

Sources and Sinks of Trace Gases in Amazonia and the Cerrado

M. M. C. Bustamante

Department of Ecology, University of Brasilia, Brasilia, Brazil

M. Keller¹

International Institute of Tropical Forestry, USDA Forest Service, Rio Piedras, Puerto Rico

D. A. Silva

Department of Ecology, University of Brasilia, Brasilia, Brazil

Data for trace gas fluxes (NO_x , N_2O , and CH_4) from the Amazon and cerrado region are presented with focus on the processes of production and consumption of these trace gases in soils and how they may be changed because of land use changes in both regions. Fluxes are controlled by seasonality, soil moisture, soil texture, topography, and fine-root dynamics. Compared to Amazonian forests where the rapid cycling of nitrogen supports large emissions of N_2O , nitrification rates and soil emissions of N oxide gases in the cerrado region are very low. Several studies report CH_4 consumption during both wet and dry seasons in forest soils, but there is occasionally net production of CH_4 during the wet season. A few studies suggest an unknown source of CH_4 from upland forests. As with N oxide emissions, there are few data on CH_4 emissions from cerrado soils, but CH_4 consumption occurs during both wet and dry seasons. Clearing natural vegetation, burning, fertilization of agricultural lands, intensive cattle ranching, and increasing dominance by legume species in areas under secondary succession after land conversion have all been identified as causes of increasing N_2O and NO emissions from tropical regions. Large uncertainties remain for regional estimates of trace gas fluxes. Improvement of models for the N oxides and CH_4 fluxes for Amazonia and the cerrado still depends upon gathering more data from sites more widely distributed across two vast biomes and more importantly on basic theory about the controls of emissions from the ecosystem to the atmosphere.

¹Also at NEON Inc., Boulder, Colorado, USA.

1. INTRODUCTION

known in Brazil as cerrado. The cerrado of Brazil, covering 2 million km², is the largest savanna biome in South America and an area of extremely rapid agricultural development [Klink and Machado, 2005]. The tropical forests of Amazonia are also suffering rapid rates of change. Deforestation in Brazil has averaged nearly 20,000 km² a⁻¹ over the past 2 decades [see Alves *et al.*, this volume] and selective logging covers a similar area [see Asner *et al.*, this volume]. The conversion of native vegetation formations to pasture and cropland causes substantial changes in biogeochemical processes, including the ecosystem-atmosphere exchange of N₂O, nitric oxide (NO), and CH₄.

Nitrous oxide is a stable greenhouse gas in the troposphere that absorbs strongly in the infrared and has a long atmospheric lifetime of about 120 years. As a result, its 100-year global warming potential is 298 times that of CO₂ [Forster *et al.*, 2007]. In the stratosphere, N₂O is destroyed by photolysis and reaction with excited oxygen, which is a source of nitric oxide that contributes to depletion of the ozone [Crutzen, 1970]. Therefore the current increase from the preindustrial atmospheric mixing ratio of 270 ppbv to 319 ppbv (in 2005) has the potential to impact global climate over the next century [Lashof and Ahuja, 1990; Prather and Ehhalt, 2001; Forster *et al.*, 2007]. The global budget of N₂O is seriously perturbed with anthropogenic sources accounting for nearly a 50% increase over natural sources from terrestrial ecosystems and the oceans [Hirsch *et al.*, 2006]. Atmospheric N₂O is produced primarily as a result of microbial processes in soils especially through denitrification and through nitrification when oxygen tensions are low. Soils of the tropical forest biome are the most important natural source for N₂O [Matson and Vitousek, 1990].

Nitric oxide (NO) is a short-lived reactive gas that influences the oxidant balance of the troposphere and the production of ozone, a component of photochemical smog and a greenhouse gas. Although most atmospheric NO is produced either by fossil fuel combustion or by lightning, biological nitrification and denitrification, as well as chemodenitrification in soils, are also important [Davidson and Kingerlee, 1997]. A global estimate of NO emissions from soils is less certain than for N₂O but is about 21 Tg N a⁻¹ [Davidson and Kingerlee, 1997].

In soils, the production and emission of N₂O and NO are mainly regulated by the same processes. These have been summarized in a conceptual model known as "the hole-in-the-pipe" [Firestone and Davidson, 1989; Davidson *et al.*, 2000]. According to this model, total emissions of N₂O and NO are proportional to the inorganic nitrogen (ammonium and nitrate ions) flowing through the nitrification and denitrification pipes. Gases leak out through holes that are regulated by soil conditions such as moisture and oxygen concentra-

tion. Anaerobic conditions are found in soils when the rate of O₂ diffusion is slower than O₂ consumption. Within the soil environment, the aerobic process of nitrification (predominant at <60% water-filled pore space (WFPS)) is maintained primarily by autotrophic bacteria and archaea [Leininger *et al.*, 2006], resulting in the conversion of ammonium (NH₄⁺) to nitrate (NO₃⁻) via nitrite (NO₂⁻). There are two functional groups of nitrifiers, namely, the ammonium oxidizing nitrifiers, which convert NH₄⁺ via hydroxylamine to NO₂⁻, and the nitrite oxidizing nitrifiers, which oxidize NO₂⁻ to NO₃⁻. Denitrification, on the other hand, is an anaerobic process (predominant at >60% WFPS) in which denitrifiers reduce NO₃⁻ (via NO₂⁻), NO, and nitrous oxide (N₂O) to molecular nitrogen (N₂). The complete denitrification pathways result in the reduction of NO₃⁻ to N₂, but significant amounts of NO and N₂O can be emitted before complete reduction to N₂. Soil pH, metallic ion composition, and soil organic matter (SOM) all control the abiotic process of chemodenitrification, whereby microbially produced NO₂⁻ is decomposed to NO and NO₂ [Davidson, 1992]. The conceptual hole-in-the-pipe model has been formalized in simulation models such as the NASA-Carnegie-Ames-Stanford approach (CASA) [Potter *et al.*, 1998] and the Terrestrial Ecosystems Model [Melillo *et al.*, 2001].

Methane (CH₄) is an important greenhouse gas, and its atmospheric concentration has more than doubled since preindustrial times from about 0.7 to about 1.8 ppm today [Spahni *et al.*, 2005; Bosquet *et al.*, 2006; Forster *et al.*, 2007]. Most atmospheric CH₄ is produced by anaerobic degradation of organic matter under conditions where anaerobic respiration by microbes is limited by the paucity of alternate electron acceptors [Fenchel *et al.*, 1998]. Natural wetlands are the most important global source of CH₄, producing up to about 200 Tg CH₄ a⁻¹ (up to 40% of the estimated total CH₄ production) [Reeburgh, 2003]. The CH₄ source from the wetlands of the Amazon Basin has been estimated to be 29 Tg CH₄ a⁻¹ [Melack *et al.*, 2004]. This important source is discussed by Melack *et al.* [this volume] together with other aspects of the wetland carbon cycle. Microbial production of CH₄ in termite guts is another natural source of CH₄ that may be important in tropical ecosystems. Although this source is generally considered to be a minor term in the global budget, it is extremely difficult to quantify and highly uncertain [Martius *et al.*, 1993]. Reaction with OH radicals and transport to the stratosphere are the primary sinks for tropospheric CH₄. In soils under aerobic conditions, CH₄ tends to be consumed from the atmosphere in a process mediated primarily by bacteria that specialize in C 1 compounds, collectively known as methylotrophs [Hanson and Hanson, 1996]. Soil CH₄ consumption accounts for less than 10% of the annual destruction of atmospheric CH₄ [Reeburgh, 2003].

2. FLUXES OF N₂O AND NO FROM NATURAL ECOSYSTEMS TO THE ATMOSPHERE

2.1. N₂O and NO Fluxes From Amazon Forest Soils

The rapid cycling of nitrogen in Amazonian forests supports large emissions of N₂O. A summary of reported average annual fluxes of NO and N₂O for forests in the Amazon regions is presented in Table 1. The data indicate annual emissions of N₂O from soils of mature Amazonian forests ranging from 1.1 [Davidson and Kingerlee, 1997] to 6.9 kg N ha⁻¹ a⁻¹ [Keller et al., 2005]. Estimates of annual emissions of NO from Amazonian forests ranged from 0.9 [Davidson et al., 2004] to 2.4 kg N ha⁻¹ a⁻¹ [Garcia-Montiel et al., 2003]. The controls of NO and N₂O fluxes including seasonality, soil moisture, soil texture, topography, and fine-root dynamics are discussed in this section.

Variability of rainfall is a more important control than the small variation in soil temperature for the emissions of N oxides from soils in forests in the Amazon region [Verchot et al., 2000; Keller et al., 2005] (Figure 1). Nitrous oxide emissions are controlled by carbon and nitrogen availability and soil aeration in relation to water saturation. Both nitrifying and denitrifying bacteria produce N₂O, but the largest emissions result from denitrification under anaerobic conditions. For example, fluxes of N₂O were generally higher during the wet season (January–June) than the dry season [Davidson et al., 2004] in Pará. The significant increase of N₂O emission in the wet season could have been due to a combined effect of increased soil water content and nitrogen mineralization. The ratios of N₂O:NO fluxes were positively correlated with volumetric water content in soils in Pará [Davidson et al., 2004]. Working on sandy soils in Rondônia (Brazil), Garcia-Montiel et al. [2003] also found over 84% of N₂O fluxes

Table 1. Summary of Reported Average Annual Fluxes of NO, N₂O and CH₄ From Natural and Managed Ecosystems in the Amazon Region

Location/ Ecosystem	Reference	NO Flux (kg N-NO ha ⁻¹ a ⁻¹)	N ₂ O Flux (kg N-N ₂ O ha ⁻¹ a ⁻¹)	CH ₄ Flux (kg CH ₄ ha ⁻¹ a ⁻¹)
Amazonas State				
Forest	Kaplan et al. [1988]	1.4	1.4 and 1.9	
Amazon region				
Forest	Davidson and Kingerlee [1997]		1.1	
Secondary forest	Davidson and Kingerlee [1997]		0.3	
Active pasture	Davidson and Kingerlee [1997]		0.5	
Old pasture	Davidson and Kingerlee [1997]		0.4	
Pará State				
Primary forest	Verchot et al. [1999, 2000]	1.5	2.4	-2.1
Secondary forest	Verchot et al. [1999, 2000]	0.7	0.9	-1.0
Active pasture	Verchot et al. [1999, 2000]	0.5	0.3	-1.3
Degraded pasture	Verchot et al. [1999, 2000]	0.3	0.1	-3.1
Forest	Davidson et al. [2004]	0.9	2.6	-1.1
	Nepstad et al. [2002]	1.7	2.3	
Primary forest clay	Keller et al. [2005]	7.9	6.5	-0.7
Primary forest sandy loam	Keller et al. [2005]	7.7	1.4	-3.5
Logged forest clay	Keller et al. [2005]	–	7.0	16.8
Logged forest sandy loam	Keller et al. [2005]	28.6	6.5	7.5
Rondônia State				
Forest	Feigl et al. [2001]		1.9–2.8	-6.7
Pasture (4 years)	Feigl et al. [2001]		~30% < than forest	3.6
Pasture (22 years)	Kirkman et al. [2002]	0.17		
Forest	Garcia-Montiel et al. [2003]	2.4	3.2	
Forest	Neill et al. [2005]	1.4	4.3	
Pasture (1–3 years)	Neill et al. [2005]	0.2	3.1–5.1	
Pasture (6 years)	Neill et al. [2005]	0.2	0.1–0.4	

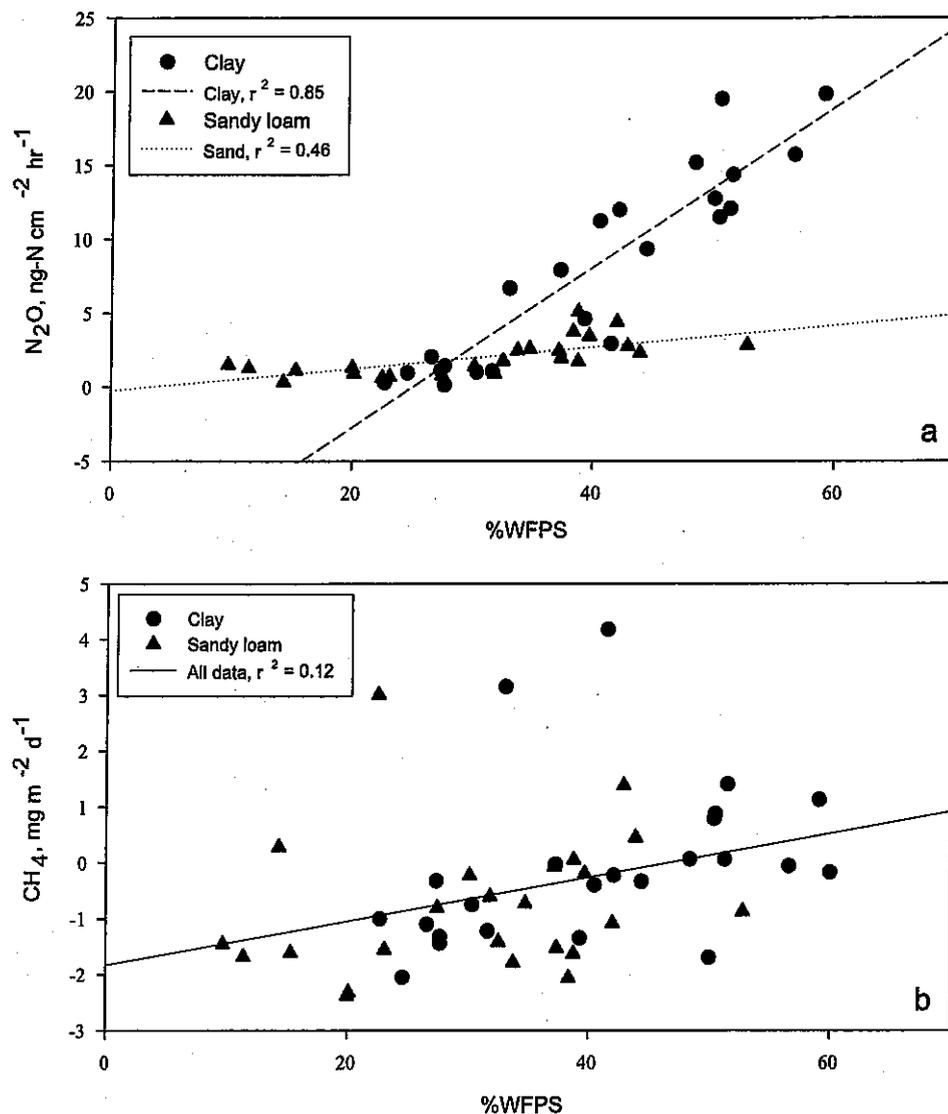


Figure 1. (a) N_2O and (b) CH_4 fluxes versus soil WFPS from clay (circles) and sandy loam Ultisol (triangles) soils from undisturbed sites in the Tapajós National Forest. Reprinted from Keller *et al.* [2005].

were emitted during the wet season. Similarly, during the wet season, soil N_2O fluxes in forest and pasture sites near Santarém, Pará, Brazil, were also positively correlated to C/N ratio in leaf litter, NH_4^+-N , and the ratio $NO_3^--N/(NO_3^--N + NH_4^+-N)$ but were negatively correlated to soil CH_4 consumption and bulk density, indicators of soil aeration [Wick *et al.*, 2005]. In contrast to N_2O , emissions of NO were more evenly distributed over the wet and dry seasons in Rondônia [Garcia-Montiel *et al.*, 2003; Vasconcelos *et al.*, 2004].

In laboratory experiments on forest soil samples collected across Brazilian Amazonia, van Dijk and Meixner

[2001] measured NO production and the rate constant of NO consumption under variable temperature and moisture conditions. NO production increased exponentially with soil temperature. Under very dry and very wet soil conditions, the response of the NO production to a change in temperature was less pronounced than under conditions of intermediate soil moisture. NO production peaked, independently of soil temperature, at soil moisture of $0.10\ g\ g^{-1}$ (0.27 and 0.38 WFPS for forest and pasture soils, respectively). On the other hand, NO consumption was most efficient at high soil temperatures ($>25^\circ C$) and under dry soil conditions ($<0.20\ g$

g^{-1} or 0.53 WFPS for forest soils). The rate constants of NO consumption were within 5% of NO release with comparable values for forest and pasture soils.

Tropical humid forests have generally high rates of net mineralization and net nitrification that can lead to the accumulation of NH_4^+ and NO_3^- during dry periods [Neill *et al.*, 1995]. The accumulation of NH_4^+ and NO_3^- in dry soils, followed by wetting, provides more favorable conditions for microbial activity and the development of soil anoxia stimulating the production of both N_2O and NO [Davidson, 1991; Garcia-Mendez *et al.*, 1991]. Soil accumulation of NH_4^+ , NO_2^- , and NO_3^- may occur in thin water films of microsites near oxidizing sites. Upon soil wetting, soil microbes can quickly use these pools, and produce pulses of N oxide gases. The effects of moisture and substrate availability on soil fluxes of NO and N_2O in an Amazonian regrowth forest were quantified by Vasconcelos *et al.* [2004] through irrigation during the dry season and removal of aboveground litter. Fluxes of N_2O and NO increased during dry season irrigation, while litter removal had no significant impact on N oxide emissions. Net soil nitrification did not respond to dry season irrigation but was somewhat reduced by litter removal. In contrast, pulse releases following wet-up events contributed relatively little to total annual emissions of N_2O and NO in the forest and pastures in studies in Rondônia [Neill *et al.*, 2005]. Curiously, an experiment investigating the effects of drought simulating the predicted climate change in the Amazon region showed no effect on NO and N_2O emissions [Davidson *et al.*, 2004].

Luizão *et al.* [2004] showed a significant differentiation of nitrogen mineralization and inorganic N concentration along a topographic gradient near Manaus, Amazonas, Brazil, with a positive rate of net N mineralization on the plateau and slope location and negative net N immobilization in the valley on sandy soils [Luizão *et al.*, 2004]. The decrease in total N concentrations followed the clay content in the topographic gradient, with higher concentrations in the clayey Oxisol and much lower concentrations for the sandy Podzol. This result explains early observations that noted considerably greater NO emissions from clay soils on plateaus as compared to sandy soils in valleys in the Manaus region [Bakwin *et al.*, 1990]. Consistent differences in soil-atmosphere fluxes of N_2O and NO with soil texture were determined by Keller *et al.* [2005] in a study over 2 years in undisturbed forest, near Santarem, Pará. Annual soil-atmosphere fluxes of N_2O (mean plus/minus standard error) were 7.9 ± 0.7 and 7.0 ± 0.6 $\text{ng N cm}^{-2} \text{h}^{-1}$ for a clay-texture Oxisol compared to 1.7 ± 0.1 and 1.6 ± 0.3 $\text{ng N cm}^{-2} \text{h}^{-1}$ for a sandy loam-texture Ultisol for 2000 and 2001, respectively (Figure 1). The annual fluxes of NO from undisturbed forest soil in 2001 were 9.0 ± 2.8 $\text{ng N cm}^{-2} \text{h}^{-1}$ for the Oxisol and

8.8 ± 5.0 $\text{ng N cm}^{-2} \text{h}^{-1}$ for the Ultisol [Keller *et al.*, 2005]. These results are consistent with earlier studies from the same region that showed significantly greater net nitrogen mineralization, net nitrification, and denitrification enzyme activity in the clay soils compared to the sandy loams [Silver *et al.*, 2000].

Along with soil texture, fine-root dynamics can affect the production and emission of trace gases, especially in tropical rain forests that are characterized by high root biomass density and rapid turnover of fine roots. Working in the Santarém region, Varner *et al.* [2003] and Silver *et al.* [2005] examined patterns in fine-root dynamics on clay and sandy loam soils in a lowland moist forest and its effect on rates of C and N trace gas fluxes. Root production did not differ significantly with soil texture. However, root decay was faster in clay than in sandy loam soil, leading to greater standing stocks of dead roots in the sandy loam. Rates of N_2O emissions were significantly greater in the clay soil (13 ± 1 $\text{ng N cm}^{-2} \text{h}^{-1}$) than in the sandy loam (1.4 ± 0.2 $\text{ng N cm}^{-2} \text{h}^{-1}$). Root mortality and decay following trenching doubled rates of N_2O emissions in the clay and tripled them in the sandy loam over a 1-year period. Trenching also increased NO fluxes, with greater fluxes in the sandy loam than in the clay soil. The authors concluded that fine-root mortality and decomposition associated with disturbance and land use change can contribute significantly to increased rates of N oxide emissions.

2.2. Interactions of NO and NO_2 With Amazonian Forest Canopy

In the uppermost soil layers, NO is simultaneously produced and consumed by microbiological processes, generally resulting in a net emission [Conrad, 1996]. However, when the soil is covered by tall vegetation, not all NO emitted from the soil leaves the canopy. A substantial portion of biogenically emitted NO can react with ozone (O_3), mixed into the canopy from aloft, to form nitrogen dioxide (NO_2) in the subcanopy atmosphere. The NO_2 can subsequently be deposited on vegetation elements [Jacob and Wofsy, 1990; Jacob and Bakwin, 1991; Meixner, 1994; Ammann *et al.*, 1999].

In a forest in Rondônia, Rummel *et al.* [2002] compared the quantity of NO emitted from the soil and fluxes above the forest canopy measured by eddy covariance and found that 92% of soil-emitted NO was consumed in the canopy during the daytime. At night, when rates of vertical mixing of O_3 into the forest canopy were much slower, about 8% of the NO was consumed, resulting in a daily reduction flux of NO from soil to atmosphere of 52%. Other studies suggested canopy consumption in the range of 60–81% [Bakwin

et al., 1990; *Jacob and Wofsy*, 1990]. On the basis of these results and on an annual soil emission of $1.4 \text{ kg N ha}^{-1} \text{ a}^{-1}$ from a forest in Rondônia, *Neill et al.* [2005] estimated that the net NO flux to the atmosphere from forest would be $0.7 \text{ kg N ha}^{-1} \text{ a}^{-1}$.

2.3. N_2O and NO Fluxes From Cerrado Soils Under Native Vegetation

Most of the cerrado vegetation occurs on dystrophic and clayey but well-drained soils. Drainage of water is very rapid even during the wet season because of the formation of soil microaggregates. Organic matter content is low and concentrated in a thin surface layer. Because cerrado soils are mainly well drained and aerated, nitrification is a more important pathway for N oxide production, and conditions favorable for denitrification are rare [*Pinto et al.*, 2002; *Varella et al.*, 2004; *Pinto et al.*, 2006].

Frequent fires in the cerrado region provoke losses of N from the ecosystem, and this is reflected in low soil N availability [*Pivello and Coutinho*, 1992; *Bustamante et al.*, 2006]. Nitrification rates in cerrado soils are very low [*Nardoto and Bustamante*, 2003], and only rarely does NO_3^- production exceed the demand by microorganisms and plant roots. The combination of low nitrification rates and the dominance of NH_4^+ in the inorganic N pools contribute to low soil emissions of N oxide gases in the cerrado region.

Fires have an impact in the trace gases emission not only as a consequence of biomass combustion but as a result of emissions by soils after fires. *Pinto et al.* [2002] measured soil fluxes of NO and N_2O in two cerrado vegetation types in plots near Brasília characterized by differing amounts of woody plant canopy cover that were either burned every 2 years or protected from fire. The two vegetation types were cerrado in the strict sense (20–50% woody plant canopy cover) and campo sujo (open and grass dominated). NO fluxes varied according to the proportion of woody cover and fire-regime. Annual fluxes of NO from the fire-protected areas were 0.1 kg N ha^{-1} for the campo sujo and 0.4 kg N ha^{-1} for the cerrado in the strict sense. An increase in the annual soil-atmosphere flux of NO with fire was observed only for the campo sujo (0.5 kg N ha^{-1}) [*Pinto*, 2003] (Table 2). NO emissions increased after burning ($1.0 \text{ ng N cm}^{-2} \text{ h}^{-1}$), but the flux diminished quickly to levels even lower than prefire levels. The timing of burning (early dry season, middle dry season, or late dry season burning) had little influence on soil NO emissions.

In the same experiment, soil moisture was the critical control on soil-atmosphere NO fluxes. Large NO fluxes were observed immediately following precipitation events that broke long droughts. NO emissions increased to 1.0 ng N

Table 2. Summary of Reported Average Daily Fluxes for Dry and Rainy Seasons and Annual Fluxes Estimation of NO and N_2O From Natural and Managed Ecosystems in the Cerrado Region^a

Ecosystem	Reference	Annual N-NO Flux	N_2O Flux		
			DS	RS	Annual
Cerrado	<i>Anderson and Poth</i> [1998]		UD		
Cerrado burned plus 45 days	<i>Anderson and Poth</i> [1998]			UD	
Cerrado burned plus 17 days	<i>Anderson and Poth</i> [1998]			UD	
Cerrado	<i>Saminéz</i> [1999]				0.3–0.5
Pasture	<i>Saminéz</i> [1999]				0.5
Soybean between lines	<i>Saminéz</i> [1999]				1.1
Soybean line	<i>Saminéz</i> [1999]				1.6
<i>Pinus</i>	<i>Saminéz</i> [1999]				0.4
<i>Eucalyptus</i>	<i>Saminéz</i> [1999]				0.3
Campo sujo	<i>Pinto et al.</i> [2002]	0.1	UD	UD	UD
Campo sujo burned	<i>Pinto</i> [2003]	0.5	UD	UD	UD
Cerrado	<i>Pinto</i> [2003]	0.4	UD	UD	UD
Cerrado burned	<i>Pinto</i> [2003]	0.4	UD	UD	UD
Fertilized pasture	<i>Pinto</i> [2003]	0.01 ^b	UD	UD	UD
Legume-grass pasture	<i>Pinto</i> [2003]	0.01 ^b	UD	UD	UD
Young pasture	<i>Pinto</i> [2003]	0.04 ^b	UD	UD	UD
Traditional pasture	<i>Pinto</i> [2003]	0.00 ^b	UD	UD	UD
Corn	<i>Fernandes</i> [2008] ^c	0.3			
Bean	<i>Fernandes</i> [2008] ^c	0.3			
Soybean	<i>Fernandes</i> [2008] ^c	0.2			
Cotton	<i>Fernandes</i> [2008] ^c	0.7			

^aAverage daily fluxes are given in $\text{mg N m}^{-2} \text{ d}^{-1}$. Annual fluxes estimations are given in $\text{kg N ha}^{-1} \text{ a}^{-1}$. Abbreviations are DS, dry season; RS, rainy season; and UD, under detection limit.

^bFlux is integrated for the wet season.

^cFlux is integrated for one crop cycle. Some crops are cultivated twice a year.

$\text{cm}^{-2} \text{h}^{-1}$ with the first rains in unburned cerrado in the strict sense and to $1.9 \text{ ng N cm}^{-2} \text{h}^{-1}$ in burned cerrado in the strict sense. Wetting of dry soil in cerrado causes an increase in NO emissions of a factor of 10 or more but that pulse was short-lived. Fluxes fell to background values within 3 days of a wetting pulse [Pinto *et al.*, 2002; Varella *et al.*, 2004].

In the cerrado, N_2O production is limited both by low N availability and by dry conditions, and fluxes of N_2O are generally very low ($<0.6 \text{ ng N cm}^{-2} \text{h}^{-1}$) [Pinto *et al.*, 2002; Varella *et al.*, 2004] regardless of the vegetation type or fire regime. Even the increase of soil water content in the wet season is not sufficient to stimulate high N_2O production.

3. EFFECTS OF LAND USE CHANGES ON N_2O AND NO EMISSIONS FROM SOIL TO THE ATMOSPHERE

Deforestation causes environmental changes resulting in changes of trace gas emissions. Immediately following clearing, the elimination of the plant sink for nutrients results in a pulse of nutrient availability, including N, in soils and streams. Emissions depend upon the prior site fertility and the rate of vegetation regrowth after disturbance. Clearing natural vegetation [Luizão *et al.*, 1989; Keller *et al.*, 1993; Davidson and Kinglerlee, 1997], burning [Levine *et al.*, 1996; Neff *et al.*, 1995; Serça *et al.*, 1998], fertilization of agricultural lands [Matson *et al.*, 1996; Mosier and Delgado, 1997; Veldkamp and Keller, 1997], intensive cattle ranching [Lima *et al.*, 2001; Primavesi *et al.*, 2004], and increasing dominance by legume species in areas under secondary succession after land conversion [Erickson *et al.*, 2002; Davidson *et al.*, 2007] have been identified as causes of increasing N_2O and NO emissions from tropical regions.

3.1. Effects of Logging on N_2O and NO Emissions From Soils

In the Brazilian Amazon region, selective logging removes timber volume in the range of only $20\text{--}60 \text{ m}^3 \text{ha}^{-1}$ (about $3\text{--}9$ trees ha^{-1}); however, current practices result in high levels of collateral damage to the forest canopy and soils [Verissimo *et al.*, 1992; Pereira *et al.*, 2002; see Asner *et al.*, this volume]. Felling a tree transfers fresh leaf and root nutrients to the soil, causing pulses of decomposition [Lodge *et al.*, 1991; Scatena *et al.*, 1996]. Loss of nutrient and water uptake by roots added to the forest floor leads to wetter sites and greater nutrient leaching [Parker, 1985; Brouwer, 1996]. In Guyana, nitrate losses from selective harvest varied in proportion to the area of soil disturbance [Brouwer, 1996].

The changes in nutrient and water cycles provoked by logging affect the soil-atmosphere exchange of trace gases.

One Large-Scale Biosphere-Atmosphere Experiment in Amazonia study approached this topic through measurement of soil-atmosphere fluxes of N_2O and NO on two soil types (clay Oxisol and sandy loam Ultisol) over 2 years (2000–2001) in both undisturbed forest (as discussed in section 2.1) and recently logged forest. Studies were conducted in the Tapajós National Forest, near Santarém, Pará, Brazil, where a demonstration logging project used reduced-impact forest management techniques [Keller *et al.*, 2005]. Keller *et al.* measured fluxes in logged areas and compared excess fluxes by subtraction of a background flux from undisturbed forest. Logging increased emissions of N_2O and NO from 30 to 350% depending upon soil conditions. Along with the hypothesized effects of changes in nutrient and water cycles discussed above, the authors found that compaction of soils by heavy machinery in skid trails and log storage decks tended to augment emissions N_2O and NO. While significant effects were measurable locally, Keller *et al.* cautioned that logging-induced fluxes were unlikely to increase regional emissions of N_2O by more than about 6%.

3.2. Emissions of N Oxides With Secondary Forest Succession

In the Amazon Basin, about 30–50% of cleared land is in some stage of secondary forest succession following agricultural abandonment [Hirsch *et al.*, 2004]. Davidson *et al.* [2007] demonstrated through the comparison of forest chronosequences (stands ranging in age from 3 to 70 years and remnant mature forests in eastern Amazonia-Pará) that young successional forests growing after agricultural abandonment on highly weathered lowland tropical soils exhibited conservative N cycling properties much like N-limited forests on younger soils in temperate latitudes. As secondary succession progressed, N cycling properties recovered with increasing availability of soil nitrate and a concomitant decrease of ammonium concentration. The dominance of a conservative P cycle typical of mature lowland tropical forests reemerged. Because of the successional shifts in N:P cycling ratios with forest age, soil emissions of N_2O were initially low and then increased gradually. N_2O emissions increased with forest age at clayey and sandy soils, although the more clay-rich site exhibited higher emissions. These results showed that increasing emissions of N_2O as the successional forests age can be attributed to the gradual recuperation of N cycling processes.

3.3. Conversion of Forest to Pasture and Crops

Following a site disturbance such as deforestation, N availability in the soil often temporarily increases, causing

significant increases in emissions of NO and N₂O. Fire is the main tool for clearing forest in Amazonia [Setzer *et al.*, 1998; Kauffman *et al.*, 1992]. An average of 19,000 km² of forests are cleared and burned each year in the region, mainly for the implementation of pastures and crops [Nepstad *et al.*, 1999]. Soil NO emissions are especially great immediately following fires. According to Neff *et al.* [1995], microbial nitrification is a critical process responsible for NO emissions throughout the clearing and burning period. Additionally, chemical denitrification of nitrite deposited in ash supported a large peak in NO fluxes for a few days following burning.

When tropical humid forests are converted to pastures, N availability in soil decreases with time [Neill *et al.*, 1995; Van Gestel *et al.*, 1993; Wick *et al.*, 2005]. Progressively smaller N oxide emissions are measured from pastures compared to old-growth forests because of a progressive decline in N availability with pasture age [Keller and Reiners, 1994; Van Gestel *et al.*, 1993; Garcia-Montiel *et al.*, 2001; Melillo *et al.*, 2001; Wick *et al.*, 2005]. Emissions of N₂O from newly created pasture in Rondônia were about 2 and a half times the forest emissions during the first 2 years (5.0 kg N ha⁻¹ a⁻¹ versus 1.9 kg N ha⁻¹ a⁻¹), but in pastures older than 3 years, N₂O fluxes were, on average, about one third lower than those from undisturbed forest (1.4 kg N ha⁻¹ a⁻¹ versus 1.9 kg N ha⁻¹ a⁻¹) [Melillo *et al.*, 2001] (Figure 2). According to Melillo *et al.* [2001], the magnitude of the NO₃⁻ pool up to 10-cm soil depth was the best predictor of N₂O across the forest-pasture chronosequence.

NO emissions following forest clearing, burning, pasture establishment, and pasture degradation follow a similar pat-

tern to that described above for N₂O emissions, except that NO is relatively more important where there is a more pronounced dry season along the eastern and southern flanks of the Amazon Basin [Davidson *et al.*, 2001]. Nitric oxide emissions did not vary with pasture age in one study in Rondônia, and mean annual NO emission from pastures was 0.2 kg N ha⁻¹ a⁻¹ compared to 1.4 kg N ha⁻¹ a⁻¹ in nearby forest [Neill *et al.*, 2005]. This study did not measure NO fluxes from pastures less than 9 years old, and Neill *et al.* recognized that younger pastures might have greater NO emissions assuming behavior similar to N₂O. Kirkman *et al.* [2002] compared forest and old pasture soils in Rondônia during two transition season periods (wet-dry and dry-wet) and observed soil-atmosphere NO fluxes from pastures that were 9 times lower than old-growth forest fluxes under similar soil moisture and temperature conditions. They attributed this pattern to the combination of a diminished velocity for the soil N cycle and lower effective soil NO diffusion rates in the pasture soils.

Over the past 40 years, large areas of cattle pasture in Amazonia have suffered declining productivity as a result of nutrient losses. Practices adopted by ranchers to restore productivity to degraded pastures have the potential to alter soil N availability and gaseous N losses from soils. These practices involve varying amounts of tillage combined with fertilizer and herbicide applications, and the planting of cash crops prior to the planting of forage grasses. Passianoto *et al.* [2003] reported on the emissions of N₂O and NO from the first 6 months of three restoration treatments for pastures in central Rondônia. The treatments were (1) control pasture; (2) conventional tillage followed by planting of forage grass (*Brachiaria brizantha*) and fertilizer addition (42 kg

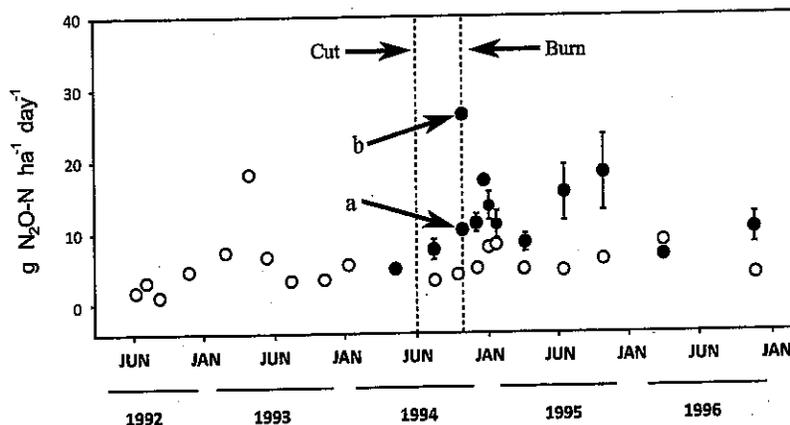


Figure 2. N₂O emissions (plus standard error) from the reference forest (open circles) and a new 3 ha pasture (solid circles) that was established for the study in 1994. The error bars for the forest measurements are within symbols. Measurements to generate the data point labeled "a" were taken 2 days before burn, and the measurements to generate the data point labeled "b" were taken 3 days after the burn. Reprinted from Melillo *et al.* [2001].

N ha⁻¹); (3) no tillage with herbicide treatment followed by two plantings, the first being rice, fertilized with 33 kg N ha⁻¹, followed by a forage grass. The cumulative N₂O and NO emissions over the first 2 months from the tillage regime (0.94 kg N-N₂O ha⁻¹ and 0.98 kg N-NO ha⁻¹) were much higher than the releases from either the no-tillage/herbicide regime (0.64 kg N-N₂O ha⁻¹ and 0.72 kg N-NO ha⁻¹) or the control pasture treatment (0.04 kg N-N₂O ha⁻¹ and 0.12 kg N-NO ha⁻¹). Tillage increased soil NH₄⁺ and NO₃⁻ pools, while these pools remained relatively constant in the control and no-tillage treatments. Cumulative rates of net N mineralization and net nitrification during the first 6 months after treatment varied widely but were highest in the tilled treatment [do Carmo et al., 2005].

In this experiment, while emissions of NO and N₂O increased with tillage and N fertilization, there were no clear relationships among rates of N fertilizer application, net mineralization, net nitrification, NO, N₂O, and total N oxide emissions. The magnitude of the increased N oxide fluxes differed based on the timing of fertilizer application relative to the presence of plants and the magnitude of plant N demand. Emissions of N oxides decreased with the use of restoration sequences that minimized reductions in pasture grass cover [do Carmo et al., 2005].

A few authors have attempted to estimate the regional effects of land use changes on the fluxes of N oxides. Potter et al. [1998] using the NASA-CASA ecosystem model estimated a total flux of 0.5 Tg N₂O-N a⁻¹ from Brazilian Amazonia. In a subsequent study [Potter et al., 2001], a version of this model was applied to two forest sites, located in the Brazilian states of Rondônia and Pará, differing in terms of seasonality of rainfall, length of the annual dry period, and soil properties. The measured fluxes of soil N₂O for forests closely matched the proposed models for the forest in Pará but not for that in Rondônia. This result suggested that algorithms controlling nitrogen trace gas fluxes, particularly in relatively sandy tropical soils require further development.

Melillo et al. [2001] used a constant value of 1.4% of modeled N mineralization to estimate N₂O emission. With this approximation, Amazon Basin-wide (area of 6.9 × 10⁶ km²) emissions from 1978 to 1995 averaged 1.3 Tg N₂O-N a⁻¹ with 0.8 Tg N₂O-N a⁻¹ for the Brazilian portion of the Basin.

3.4. Conversion of Cerrado to Pasture and Crops

Planted pastures (mainly *Brachiaria* spp.) are the most extensive land use in the cerrado, and with an area of approximately 50 million ha they occupy nearly one fourth of the biome [Sano et al., 2000]. In well-managed pastures on clayey soils in the cerrado region, productivity and long-term soil C stocks can surpass levels for native vegetation

[Corazza et al., 1999; Bustamante et al., 2006]. On the other hand, poor management practices, especially overgrazing, lead to pasture degradation after a few years. According to Oliveira et al. [2004], degraded pastures in the tropical region of Brazil occupy 25 million ha.

Although few studies have been conducted on N oxide emissions from pasture soils in the cerrado region (Table 2), they suggest a decrease in emissions with pasture age as presented in section 3.3 for the Amazon region. Varella et al. [2004] measured fluxes of NO in a 20-year-old *B. brizantha* pasture in central Brazil and found annual NO emissions of only 0.1 kg N ha⁻¹ a⁻¹. Emissions of soil N₂O were below the detection limit (<0.6 ng N-N₂O cm⁻² h⁻¹ = 0.5 kg N ha⁻¹ a⁻¹). Saminéz [1999] measured annual N₂O soil emission of 0.5 kg N ha⁻¹ a⁻¹ in both native cerrado and in a 5-year-old *Andropogon gayannus* pasture.

Because planted pastures in the cerrado tend to lose productivity with time, ranchers use a variety of agronomic approaches including tillage and fertilization to reform their pastures. Pinto et al. [2006] studied the effects of pasture reformation on N dynamics (net N mineralization, net nitrification, available inorganic N and NO, and N₂O gas fluxes). The study focused on three areas of cerradão (closed savanna woodland) converted to *B. brizantha* in 1991 that exhibited characteristics of degradation after 9 years. In 1999, different restoration treatments were tested: (1) fertilization (60 kg N ha⁻¹ and 12 kg P ha⁻¹); (2) association of grasses and legumes (*B. brizantha* and *Stylosanthes guianensis*) with addition of 12 kg P ha⁻¹, and (3) a traditional plot without management. These treatments were also compared with a fourth area of cerradão converted to *B. brizantha* pasture in 1999 (young pasture). Measurements were carried out during the wet season of 2001–2002. Ammonium was the predominant inorganic N form in the soils. All plots showed high variability of soil N gases emissions. Peak emissions of NO (3.6 ng N-NO cm⁻² h⁻¹) and N₂O (6.7 ng N-N₂O cm⁻² h⁻¹) were probably caused by cattle urination and defecation that led to an irregular distribution of organic residues. Despite these peaks of N gas emissions, overall nitrogen oxide emissions were low and only amounted to 0.03 kg N ha⁻¹ during the January to April growing season. A water addition experiment during the dry season (September 2002) indicated that the transition from dry to wet season might be an important period for the production of NO in the young pasture with fluxes ranging from 6.8 ng N-NO cm⁻² h⁻¹ within an hour after watering to 3.0 ng N-NO cm⁻² h⁻¹ 2 days after the treatment.

In 2006, approximately 14 million ha of cerrado were cropped with soybean, maize, cotton, common bean, and rice (see the Companhia Nacional de Abastecimento Web site at <http://www.conab.gov.br>). Soybean production catalyzed the agricultural expansion in the cerrado during the last 2

decades. This crop occupies more than 6 million ha in the plateau regions of the cerrado. However, continuous monoculture of soybeans coupled with inadequate tillage practices has caused severe erosion and soil degradation [Resck *et al.*, 1991]. Because of the problems associated with conventional systems, low-tillage agriculture was introduced. In 1989–1990, low-tillage agriculture in Brazil occupied an area of 1×10^6 ha, and by 2004 it had expanded to 23.6×10^6 ha (see the Federação Brasileira de Plantio Direto na Palha Web site at <http://www.febrapdp.org.br>). Of this total low-tillage area, about 8×10^6 ha were in the cerrado region [Duarte *et al.*, 2007].

Few studies track the effects of the conversion of cerrado to row crops for nitrogen oxide emissions. Work done to date has shown that N_2O emissions are not great. Results from a soybean-corn crop rotation showed that N_2O flux increased modestly from $0.8 \text{ ng } N_2O\text{-N cm}^{-2} \text{ h}^{-1}$ to $2.5 \text{ ng } N_2O\text{-N cm}^{-2} \text{ h}^{-1}$ under soybean cultivation [Saminéz, 1999] compared to other published accounts of elevated emissions from tropical agricultural soils. Low emissions may be explained by the relatively dry cerrado climate that does not favor large N_2O emissions. Metay *et al.* [2007] studied two 5-year-old systems during a cropping cycle in Goiânia, Goiás: tillage with disking in the first 15 cm and no tillage with a direct-sowing mulch-based crop system and an additional cover crop. Emissions of N_2O were very low, and no significant difference between treatments was observed. Monthly mean N_2O emissions increased exponentially with monthly mean (WFPS) in the 0- to 10-cm layer.

NO emissions may be quantitatively more important for N cycling than N_2O emissions in croplands in the cerrado region. Carvalho *et al.* [2006] compared NO fluxes in a cornfield under no-tillage and tillage systems fertilized with urea. Irrigation was performed immediately following the fertilization. No significant differences in nitrogen oxide fluxes were found between plots under tillage and no-tillage systems. The response to fertilization was rapid. Following broadcast fertilization, high NO fluxes were measured 15 min ($5.4 \text{ ng N cm}^{-2} \text{ h}^{-1}$) and 3 days after N fertilization ($4.8 \text{ ng N cm}^{-2} \text{ h}^{-1}$), but fluxes decreased to $1.2 \text{ ng N cm}^{-2} \text{ h}^{-1}$ after 5 days.

Unfortunately, the database related to N oxide emissions in the cerrado is even more restricted than in Amazonia. Most of the data are from the core region of the cerrado (state of Goiás and the federal district) and these studies have focused on the most common soil types in the cerrado region (Latossolos Vermelho-Escuro and Vermelho-Amarelo in the Brazilian system and Acrustox in the U.S. Department of Agriculture taxonomy system). The diversity of crop systems and management practices in the region limit extrapolation.

4. METHANE FLUX BETWEEN UPLAND ECOSYSTEMS OF AMAZONIAN FOREST AND CERRADO AND THE ATMOSPHERE

4.1. Exchange of CH_4 Between Upland Soils and the Atmosphere in Amazon Forests and the Cerrado

In general, well-drained soils consume atmospheric CH_4 , and by convention these fluxes are shown as negative. Early studies from well-drained upland forest soils in Amazonia conform to global trends [Keller *et al.*, 1983, 1986; Steudler *et al.*, 1996]. On the basis of the results of 22 studies from humid tropical forests, Potter *et al.* [1996] reported an average flux of CH_4 from the atmosphere to soil of $-3.8 \pm 0.6 \text{ kg } CH_4 \text{ ha}^{-1} \text{ a}^{-1}$. Several studies report CH_4 consumption during both wet and dry seasons in forest soils in the municipalities of Santarém and Belterra (Pará) although all observe occasional net production of CH_4 during the wet season [Davidson *et al.*, 2004; Wick *et al.*, 2005; Keller *et al.*, 2005]. Keller *et al.* [2005] compared soil texture effects CH_4 fluxes and found annual average (plus/minus standard error) fluxes of -0.3 ± 0.2 and $-0.1 \pm 0.9 \text{ mg } CH_4 \text{ m}^{-2} \text{ d}^{-1}$ on a clay-textured Oxisol and -1.0 ± 0.2 and $-0.9 \pm 0.3 \text{ mg } CH_4 \text{ m}^{-2} \text{ d}^{-1}$ on a sandy loam Ultisol for two subsequent years (2000 and 2001) with greater variability of CH_4 fluxes in the Oxisol than in the Ultisol, especially during the wet season. The size of the regional CH_4 sink was calculated by Davidson and Artaxo [2004], who estimated the net soil uptake of CH_4 as 1 to 3 Tg $CH_4 \text{ a}^{-1}$.

In general, studies of soil CH_4 in Amazon forests demonstrate that soil CH_4 consumption is limited by gas diffusivity [Verchot *et al.*, 2000]. Net CH_4 production has also been associated with soil respiration possibly because high rates of soil respiration create anaerobic microsites resulting in CH_4 production [Verchot *et al.*, 2001]. Manipulations of soil moisture confirm that moisture controls CH_4 fluxes. In an experiment investigating the effects of drought, in Amazonian forest, soil consumption of atmospheric CH_4 was increased on soils affected by drought by a factor of >4 [Davidson *et al.*, 2004]. Vasconcelos *et al.* [2004] reported significantly lower CH_4 fluxes in the dry season ($-0.3 \pm 0.1 \text{ mg } CH_4 \text{ m}^{-2} \text{ d}^{-1}$) than in the wet season ($0.1 \pm 0.1 \text{ mg } CH_4 \text{ m}^{-2} \text{ d}^{-1}$) in a secondary forest and that irrigation during the dry season increased CH_4 efflux in relation to control plots (0.2 ± 0.4 and $-0.5 \pm 0.2 \text{ mg } CH_4 \text{ m}^{-2} \text{ d}^{-1}$, respectively).

4.2. Effects of Land Use Changes on the Soil-Atmosphere Exchange of CH_4

Soil aeration is the primary control on CH_4 flux. As observed in Costa Rica [Keller *et al.*, 1993; Keller and Rein-

ers, 1994], soil compaction resulting from forest to pasture conversion restricts soil-atmosphere gas exchange and leads to diminished CH₄ consumption. Along with compaction, other factors that favor CH₄ emission from pasture soils in the Amazon region include higher pH values, lower availability of alternate electron acceptors such as N-NO₃⁻, and possibly greater availability of organic matter [Feigl *et al.*, 2001].

Methane fluxes between soils and the atmosphere were measured in two tropical forest-to-pasture chronosequences in the state of Rondônia, Brazil [Stuedler *et al.*, 1996]. Forest soils always showed a net consumption of atmospheric CH₄ with maximum uptake rates in the dry season. Pasture soils consumed atmospheric CH₄ during the dry season but at lower rates than those in the forests. When soil moisture increased in the pasture soils, they became a source of CH₄ to the atmosphere.

Integrated over the year, forest soils were a net sink of approximately -1.7 mg CH₄ m⁻² d⁻¹, while pastures were a net source of about +1.0 mg CH₄ m⁻² d⁻¹. Thus forest-to-pasture conversion resulted in a net change in the soil flux of CH₄ from the soil of almost 2.7 mg CH₄ m⁻² d⁻¹.

Logging in Brazilian Amazonia annually affects an area almost as large as the area clear-cut for conversion to agriculture and pasture [Asner *et al.*, 2005]. Logging operations depend on heavy machinery that compacts forest soils, leading to a change from CH₄ consumption to CH₄ production [Keller *et al.*, 2005]. Ground damage is limited to only a portion of the logged area that depends upon the intensity of harvest and the quality of the harvest management [Pereira

et al., 2002]. Critically, CH₄ production is dominated by small areas known as log decks that are used to stage logs for trucking to sawmills. These log decks occupy approximately 1–2% of the logged area dependent upon management, and they become waterlogged in the wet season because the compacted soils do not readily drain. Waterlogged decks emit CH₄ at rates similar to tropical swamps while they are inundated, accounting for >80% of the CH₄ emitted in logged areas.

As pointed out for N oxide emissions, there are few data on CH₄ emissions from cerrado soils (Table 3). In the first measurements of CH₄ flux made on cerrado soils [Anderson and Poth, 1998], newly burned cerrado had a CH₄ flux of -4.4 mg CH₄ m⁻² d⁻¹ that increased to -20.4 mg CH₄ m⁻² d⁻¹ at sites burned 30 days earlier. However, in an area burned 1 year before, CH₄ uptake by soils had disappeared. CH₄ fluxes were not correlated with any soil chemical parameters measured [Poth *et al.*, 1995]. Poth *et al.* hypothesized that the absence of uptake by unburned soils would indicate the presence of a balance between the source of soil CH₄, possibly the foraging termite community, and the sink for CH₄, oxidation by the soil microbiota [Seiler *et al.*, 1984]. Sanhueza [2007] has presented limited measurements indicating that savanna grasses in the Venezuelan llanos produced small amounts of CH₄. Saminéz [1999] compared fluxes of CH₄ from Oxisols under cerrado native vegetation, 5-year-old pasture, soybean-corn rotation, and eucalyptus and pine plantations. CH₄ consumption occurred under all land uses during both wet and dry seasons although values during the wet season were lower (Table 3). Low but positive CH₄

Table 3. Summary of Reported Average Daily Fluxes for Dry and Rainy Seasons and Annual Flux Estimation of CH₄ From Natural and Managed Ecosystems in the Cerrado Region

Reference	Vegetation Cover/ Land Use	CH ₄ Flux		
		Dry Season (mg CH ₄ m ⁻² d ⁻¹)	Rainy Season (mg CH ₄ m ⁻² d ⁻¹)	Annual (kg CH ₄ ha ⁻¹ a ⁻¹)
<i>Poth et al.</i> [1995]	cerrado	1.12		
	cerrado burned plus 2 days	-3.93		
	cerrado burned plus 30 days	-20.22		
<i>Anderson and Poth</i> [1998]	cerrado	-1.68		
	cerrado burnt plus 45 days	-1.01		
	cerrado burnt plus 17 days	-1.03		
<i>Saminéz</i> [1999]	cerrado		-1.24	-5.5 and -6.0
	pasture		-0.88	-4.0
	soybean between lines		-0.69	-3.3
	soybean line		-1.09	-2.3
	<i>Pinus</i>		-1.17	-4.8
	<i>Eucalyptus</i>		-1.39	-5.6
<i>Metay et al.</i> [2007]	rice, tillage (15 cm)			0.54
	rice, direct seeding mulch			0.33

fluxes were measured by *Metay et al.* [2007] in a cultivated cerrado area under low till ($0.33 \text{ kg CH}_4 \text{ ha}^{-1} \text{ a}^{-1}$) and tillage ($0.53 \text{ kg CH}_4 \text{ ha}^{-1} \text{ a}^{-1}$).

4.3. Methane Production by Ruminant Livestock

Brazil has the largest commercial cattle herd in the world, and it is second only to India in total cattle population [*Lerner et al.*, 1988]. The cattle population of Brazil is increasing rapidly, reaching 207 million head in 2005, with a concentration of animals in the center west region (mainly cerrado, 72×10^6 head) and north region (Amazon, 42×10^6 head) (see the Banco de Dados Agregados Web site at <http://www.sidra.ibge.gov.br>).

One result of the cattle population increase is that emissions from livestock have become a significant source of atmospheric CH_4 . Ruminants generate CH_4 as a by-product of the anaerobic digestion of food in the rumen. CH_4 is released mainly by exhalation and eructation. The CH_4 production rate is affected by factors such as quantity and quality of feed, body weight, age, and exercise and varies among animal species as well as among individuals of the same species [*Mosier et al.*, 1998]. CH_4 emission from dairy cattle fed with tropical grasses (between 121 and 147 $\text{kg CH}_4 \text{ a}^{-1}$ per animal) is greater than emissions from dairy cattle in temperate climate (between 100 and 118 $\text{kg CH}_4 \text{ a}^{-1}$ per animal) probably because of differences in forage quality [*Primavesi et al.*, 2004]. The estimate of CH_4 emissions from all cattle raised in Brazil (including beef and dairy cattle) for 1994 was 9.77 $\text{Tg CH}_4 \text{ a}^{-1}$ (96% from enteric fermentation and 4% from animal wastes) with beef cattle contributing 81% of the total. Of this total, the center west region (most of the cerrado) makes the greatest contribution (3.09 $\text{Tg CH}_4 \text{ a}^{-1}$), representing 30% of the total [*Lima et al.*, 2001].

4.4. Atmospheric CH_4 Measurements and CH_4 Sources

Evidence from satellite sensors as well as ground- and aircraft-based in situ sampling suggests that the CH_4 emissions of the Amazon region have been underestimated. *Frankenberg et al.* [2005] compared total column CH_4 concentrations retrieved using the Scanning Imaging Absorption Spectrometer for Atmospheric Cartography instrument on the European ENVISAT satellite with a global atmospheric chemistry and transport model. On the basis of several months of observations from 2003, they concluded that tropical forest-derived CH_4 emissions have been underestimated by at least 30 $\text{Tg CH}_4 \text{ a}^{-1}$ representing more than 5% of global annual emissions. In a subsequent compilation of data for 2003 and 2004, *Frankenberg et al.* [2006] confirmed anomalous column abundances of CH_4 over

Amazonia compared to accepted emission inventories. These anomalies can be accommodated in part with an increased wetland source in Amazonia of 41 $\text{Tg CH}_4 \text{ a}^{-1}$ as suggested by an inverse model analysis [*Bergamaschi et al.*, 2007]. However, this wetland source is substantially greater than the most complete bottom-up estimate of Amazon Basin wetland CH_4 emissions (29 $\text{Tg CH}_4 \text{ a}^{-1}$ [*Melack et al.*, 2004]).

Measurements of CH_4 mixing ratios in the canopy layer of three forest sites across Brazilian Amazonia (Caxiuanã National Forest in Pará, Cuieiras Reserve in Amazonas, and Sinop in Mato Grosso) in both wet and dry seasons showed net CH_4 emissions ranging from 2 to 21 $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ [*do Carmo et al.*, 2006]. While the measurements are sparse, they suggest an unknown source of CH_4 from upland forests (as opposed to wetlands) of between 4 and 38 $\text{Tg CH}_4 \text{ a}^{-1}$ if extrapolated over the Amazon forest area. Estimates of CH_4 emissions based on episodic aircraft sampling from 2001 through 2006 by *Miller et al.* [2007] averaged $35 \pm 23 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ and $20 \pm 17 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ between the Brazilian coast and the interior Amazonian cities of Santarém and Manaus, respectively. These are also greater than the estimates of average CH_4 emissions for the wetlands of the region (16 $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ [*Miller et al.*, 2007]).

What sources could account for greater CH_4 emissions in Amazonia compared to bottom-up inventories? While recently, laboratory experiments have indicated that aerobic production of CH_4 by plants may play a significant role in the atmospheric budget of CH_4 [*Keppeler et al.*, 2006], the early estimates may have exaggerated the magnitude of the source. Limited evidence from field studies in Venezuelan savannas supports the plant source although with a smaller magnitude [*Sanhueza*, 2007]. The extrapolation of the laboratory study has been controversial, and several analyses indicate that even if the laboratory results are reliable, the global importance of plants as a CH_4 source has been exaggerated [*Kirschbaum et al.*, 2006; *Houweling et al.*, 2006; *Ferretti et al.*, 2007]. A recent laboratory study using ^{13}C -labeled plants found no evidence for plant CH_4 emission above trace levels that would be globally insignificant [*Dueck et al.*, 2007]. It remains difficult to justify a plant source of CH_4 that could account for excess CH_4 observed over Amazonia. Other known sources that may be underestimated in current inventories include biomass burning (especially the manufacture of charcoal) and termite-derived CH_4 [*Christian et al.*, 2007].

5. CONCLUSIONS

Emissions of N_2O and NO from soils of mature Amazonian forests range from about 1 to 7 $\text{kg N ha}^{-1} \text{ a}^{-1}$ and 1 to 3 $\text{N ha}^{-1} \text{ a}^{-1}$, respectively. Environmental controls are mainly

the variability of rainfall and soil texture as influences on soil moisture content with higher fluxes on clayey soils. In addition, fine-root dynamics affect the production and emission of trace gases, especially in tropical rain forests that are characterized by a large biomass and rapid turnover of fine roots. The proportion of N oxides emitted from soil to atmosphere is also dependent on the interaction with the vegetation canopy. Studies indicated a daily reduction flux of NO from soil to atmosphere of about 50%.

Land use change does not necessarily lead to a greater emission of greenhouse gases. Logging increased emissions of N₂O and NO from 30 to 350% depending upon soil conditions, but logging-induced fluxes were unlikely to increase regional emissions of N₂O by more than about 6%. Conversions of tropical forests to cattle pastures do not cause long-term increases in the contribution of soil emissions to atmospheric N₂O or NO. Lower N oxide emissions measured from pastures compared to old-growth forests are related to a progressive decline in N availability with pasture age combined with strongly anaerobic conditions in some pastures during the wet season. Compared to the primary forest, predicted changes in soil nitrogen cycling lead to a doubling in annual emissions of N₂O gas during the first year following deforestation with lower emissions thereafter (Figure 3). After pasture abandonment and with forest regrowth soil emissions of N₂O were initially lower and then increased gradually. Comparisons of N oxide emissions from agricultural areas indicated that soil preparation had an effect, with higher fluxes under tillage. Studies of intensively managed agriculture in Amazonia are still rare, but the evidence so far accumulated indicates that natural ecosystems often emit more nitrogen oxides than agroecosystems.

In the case of the cerrado, the combination of low nitrification rates and the dominance of NH₄⁺ in the inorganic N pools contribute to low soil emissions of N oxide gases. Large NO fluxes have been observed immediately following precipitation events that broke long drought periods, but these pulses are short-lived and contribute only slightly to annual emissions. NO emissions increased after burning, but again the flux returned quickly to prefire or even lower levels. Soil moisture and vegetation type were more important in controlling NO fluxes than fire regime. In the cerrado, N₂O production is limited both by low N availability and by dry conditions; fluxes of N₂O are generally very low regardless of the vegetation type or fire regime. Although few studies have been conducted on N oxide emissions from pasture soils in the cerrado region, the existing data suggest a decrease in emissions with pasture age as observed for Amazonia. The conversion of cerrado to row crops does not contribute significantly to N₂O emissions, but NO emissions appear to be more important. However, the association of N

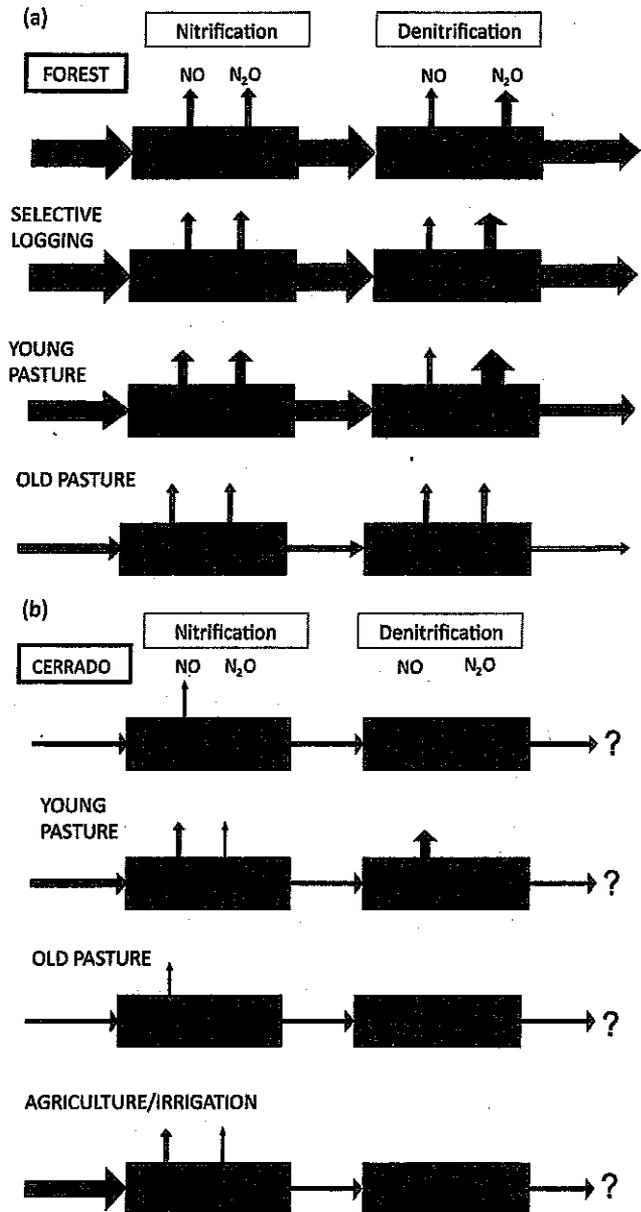


Figure 3. Fluxes of inorganic nitrogen for (a) moist forest and (b) cerrado environments schematically represented by a modified hole-in-the-pipe model. The relative widths of the horizontal arrows to the left of the boxes represent nitrification and denitrification processes and mineralized N or fertilizer N entering into the soil system. Horizontal arrows on the far right represent the presumed losses of N₂ through denitrification. These losses have not been well quantified and may be negligible in the cerrado as noted by the question mark. The relative widths of the vertical arrows represent the gaseous losses of NO and N₂O from the nitrification and denitrification processes. Where no arrows are shown, losses are below the measurable threshold.

fertilization with irrigation could lead to higher N₂O emissions (Figure 3).

In general, studies of soil CH₄ in Amazonian forests demonstrate that soil CH₄ consumption is limited by gas diffusivity. On an annual basis, undisturbed forest soils always showed a net consumption of atmospheric CH₄ with maximum uptake rates in the dry season. Pasture soils consumed atmospheric CH₄ during the dry season but at lower rates than those in the forests. When soil moisture increased in the pasture soils, they became a source of CH₄ to the atmosphere, and thus forest-to-pasture conversion resulted in a net change in the direction of the flux of CH₄ from the soil. Measurements of CH₄ mixing ratios in the canopy layer of three forest sites across Brazilian Amazonia in both wet and dry seasons showed evidence for net CH₄ emission in upland forests. This indicates the existence of an unknown source of CH₄ from upland forests.

As pointed out for N oxide emissions, there are few data on CH₄ emissions from cerrado soils, but they indicated a predominance of CH₄ consumption over emission under different land uses during both wet and dry seasons.

Davidson and Artaxo [2004] have summed the 100-year global warming potentials (GWP) of the annual sources and sinks of CH₄, N₂O, and CO₂, indicating that the Amazonian forest-river system currently may be nearly balanced in terms of net GWP for these biogenic atmospheric gases. Unfortunately, large uncertainties remain for these estimates. There is still a lack good predictive models for regionalization of site-specific data. The current models lack geographic data for parameterization and testing and, more importantly, basic theory on the controls of emissions from the ecosystem to the atmosphere. From a regional perspective, the unknown source of CH₄ from upland forests is the greatest uncertainty. Improvement of models for the N oxides and CH₄ fluxes for Amazonia and the cerrado still depends upon gathering more data from sites with different edaphic and vegetation characteristics, more widely distributed across two vast biomes.

Acknowledgment. Mercedes Bustamante and Dulce Alves Silva acknowledge support from the LBA-ND07 project.

REFERENCES

- Alves, D. S., D. C. Morton, M. Batistella, D. A. Roberts, and C. Souza Jr. (2009), The changing rates and patterns of deforestation and land use in Brazilian Amazonia, *Geophys. Monogr. Ser.*, doi:10.1029/2008GM000722, this volume.
- Ammann, M., R. Siegwolf, F. Pichlmayer, M. Suter, M. Saurer, and C. Brunold (1999), Estimating the uptake of traffic-derived NO₂ from ¹⁵N abundance in Norway spruce needles, *Oecologia*, 118, 124–131.
- Anderson, J. C., and M. A. Poth (1998), Controls on fluxes of trace gases from Brazilian cerrado soils, *J. Environ. Qual.*, 27, 1117–1124.
- Asner, G. P., D. E. Knapp, E. N. Broadbent, P. J. C. Oliveira, M. Keller, and J. N. Silva (2005), Selective logging in the Brazilian Amazon, *Science*, 310, 480–482.
- Asner, G. P., M. Keller, M. Lentini, F. Merry, and C. Souza Jr. (2009), Selective logging and its relation to deforestation, *Geophys. Monogr. Ser.*, doi:10.1029/2008GM000723, this volume.
- Bakwin, P. S., S. C. Wofsy, S.-M. Fan, M. Keller, S. E. Trumbore, and J. M. Da Costa (1990), Emission of nitric oxide (NO) from tropical forest soils and exchange of NO between the forest canopy and atmospheric boundary layers, *J. Geophys. Res.*, 95, 16,755–16,764.
- Bergamaschi, P., et al. (2007), Satellite cartography of atmospheric methane from SCIAMACHY on board ENVISAT: 2. Evaluation based on inverse model simulations, *J. Geophys. Res.*, 112, D02304, doi:10.1029/2006JD007268.
- Bosquet, P., P. Ciais, and J. B. Miller (2006), Contribution of anthropogenic and natural sources to atmospheric methane variability, *Nature*, 443, 439–443.
- Brouwer, L. C. (1996), *Nutrient Cycling in Pristine and Logged Tropical Rain Forest: A Study in Guyana, Tropenbos Guyana Ser.*, vol. 1, Elinkwijk Press, Utrecht, Netherlands.
- Bustamante, M. M. C., M. Corbells, E. Scopel, and R. Roscoe (2006), Soil carbon storage and sequestration potential in the cerrado region of Brazil, in *Carbon Sequestration in Soils of Latin America*, edited by R. Lal et al., pp. 285–304, Harworth, Binghamton, N. Y.
- Carvalho, A. M., M. M. C. Bustamante, A. R. Kozovits, L. N. Miranda, L. J. Vivaldi, and D. M. Sousa (2006), Emissões de óxidos de nitrogênio associadas à aplicação de uréia sob plantio convencional e direto, *Pesqui. Agropecu. Bras.*, 41, 679–685.
- Christian, T. J., R. J. Yokelson, J. A. Carvalho Jr., D. W. T. Griffith, E. C. Alvarado, J. C. Santos, T. G. S. Neto, C. A. G. Veras, and W. M. Hao (2007), The tropical forest and fire emissions experiment: Trace gases emitted by smoldering logs and dung from deforestation and pasture fires in Brazil, *J. Geophys. Res.*, 112, D18308, doi:10.1029/2006JD008147.
- Conrad, R. (1996), Soil microorganisms as controllers of atmospheric trace gases (H₂, CO, CH₄, OCS, N₂O, and NO), *Microbiol. Rev.*, 60, 609–640.
- Corazza, E. J., J. E. Silva, D. V. S. Resçk, and A. C. Gomes (1999), Comportamento de diferentes sistemas de manejo como fonte ou depósito de carbono em relação a vegetação de Cerrado, *Rev. Bras. Cien. Solo*, 23, 425–432.
- Crutzen, P. J. (1970), The influence of nitrogen oxides on the atmospheric ozone content, *Q. J. R. Meteorol. Soc.*, 96, 320–325.
- Davidson, E. A. (1991), Fluxes of nitrous 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. Whitman, pp. 219–235, Am. Soc. for Microbiol., Washington, D. C.
- Davidson, E. A. (1992), Sources of nitric oxide and nitrous oxide following wetting of dry soil, *Soil Sci. Soc. Am. J.*, 56, 95–102.
- Davidson, E. A., and P. Artaxo (2004), Globally significant changes in biological processes of the Amazon Basin: Results of large-

- scale biosphere-atmosphere experiment, *Global Change Biol.*, *10*, 519–529.
- Davidson, E. A., and W. Kinglerlee (1997), A global inventory of nitric oxide emissions from soils, *Nutr. Cycling Agroecosyst.*, *48*, 37–50.
- Davidson, E. A., M. Keller, H. W. Erickson, L. V. Verchot, and E. Veldkamp (2000), Testing a conceptual model of soil emissions of nitrous and nitric oxides, *BioScience*, *50*, 667–680.
- Davidson, E. A., M. M. C. Bustamante, and A. S. Pinto (2001), Emissions of nitrous oxide and nitric oxide from soils of native and exotic ecosystems of the Amazon and cerrado regions of Brazil, *Sci. World*, *1*, 312–319.
- Davidson, E. A., F. Y. Ishida, and D. C. Nepstad (2004), Effects of an experimental drought on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest, *Global Change Biol.*, *10*, 718–730.
- Davidson, E. A., et al. (2007), Recuperation of nitrogen cycling in Amazonian forests following agricultural abandonment, *Nature*, *447*, 995–999.
- do Carmo, J. B., C. Neill, D. C. Garcia-Montiel, M. de C. Piccolo, C. C. Cerri, P. A. Steudler, C. A. de Andrade, C. C. Passianoto, B. J. Feigl, and J. M. Melillo (2005), Nitrogen dynamics during till and no-till pasture restoration sequences in Rondônia, Brazil, *Nutr. Cycling Agroecosyst.*, *71*, 213–225.
- do Carmo, J. B., M. Keller, J. D. Dias, P. B. de Camargo, and P. Crill (2006), A source of methane from upland forests in the Brazilian Amazon, *Geophys. Res. Lett.*, *33*, L04809, doi:10.1029/2005GL025436.
- Duarte, J. O., J. C. Garcia, and M. J. Matoso (2007), Área de plantio direto e área plantada com sorgo no Cerrado: Existe alguma correlação entre elas?, *Comun. Téc.* *151*, 8 pp., Embrapa Milho e Sorgo, Sete Lagoas, Brazil.
- Dueck, T. A., et al. (2007), No evidence for substantial aerobic methane emission by terrestrial plants: A ^{13}C -labelling approach, *New Phytol.*, *175*, 29–35.
- Erickson, H., E. A. Davidson, and M. Keller (2002), Former land-use and tree species affect nitrogen oxide emissions from a tropical dry forest, *Oecologia*, *130*, 297–308.
- Feigl, B., M. Bernoux, C. C. Cerri, and M. C. Piccolo (2001), O efeito da sucessão floresta/pastagem sobre o estoque de carbono e o fluxo de gases em solos da Amazônia, in *Mudanças Climáticas Globais e a Agropecuária Brasileira*, edited by M. A. Lima, O. M. R. Cabral, and J. D. G. Miguez, pp. 257–271, Embrapa Meio Ambiente, Jaguariúna, Brazil.
- Fenchel T., G. M. King, and T. H. Blackburn (1998), *Bacterial Biogeochemistry: The Ecophysiology of Mineral Cycling*, Academic, San Diego, Calif.
- Fernandes, E. B. (2008), Emissões de CO_2 , NO_x e N_2O de solos sob diferentes sistemas de cultivo no cerrado, Ph.D. thesis, 138 pp., Univ. of Brasília, Brasília, Brazil.
- Ferretti, D. F., J. B. Miller, J. W. C. White, K. R. Lassey, D. C. Lowe, and D. M. Etheridge (2007), Stable isotopes provide revised global limits of aerobic methane emissions from plants, *Atmos. Chem. Phys.*, *7*, 237–241.
- Firestone, M., and E. A. Davidson (1989), Microbial basis of NO and N_2O production and consumption, in *Exchange of Trace Gases Between Ecosystems and the Atmosphere*, edited by M. O. Andreae and D. S. Schimel, pp. 7–21, John Wiley, New York.
- Forster, P., et al. (2007), Changes in atmospheric constituents and in radiative forcing, in *Climate Change 2007: The Physical Science Basis: Working Group I Contribution to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by S. Solomon et al., pp. 129–234, Cambridge Univ. Press, Cambridge, U. K.
- Frankenberg, C., J. F. Meirink, M. van Weele, U. Platt, and T. Wagener (2005), Assessing methane emissions from global space-borne observations, *Science*, *308*, 1010–1014.
- Frankenberg, C., J. F. Meirink, P. Bergamaschi, A. P. H. Goede, M. Heimann, S. Körner, U. Platt, M. van Weele, and T. Wagner (2006), Satellite cartography of atmospheric methane from SCLAMACHY on board ENVISAT: Analysis of the years 2003 and 2004, *J. Geophys. Res.*, *111*, D07303, doi:10.1029/2005JD006235.
- García-Mendez, G., J. M. Mass, P. A. Matson, and P. M. Vitousek (1991), Nitrogen transformations and nitrous oxide flux in a tropical deciduous forest in México, *Oecologia*, *88*, 362–366.
- García-Montiel, D. C., P. A. Steudler, M. C. Piccolo, J. 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.
- García-Montiel, D. C., P. A. Steudler, M. C. Piccolo, J. Melillo, C. Neill, and C. C. Cerri (2003), Nitrogen oxide emissions following wetting of dry soils in forest and pastures in Rondônia, *Biogeochemistry*, *64*, 319–336.
- Hanson, R. S., and T. E. Hanson (1996), Methanotrophic bacteria, *Microbiol. Rev.*, *60*, 439–471.
- Hirsch, A., W. S. Little, R. A. Houghton, N. A. Scott, and J. D. White (2004), The net carbon flux due to deforestation and forest re-growth in the Brazilian Amazon: Analysis using a process-based model, *Global Change Biol.*, *10*, 908–924.
- Hirsch, A. I., A. M. Michalak, L. M. Bruhwiler, W. Peters, E. J. Dlugokencky, and P. P. Tans (2006), Inverse modeling estimates of the global nitrous oxide surface flux from 1998–2001, *Global Biogeochem. Cycles*, *20*, GB1008, doi:10.1029/2004GB002443.
- Houweling, S., T. Röckmann, I. Aben, F. Keppler, M. Krol, J. F. Meirink, E. J. Dlugokencky, and C. Frankenberg (2006), Atmospheric constraints on global emissions of methane from plants, *Geophys. Res. Lett.*, *33*, L15821, doi:10.1029/2006GL026162.
- Jacob, D. J., and P. S. Bakwin (1991), Cycling of NO_x in tropical forest canopies, in *Microbial Production and Consumption of Greenhouse Gases: Methane, Nitrogen Oxides and Halomethanes*, edited by J. E. Roger and W. B. Whitman, pp. 237–253, Am. Soc. for Microbiol., Washington, D. C.
- Jacob, D. J., and S. C. Wofsy (1990), Budgets of reactive nitrogen, hydrocarbons, and ozone over the Amazon forest during the wet season, *J. Geophys. Res.*, *95*, 16,737–16,754.
- Kaplan, W. A., S. C. Wofsy, M. Keller, and J. M. Da Costa (1988), Emission of NO and deposition of O_3 in a tropical forest system, *J. Geophys. Res.*, *93*, 1389–1395.
- Kauffman, J. B., K. M. Till, and R. W. Shea (1992), Biogeochemistry of deforestation and biomass burning, in *The Impact of Human Activities on the Environment*, edited by D. A. Dunnette and R. J. O'Brien, *ACS Symp. Ser.*, *483*, 426–456.

- Keller, M., and W. A. Reiners (1994), Soil-atmosphere exchange of nitrous oxide, nitric oxide, and methane under secondary succession of pasture to forest in the Atlantic lowlands of Costa Rica, *Global Biogeochem. Cycles*, *8*, 399–409.
- Keller, M., T. J. Goreau, S. C. Wofsy, W. A. Kaplan, and M. B. McElroy (1983), Production of nitrous oxide and consumption of methane by forest soils, *Geophys. Res. Lett.*, *10*, 1156–1159.
- Keller, M., W. A. Kaplan, and S. C. Wofsy (1986), Emissions of N_2O , CH_4 and CO_2 from tropical forest soils, *J. Geophys. Res.*, *91*, 11,791–11,802.
- Keller, M., E. Veldkamp, A. M. Weitz, and W. A. Reiners (1993), Pasture age affects on soil-atmosphere trace gas exchange in a deforested area of Costa Rica, *Nature*, *365*, 244–246.
- Keller, M., R. Varner, J. D. Dias, H. Silva, P. Crill, R. C. de Oliveira Jr., and G. P. Asner (2005), Soil-atmosphere exchange of nitrous oxide, nitric oxide, methane, and carbon dioxide in logged and undisturbed forest in the Tapajos National Forest, Brazil, *Earth Interact.*, *9*(23), EI125, doi:10.1175/EI125.1.
- Keppler, F., J. T. G. Hamilton, M. Braß, and T. Röckmann (2006), Methane emissions from terrestrial plants under aerobic conditions, *Nature*, *439*, 187–191.
- Kirkman, G. A., A. Gut, C. Ammann, L. V. Gatti, A. M. Cordova, M. A. L. Moura, M. O. Andreae, and F. X. Meixner (2002), Surface exchange of nitric oxide, nitrogen dioxide, and ozone at a cattle pasture in Rondônia, Brazil, *J. Geophys. Res.*, *107*(D20), 8083, doi:10.1029/2001JD000523.
- Kirschbaum, M. U. F., D. Bruhn, D. M. Etheridge, J. R. Evans, G. D. Farquhar, R. M. Gifford, K. I. Paul, and A. J. Winters (2006), A comment on the quantitative significance of aerobic methane release by plants, *Funct. Plant Biol.*, *33*, 521–530.
- Klink, C. A., and R. B. Machado (2005), Conservation of the Brazilian cerrado, *Conserv. Biol.*, *19*, 707–713.
- Lashof, D. A., and D. R. Ahuja (1990), Relative global warming potentials of greenhouse gas emissions, *Nature*, *344*, 529–531.
- Leininger, S., T. Urich, M. Schloter, L. Schwark, J. Qi, G. W. Nicol, J. I. Prosser, S. C. Schuster, and C. Schleper (2006), Archaea predominate among ammonia-oxidizing prokaryotes in soils, *Nature*, *442*, 806–809.
- Lerner, J., E. Matthews, and I. Fung (1988), Methane emission from animals: A global high-resolution data base, *Global Biogeochem. Cycles*, *2*, 139–156.
- Levine, J. S., E. L. Winstead, D. A. B. Parsons, M. C. Scholes, R. J. Scholes, W. R. Cofer III, D. R. Cahoon Jr., and D. I. Sebacher (1996), Biogenic soil emissions of nitric oxide (NO) and nitrous oxide (N_2O) from savannas in South Africa: The impact of wetting and burning, *J. Geophys. Res.*, *101*, 23,689–23,697.
- Lima, M. A., R. C. Boeira, V. L. S. Castro, M. A. V. Ligo, O. M. R. Cabral, R. F. Vieira, and A. J. B. Luiz (2001), Estimativa das emissões de gases de efeito estufa provenientes de atividades agrícolas no Brasil, in *Mudanças climáticas Globais e a Agropecuária Brasileira*, edited by M. A. Lima, O. M. R. Cabral, and J. D. G. Miguez, pp. 169–189, Embrapa Meio Ambiente, Jaguariúna, Brazil.
- Lodge, D. J., F. N. Scatena, C. E. Asbury, and M. J. Sanchez (1991), Fine litterfall and related nutrient inputs resulting from hurricane Hugo in subtropical wet and lower montane rain forests of Puerto Rico, *Biotropica*, *23*, 336–342.
- Luizão, F., P. Matson, G. Livingston, R. Luizão, and P. Vitousek (1989), Nitrous oxide flux following tropical land clearing, *Global Biogeochem. Cycles*, *3*, 281–285.
- Luizão, R. C. C., F. J. Luizão, R. Q. Paiva, T. F. Monteiro, L. S. Sousa, and B. Kruijts (2004), Variation of carbon and nitrogen cycling process along a topographic gradient in a central Amazonian forest, *Global Change Biol.*, *10*, 592–600.
- Martius, C., R. Wassmann, U. Thein, A. Bandeira, H. Rennenberg, W. Junk, and W. Seiler (1993), Methane emission from wood-feeding termites in Amazonia, *Chemosphere*, *26*, 623–632.
- Matson, P. A., C. Billow, S. Hall, and J. Zachariassen (1996), Fertilization practices and soil variations control nitrogen oxide emissions from tropical sugar cane, *J. Geophys. Res.*, *101*, 18,533–18,545.
- Matson, P. A., and P. M. Vitousek (1990), Ecosystem approach for the development of a global nitrous oxide budget, *Bioscience*, *40*, 667–672.
- Meixner, F. X. (1994), Surface exchange of odd nitrogen oxides, *Nova Acta Leopold.*, *288*, 299–348.
- Melack, J. M., L. L. Hess, M. Gastil, B. R. Forsberg, S. K. Hamilton, I. B. T. Lima, and M. L. M. Novo (2004), Regionalization of methane emissions in the Amazon Basin with microwave remote sensing, *Global Change Biol.*, *10*, 530–544.
- Melack, J. M., E. M. L. M. Novo, B. R. Forsberg, M. T. F. Piedade, and L. Maurice (2009), Floodplain ecosystem processes, *Geophys. Monogr. Ser.*, doi:10.1029/2008GM000721, this volume.
- Melillo, J. M., P. A. Steudler, B. J. Feigl, C. Neill, D. Garcia, M. C. Piccolo, C. C. Cerri, and H. Tian (2001), Nitrous oxide emissions from forests and pastures of various ages in the Brazilian Amazon, *J. Geophys. Res.*, *106*, 34,179–34,188.
- Metay, A., R. Oliver, E. Scopel, J. M. Douzet, J. A. A. Moreira, F. Maraux, B. J. Feigl, and C. Feller (2007), N_2O and CH_4 emissions from soils under conventional and no-till management practices in Goiania (cerrados, Brazil), *Geoderma*, *114*, 78–88.
- Miller, J. B., L. V. Gatti, M. T. S. d'Amelio, A. M. Crotwell, E. J. Dlugokencky, P. Bakwin, P. Artaxo, and P. P. Tans (2007), Airborne measurements indicate large methane emissions from the eastern Amazon basin, *Geophys. Res. Lett.*, *34*, L10809, doi:10.1029/2006GL029213.
- Mosier, A. R., and J. A. Delgado (1997), Methane and nitrous oxide fluxes in grass lands in western Puerto Rico, *Chemosphere*, *35*, 2059–2082.
- Mosier, A. R., J. M. Duxbury, J. R. Freney, O. Heinemeyer, K. Minami, and D. W. Johnson (1998), Mitigation agricultural emissions of methane, *Clim. Change*, *40*, 39–80.
- Nardoto, G. B., and M. M. C. Bustamante (2003), Effects of fire on soil nitrogen dynamics and microbial biomass in savannas of central Brazil, *Pesqui. Agropecu. Bras.*, *38*, 955–962.
- Neff, J. C., M. Keller, E. A. Holland, A. W. Weitz, and E. Veldkamp (1995), Fluxes of nitric oxide from soils following the clearing and burning of a secondary tropical rain forest, *J. Geophys. Res.*, *100*, 25,913–25,922.

- Neill, C., M. C. Piccolo, P. A. Steudler, J. M. Melillo, B. J. Feigl, and C. C. Cerri (1995), Nitrogen dynamics in soils of forests and active pastures in the western Brazilian Amazon Basin, *Soil Biol. Biochem.*, 27, 1167–1175.
- Neill, C., P. A. Steudler, D. C. Garcia-Montiel, J. M. Melillo, B. J. Feigl, M. C. Piccolo, and C. C. Cerri (2005), Rates and controls of nitrous oxide and nitric oxide emissions following conversion of forest to pasture in Rondônia, *Nutr. Cycling Agroecosyst.*, 71, 1–15.
- Nepstad, D. C., et al. (1999), Large-scale impoverishment of Amazonian forests by logging and fire, *Nature*, 398, 505–508.
- 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.
- Oliveira, O. C., I. P. Oliveira, S. Urquiaga, B. J. R. Alves, and R. M. Boddey (2004), Chemical and biological indicator of decline/degradation of *Brachiaria* pastures in the Brazilian cerrado, *Agric. Ecosyst. Environ.*, 103, 289–300.
- Parker, G. G. (1985), The effect of disturbance on water and solute budgets of hillslope tropical rainforest in northeastern Costa Rica, Ph.D. thesis, Univ. of Ga., Athens.
- Passianoto, C. C., T. Ahrens, B. J. Feigl, P. A. Steudler, J. B. do Carmo, and J. M. Melillo (2003), Emissions of CO₂, N₂O, and NO in conventional and no-till management practices in Rondônia, Brazil, *Biol. Fertil. Soils*, 38, 200–208.
- Pereira, R., J. C. Zweede, G. P. Asner, and M. Keller (2002), Forest canopy damage and recovery in reduced impact and conventional logging in eastern Para, Brazil, *For. Ecol. Manage.*, 168, 77–89.
- Pinto, A. de S. (2003), Contribuição dos solos de cerrado do Brasil Central para as emissões de gases traço (CO₂, N₂O e NO): Sazonalidade, queimadas prescritas e manejo de pastagens degradadas, Ph.D. thesis, 114 pp., Univ. de Brasília, Brasília.
- Pinto, A. de S., M. M. C. Bustamante, K. Kisselle, R. Burke, R. Zepp, L. T. Viana, R. F. Varella, and M. Molina (2002), Soil emissions of N₂O, NO, and CO₂ in Brazilian savannas: Effects of vegetation type, seasonality, and prescribed fires, *J. Geophys. Res.*, 107(D20), 8089, doi:10.1029/2001JD000342.
- Pinto, A. de S., M. M. C. Bustamante, M. R. S. S. da Silva, K. W. Kisselle, M. Brossard, R. Kruger, R. G. Zepp, and R. A. Burke (2006), Effects of different treatments of pasture restoration on soil trace gas emissions in the cerrados of central Brazil, *Earth Interact.*, 10(1), E1146, doi:10.1175/E1146.1.
- Pivello, V. R., and L. M. Coutinho (1992), Transfer of macro-nutrients to the atmosphere during experimental burnings in an open cerrado (Brazilian savanna), *J. Trop. Ecol.*, 8, 487–497.
- Poth, M., I. C. Anderson, H. S. Miranda, A. C. Miranda, and P. J. Riggan (1995), The magnitude and persistence of soil NO, N₂O, CH₄ and CO₂ fluxes from burned tropical savanna in Brazil, *Global Biogeochem. Cycles*, 9, 503–513.
- Potter, C., E. Davidson, D. Nepstad, and C. R. de Carvalho (2001), Ecosystem modeling and dynamic effects of deforestation on trace gas fluxes in Amazon tropical forests, *For. Ecol. Manage.*, 152, 97–117.
- Potter, C. S., E. A. Davidson, and L. V. Verchot (1996), Estimation of global biogeochemical controls and seasonality in soil methane consumption, *Chemosphere*, 32, 2219–2246.
- Potter, C. S., E. A. Davidson, S. A. Klooster, D. C. Nepstad, G. H. De Negreiros, and V. Brooks (1998), Regional application of an ecosystem production model for studies of biogeochemistry in Brazilian Amazonia, *Global Change Biol.*, 4, 315–334.
- Prather, M., and D. Ehhalt (2001), Atmospheric chemistry and greenhouse gases, in *Climate Change 2001: The Scientific Basis: Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*, edited by J. T. Houghton et al., pp. 239–288, Cambridge Univ. Press, Cambridge, U. K.
- Primavesi, O., R. T. S. Frighetto, M. S. Pedreira, M. A. Lima, T. T. Berchielli, and P. F. Barbosa (2004), Metano entérico de bovinos leiteiros em condições tropicais brasileiros, *Pesqui. Agropecu. Bras.*, 39, 277–283.
- Reeburgh, W. S. (2003), Global methane biogeochemistry, in *Treatise on Geochemistry*, vol. 4, *The Atmosphere*, edited by R. F. Keeling, pp. 65–89, Elsevier, New York.
- Resck, D. V. S., J. Pereira, and J. E. da Silva (1991), Dinâmica da matéria orgânica na Região dos Cerrados, *Doc. 36*, Empresa Bras. de Pesqui. Agropecu., Planaltina, Brazil.
- Rummel, U., C. Ammann, A. Gut, F. X. Meixner, and M. O. Andreae (2002), Eddy covariance measurements of nitric oxide flux within an Amazonian rain forest, *J. Geophys. Res.*, 107(D20), 8050, doi:10.1029/2001JD000520.
- Saminêz, T. C. O. (1999), Efeito do sistema de cultivo, tensão da água biomassa microbiana e temperatura do solo nos fluxos de CH₄ e N₂O em solos de cerrados, MSc. thesis, 99 pp., Univ. de Brasília, Brasília.
- Sanhueza, E. (2007), Methane soil-vegetation-atmosphere fluxes in tropical ecosystems, *Interciencia*, 32, 30–34.
- Sano, E. E., A. O. Barcellos, and H. S. Bezerra (2000), Assessing the spatial distribution of cultivated pastures in the Brazilian savanna, *Pasturas Trop.*, 22, 2–15.
- Scatena, F. N., S. Moya, C. Estrada, and J. D. Chinea (1996), The first five years in the reorganization of aboveground biomass and nutrient use following hurricane Hugo in Bisley Experimental watersheds, Luquillo Experimental Forest, Puerto Rico, *Biotropica*, 28, 424–440.
- Seiler, W., R. Conrad, and D. Scharffe (1984), 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.
- Serça, D., R. Delmas, X. L. Roux, A. B. Parsons, M. C. Scholes, L. Abbadie, R. Lensi, O. Ronce, and L. Labrousse (1998), Comparison of nitrogen monoxide emissions from several African tropical ecosystems and influence of season and fire, *Global Biogeochem. Cycles*, 12, 637–651.
- Setzer, A. W., M. C. Pereira, A. C. P. Pereira, and S. O. Almeida (1998), Relatório de atividades do projeto IBDF-INPE “SEQE”-ano 1987, *Publ. INPE_4534-RPE/565*, INPE, Inst. Nac. de Pesqui. Espaciais, São José dos Campos, Brazil.
- Silver, W. L., J. Neff, M. McGroddy, E. Veldkamp, M. Keller, and R. Cosme (2000), Effects of soil texture on belowground carbon and nutrient storage in a lowland Amazonian forest ecosystem, *Ecosystems*, 3, 193–209.

- Silver, W. L., A. W. Thompson, M. E. McGroddy, R. K. Varner, J. D. Dias, H. Silva, P. M. Crill, and M. Keller (2005), Fine root dynamics and trace gas fluxes in two lowland tropical forest soils, *Global Change Biol.*, *11*, 290–306.
- Spahni, R., et al. (2005), Atmospheric methane and nitrous oxide of the late Pleistocene from Antarctic ice cores, *Science*, *310*, 1317–1321.
- Stuedler P. A., R. D. Jones, M. S. Castro, J. M. Melillo, and D. L. Lewis (1996), Microbial controls of CH₄ oxidation in temperate forest and agricultural soils, in *Microbiology of Atmospheric Trace Gases*, edited by J. C. Murrell and D. P. Kelly, *NATO ASI Ser., Ser. 1*, vol. 39, pp. 69–85, Springer, Berlin.
- van Dijk, S. M., and F. X. Meixner (2001), Production and consumption of NO in forest and pasture soils from the Amazon Basin, *Water Air Soil Pollut. Focus*, *1*, 119–130.
- Van Gestel, M., R. Merckx, and K. Vlassak (1993), Microbial biomass responses to soil drying and rewetting: The fate of fast- and slow-growing microorganisms in soils from different climates, *Soil Biol. Biochem.*, *25*, 109–123.
- Varella, R. F., M. M. C. Bustamante, A. S. Pinto, K. W. Kisselle, R. V. Santos, R. A. Burke, R. G. Zeep, and L. T. Viana (2004), Soil fluxes of CO₂, CO, NO and N₂O from an old pasture and from native savanna in Brazil, *Ecol. Appl.*, *14*(sp4), 221–231.
- Varner, R. K., M. Keller, J. R. Robertson, J. D. Dias, H. Silva, P. M. Crill, M. McGroddy, and W. L. Silver (2003), Experimentally induced root mortality increased nitrous oxide emission from tropical forest soils, *Geophys. Res. Lett.*, *30*(3), 1144, doi:10.1029/2002GL016164.
- 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, 10.1029/2003GB002210
- Veldkamp, E., and M. Keller (1997), Nitrogen oxide emissions from a banana plantation in the humid tropics, *J. Geophys. Res.*, *102*, 15,889–15,898.
- Verchot, L. V., E. A. Davidson, 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.
- Verchot, L. V., Z. Holmes, L. Mulon, P. M. Groffman, and G. M. Lovett (2001), Gross vs net rates of N mineralization and nitrification as indicators of functional differences between forest types, *Soil Biol. Biochem.*, *33*, 1889–1901.
- Verissimo, A., P. Barreto, M. Mattos, R. Tarifa, and C. Uhl (1992), Logging impacts and prospects for sustainable forest management in an old Amazonian frontier: The case of Paragominas, *For. Ecol. Manage.*, *55*, 169–199.
- Wick, B., E. Veldkamp, W. Z. de Mello, M. Keller, and P. Crill (2005), Nitrous oxide fluxes and nitrogen cycling along a pasture chronosequence in central Amazonia, Brazil, *Biogeosci. Discuss.*, *2*, 499–535.

M. M. C. Bustamante and D. A. Silva, Department of Ecology, University of Brasília, Asa Norte ICC Sul, Brasília, DF CEP 70910-900, Brazil. (mercedes@unb.br)

M. Keller, NEON Inc., 5340 Airport Boulevard, Boulder, CO 80301, USA.