figure 1a), resulting

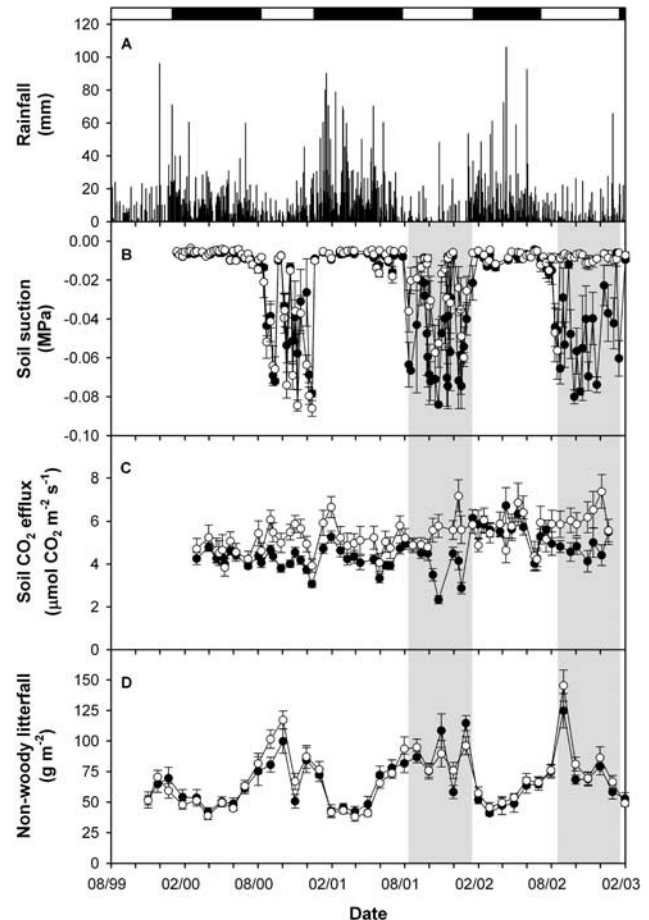


Figure 1. Effects of rainfall patterns and dry-season irrigation on soil moisture status, soil respiration, and non-woody litterfall: (a) daily rainfall at the study site, (b) soil suction, (c) soil CO₂ efflux, and (d) non-woody litterfall. In Figures 1b–1d, solid and open circles represent means (\pm SE) for control and irrigation treatments, respectively ($n = 4$ for soil suction and $n = 12$ for soil CO₂ efflux and non-woody litterfall per sampling date). Shaded areas indicate the dry season irrigation periods. White and black horizontal bars mark dry and wet seasons, respectively.

in lower soil suction during this period (Figure 1b). The dry-season irrigation resulted in significantly ($P < 0.0001$) less negative soil suction in control plots for most of the dates in 2001 and 2002 (Figure 1b). During the 2001 dry season, soil suction was -0.052 ± 0.003 and -0.024 ± 0.002 MPa in control and irrigated plots, respectively; corresponding values for the 2002 dry season were -0.046 ± 0.003 and -0.013 ± 0.002 MPa.

[25] There was a significant effect of date and the interaction between treatment and date on soil CO₂ efflux (Table 1). Soil CO₂ efflux for irrigated plots was significantly higher than for control plots during the dry-season irrigation ($P < 0.0001$, Figure 1c). There was also a significant effect of date and the interaction between treatment and date on soil CO₂ efflux for the pretreatment period ($P < 0.0001$); however, pretreatment differences between

Table 1. *F* Statistics and Associated Significance Levels for the Effect of Treatments (Irrigation and Litter Removal), Sampling Date, and Their Interaction on Soil Trace Gas Fluxes and Non-Woody Litterfall in a Tropical Regrowth Forest Stand in Eastern Amazonia^a

Variable	Irrigation Experiment			Litter Removal Experiment		
	Treatment	Date	Treatment × Date	Treatment	Date	Treatment × Date
Soil CO ₂ efflux	2.55 (ns)	9.48 (P < 0.001)	5.02 (P < 0.001)	3.10 (ns)	9.63 (P < 0.001)	3.24 (P < 0.001)
Soil NO efflux	0.04 (ns)	5.46 (P < 0.001)	1.50 (ns)	3.29 (ns)	7.65 (P < 0.001)	2.21 (P < 0.005)
Soil N ₂ O efflux	0.93 (ns)	4.20 (P < 0.001)	1.00 (ns)	0.32 (ns)	6.42 (P < 0.001)	1.68 (P < 0.005)
Soil CH ₄ efflux	0.91 (ns)	2.14 (P < 0.01)	1.22 (ns)	<0.01 (ns)	2.21 (P < 0.001)	0.77 (ns)
Non-woody litterfall	0.24 (ns)	45.27 (P < 0.001)	1.62 (P < 0.01)	0.27 (ns)	32.91 (P < 0.001)	1.18 (ns)

^aUsing PROC MIXED, SAS System version 9.0. P values are indicated in parentheses (ns: not significant). Significant “treatment” effects (not observed) would indicate temporally consistent differences between treatment and control both pre- and post-treatment and across seasons, significant “date” effects are generally indicative of seasonal trends that affect both treatment and control measurements, and “treatment × date” effects indicate a significant difference between the treatment and control measurements that occurs after the treatment was initiated.

plots did not affect the significance of the dry-season irrigation effect. In the 2001 dry season irrigation period, soil CO₂ efflux values were 3.91 ± 0.13 and 5.54 ± 0.19 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for control and irrigated plots, respectively; corresponding values for the 2002 dry season were 4.76 ± 0.19 and 6.21 ± 0.25 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

[26] The lowest mean soil CO₂ efflux rate (2.33 ± 0.19 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), which occurred in the control treatment on 24 October 2001 (Figure 1c), coincided with a successive decrease in soil water status (to -0.084 MPa) caused by a long dry spell of 24 days without rain out of a total of 31 days, with total precipitation of only 9 mm during the 31-day period. A 93% increase in the control plot soil CO₂ efflux in the subsequent measurement coincided with an increase in soil water status (to -0.008 MPa) following two consecutive rainy days (19 and 26 mm) after the long dry spell, and immediately prior to the soil respiration measurement; no increased soil CO₂ efflux was observed for irrigated plots. The pulse in soil CO₂ efflux was then followed by a decrease in CO₂ emissions associated with another dry period.

[27] Non-woody litterfall was significantly affected by date and by the interaction between date and treatment (Table 1, Figure 1d); the significant effect of the interaction was not associated with differences between treatments within dry-season irrigation periods ($P > 0.63$). Non-woody litterfall in the dry season was significantly higher than in the wet season ($P < 0.0001$).

[28] Annual soil C efflux was significantly higher in 2002 than in 2001 ($P < 0.0001$) (Table 2). The effects of treatment and the interaction between treatment and date were marginally significant ($P < 0.07$ and $P < 0.10$, respectively). Annual litterfall C was not affected by treatment or year (Table 2); although the interaction between treatment and year was marginally significant ($P < 0.053$), it is not readily attributable to a treatment effect.

[29] The significant effect of date on NO efflux (Table 1, Figure 2b) was largely due to a single value measured in the end of July 2002; wet versus dry season contrasts indicated non-significant seasonal differences in NO efflux. For N₂O (Figure 2c), the wet season efflux was significantly higher than the dry season efflux (5.62 ± 0.50 and 2.41 ± 0.47 $\mu\text{g N m}^{-2} \text{ h}^{-1}$, respectively; $P < 0.0001$). During dry-season irrigation, treatment versus control contrasts indicated that N₂O efflux in irrigated plots was significantly higher than in

control plots (4.18 ± 0.87 and 2.34 ± 0.75 $\mu\text{g N m}^{-2} \text{ h}^{-1}$, respectively; $P < 0.05$).

[30] Date was again the only factor to have a significant effect on CH₄ efflux (Table 1, Figure 2d). Methane efflux in the dry season was significantly lower than in the wet season (-0.348 ± 0.118 and 0.128 ± 0.118 $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$, respectively; $P < 0.0001$). During dry-season irrigation, treatment versus control contrasts indicated that CH₄ efflux in irrigated plots was also significantly higher than in control plots (0.226 ± 0.361 and -0.526 ± 0.185 $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$, respectively; $P < 0.01$). The net CH₄ emissions were generally close to zero, with most chambers generally showing net uptake of CH₄ (77% in control plots and 80% in irrigated plots). The range of CH₄ efflux for the whole experimental period was -5.00 to 22.03 $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$. Two chambers with very high effluxes (5.93 and 9.97 $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$) drove the large variability in the mean efflux for the control plot in March 2001, while the high variability for the irrigation means in September and October 2001 was driven by one chamber (9.08 and 10.30 $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$). The apparent high mean net production of CH₄ for irrigated plots in September (0.884 ± 1.353 $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$) and October (0.879 ± 1.187 $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$) 2001 becomes net consumption (-0.461 ± 0.172 and -0.292 ± 0.223 $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$) if we exclude the high efflux chambers from the calculation of means. There was no significant effect of irrigation on net nitrification rates for control and irrigated plots (0.11 ± 0.02 and 0.11 ± 0.03 $\mu\text{g N g}^{-1} \text{ soil d}^{-1}$, respectively).

5.2. Litter Removal Experiment

[31] Soil suction (Figure 3b) was significantly less negative in the wet season than in the dry season ($P < 0.0001$).

Table 2. Annual Soil Carbon Efflux and Non-Woody Litterfall Carbon for Control, Irrigated, and Litter Removal Plots in a Tropical Regrowth Forest Stand in Eastern Amazonia^a

Treatment	Soil C Efflux, $\text{g m}^{-2} \text{ yr}^{-1}$		Non-Woody Litterfall C, $\text{g m}^{-2} \text{ yr}^{-1}$	
	2001	2002	2001	2002
Control	1593 ± 74	1988 ± 126	410 ± 28	383 ± 27
Irrigation	2021 ± 154	2237 ± 158	398 ± 24	415 ± 24
Litter removal	-	1429 ± 165	-	368 ± 14

^aMean \pm SE, $n = 12$ per treatment.

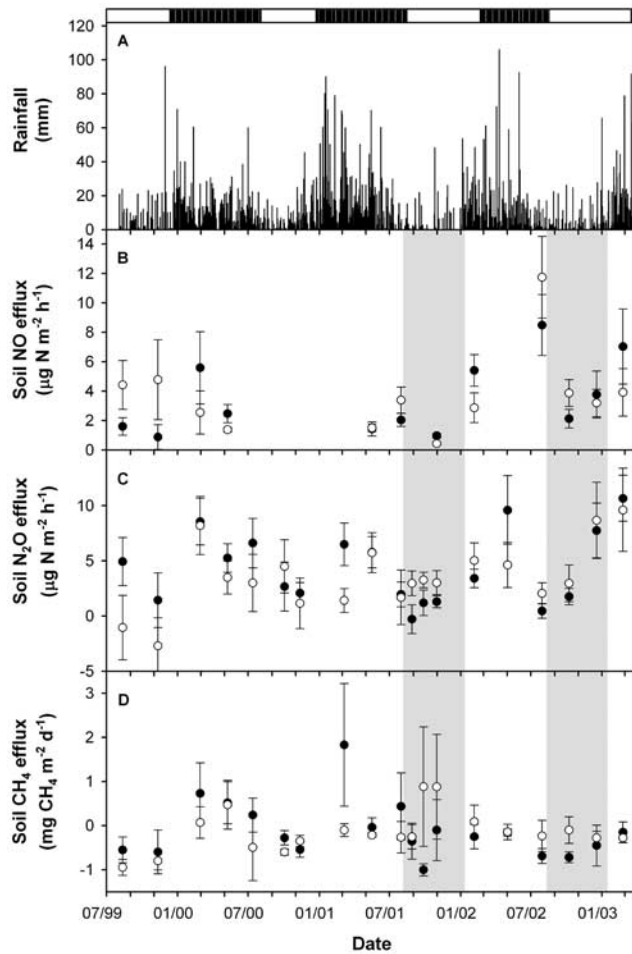


Figure 2. Effects of rainfall patterns and dry-season irrigation on N-oxide and methane effluxes: (a) daily rainfall at the study site, (b) soil NO efflux, (c) soil N₂O efflux, and (d) soil CH₄ efflux. In Figures 2b–2d, solid and open circles represent means (\pm SE) for control and irrigation treatments, respectively ($n = 8$ per sampling date). Shaded areas indicate the dry season irrigation periods. White and black horizontal bars mark dry and wet seasons, respectively.

Soil CO₂ efflux during the pretreatment period (Figure 3c) for litter removal and control plots did not differ significantly (4.18 ± 0.12 and $4.24 \pm 0.08 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively; $P = 0.87$). During the litter manipulation period, soil CO₂ efflux in litter removal plots was significantly lower than in control plots (3.54 ± 0.17 and $4.90 \pm 0.18 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively; $P < 0.001$). This difference was not homogeneous throughout the experimental period and followed a trajectory that can be divided in three phases. In the first phase, corresponding with the dry season and the early rainy season, the difference between treatment and control measurements was apparent for nearly all of the measurements made during the first 6 months of litter removal. The second phase, from 6 to 10 months after the beginning of litter removal, corresponded with the middle to late rainy season. During this phase, there

were fewer measurements in which the difference between treatment means was significant. In the third phase, corresponding with the following dry season, the difference in soil CO₂ efflux between treatments was uniformly significant, and persisted through the end of the measurement period.

[32] Non-woody litterfall in control and litter removal plots was significantly affected only by date (Table 1, Figure 3d), and was significantly higher in the dry season than in the wet season ($P < 0.0001$). Aboveground litter respiration represented $22 \pm 2\%$ of total soil respiration for the whole litter removal period and was 22 ± 2 , 16 ± 4 , and $28 \pm 2\%$ of total soil respiration during the first, second, and third phases, respectively. Annual soil C

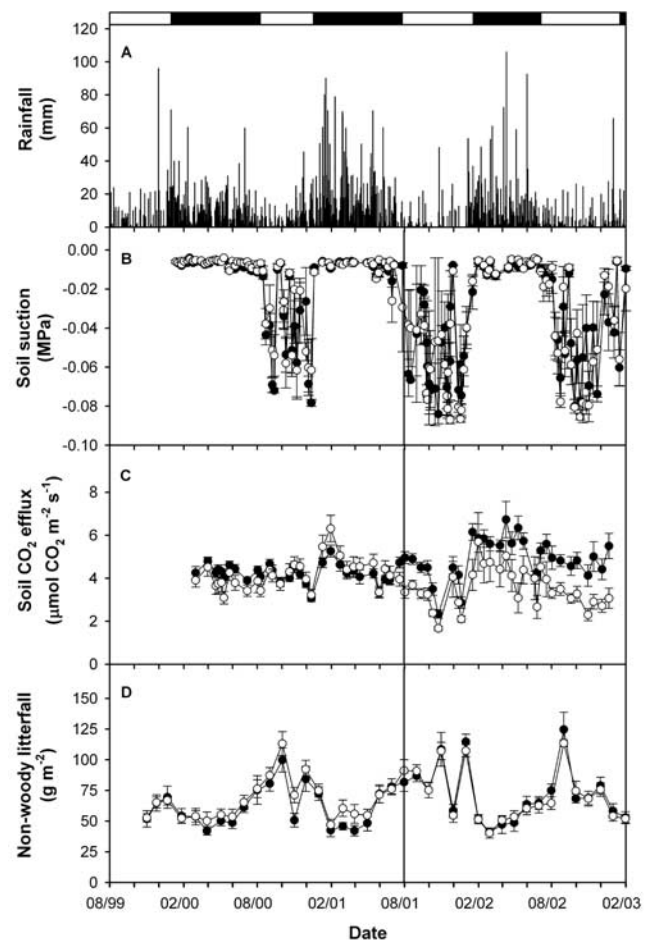


Figure 3. Effects of rainfall patterns and litter removal on soil moisture status, soil respiration, and non-woody litterfall: (a) daily rainfall at the study site, (b) soil suction, (c) soil CO₂ efflux, and (d) non-woody litterfall. In Figures 3b–3d, solid and open circles represent means (\pm SE) for control and litter removal treatments, respectively ($n = 4$ for soil suction and $n = 12$ for soil CO₂ efflux and non-woody litterfall per sampling date). The vertical line indicates the beginning of the litter removal treatment. White and black horizontal bars mark dry and wet seasons, respectively.

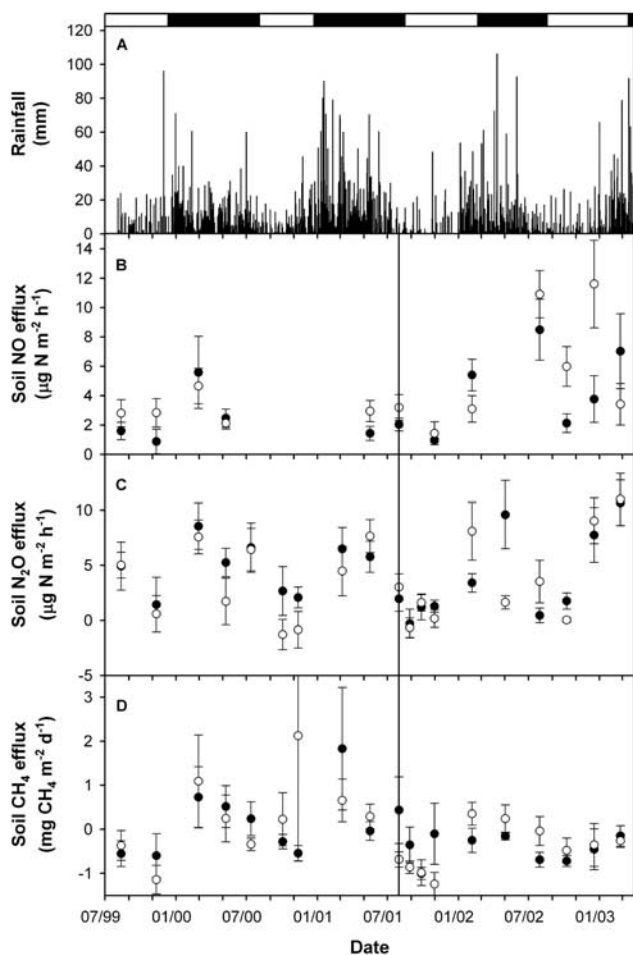


Figure 4. Effects of rainfall patterns and litter removal on N-oxide and methane effluxes: (a) daily rainfall at the study site, (b) soil NO efflux, (c) soil N₂O efflux, and (d) soil CH₄ efflux. In Figures 4b–4d, solid and open circles represent means (\pm SE) for control and litter removal treatments, respectively ($n = 8$ per sampling date). The vertical line indicates the beginning of the litter removal treatment. White and black horizontal bars mark dry and wet seasons, respectively.

efflux was significantly lower ($P < 0.05$) in litter removal than in control plots in 2002 (Table 2). There was no significant difference in annual litterfall C between control and litter removal treatments in 2002 (Table 2).

[33] The significant interaction effect on N oxide emissions (Table 1) was not related to a consistent effect of litter removal on either NO or N₂O effluxes (Figures 4b and 4c, respectively); the difference between treatments for both gases during the litter removal period was non-significant. Emissions of CH₄ (Figure 4d) in the dry season were significantly lower than in the wet season (-0.420 ± 0.164 and 0.287 ± 0.113 mg CH₄ m⁻² d⁻¹, respectively; $P < 0.01$).

[34] Mean net nitrification rates in control plots were marginally higher ($P = 0.06$) than in litter removal

plots (0.11 ± 0.02 and 0.07 ± 0.01 µg N g⁻¹ soil d⁻¹, respectively).

6. Discussion

6.1. Soil CO₂ Efflux, Non-Woody Litterfall, and Belowground C Allocation

[35] The soil CO₂ efflux rates measured in our study are within the range of data reported for tropical forests and are consistent with several other studies in Amazonian forests [Davidson *et al.*, 2000; Verchot *et al.*, 2000; Cattânio *et al.*, 2002; Fernandes *et al.*, 2002; Nepstad *et al.*, 2002] and in tropical forests elsewhere [Ishizuka *et al.*, 2002; Kiese and Butterbach-Bahl, 2002] that reported higher emissions of CO₂ during the wet season than in the dry season. We have also shown strong pulses of CO₂ efflux in response to rain events during dry periods (soil wet-up events), as observed in old-growth forests in the Brazilian Amazon [Davidson *et al.*, 2000] and in Costa Rica [Schwendenmann *et al.*, 2003]. Our dry-season irrigation experiment further demonstrates the constraint that moisture availability exerts on soil CO₂ efflux.

[36] Soil CO₂ efflux as measured in the field mainly integrates root and microbial respiration, and we have not determined if the reduction in soil respiration in the dry season was caused by decreased activity of microbes, roots, or both. However, a laboratory study with soil from the same site showed a significant increase in microbial basal respiration during the 2001 wet season compared to the previous dry season [Rangel-Vasconcelos, 2002], as observed in other tropical forests [Luizao *et al.*, 1992; Cleveland *et al.*, 2003]. Although microbial respiration rates determined under laboratory conditions cannot be compared to rates obtained in the field with chamber techniques, those results suggest that reduction in soil microbial activity during the dry season likely contributed to the observed lower rates of soil respiration during this period at our site. Likewise, reduced activity of microbes in decomposing aboveground litter during the dry season could have contributed to lower soil CO₂ efflux in non-irrigated plots. Borken *et al.* [2003] have recently shown that microbial respiration of the O horizon can contribute significantly to CO₂ pulses after soil wet-up events in a temperate forest. Wieder and Wright [1995] have also observed higher litter mass loss under irrigation compared with no irrigation in a tropical forest in Panama. Finally, lower soil CO₂ efflux during the dry season could also have resulted from constrained root respiration due to decreased root growth [Cattânio *et al.*, 2002] or decreased flux of photosynthates to roots, which limits root respiration itself [Högberg *et al.*, 2001] and/or rhizospheric microbial respiration [Kuzyakov and Cheng, 2001]. Further research on differentiating root from microbial respiration and aboveground litter from soil respiration are needed to better understand how moisture constrains CO₂ efflux from tropical forest soils.

[37] The variation in the size of the difference of soil CO₂ efflux between control and litter removal throughout the manipulation period followed a trajectory that can be linked to altered substrate availability and variation in soil water status due to the seasonality of rainfall. In the first phase

of this trajectory, the early impact of litter removal on soil respiration suggests that CO₂ efflux associated with microbial decomposition of aboveground litter and superficial root respiration represents a substantial proportion (about 22% in the present study) of total soil respiration [Raich and Schlesinger, 1992]. During the second phase, an interaction between substrate availability and rainfall seasonality appears to influence the variation in soil CO₂ efflux. The difference between control and litter removal plots decreased during some dates in the second phase, suggesting that the contribution of belowground respiration was relatively higher during the wet season. The third phase may be characterized by the depletion of labile soil carbon and, therefore, an increase in the difference in soil CO₂ efflux between treatments. Although this phase is also coincident with the 2002 dry season, its length and consistency (i.e., lack of responsiveness to dry-season wet-up events) lead us to suspect that, due to the removal of the litter layer, substrate availability has become a larger constraint on soil respiration than reduced moisture availability.

[38] The estimated annual soil C efflux measured in our control plots is comparable to another estimate for eastern Amazonian forests in Brazil [Davidson *et al.*, 2000] and is higher than estimates for tropical old-growth forests elsewhere [Ishizuka *et al.*, 2002; Schwendenmann *et al.*, 2003]. We observed lower total rainfall and higher annual soil C efflux in 2002 than in 2001, suggesting that the interannual variability in soil C efflux was not caused by differences in annual rainfall. Pulses of CO₂ associated with rainfall events observed in this study are consistent with the hypothesis that rainfall distribution, rather than total rainfall, may better explain annual variability in soil C efflux. Differences in annual soil C efflux between irrigation and control plots are also consistent with a substantial moisture constraint on soil respiration.

[39] Non-woody litterfall rates measured in our study are within the range reported for Amazonian forests [Scott *et al.*, 1992; Smith *et al.*, 1998] and tropical forests elsewhere [Cuevas *et al.*, 1991; Clark *et al.*, 2001]. The lack of irrigation effects on litterfall rates in the dry season, as also reported in a semideciduous lowland forest in Panama [Wieder and Wright, 1995], suggests that increased litterfall usually observed during this period [Scott *et al.*, 1992; Smith *et al.*, 1998] is not triggered by changes in soil moisture availability, but by other factors (e.g., increased atmospheric vapor pressure deficits [Wright and Cornejo, 1990]).

[40] Litter removal can result in nutrient deficiency, which may ultimately lead to reduced aboveground net primary productivity (ANPP) in tropical forests [Harrington *et al.*, 2001]. Our results indicate that the total period of litter manipulation was not long enough to substantially affect ANPP since litterfall, an index of ANPP, has not yet been altered by the litter removal treatment.

[41] On the basis of our annual soil C efflux and non-woody litterfall C estimates, we can calculate a C efflux:litterfall C ratio of 4.0–5.2 for our control plots, consistent with the mean value of 4.16 reported by Davidson *et al.* [2002] for young forests. Total belowground carbon allocation (TBCA) estimated by the difference between annual

basis C fluxes in soil respiration and litterfall [Raich and Nadelhoffer, 1989] is underestimated for regrowth forests if C storage in roots and soil is not accounted for [Davidson *et al.*, 2002]. However, simple calculation of TBCA based only on soil respiration and litterfall can provide a lower limit of TBCA for regrowth forests. For our site, the ratio between annual soil C efflux and annual litterfall C indicates that TBCA relative to litterfall is similar to values for other regrowth forest site in the eastern Amazon [Davidson *et al.*, 2002] and higher than those of mature forests [Raich and Nadelhoffer, 1989; Davidson *et al.*, 2002], consistent with increased allocation of C to belowground structures as a mechanism by which regrowth forests cope with the demands for water and nutrients [Davidson *et al.*, 2002].

[42] Differences in annual soil C efflux between litter removal and control plots are consistent with a substantial substrate constraint on soil respiration. In 2002, the amount of carbon in litterfall ($368 \pm 14 \text{ g C m}^{-2} \text{ yr}^{-1}$) was well within 1 standard error of the mean difference in soil C efflux between control and litter removal ($559 \pm 291 \text{ g C m}^{-2} \text{ yr}^{-1}$). This substantial difference in soil C efflux also suggests that ~20% of total soil C efflux is due to litter respiration, with the remaining ~80% due to belowground respiration; this is consistent with results obtained in litter removal studies in forest ecosystems in other climatic regions [Bowden *et al.*, 1993; Jandl and Sollins, 1997; Rey *et al.*, 2002].

6.2. Nitrogen Oxide Emissions

[43] Nitric and nitrous oxide effluxes measured in this study both in wet or dry seasons are among the lowest reported for either regrowth or old-growth tropical forests in the Brazilian Amazon [Verchot *et al.*, 1999; Garcia-Montiel *et al.*, 2001; Catt nio *et al.*, 2002; Nepstad *et al.*, 2002] and tropical forests elsewhere [Erickson *et al.*, 2001; Ishizuka *et al.*, 2002; Palm *et al.*, 2002]. These low N oxide effluxes may result from low rates of N cycling, as indicated by the very low net nitrification rates we found in both seasons compared to other studies for Amazonian forests [Neill *et al.*, 1997; Palm *et al.*, 2002; Garcia-Montiel *et al.*, 2003a]. The thin concretionary soils of this site, along with the recent history of repeated slash-and-burn cycles and the high litterfall C:N ratios, are consistent with a very conservative nitrogen cycle and low rates of both nitrification and denitrification. Although fluxes were consistently low, slightly higher efflux of N₂O in the wet season compared to the dry season reported here has also been observed in other tropical forests [Verchot *et al.*, 1999; Garcia-Montiel *et al.*, 2001; Catt nio *et al.*, 2002; Erickson *et al.*, 2002; Kiese and Butterbach-Bahl, 2002; Nepstad *et al.*, 2002]. Consistent with the results obtained by Nobre *et al.* [2001], we also found a significant effect of irrigation on N₂O efflux. Higher N₂O efflux associated with wetter soil conditions during both the wet season and dry-season irrigation periods likely resulted from increased denitrification [Davidson, 1991].

[44] The effects of litter removal on N oxide fluxes are not clear and are difficult to interpret since the fluxes are inherently very low at our site. If N trace gas emissions were already limited by N availability in this infertile soil,

the removal of litter might be expected to decrease emissions further. However, that decrease would be difficult to detect relative to the naturally low emissions that were already frequently near detection limits prior to litter removal.

6.3. Methane Emissions

[45] Methane fluxes measured at our site are in the lower range of both net consumption and net production fluxes found for tropical forests [Verchot *et al.*, 2000; Palm *et al.*, 2002; Kiese *et al.*, 2003]. Higher net consumption of CH₄ in the dry season and lower net consumption (or even small net production) in the wet season observed in our study is consistent with the pattern of CH₄ emissions measured in other Brazilian Amazonian forests [Verchot *et al.*, 2000; Cattânio *et al.*, 2002; Nepstad *et al.*, 2002] and tropical forests elsewhere [Kiese *et al.*, 2003]. Increased net CH₄ production during the wet season as well as during the irrigation period in our study suggests that higher soil water status decreased soil aeration leading to an increase in methanogenesis [Davidson and Schimel, 1995]. Although decreased aeration during the wet season could have resulted in higher efflux of CH₄ and N₂O, higher soil CO₂ efflux associated with wetter soil conditions could also have contributed to the increased efflux of CH₄ and N₂O because of the consumption of O₂ in the respiration process [Verchot *et al.*, 2000; Palm *et al.*, 2002].

7. Conclusions

[46] We conclude that soil CO₂ efflux is strongly linked to soil moisture and substrate availability as indicated from the responses of CO₂ emissions to soil wet-up events, dry-season irrigation, and litter removal for this tropical regrowth stand. On an annual basis, this regrowth stand allocates a large amount of C to belowground structures relative to litterfall C. Reducing dry season water limitation increased soil respiration by about 40 and 30% in the two dry seasons studied, corresponding to annual increases of 27 and 13% in 2001 and 2002, respectively. Removing aboveground litter reduced annual soil respiration by 28% in 2002.

[47] In general, N oxide emissions were very low, probably due to the inherently low rates of nitrogen cycling at this site. Emissions of N₂O and CH₄ were constrained by low moisture availability, while emissions of NO were not affected by irrigation. We were unable to detect more severe substrate limitation induced by the litter removal treatment on N oxide and CH₄ emissions. The substantial impacts of soil moisture and aboveground litter on soil CO₂ efflux shown in this study suggest that alterations in the availability of these resources that may result from climate and land-use changes in tropical regions could have significant effects on regional CO₂ fluxes.

[48] **Acknowledgments.** We thank Osorio Oliveira, Glebson Sousa, and Evandro da Silva for their assistance in the field, and Raimundo Nonato da Silva (UFRA) for logistical support. We also thank two anonymous reviewers for insightful comments on the manuscript. This research was conducted under cooperative agreements between the University of Florida, Universidade Federal Rural da Amazônia, and Empresa Brasileira de Pesquisa Agropecuária-Amazônia Oriental. This research was supported by grants to Zarin from the Andrew Mellon Foundation, grants NCC5-332

and NCC5-686 of NASA's Terrestrial Ecology Program to Davidson as part of the Large-scale Biosphere-Atmosphere (LBA) project, and by the Florida Agricultural Experimental Station, and was approved for publication as Journal Series R-10110.

References

- Borken, W., E. A. Davidson, K. Savage, J. Gaudinski, and S. E. Trumbore (2003), Drying and wetting effects on carbon dioxide release from organic horizons, *Soil Sci. Soc. Am. J.*, *67*, 1888–1896.
- Bowden, R. D., K. J. Nadelhoffer, R. D. Boone, J. M. Melillo, and J. B. Garrison (1993), Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest, *Can. J. For. Res.*, *23*, 1402–1407.
- Cattânio, J. H., E. A. Davidson, D. C. Nepstad, L. V. Verchot, and I. L. Ackerman (2002), Unexpected results of a pilot throughfall exclusion experiment on soil emissions of CO₂, CH₄, N₂O, and NO in eastern Amazonia, *Biol. Fertil. Soils*, *36*, 102–108.
- Clark, D. A., S. Brown, D. W. Kicklighter, J. Q. Chambers, J. R. Thomlinson, J. Ni, and E. A. Holland (2001), Net primary production in tropical forests: An evaluation and synthesis of existing field data, *Ecol. Appl.*, *11*, 371–384.
- Cleveland, C. C., A. R. Townsend, S. K. Schmidt, and B. C. Constance (2003), Soil microbial dynamics and biogeochemistry in tropical forests and pastures, southwestern Costa Rica, *Ecol. Appl.*, *13*, 314–326.
- Coelho, R. F. R., D. J. Zarin, I. S. Miranda, and J. M. Tucker (2004), Análise florística e estrutural de uma floresta em diferentes estágios sucessionais no município de Castanhal, Pará, *Acta Amazon.*, *33*, 563–582.
- Cuevas, E., S. Brown, and A. E. Lugo (1991), Above- and belowground organic matter storage and production in a tropical pine plantation and a paired broadleaf secondary forest, *Plant Soil*, *135*, 257–268.
- Davidson, E. A. (1991), Fluxes of nitrous oxide and nitric oxide from terrestrial ecosystems, in *Microbial Production and Consumption of Greenhouse Gases: Methane, Nitrogen Oxides, and Halomethanes*, edited by J. E. Rogers and W. B. Whitmann, pp. 219–235, Am. Soc. for Microbiol., Washington, D. C.
- Davidson, E. A., and D. S. Schimel (1995), Microbial processes of production and consumption of nitric oxide, nitrous oxide and methane, in *Biogenic Trace Gases: Measuring Emissions From Soil and Water*, edited by P. A. Matson and R. C. Harriss, pp. 327–357, Blackwell Sci., Malden, Mass.
- Davidson, E. A., P. A. Matson, P. M. Vitousek, R. Riley, K. Dunkin, G. García-Méndez, and J. M. Maass (1993), Processes regulating soil emissions of NO and N₂O in a seasonally dry tropical forest, *Ecology*, *74*, 130–139.
- Davidson, E. A., L. V. Verchot, J. H. Cattânio, I. L. Ackerman, and J. E. M. Carvalho (2000), Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia, *Biogeochemistry*, *48*, 53–69.
- Davidson, E. A., et al. (2002), Belowground carbon allocation in forests estimated from litterfall and IRGA-based soil respiration measurements, *Agric. For. Meteorol.*, *113*, 39–51.
- Erickson, H., M. Keller, and E. A. Davidson (2001), Nitrogen oxide fluxes and nitrogen cycling during postagricultural succession and forest fertilization in the humid tropics, *Ecosystems*, *4*, 67–84.
- Erickson, H., E. Davidson, and M. Keller (2002), Former land-use and tree species affect nitrogen oxide emissions from a tropical dry forest, *Oecologia*, *130*, 297–308.
- Fearnside, P. M. (1996), Amazonian deforestation and global warming: Carbon stocks in vegetation replacing Brazil's Amazon forest, *For. Ecol. Manage.*, *80*, 21–34.
- Fernandes, S. A. P., M. Bernoux, C. C. Cerri, B. J. Feigl, and M. C. Piccolo (2002), Seasonal variation of soil chemical properties and CO₂ and CH₄ fluxes in unfertilized and P-fertilized pastures in an Ultisol of the Brazilian Amazon, *Geoderma*, *107*, 227–241.
- Firestone, M. K., and E. A. Davidson (1989), Microbiological basis of NO and N₂O production and consumption in soil, in *Exchange of Trace Gases Between Terrestrial Ecosystems and the Atmosphere*, edited by M. O. Andreae and D. S. Schimel, pp. 7–21, John Wiley, Hoboken, N. J.
- Fortini, L. B., S. S. Mulkey, D. J. Zarin, S. S. Vasconcelos, and C. J. R. D. Carvalho (2003), Drought constraints on leaf gas exchange by *Miconia ciliata* (Melastomataceae) in the understorey of an eastern Amazonian regrowth forest stand, *Am. J. Bot.*, *90*, 1064–1070.
- García-Montiel, D. C., P. A. Steudler, M. C. Piccolo, J. M. Melillo, C. Neill, and C. C. Cerri (2001), Controls on soil nitrogen oxide emissions from forest and pastures in the Brazilian Amazon, *Global Biogeochem. Cycles*, *15*, 1021–1030.

- Garcia-Montiel, D. C., J. M. Melillo, P. A. Steudler, C. C. Cerri, and M. C. Piccolo (2003a), Carbon limitations to nitrous oxide emissions in a humid tropical forest of the Brazilian Amazon, *Biol. Fertil. Soils*, *38*, 267–272.
- Garcia-Montiel, D. C., P. A. Steudler, M. C. Piccolo, C. Neill, J. M. Melillo, and C. C. Cerri (2003b), Nitrogen oxide emissions following wetting of dry soils in forest and pastures in Rondônia, Brazil, *Biogeochemistry*, *64*, 319–336.
- Harrington, R. A., J. H. Fownes, and P. M. Vitousek (2001), Production and resource use efficiencies in N- and P-limited tropical forests: A comparison of responses to long-term fertilization, *Ecosystems*, *4*, 646–657.
- Hart, S. C., J. M. Stark, E. A. Davidson, and M. K. Firestone (1994), Nitrogen mineralization, immobilization, and nitrification, in *Methods of Soil Analysis: Part 2. Microbiological and Biochemical Properties*, edited by R. W. Weaver, J. S. Angle, and P. S. Bottomley, pp. 985–1018, Soil Sci. Soc. of Am., Madison, Wis.
- Högberg, P., A. Nordgren, N. Buchmann, A. F. S. Taylor, A. Ekblad, M. N. Högberg, G. Nyberg, N. Ottosson-Löfvenius, and D. J. Read (2001), Large-scale forest girdling shows that current photosynthesis drives soil respiration, *Nature*, *411*, 789–792.
- Ishizuka, S., H. Tsuruta, and D. Murdiyarso (2002), An intensive field study on CO₂, CH₄, and N₂O emissions from soils at four land-use types in Sumatra, Indonesia, *Global Biogeochem. Cycles*, *16*(3), 1049, doi:10.1029/2001GB001614.
- Jandl, R., and P. Sollins (1997), Water-extractable soil carbon in relation to the belowground carbon cycle, *Biol. Fertil. Soils*, *25*, 196–201.
- Jipp, P. H., D. C. Nepstad, D. K. Cassel, and C. R. D. Carvalho (1998), Deep soil moisture storage and transpiration in forests and pastures of seasonally-dry Amazonia, *Clim. Change*, *39*, 395–412.
- Johnson, C. H., D. J. Zarin, and A. H. Johnson (2000), Post-disturbance aboveground biomass accumulation in global secondary forests, *Ecology*, *81*, 1395–1401.
- Kiese, R., and K. Butterbach-Bahl (2002), N₂O and CO₂ emissions from three different tropical forest sites in the wet tropics of Queensland, Australia, *Soil Biol. Biochem.*, *34*, 975–987.
- Kiese, R., B. Hewett, A. Graham, and K. Butterbach-Bahl (2003), Seasonal variability of N₂O emissions and CH₄ uptake by tropical rainforest soils of Queensland, Australia, *Global Biogeochem. Cycles*, *17*(2), 1043, doi:10.1029/2002GB002014.
- Kuzyakov, Y., and W. Cheng (2001), Photosynthesis controls of rhizosphere respiration and organic matter decomposition, *Soil Biol. Biochem.*, *33*, 1915–1925.
- Lean, J., C. B. Bunton, C. A. Nobre, and P. R. Rowntree (1996), The simulated impact of Amazonian deforestation on climate using measured ABRACOS vegetation characteristics, in *Amazonian Deforestation and Climate*, edited by J. H. C. Gash et al., pp. 549–576, John Wiley, Hoboken, N. J.
- Luizao, R. C. C., T. A. Bonde, and T. Rosswall (1992), Seasonal variation of soil microbial biomass—The effects of clearfelling a tropical rainforest and establishment of pasture in the Central Amazon, *Soil Biol. Biochem.*, *24*, 802–813.
- Neill, C., M. C. Piccolo, C. C. Cerri, P. A. Steudler, J. M. Melillo, and M. Brito (1997), Net nitrogen mineralization and net nitrification rates in soils following deforestation for pasture across the southwestern Brazilian Amazon Basin landscape, *Oecologia*, *110*, 243–252.
- Nepstad, D. C., et al. (2002), The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon forest, *J. Geophys. Res.*, *107*(D20), 8085, doi:10.1029/2001JD000360.
- Nobre, A. D., M. Keller, P. M. Crill, and R. C. Harriss (2001), Short-term nitrous oxide profile dynamics and emissions response to water, nitrogen and carbon additions in two tropical soils, *Biol. Fertil. Soils*, *34*, 363–373.
- Palm, C. A., J. C. Alegre, L. Arevalo, P. K. Mutuo, A. R. Mosier, and R. Coe (2002), Nitrous oxide and methane fluxes in six different land use systems in the Peruvian Amazon, *Global Biogeochem. Cycles*, *16*(4), 1073, doi:10.1029/2001GB001855.
- Potter, C. S., and S. A. Klooster (1998), Interannual variability in soil trace gas (CO₂, N₂O, NO) fluxes and analysis of controllers on regional to global scales, *Global Biogeochem. Cycles*, *12*, 621–635.
- Raich, J. W., and K. J. Nadelhoffer (1989), Belowground carbon allocation in forest ecosystems: Global trends, *Ecology*, *70*, 1346–1354.
- Raich, J. W., and W. H. Schlesinger (1992), The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate, *Tellus, Ser. B*, *44*, 81–99.
- Rangel-Vasconcelos, L. G. T. (2002), Biomassa microbiana de solo sob vegetação secundária na Amazônia oriental, M.S. thesis, Fac. de Ciênc. Agrárias do Pará, Belém, Brazil.
- Rey, A., E. Pegoraro, V. Tedeschi, I. D. Parri, P. G. Jarvis, and R. Valentini (2002), Annual variation in soil respiration and its components in a coppice oak forest in central Italy, *Global Change Biol.*, *8*, 851–866.
- Schwendenmann, L., E. Veldkamp, T. Brenes, J. J. O'Brien, and J. Mackensen (2003), Spatial and temporal variation in soil CO₂ efflux in an old-growth neotropical rain forest, La Selva, Costa Rica, *Biogeochemistry*, *64*, 111–128.
- Scott, D. A., J. Proctor, and J. Thompson (1992), Ecological studies on a lowland evergreen rain forest on Maracá Island, Roraima, Brazil: II. Litter and nutrient cycling, *J. Ecol.*, *80*, 705–717.
- Shuttleworth, W. J., et al. (1984), Eddy correlation measurements of energy partition for Amazonian forests, *Q. J. R. Meteorol. Soc.*, *110*, 1143–1162.
- Smith, K., H. L. Gholz, and F. D. A. Oliveira (1998), Litterfall and nitrogen-use efficiency of plantations and primary forest in the eastern Brazilian Amazon, *For. Ecol. Manage.*, *109*, 209–220.
- Tenório, A. R. D. M., et al. (1999), Mapeamento dos solos da estação de piscicultura de Castanhal, PA, *FCAP Informe Tec.*, *25*, 5–26.
- Verchot, L. V., E. A. Davidson, J. H. Cattânio, I. L. Ackerman, H. E. Erickson, and M. Keller (1999), Land use change and biogeochemical controls of nitrogen oxide emissions from soils in eastern Amazonia, *Global Biogeochem. Cycles*, *13*, 31–46.
- Verchot, L. V., E. A. Davidson, J. H. Cattânio, and I. L. Ackerman (2000), Land-use change and biogeochemical controls of methane fluxes in soils of eastern Amazonia, *Ecosystems*, *3*, 41–56.
- Vitousek, P. M., and P. A. Matson (1992), Tropical forests and trace gases: Potential interactions between tropical biology and the atmospheric sciences, *Biotropica*, *24*, 233–239.
- Wieder, R. K., and S. J. Wright (1995), Tropical forest litter dynamics and dry season irrigation on Barro Colorado Island, Panama, *Ecology*, *76*, 1971–1979.
- Wright, S. J., and F. H. Cornejo (1990), Seasonal drought and leaf fall in a tropical forest, *Ecology*, *71*, 1165–1175.
- Zarin, D. J., M. J. Ducey, J. M. Tucker, and W. A. Salas (2001), Potential biomass accumulation in Amazonian regrowth forests, *Ecosystems*, *4*, 658–668.

D. V. Aragão and M. M. Araújo, Departamento de Ciências Florestais, Universidade Federal Rural da Amazônia, P.O. Box 917, Belém, PA, 66077-530, Brazil.

M. Capanu and R. Littell, Department of Statistics, University of Florida, P.O. Box 118545, Gainesville, FL 32611-8545, USA.

E. A. Davidson, Woods Hole Research Center, P.O. Box 296, Woods Hole, MA 02543, USA.

F. de Assis Oliveira, Departamento de Ciências do Solo, Universidade Federal Rural da Amazônia, P.O. Box 917, Belém, PA, 66077-530, Brazil.

C. J. R. de Carvalho, Embrapa Amazônia Oriental, P.O. Box 48, Belém, PA, 66077-530, Brazil.

F. Y. Ishida and E. B. Santos, Instituto de Pesquisa Ambiental da Amazônia, Av. Nazaré 669, Belém, PA, 66035-170, Brazil.

W. H. McDowell, Department of Natural Resources, University of New Hampshire, 219 James Hall, Durham, NH 03824, USA.

L. G. T. Rangel-Vasconcelos, Soil and Water Science Department, University of Florida, P.O. Box 110510, Gainesville, FL 32611-0510, USA.

S. S. Vasconcelos and D. J. Zarin, School of Forest Resources and Conservation, University of Florida, P.O. Box 110760, Gainesville, FL 32611-0760, USA. (zarin@ufl.edu)