

## The magnitude and persistence of soil NO, N<sub>2</sub>O, CH<sub>4</sub>, and CO<sub>2</sub> fluxes from burned tropical savanna in Brazil

Mark Poth,<sup>1</sup> Iris Cofman Anderson,<sup>2</sup> Heloisa Sinatora Miranda,<sup>3</sup>  
Antonio Carlos Miranda,<sup>3</sup> Philip J. Riggan<sup>1</sup>

**Abstract.** Among all global ecosystems, tropical savannas are the most severely and extensively affected by anthropogenic burning. Frequency of fire in cerrado, a type of tropical savanna covering 25% of Brazil, is 2 to 4 years. In 1992 we measured soil fluxes of NO, N<sub>2</sub>O, CH<sub>4</sub>, and CO<sub>2</sub> from cerrado sites that had been burned within the previous 2 days, 30 days, 1 year, and from a control site last burned in 1976. NO and N<sub>2</sub>O fluxes responded dramatically to fire with the highest fluxes observed from newly burned soils after addition of water. Emissions of N-trace gases after burning were of similar magnitude to estimated emissions during combustion. NO fluxes immediately after burning are among the highest observed for any ecosystem studied to date. These rates declined with time after burning and had returned to control levels 1 year after the burn. An assessment of our data suggested that tropical savanna, burned or unburned, is a major source of NO to the troposphere. Cerrado appeared to be a minor source of N<sub>2</sub>O and a sink for atmospheric CH<sub>4</sub>. Burning also elevated CO<sub>2</sub> fluxes, which remained detectably elevated 1 year later.

### Introduction

One of the keys to understanding global atmospheric change is to understand the interactions between land management practices and the influence of these actions on the magnitude and direction of ecosystem trace gas exchange. Many of the atmospheric trace gases of interest are the direct or indirect products of biological activity. Consequently, tropical biomes of high biological activity are important contributors to the global trace gas budget. The emissions data available on what are a wide variety of tropical ecosystems supports the importance of tropical ecosystems as sources of NO, N<sub>2</sub>O [Keller *et al.*, 1983; Keller *et al.*, 1986; Seiler and Conrad, 1987; Kaplan *et al.*, 1988; Goreau and de Mello, 1988; Johansson and Sanhueza, 1988; Luizao *et al.*, 1989; Garcia-Mendez *et al.*, 1991] and methane [Keller *et al.*, 1986; Hao *et al.*, 1988]. An understanding of how biosphere/atmosphere trace gas exchanges are modified by various land use practices is lacking [Keller *et al.*, 1992; Davidson *et al.*, 1993]. Without such data, projections or assessments cannot be made of the numerous land use options available. We need

more trace gas exchange data and a better understanding of the mechanisms involved in order to select optimal strategies for mitigating emissions.

Disturbance can greatly alter soil processes and trigger changes in the emission rates of important trace gases. For example, grassland fertilizations can stimulate N<sub>2</sub>O emissions and depress methane uptake [Mosier *et al.*, 1991]. This is the result of the stimulation of soil nitrification and denitrification processes and the inhibiting effects of ammonium on the biological oxidation of methane. Flooding caused by new reservoirs has increased CO<sub>2</sub> and CH<sub>4</sub> emissions [Rudd *et al.*, 1993] by changing oxygen availability to what used to be forest soils. Fire in California chaparral dramatically stimulated NO and N<sub>2</sub>O emissions for over 6 months [Anderson and Poth, 1989] by converting nitrogen into more available forms for nitrification and temporarily reducing competition for nitrogen from plant uptake. Conversely, in burned tall grass prairie, little N<sub>2</sub>O was released from burned soils because of uptake by the surviving grasses [Groffman *et al.*, 1993]. Fire is certainly a potent force in the tropics [Crutzen and Andreae, 1990; Riggan *et al.*, 1993], yet information on the influence of fire on soil emissions of important trace gases is limited [Luizao and Matson, 1989; Hao *et al.*, 1988].

Cerrado, a tropical vegetation type unique to South America, covers 2 million km<sup>2</sup> or about 25% of Brazil. Fires set by man or by lightning are common in the dry season and have been occurring in these ecosystems for thousands of years [Goodland, 1971]. Cerrado is made up of diverse plant communities covering a continuum from

<sup>1</sup>U.S. Department of Agriculture, Forest Service Research, Riverside, California.

<sup>2</sup>Virginia Institute of Marine Science, College of William and Mary, Gloucester point, Virginia.

<sup>3</sup>Departamento de Ecología, Universidade de Brasília, Brasília, Brasil.

Copyright 1995 by the American Geophysical Union.

open tropical grassland to savanna (campo limpio) to cerrado, a closed canopy semideciduous forest. Five distinct plant communities are recognized [Goodland, 1971; Coutinho, 1982]. The gradient of cerrado vegetation has been hypothesized to follow gradients in soil fertility and fire use. Fire is very common in grasslands and savannas but is a rare occurrence in the mature closed canopy cerrado forests [Goodland, 1971]. Fuel characteristics and direct fire emissions rates have been reported for cerrado by Ward *et al.* [1992]. This paper reports the first measurements of trace gas fluxes from cerrado soils and the effects of burning on changing flux rates, and also assesses the importance of fire disturbance of tropical savanna on the global budget of trace gases.

## Methods

### Study Site

Our study was conducted within the research and ecological reserve operated by the Instituto Brasileiro de Geografia e Estatística (IBGE), located 20 km south of Brasília, District Federal (15°55'58"S, 47°51'02"W). The climate is tropical (Köppen's Aw) with mean annual precipitation of 1100-1600 mm. This area of the tropics is characterized by distinct wet (October to March) and dry (April to September) seasons with 90% of the precipitation falling in the wet season. The mean relative humidity is 64%, but it can be as low as 18% during the driest periods. The annual mean maximum temperature is 25°C and the annual mean minimum temperature 16°C (climate data courtesy of the Reserva Ecológica, IBGE, 1980-1989). Soils are dystrophic, deep, and well-drained red latosols.

Current research at IBGE has been carried out in three experimental sites with different physiognomic forms: cerrado, closed canopy semideciduous forest; cerrado, a dense scrub of shrubs and trees (in a strict sense), and campo sujo, a grassland with scattered shrubs [Goodland, 1971]. Plots are burned every 4 years (in August), or every 2 years (in either June, August, or September). Long-term control plots have not burned since 1976. Plot size ranges from 1 to 5 ha. The overall design includes 37 plots.

The work we report on here was done during late August of 1992. Burning was carried out by the Reserva Ecológica - IBGE technicians in conjunction with Universidade de Brasília staff. Fires were usually started at 1400 LT. Fires spread quickly and typically were completed within 30 min.

We measured fluxes of NO, N<sub>2</sub>O, CH<sub>4</sub>, and CO<sub>2</sub> from cerrado sites that had been burned within the previous 2 days. We also made measurements on plots 30 days and 1 year after burning and from long-term control plots that have remained unburned since 1976. Although we made measurements at replicate plots, all of these are within the Reserva Ecológica - IBGE.

### Plant Biomass and Fuel Consumption

To partially characterize the fire at these sites, we measured total fuel consumption during the fire by determining the plant biomass before and after burning. On the basis of previous prescribed fire experiments, we have defined fuel for the cerrado simply as the living or dead parts of the vegetation found from the soil surface to a height of 2 m. Tree trunks and stems with a diameter greater than 6 mm are excluded. To estimate fuel, five transect lines of 15 m were established in each plot. For each transect, five subplots (25x25 cm) at 3-m intervals were used to sample the fuel. All fuel within the subplot was clipped at ground level, and together with the litter on the soil surface, taken to the laboratory. In the laboratory, fuel was separated into live and dead grasses, leaves, and stems. The fuel was dried at 80°C for 48 hours, allowed to cool, and weighed. For higher shrubs and trees, the fuel was sampled in a subplot 1-m wide, 5-m long, and 2-m high in the middle of each transect. After the fire, a similar transect was used to collect and estimate the amount of unburned fuel.

### Flux Measurements

Fluxes of NO, N<sub>2</sub>O, CH<sub>4</sub>, and CO<sub>2</sub> were measured using a closed box flux technique [Anderson and Levine, 1987]. One day prior to making flux measurements at each plot, six stainless steel frames, covering an area of 0.581 m<sup>2</sup> were driven 2.5 cm into the soil. In order to measure fluxes of either CO<sub>2</sub> or NO, a Teflon-lined, expanded-cell polycarbonate box fitted with a fan and with a total volume of 150.5 L (including the frame volume) was placed over the frame. The base of the flux box was sealed to the frame via a Teflon-covered foam lining. Two openings (0.64 cm) in the top of the flux box prevented pressure changes from developing during sampling. For N<sub>2</sub>O and CH<sub>4</sub> measurements, a flux box with a total volume of 76.9 L was used in order to increase sensitivity. Because we made measurements during the dry season, soils were relatively dry. After measuring trace gas flux rates of dry soils, we added distilled water equivalent to a 1-cm rainfall. After 30 min, gas flux measurements were repeated. We sampled a new plot each day.

### Inhibitors and Soil Amendments

To assess the roles of different microbial communities in producing the observed fluxes of trace gases, we employed two nitrification inhibitors: acetylene and allylthiourea (ATU). Acetylene was added to the flux box to a concentration of 1% and allowed to react with the soil for 1 hour. The flux cover was then removed and gas allowed to disperse for 10 min. This was done to eliminate acetylene interference with NO measurements and

achieve inhibition of nitrification. A solution of 200- $\mu$ M ATU was added to the soil 1 hour before measurements began. The amount added was equivalent to 1 cm of rainfall.

Soils in the unburned plots might have been substrate limited for NO or N<sub>2</sub>O production. To test for this, unburned soils were amended with 10-mM-N ammonium chloride or potassium nitrate solutions equivalent to 1 cm of rainfall 1 hour prior to initial measurements.

### Analysis of Carbon Dioxide

Immediately upon setting the flux chamber on its frame, CO<sub>2</sub> was analyzed in sample air over a 3-min period using a LiCor 6200 photosynthesis system with integrated infrared gas analyzer and data system. (All manufacturer and brand names are used for information only. No endorsement is intended.) The instrument was modified by removing the cuvette and substituting the flux box cover system described above as the input source. Standard errors for CO<sub>2</sub> fluxes using this system were <1% of the rates measured.

### Analysis of Nitric Oxide

Immediately following the 3-min sampling period for CO<sub>2</sub>, the sample stream was switched to a system for analysis of NO, which was detected over an 8-min period using a Luminox, nitrogen dioxide (NO<sub>2</sub>) detector (Model LMA-3, Scintrex-Unisearch, Toronto, Canada) as described by *Anderson and Poth* [1989]. Sample air from the flux box, pumped at approximately 2.8 L min<sup>-1</sup> by a Teflon bellows and a battery-operated pump, was dried by passage through nafion tubing (Type 815, Dupont perfluorinated polymer, Perma Pure, Inc., Toms River, N.J.) packed in indicating silica gel. NO in the dried sample gas was converted to NO<sub>2</sub> by passage through a tube (7.6 cm) containing 10% chromium trioxide on firebrick (30/60 mesh, Chromosorb P, Altech) before being pumped to a tee inlet on the LMA-3 NO<sub>2</sub> detector, which then sampled the gas stream at the rate of 1.5 L min<sup>-1</sup>. A three-way valve, which switched flow of sample air from the converter tube to a blank tube, allowed measurement of either background NO<sub>2</sub> in sample air (following passage through the blank tube) or NO + NO<sub>2</sub> (following passage through the converter tube). The chromium trioxide/firebrick was replaced whenever we observed a decrease in converter efficiency during calibration. Calibrations and measurements of flow rates through the pumping system and the LMA-3 were performed at the beginning and at the end of each day of data collection. During calibration, the LMA-3 was zeroed with room air which was passed first through a column containing pellets of alumina coated with KMnO<sub>4</sub> (Purafil, Southeastern Engineering Co.,

Midlothian, Va). This column reduces the background NO in room air to approximately 2 to 4 ppbv (parts per billion by volume) and obviates the need for transporting cylinders of zero air to field sites. For calibration NO (approximately 9 ppmv, Scott Environmental Technology, Plumsteadville, Pa.) was mixed with room air (after passage through KMnO<sub>4</sub> coated alumina) providing known concentrations of NO ranging from 20 to 50 ppbv. Gas flows were controlled with mass flow controllers (Tylan, model FC 280). Fluxes of NO were calculated from the slope of the regression line of NO versus time (4 - 8 min) after correction of the NO concentration for dilution during sampling.

### Analysis of CH<sub>4</sub> and N<sub>2</sub>O

For analysis of CH<sub>4</sub> and N<sub>2</sub>O, samples were taken through a septum on the top of the flux box every 20 min for 1 hour using 60-mL disposable plastic syringes with rubber plunger tips and fitted with three-way stopcocks. Samples were analyzed for N<sub>2</sub>O using a gas chromatograph (Hewlett Packard, model 5890, Palo Alto, Calif.) with electron capture detector and 10-port valve allowing backflushing of the column following each sample run. The detector temperature was 330°C, oven temperature was 50°C, the column was a 2-m porapak Q, and argon plus 5% methane was the carrier gas at a flow rate of 30 mL min<sup>-1</sup>. CH<sub>4</sub> in these samples was measured by gas chromatography with a flame ionization detector. The column was 2-m stainless-steel, containing molecular sieve 5 Å. Detector temperature was 250°C and the column 70°C. Helium was used as the carrier gas at a flow rate of 30 mL min<sup>-1</sup>.

### KCl-Extractable Soil NH<sub>4</sub><sup>+</sup>, NO<sub>2</sub><sup>-</sup>, and NO<sub>3</sub><sup>-</sup>

At the study site, composite samples (five subsamples each) were taken from the top 2-cm of soil both around each of the flux box frames and within each frame at the completion of the experiment. These samples were taken immediately after the completion of flux measurements. Soils were air dried, sealed in whirl-pak bags, and extracted with 2-M KCl upon return to the laboratory, using a modification of the technique of *Keeney and Nelson* [1982]. A 5-g sample of soil was weighed into a 50-mL screw cap centrifuge tube. The tube was sealed after adding 50-ml of 2 M KCl and mixed with a wrist action shaker for 1 hour. The tube was then centrifuged and the supernatant used for analysis. Ammonium was determined colorimetrically by an automated indophenol method (Technicon Industrial Method 780-86T), nitrite via diazotization (Technicon Industrial Method 784-86T), and nitrate + nitrite by copperized cadmium reduction in combination with diazotization (Technicon Industrial Method 818-86T), using a Technicon Traacs autoanalyzer, Model 800 (Technicon Corporation, Terrytown, N.Y).

### Percent Moisture

Samples for analysis of percent moisture were taken as described above, stored for less than 30 min in whirl-pak bags, weighed, and dried to constant weight at 105°C. Percent moisture is reported as percent of dry weight.

### Measured pH

A 1:1 soil water paste was prepared with glass-distilled water and allowed to stand for 1 hour. The soil was then stirred and the pH measured using a Beckman, model 71 pH meter with temperature compensation.

### Soil and Air Temperatures

During each flux measurement, temperature was measured both within the flux box at approximately half height and in the soil at a depth of 2 cm. A National Institute of Standards and Technology (NIST)-calibrated thermometer equipped with thermistor probes was used.

### Enumeration of Autotrophic Nitrifiers

Autotrophic nitrifier populations were estimated using a five-tube most probable number (MPN) procedure [Schmidt and Belser, 1982]. After inoculation, tubes were incubated at room temperature for 30 days. Positive tubes were those containing nitrate and/or nitrite, determined colorimetrically [Schmidt and Belser, 1982].

### Statistics

For measured variables, normal probability plots were used to assess the distribution of the data. To determine

the relationships between measured soil parameters and trace gas fluxes, we used regression analysis and calculated Pearson's coefficient of determination and associated *p* values. Because of observed nonlinearity in probability plots and to be conservative in testing for differences between burn treatments and water amendments, we used the Kurskal-Wallis one-way analysis of variance, a nonparametric technique. All analyses were performed with the Systat (V.5.1) package for Macintosh computers [Wilkinson, 1989].

## Results

### Plant Biomass and Fuel Consumption

The measured (all leaves and stems less than 6 mm) plant biomass plot averages in campo sujo and cerrado, in a strict sense, stands varied, respectively, from 0.67 (SD 0.08) kg m<sup>-2</sup> to 0.082 (SD 0.09) kg m<sup>-2</sup>, and from 0.75 (SD 0.09) kg m<sup>-2</sup> to 1.24 (SD 0.13) kg m<sup>-2</sup>. In the cerrado areas, grasses were less than 30% of the total fuel load and dead leaves from the litter layer accounted for 36-39%. The fire consumed 81-98% of the fuel in campo sujo plots and 68-97% in the cerrado plots. Remaining biomass consisted mainly of larger stems in burned areas with occasional unburned islands accounting for the remainder.

### Soil Chemical Responses to Fire

The fire had a dramatic effect on soil chemistry (Table 1). Burning increased the concentration of extractable ammonium. There was no clear effect of fire on soil

**Table 1.** Comparison of Soil Chemical Characteristics for Cerrado Soils Along a Burning Chronosequence

	Unburned	Burned	Burned + 30 Days
Exchangeable NH <sub>4</sub> <sup>+</sup> (mg kg-soil <sup>-1</sup> )	14.4 (1.4)	42.9 (2.7)	26.6 (3.7)
Exchangeable NO <sub>3</sub> <sup>-</sup> (mg kg-soil <sup>-1</sup> )	11.5 (1.71)	14.5 (1.4)	5.88 (1.65)
Exchangeable NO <sub>2</sub> <sup>-</sup> (mg kg-soil <sup>-1</sup> )	0.64 (0.13)	0.57 (0.06)	0.63 (0.29)
pH	3.74 (0.50)	4.17 (0.04)	3.88 (0.02)
Total N (%)	0.260 (0.012)	0.320 (0.009)	0.283 (0.015)
Total C (%)	5.18 (0.28)	6.06 (0.28)	5.53 (0.36)

Values shown are means (standard error).

extractable  $\text{NO}_2^-$  and  $\text{NO}_3^-$ . Detectable concentrations of  $\text{NO}_2^-$  were relatively high in all soils. Soil pH also increased measurably in the top 2 cm of the soil due to the addition of ash produced by the fire.

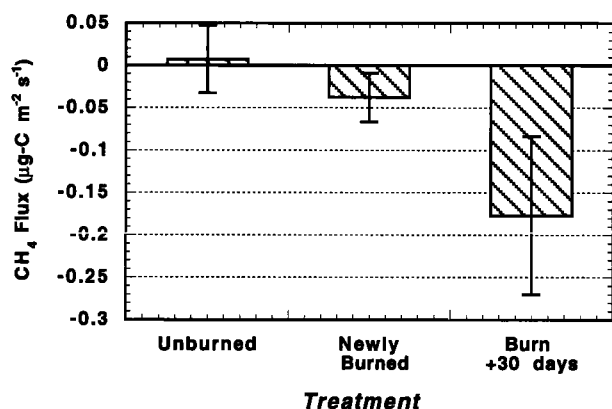
### CH<sub>4</sub> and CO<sub>2</sub> Fluxes

Cerrado that is unburned has no significant flux of CH<sub>4</sub> (Figure 1). Newly burned cerrado had a CH<sub>4</sub> flux rate of  $-0.038$  (SE=0.029)  $\mu\text{g-C m}^{-2} \text{s}^{-1}$  that increased to  $-0.177$  (SE=0.093)  $\mu\text{g-C m}^{-2} \text{s}^{-1}$  at sites burned 30 days earlier. By 1 year after the fire, CH<sub>4</sub> uptake by soils had disappeared. CH<sub>4</sub> fluxes were not correlated with any soil chemical parameter (Table 2).

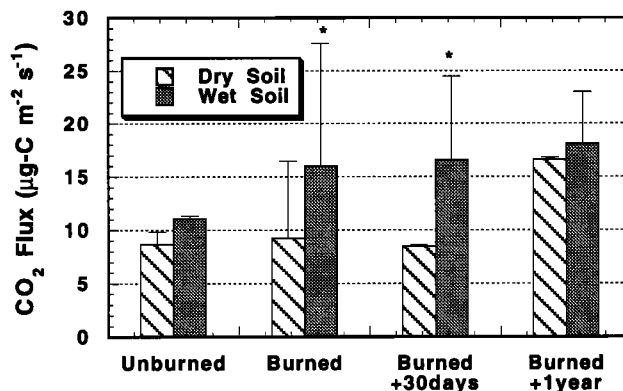
CO<sub>2</sub> fluxes were higher for burned cerrado than for the unburned control (Figure 2). At sites burned 1 year earlier and at the long-term fire exclusion sites, CO<sub>2</sub> fluxes were insensitive to water additions. In contrast, newly burned sites and sites burned 30 days earlier responded strongly to water additions. CO<sub>2</sub> fluxes were correlated with NO fluxes and soil exchangeable  $\text{NH}_4^+$ ,  $\text{NO}_3^-$  and  $\text{NO}_2^-$  (Table 2). CO<sub>2</sub> flux and soil temperature are not well correlated with analysis yielding a high Q<sub>10</sub> of about five (Figure 3). There were no significant changes in CO<sub>2</sub> flux with the addition of  $\text{NH}_4^+$  or  $\text{NO}_3^-$ . The nitrification inhibitors C<sub>2</sub>H<sub>2</sub> and ATU also had no effect.

### NO and N<sub>2</sub>O Fluxes

The variation in the NO fluxes measured is shown with a probability plot (Figure 4). The variance is large and apparently not normally distributed when examined across all treatments. NO fluxes from sites burned the previous



**Figure 1.** Methane fluxes for cerrado (tropical savanna) near Brasília, Brazil, as a function of time since burning. Values shown are means (SE). All treatments were significantly different ( $p < 0.05$ ).



**Figure 2.** Carbon dioxide fluxes for cerrado (tropical savanna) near Brasília, Brazil, as a function of time since burning. Change in flux with the addition of 1 cm of water is shown by the gray bars (asterisk indicates a significant increase  $p < 0.05$  with the addition of water).

day and 1 month earlier were significantly higher than those from unburned control sites and were dramatically increased by the addition of water (Figure 5). Soil N<sub>2</sub>O fluxes were significantly higher in burned plots than unburned plots but dropped back to unburned levels within 30 days. Both NO and N<sub>2</sub>O fluxes were significantly correlated with pH. Here, pH increases as a result of the ash deposited by burning. NO flux was also correlated with soil exchangeable  $\text{NH}_4^+$  but uncorrelated with  $\text{NO}_3^-$  and other soil chemical parameters (Figure 6 and Table 2). NO flux and temperature were poorly correlated with a Q<sub>10</sub> of about 3.8 (Figure 3). N<sub>2</sub>O fluxes were weakly but significantly correlated with soil total N (Table 2). There were no significant changes in NO and N<sub>2</sub>O fluxes with the addition of  $\text{NH}_4^+$  or  $\text{NO}_3^-$ . The nitrification inhibitors C<sub>2</sub>H<sub>2</sub> and ATU also had no effect.

### Discussion

CH<sub>4</sub> uptake is observable after the fire in spite of the biocidal effects of fire at the soil surface (Figure 1). Cerrado fires produce temperatures that would destroy microorganisms within the top few millimeters of the soil surface [Dunn *et al.*, 1985]. This amount of soil heating would only be enough to destroy a small fraction of the total soil microorganism population within the greater soil profile. Curiously, the unburned cerrado had no measurable CH<sub>4</sub> uptake or production. This agrees with observations for tropical savanna in Venezuela [Hao *et al.*, 1988].

There is a source of methane in cerrado soils. Burning in cerrado is done during the dry season, and these fires were carried out in the dry season. Hence there were no soil sites suitably anaerobic from water logging for methane formation. Termites are common in cerrado, and

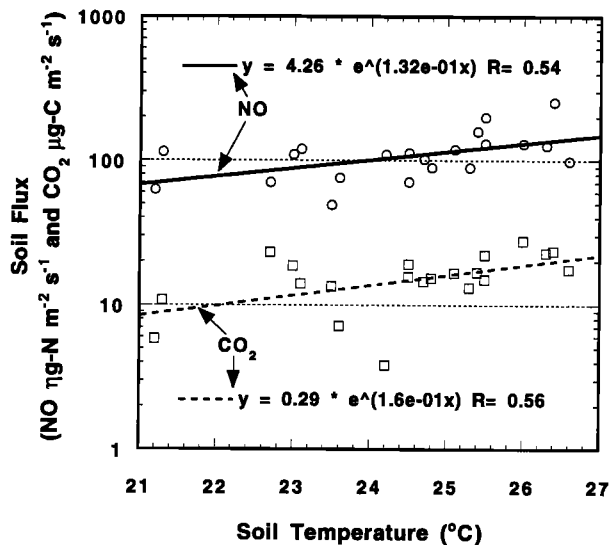
**Table 2.** Correlation Matrix (Values of  $\rho$ ) for Trace Gas Fluxes, Soil Chemical Parameters and the Most Probable Number of Soil Chemoautotrophic Ammonium Oxidizers

	CO <sub>2</sub> Flux	CH <sub>4</sub> Flux	N <sub>2</sub> O Flux	NO Flux	pH	NH <sub>4</sub> <sup>+</sup>	NO <sub>3</sub> <sup>-</sup>	NO <sub>2</sub> <sup>-</sup>	Total N	Total C	MPN
CO <sub>2</sub> Flux	1										
CH <sub>4</sub> Flux	0.29	1									
N <sub>2</sub> O Flux	-0.34	0.27	1								
NO Flux	0.61*	0.13	0.20	1							
pH	-0.04	-0.09	-0.51*	0.37*	1						
NH <sub>4</sub> <sup>+</sup>	0.52*	0.01	-0.41	0.76*	0.76*	1					
NO <sub>3</sub> <sup>-</sup>	-0.46*	0.26	0.20	0.16	0.21	0.11	1				
NO <sub>2</sub> <sup>-</sup>	0.64*	0.27	-0.35	0.13	-0.01	-0.18	-0.06	1			
Total N	0.21	-0.22	-0.47*	0.35	0.26	0.68*	0.24	-0.19	1		
Total C	0.11	-0.16	-0.42	-0.20	0.05	0.49*	0.24	-0.19	0.92*	1	
MPN	0.17	0.12	-0.10	0.16	0.05	0.09	-0.02	-0.07	0.16	0.06	1
Soil H <sub>2</sub> O	0.34	-0.21	0.05	0.30	-0.50*	-0.02	-0.51*	-0.40	0.01	0.10	-0.16

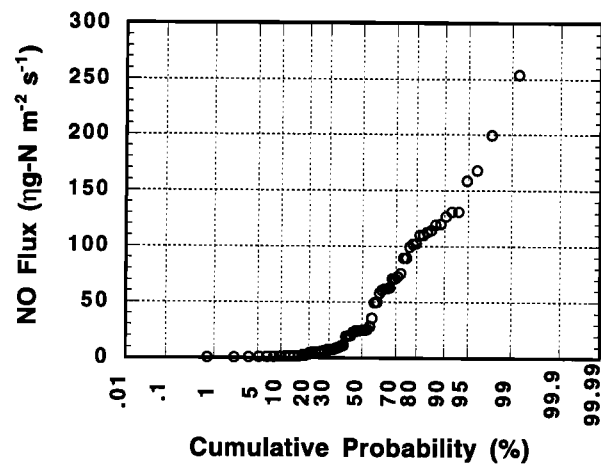
Significance level is \* for  $p < 0.05$ .

our research site was no exception. Arboreal and surface termite nests are a very common sight. Termites, and especially tropical termites, can produce measurable quantities of CH<sub>4</sub> [Zimmerman *et al.*, 1982] although recent information indicates that this is a small part of the global total released to the atmosphere [Martius *et al.*, 1993]. Termites in tropical savannas typically forage through a complex system of underground passages, and many species build underground galleries. The net effect of this dispersal of termites during food gathering would be to disperse the source of methane generation and diffusion into

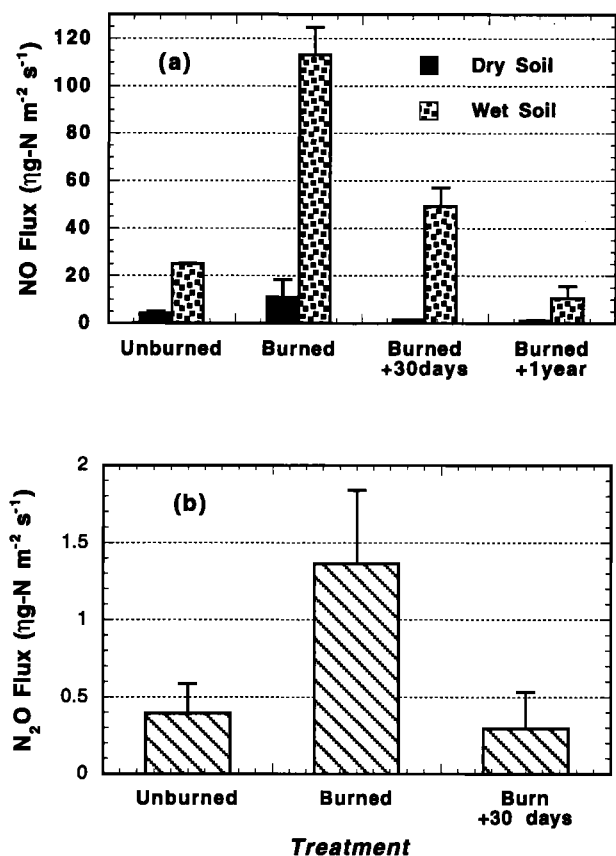
soil [Striegl, 1993]. We hypothesize that as a result of a decline in available food due to burning of above ground biomass, there is a decrease in termite foraging activity in burned cerrado, as has been observed with other insects [De Olivera and Franklin, 1993]. Presumably, they focus foraging attention on unburned islands within the fire area or adjacent unburned areas. This effect is probably very transitory, since vegetation begins to regrow even before the rains arrive. While the source of CH<sub>4</sub> is thereby reduced, the potential to oxidize CH<sub>4</sub> will remain relatively steady; thus we would expect to observe net uptake of CH<sub>4</sub> by burned soils. Because soil methane oxidation has been shown to be inhibited by increases in available soil



**Figure 3.** Relationships between soil nitric oxide and carbon dioxide fluxes and soil temperature.



**Figure 4.** Probability plot of all soil nitric oxide fluxes. Note that all fluxes greater than 20 ng-N m<sup>-2</sup> s<sup>-1</sup> are from soils that have had water added.



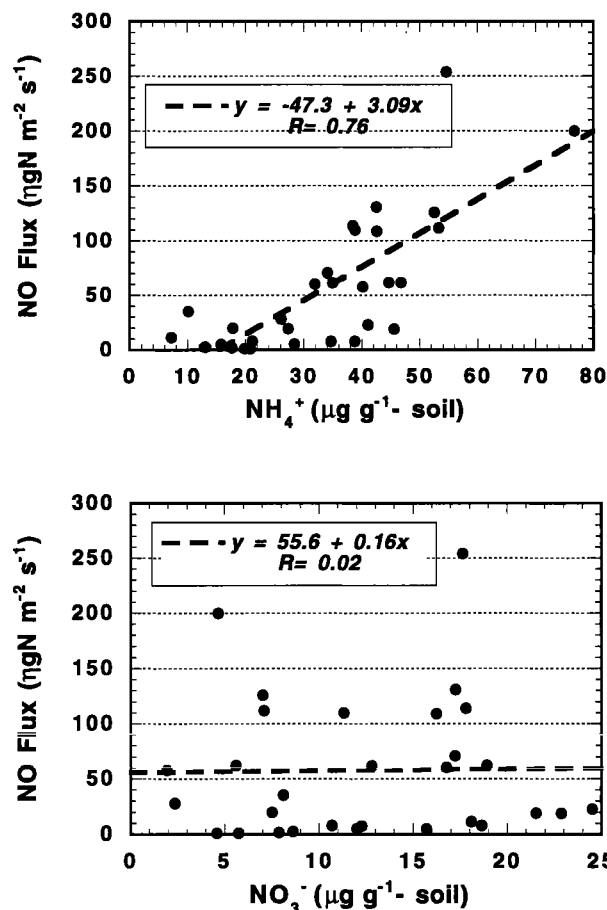
**Figure 5.** (a) Nitric oxide and (b) nitrous oxide fluxes for cerrado (tropical savanna) near Brasília, Brazil, as a function of time since burning. Change in NO flux with the addition of 1 cm of water is shown by the shaded bars. All NO fluxes were significantly higher with the addition of water ( $p < 0.05$ ). N<sub>2</sub>O fluxes were not significantly different with water addition and the values shown are the mean of wet and dry soil measurements.

ammonium [Mosier *et al.*, 1991], and because soil exchangeable NH<sub>4</sub><sup>+</sup> concentrations at these cerrado sites were high relative to controls (Table 1), our observations of CH<sub>4</sub> uptake probably represent a conservative measure of the overall CH<sub>4</sub> oxidation rate for these soils. This uptake is probably observable only when termite foraging has been dramatically reduced or redirected to unburned areas for a brief period before vegetation begins regrowing. New plant growth is observable within days.

The absence of uptake by unburned cerrado soils indicates the presence of an equilibrium between the source of soil methane, presumably the foraging termite community, and the sink for methane, oxidation by the soil microflora [Seiler *et al.*, 1984]. Although this is the case for soils, it may not be the case for termite nests. The larger populations of termites in nests do produce measurable fluxes from the nests [Martius *et al.*, 1993].

To evaluate the importance of tropical soil CH<sub>4</sub> uptake, we need to project our observed rates at this one site to all tropical soils. If we extrapolate the observed methane uptake rate for soils at the burned site of 0.038 (SE=0.029) μg m<sup>-2</sup> s<sup>-1</sup> to all tropical savanna soils (15 × 10<sup>12</sup> m<sup>2</sup>), we calculate a total uptake of 18 Tg CH<sub>4</sub> y<sup>-1</sup>. This is 70% of the estimated global total termite methane emission of 26 Tg CH<sub>4</sub>-C y<sup>-1</sup> [Martius *et al.*, 1993]. It is speculative to extend our results from one site to all tropical savannas as we have done above. Certainly, further work will be required to verify CH<sub>4</sub> uptake by tropical savanna soils. If our hypothesis concerning termite induced CH<sub>4</sub> oxidation by soils is correct, then unburned soils should demonstrate strong CH<sub>4</sub> oxidation in a laboratory setting.

An alternative hypotheses might explain the uptake of CH<sub>4</sub> by burned soils. Burning might increase the diffusion of CH<sub>4</sub> into the soil, and hence CH<sub>4</sub> oxidation, by opening root channels and removing litter layers. If CH<sub>4</sub> oxidation is diffusion limited, then removing plants and litter layers



**Figure 6.** Relationships between soil KCl extractable ammonium and nitrate and soil nitric oxide flux for cerrado (tropical savanna) near Brasília, Brazil. The relationship for ammonium is significant ( $p < 0.05$ ).

in the field (perhaps by raking away litter and clipping plants) should increase diffusion to the soil and increase  $\text{CH}_4$  oxidation.

$\text{CO}_2$  fluxes were up to 30 times higher than those reported for tropical savanna in Venezuela [Hao *et al.*, 1988] but were comparable to rates observed in Florida pine plantations [Castro *et al.*, 1994] and California Chaparral [Anderson and Poth, 1989]. Fire increased emissions ( $p=0.057$ ) when low water availability did not limit soil microbial activity (Figure 2). The effects of fire in elevating  $\text{CO}_2$  fluxes were very persistent, lasting for a year. Burning may have longer lasting effects than other anthropogenic disturbances that stimulate emissions, like fertilization [Castro *et al.*, 1994; Matson *et al.*, 1992]. Fertilization initially increases available N and so may stimulate C mineralization and associated  $\text{CO}_2$  fluxes briefly. Fire, on the other hand, by killing plants, eliminates initial plant competition for N and leaves partially burned plant material and roots available for decomposition. Fire may indirectly make soil organic matter more available for microbial decomposition as a result of the rise in soil pH. This could be a consequence of the greater solubility of humic and fulvic acids at higher pH [Schnitzer, 1982]. The net result of all of these factors combined may be a more persistent temporal effect on C mineralization. The effects of fire on C mineralization and  $\text{CO}_2$  flux were much more persistent than on NO flux that had returned to control levels 1 year after the fire. The difference may be due to the more persistent supply of C for mineralization and reestablishment of the plant community and a decrease in the availability of soil N.

NO flux in cerrado is correlated with  $\text{NH}_4^+$  availability (Table 2) as in other wildland and agricultural ecosystems [Papen *et al.*, 1993; Sanhueza *et al.*, 1990; Shepherd *et al.*, 1991]; yet, addition of  $\text{NH}_4^+$  did not significantly increase NO flux rates at the unburned site. Our MPN determinations isolated chemoautotrophic nitrifiers from cerrado soils. The substrate for chemoautotrophic nitrifiers is ammonia rather than ammonium ion. This is a result of the specificity of the ammonia oxidizing enzyme for ammonia [Suzuki *et al.*, 1974] and the much better transport of ammonia rather than ammonium into bacterial cells [Kleiner, 1985]. The stimulation of NO fluxes at the burned site may be due to the key combination of increased soil  $\text{NH}_4^+$ , providing substrate, and increased soil pH. The result is greater  $\text{NH}_3$  uptake by nitrifiers and more nitrification and associated trace gas production.

Nitrifiers were the apparent source of N trace gas emissions.  $\text{C}_2\text{H}_2$  and ATU, both inhibitors of nitrification, failed to reduce N trace gas fluxes. Though well-known inhibitors of autotrophic nitrification, these inhibitors will be far less effective if the nitrifiers in these acidic soils are heterotrophic [Anderson *et al.*, 1993] rather

than acid tolerant autotrophic strains [Martikainen and De Boer, 1993]. Alternatively, the ineffectiveness of inhibitors may be due to the coupling of nitrifier production of  $\text{NO}_2^-$  to the chemodenitrification of this product to NO. If the pool of soil  $\text{NO}_2^-$  is large enough, chemodenitrification may not decrease immediately upon the addition of a nitrification inhibitor [Davidson, 1993]. Evidence that nitrification is the source of N trace gases includes the higher NO and  $\text{N}_2\text{O}$  fluxes in response to burning which increases soil pH and N availability, conditions that favor nitrifiers. The high NO: $\text{N}_2\text{O}$  ratio of about 50 between these fluxes reflects generally aerobic conditions [Davidson, 1993]. Since soils remained aerobic and there was no correlation between N trace gas fluxes and soil nitrate, we conclude that there was no heterotrophic denitrification producing N trace gases. The  $Q_{10}$  values for both NO and  $\text{CO}_2$  soil emissions after wetting are high, and the linearity of the relationship with temperature was poor (Figure 3). This is probably due to the number of interacting biological and physical factors involved and is indicative of changing conditions. As a result, models of biogenic trace gas fluxes from soil should carefully consider other variables such as soil moisture.

The mean NO flux ( $113 \text{ ng-N m}^{-2} \text{ s}^{-1}$ , Figure 5a) from cerrado soils after fire and with the addition of water is among the highest ever observed. We used our data on emission rate changes with time after burning and with and without water limitations to calculate and estimate the annual emission of NO from cerrado. We assumed that the rainy season in the cerrado lasts for 6 months and that the frequency of burning is 2 years. For both the wet and the dry seasons, mean daily fluxes, as displayed in Figure 5a, at the newly burned site were assumed to last for 14 days and fluxes at the month-old burn for 30 days. Wet and dry rates from unburned cerrado were used for the remainder of the wet and dry seasons, respectively.

The total NO emission observed is high relative to fluxes from other ecosystems (Table 3). The calculation of regional and ecosystem emissions is very problematic [Keller and Goldstein, 1994]: to compare the relative importance of direct fire emissions with subsequent biogenic emissions from soil, we extended our results to all tropical savanna. On the basis of this tentative extension of our data, post-fire soil emissions of NO ( $3.9 \text{ Tg y}^{-1}$ ) nearly equal direct emissions during fire ( $4.4 \text{ Tg y}^{-1}$ , Table 3). The magnitude and importance of biogenic emissions in tropical savannas will need to be confirmed by other studies, preferably at other sites.

Biogenic emissions from post-fire soils will have much different temporal and spatial distributions than emissions during burning. Direct emissions of NO from fire will end with the arrival of the rainy season. Biogenic emissions that have been water limited during the dry season, when fires are most abundant, will peak during the early part of

**Table 3.** Global Annual Emissions of NO and N<sub>2</sub>O from Burned and Unburned Ecosystems

Ecosystem	Area		Emissions TgN yr <sup>-1</sup>					
	Burned yr <sup>-1</sup>	Total	Undisturbed		During Burn		Postburn	
	10 <sup>12</sup> m <sup>2</sup>		NO	N <sub>2</sub> O	NO	N <sub>2</sub> O	NO	N <sub>2</sub> O
Cerrado (Brazil)	0.90 <sup>a</sup>	1.8 <sup>a</sup>	0.41 <sup>b</sup>	-	-	-	0.5 <sup>b</sup>	0.02
Tropical Savanna	7.5 <sup>c</sup>	15.3 <sup>c</sup>	6.24 <sup>d</sup>	1.4 <sup>e</sup>	4.4 <sup>c</sup>	0.38 <sup>c</sup>		
			3.5 <sup>b</sup>				3.9 <sup>b</sup>	0.07
Tropical Forests	0.44 <sup>c</sup>	14.8 <sup>f</sup>	4.8 <sup>g</sup>	3.1 <sup>f</sup>	1.5 <sup>c</sup>	0.13 <sup>c</sup>	-	-
				2.2 <sup>e</sup>				
Temperate Forests	0.95 <sup>c</sup>	9.0 <sup>h</sup>	0.16 <sup>i</sup>	-	1.4 <sup>c</sup>	0.12 <sup>c</sup>		
(United States, Australia)			0.1 <sup>h</sup>	0.4 <sup>j</sup>				
Chaparral (United States)	0.2 <sup>k</sup>	4.0 <sup>h</sup>	0.04 <sup>l</sup>	-	-	-	0.12 <sup>l</sup>	0.03

<sup>a</sup>Ward, et al. [1992].

<sup>b</sup>This study (see text).

<sup>c</sup>Andreae [1993].

<sup>d</sup>Johansson and Sanhueza [1988]. Annualized estimated emissions take into account wet vs. dry conditions and assume a rainy season of 7 mo.

<sup>e</sup>Sanhueza et al., [1990]. This estimate includes measurements made during the dry and the rainy seasons.

<sup>f</sup>Matson and Vitousek [1990]. This estimate is based upon mean fluxes of N<sub>2</sub>O from moist tropical forests subdivided into 5 classes based upon fertility and degree of flooding.

<sup>g</sup>Calculated from mean of NO fluxes by Kaplan et al. [1988].

<sup>h</sup>Davidson [1991].

<sup>i</sup>I. C. Anderson et al., Regulation of nitric oxide, nitrous oxide and carbon dioxide emissions from temperate coniferous forest soils disturbed by clearcutting or burning, submitted to *Biogeochemistry*, 1995.

<sup>j</sup>Castro et al. [1993].

<sup>k</sup>Assuming a burn frequency of 20 years.

<sup>l</sup>Anderson and Poth, [1989].

the wet season. The peak of soil NO emissions just at the start of the rainy season may help sustain conditions for ozone formation by providing NO just as the direct source from fire is waning. This chain of events may partially explain observations of sustained high ozone concentrations in the tropics [Delaney et al., 1985].

The importance of tropical savannas, like the cerrado, as significant global sources of NO is becoming clear [Davidson, 1991, Levine et al., 1995]. The mean soil emissions of NO observed in this study are among the highest observed for any ecosystem thus far studied (Table 3). Emissions of NO from tropical systems appear to be much greater than from temperate ecosystems, agroecosystems, and boreal ecosystems.

In summary, we have provided some of the first information on the flux of trace gases from tropical savanna soils in Brazil. An assessment of our data suggests that tropical savanna, burned or unburned, is a major source of NO to the troposphere. Cerrado appears to be a minor source of N<sub>2</sub>O and a sink for atmospheric CH<sub>4</sub>.

Burning also elevated CO<sub>2</sub> fluxes, which remained detectably elevated 1 year later. It is clear that fire is important in regulating the exchange of trace gases between cerrado soils and the atmosphere.

**Acknowledgments.** We are grateful for the financial support provided for this work by the USDA - Forest Service, Pacific Global Change Research Program, the Universidade de Brasília (UnB) and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). Invaluable assistance was provided by Diane Bellis, Robert Glaubig, and the Director, Staff and Fire Brigade of the IBGE reserve. Helpful comments were provided by Eric Davidson, Michael Keller and an anonymous reviewer.

**References**

Anderson, I. C., and J. S. Levine, Simultaneous field measurements of biogenic emissions of nitric oxide and nitrous oxide, *J. Geophys. Res.* 92, 956-976, 1987.

- Anderson, I. C., and M. A. Poth, Semiannual losses of nitrogen as NO and N<sub>2</sub>O from unburned and burned chaparral, *Global Biogeochem. Cycles*, 3(2), 121-135, 1989.
- Anderson, I. C., M. A. Poth, J. Homstead, and D. J. Burdige, A comparison of NO and N<sub>2</sub>O production by the autotrophic nitrifier, *Nitrosomonas europaea* and the heterotrophic nitrifier, *Alcaligenes faecalis*, *Appl. Environ. Microbiol.* 59, 3525-3533, 1993.
- Andreae, M. O., The influence of tropical biomass burning on climate and the atmospheric environment in Chapman and Hall, *Biogeochemistry of Global Change: Radiatively Active Trace Gases* edited by R. S. Ormland, pp. 113-150, New York, 1993.
- Castro, M. S., P. A. Steudler, J. M. Melillo, J. D. Aber, and S. Millham, Exchange of N<sub>2</sub>O and CH<sub>4</sub> between the atmosphere and soils in spruce-fir forests of the northeastern United States, *Biogeochemistry*, 18, 119-135, 1993.
- Castro, M. S., W. T. Peterjohn, J. M. Melillo, P. A. Steudler, H. L. Gholz, and D. Lewis, Effects of nitrogen fertilization on the fluxes of N<sub>2</sub>O, CH<sub>4</sub>, and CO<sub>2</sub> from soils in Florida slash pine plantations, *Can. J. For. Res.*, 24, 9-13, 1994.
- Coutinho, L. M., Ecological effects of fire in the Brazilian cerrado, in *Ecology of Tropical Savannas* edited by B. J. Huntley and B. H. Walker, Springer-Verlag, pp. 273-291, New York, 1982.
- Crutzen, P. J., and M. O. Andreae, Biomass burning in the tropics: Impact on atmospheric chemistry and biogeochemical cycles, *Science* 250, 1669-1678, 1990.
- Davidson, E. A., 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 Amer. Soc. of Microbiol., J. E. Rogers and W. B. Whitman, pp. 219-235, Washington, D.C., 1991.
- Davidson, E. A., Soil water content and the ratio of nitrous oxide to nitric oxide emitted from soil in Chapman and Hall, *Biogeochemistry of Global Change: Radiatively Active Trace Gases*, edited by R. S. Ormland, pp. 369-386, New York, 1993.
- Davidson, E. A., P. A. Matson, P. M. Vitousek, R. Riley, K. Dunkin, G. Garcia-Mendez, and J. M. Maass, Processes regulating soil emissions of NO and N<sub>2</sub>O in a seasonally dry tropical forest, *Ecology*, 74, 130-139, 1993.
- Delaney, A. C., P. Haagensen, S. Walters, A. F. Watrburg, and P. J. Crutzen, Photochemically produced ozone in the emission from large scale vegetation fires, *J. Geophys. Res.*, 90(D1), 2425-2429, 1985.
- De Olivera, E. P., and E. Franklin, The effect of fire on soil mesofauna: Recolonization of burnt areas, *Pesq. Agropec. Bras.*, 28, 357-369, 1993.
- Dunn, P. H., D. R. Reynolds, M. Poth, and S. C. Barro, Effects of fire on soil microflora in the tropics, *Proceedings of the silver jubilee symposium, International Society for Tropical Ecology*, edited by Chowk, Bhargava Book Depot, 295-301, Varanasi, India, 1985.
- Garcia-Mendez, G., J. M. Maass, P. A. Matson, and P. Vitousek, Nitrogen transformations and nitrous oxide flux in a tropical deciduous forest in Mexico, *Oecologia*, 88, 362-366, 1991.
- Goodland, R. L., A physiognomic analysis of the 'cerrado' vegetation of central Brazil, *J. Ecol.* 59, 411-419, 1971.
- Goreau, T. J., and W. Z. de Mello, Tropical deforestation: Some effects on atmospheric chemistry, *Ambio*, 17, 275-281, 1988.
- Groffman, P. M., C. W. Rice, and J. M. Tiedje, Denitrification in a tallgrass prairie landscape, *Ecology*, 74 (3), 355-862, 1993.
- Hao, W. M., D. Scharffe, P. J. Crutzen, and E. Sanhueza, Production of N<sub>2</sub>O, CH<sub>4</sub>, and CO<sub>2</sub> from soils in the tropical savanna during the dry season, *J. Atmos. Chem.* 7, 93-105, 1988.
- Johansson, C., and E. Sanhueza, Emission of NO from Savanna Soils during rainy season, *J. Geophys. Res.* 93(D11), 14,193-14,198, 1988.
- Kaplan, W. A., S. C. Wofsy, M. Keller, and J. M. da Costa, Emission of NO and deposition of O<sub>3</sub> in a tropical forest system, *J. Geophys. Res.* 93, 1389-1395, 1988.
- Keeney, D. R., and D. W. Nelson, Nitrogen - Inorganic Forms in *Methods of Soil Analysis*, 2nd. ed, Agron. Soc. Amer., Madison, Wisc., edited by A.L. Page, R. H. Miller, and D. R. Keeney, pp. 643-693, 1982.
- Keller, A. A., and R. A. Goldstein, Propagation of uncertainty in carbon emission scenarios through the global carbon cycle, *World Res. Rev.*, 6, 304-315, 1994.
- Keller, M., et al., Tropical land use change and trace gas emissions, *Ecol. Bull.*, 42, 156-163, 1992.
- Keller, M., T. J. Goreau, S. C. Wofsy, W. A. Kaplan, and M. B. McElroy, Production of nitrous oxide and consumption of methane by forest soils, *Geophys. Res. Lett.* 10, 1156-1159, 1983.
- Keller, M., W. A. Kaplan, and S. C. Wofsy, Emissions of N<sub>2</sub>O, CH<sub>4</sub> and CO<sub>2</sub> from tropical forest soils, *J. Geophys. Res.*, 91, 11,791-11,802, 1986.
- Kleiner, D., Bacterial ammonium transport, *FEMS Microbiol. Rev.*, 32, 87-100, 1985.
- Levine, J. S., W. R. Cofer, D. R. Cahoon, and E. L. Winstead, Biomass burning a driver for global change, *Environ. Sci. Technol.*, 29, 120-125, 1995.
- Luizao, F., P. Matson, G. Livingston, R. Luizao, and P. Vitousek, Nitrous oxide flux following tropical land

- clearing, *Global Biogeochem. Cycles*, 3, 281-285, 1989.
- Martikainen, P. J., and W. De Boer, Nitrous oxide production and nitrification in acid soil from a dutch coniferous forest, *Soil Biol Biochem.*, 25, 343-347, 1993.
- Martius, C., R. Wassmann, U. Thein, A. Banderia, H. Rennenberg, W. Junk, and W. Seiler, Methane emissions from wood feeding termites in amazonia, *Chemosphere*, 26, 623-632, 1993.
- Matson, P. A., and P. M. Vitousek, Ecosystem approach to a global nitrous oxide budget, *BioScience*, 19, 228-235, 1990.
- Matson, P. A., T. G. Stith, C. Volkmann, C. Billow, and C. C. Grier, Soil nitrogen cycling and nitrous oxide flux in a Rocky Mountain Douglas-fir forest: Effects of fertilization, irrigation and carbon addition, *Biogeochemistry*, 18, 101-117, 1992.
- Mosier, A., D. Schimel, D. Valentine, K. Bronson, and W. Parton, Methane and nitrous oxide fluxes in native, fertilized and cultivated grasslands, *Nature*, 350, 330-332, 1991.
- Papen, H., B. Hellmann, H. Papke, and H. Rennenberg, Emission of N-oxides from acid irrigated and limed soils of a coniferous forest in Bavaria, in Chapman and Hall, *Biogeochemistry of Global Change: Radiatively Active Trace Gases*, edited by R. S. Oremland, pp. 245-260, New York, 1993.
- Riggan, P. J., J. A. Brass, and R. N. Lockwood, Assessing fire emissions from tropical savanna and forests of central Brazil, *Photogramm. Eng. Remote Sens.*, 59, 1009-1015, 1993.
- Rudd, J. W. M., R. Harris, C. A. Kelly, and R. E. Hecky, Are hydroelectric reservoirs significant sources of greenhouse gasses?, *Ambio*, 22, 246-248, 1993.
- Sanhueza, E. W., M. Hao, D. Scharfe, L. Donoso, and P. J. Crutzen, N<sub>2</sub>O and NO emissions from soils of the northern part of the Guayana Shield, Venezuela, *J. Geophys. Res.* 95(D13), 22,481-22,488, 1990.
- Schmidt, E. L., and L. W. Belser, Nitrifying Bacteria, in *Methods of Soil Analysis*, edited by A. L. Page, R. H. Miller, and D. R. Keeney, pp. 1027-1042, Agron. Soc. of Am., Madison, Wisc., 1982.
- Schnitzer, M., Organic Matter Characterization, in *Methods of Soil Analysis*, edited by A. L. Page, R. H. Miller, and D. R. Keeney, pp. 581-593, Agron. Soc. of Am., Madison, Wisc., 1982.
- Seiler, W., and R. Conrad, Contributions of tropical ecosystems to the global budget of trace gases especially CH<sub>4</sub>, H<sub>2</sub>, CO and N<sub>2</sub>O, in *The geophysiology of Amazonia*, edited by R. E. Dickenson, pp. 133-160, John Wiley, New York, 1987.
- Seiler, W., R. Conrad, and D. Scharffe, Field studies of methane emission from termite nests into the atmosphere and measurements of methane uptake by tropical soils, *J. Atmos. Chem.*, 1, 171-186, 1984.
- Shepherd, M. F., S. Barzetti, and D. R. Hastie, The production of atmospheric NO<sub>x</sub> and N<sub>2</sub>O from a fertilized agricultural soil, *Atmos. Environ.*, 25A9, 1961-1969, 1991.
- Striegl, R. G., Diffusional limits to the consumption of atmospheric methane by soils, *Chemosphere*, 26, 715-720, 1993.
- Suzuki, I., U. Dular, and S. C. Kwok, Ammonia or ammonium ion as substrate for oxidation by *Nitrosomonas europaea* cells and extracts, *J. Bacteriol.*, 120, 556-558, 1974.
- Ward, D. E., R. A. Susott, J. B. Kaufman, R. E. Babbit, D. L. Cummings, B. Dias, B. N. Holben, Y. J. Kaufman, R. A. Rasmussen, and A. W. Setzer, Smoke and fire characteristics for cerrado and deforestation burns in Brazil: BASE-B experiment, *J. Geophys. Res.*, 97, 14,601-14,619, 1992.
- Wilkinson, L., *SYSTAT: The System for Statistics*, SYSTAT, Inc., Evanston, Ill., 1989.
- Zimmerman, P. R., J. P. Greenberg, S. O. Wandinga, and P. J. Crutzen, Termites: A potentially large source of atmospheric methane, carbon dioxide, and molecular hydrogen, *Science*, 218, 563-565, 1982.
- 
- I. Cofman Anderson, Virginia Institute of Marine Science, College of William and Mary, P.O. Box 1346, Gloucester Point, VA 23062. (e-mail: iris@merlin.bio.vims.edu)
- H. Sinatora Miranda and A. C. Miranda, Departamento de Ecología, Universidade de Brasília, 70910-900, Brasília, D.F. Brasil. (e-mail: h.miranda@guarany.cpd.unb.br; a.miranda@guarany.cpd.unb.br)
- M. Poth and P. J. Riggan, USDA Forest Service Research, 4955 Canyon Crest Drive, Riverside, CA 92507. (e-mail: /s=3dm.poth/ou1=3ds27L05a@mhs#fsbo.attmail.com, /s=3dp.riggan/ou1=3ds27L05a@mhs#fsbo.attmail.com)

(Received November 30, 1994; revised June 30, 1995; accepted July 5, 1995.)