Ecosystems (2000) 3: 41–56
DOI: 10.1007/s100210000009

ECOSYSTEMS

ORIGINAL ARTICLES

Land-Use Change and Biogeochemical Controls of Methane Fluxes in Soils of Eastern Amazonia

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ABSTRACT

Tropical soils account for 10%–20% of the 15–35 Tg of atmospheric methane (CH_4) consumed annually by soils, although tropical deforestation could be changing the soil sink. The objectives of this study were (a) to quantify differences in soil CH_4 fluxes among primary forest, secondary forest, active pasture, and degraded pasture in eastern Amazonia; and (b) to investigate controlling mechanisms of CH_4 fluxes, including N availability, gas-phase transport, and soil respiration. At one ranch, Fazenda Vitória, annual uptake estimates (kg $CH_4 ha^{-1} y^{-1}$) based on monthly measurements were: primary forest, 2.1; secondary forest, 1.0; active pasture, 1.3; degraded pasture, 3.1. The lower annual uptake in the active pasture compared with the primary forest was due to CH_4 production during the wet season in the pasture soils, which is consistent with findings from other studies. In contrast, the degraded pasture was never a CH_4 source. Expressing uptake as a negative flux and emission as a positive flux, CH_4 fluxes were positively correlated with CO_2 fluxes, indicating that root and microbial respiration in the productive pastures, and to a lesser extent in the primary forest, contributed to the formation of anaerobic microsites where CH_4 was produced, whereas this productivity was absent in the degraded pasture. In all land uses, uptake rates of atmospheric CH_4 were greater in the dry season than in the wet season, indicating the importance of soil water content and gas transport on CH_4 fluxes. These clay soils had low annual uptake rates relative to reported rates on sandy soils, which also is consistent with gas transport within the soil being a limiting factor. Nitrogen availability indices did not correlate with CH_4 fluxes, indicating that inhibition of CH_4 oxidation was not an important mechanism explaining differences among land uses. At another ranch, Fazenda Agua Parada, no significant effect of pasture age was observed along a chronosequence of pasture ages. We conclude that land-use change can either increase or decrease the soil sink of CH_4, depending on the duration of wet and dry seasons, the effects of seasonal precipitation on gas-phase transport, and the phenology and relative productivity of the vegetation in each land use.

Key words: CH_4; Amazon basin; Brazil; methanotrophy; methanogenesis; deforestation; rainforests; tropical forests; tropical pastures.

Received 19 January 1999; accepted 4 August 1999.
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INTRODUCTION

Methanotrophy (bacterial oxidation of CH_4) in soils accounts for approximately 8% of the sink for atmospheric CH_4 or between 15 and 35 Tg of atmospheric CH_4 annually (Potter and others 1996).

The magnitude of this sink is of the same order as the rate of atmospheric CH_4 accumulation (Prather and others 1995). However, the relatively small sink estimate understates the importance of this process because soils also produce CH_4, and methanotrophy plays an important role in regulating the net flux of CH_4 between the soil and the atmosphere. In fact, one estimate of soil methanotrophy suggests that as much as 50% of the CH_4 produced in soils and sediments is consumed therein and that the global soil CH_4 sink exceeds the atmospheric OH^- sink (Reeburgh and others 1993). Therefore, the impact of human alterations of soil methanotrophy has potentially significant consequences for atmospheric accumulation of this potent greenhouse gas.

Humid tropical forests probably account for 10–20% of the soil sink for atmospheric CH_4 globally (Potter and others 1996). In the Brazilian Amazon region, deforestation rates are estimated to have been between 11,000 and 29,000 $km^2\ y^{-1}$ during the period 1978–97, and a total area of 532,000 km^2 had been deforested as of August 1997 (INPE Website http://www.inpe.br/Informacoes_Eventos/amz/amz.html). This cleared land is primarily used as pasture, with some degraded pasture having been abandoned and undergoing secondary succession (INPE 1996; Nepstad and others 1997). A few studies have examined the effects of deforestation and pasture creation on CH_4 sink strength, and conclusions suggest that conversion of primary forest to pastures results in decreased net CH_4 uptake in soils. Keller and others (1993) and Keller and Reiners (1994) reported that upland tropical forests in Costa Rica were sinks for atmospheric CH_4 and that pastures were sources. Similar results were reported for the central Amazon by Goreau and de Mello (1988). Steudler and others (1996) reported that forests of western Brazilian Amazonia were sinks throughout the year but that pastures were sinks only during the dry season. During the wet season, pastures became CH_4 sources, and the net annual flux from pastures was positive (source to the atmosphere).

The soil–atmosphere CH_4 flux is the result of the balance between the two offsetting processes of methanogenesis and methanotrophy. Several factors are known to contribute to the spatial and temporal variability of observed fluxes including, soil carbon, substrate quality, temperature, moisture, soil diffusivity, microbial activity, pH, and N availability (Born and others 1990; Dörr and others 1993; Striegl 1993; Steudler and others 1996). Some generalizations now can be drawn from these studies. In well-drained soils in which CH_4 concentrations are at ambient atmospheric levels, gas-phase transport of CH_4 limits soil uptake, and the effect of temperature is weak or nonexistent. In poorly drained soils, when CH_4 concentrations greatly exceed atmospheric concentrations, oxidation reactions can become saturated so that enzyme activity rather than gas-phase transport or gas–water exchange limits oxidation. In this case, soils emit CH_4, and there is a parabolic relationship between the rate of production and temperature (Whalen and Reeburgh 1996). However, other factors have been shown to have important roles in controlling CH_4 consumption. Fertilizer experiments have shown that high levels of N availability reduce methanotrophy (for example, Steudler and others 1989; Mosier and others 1991; Sitaula and Bakken 1993; Hütsch 1996), and laboratory culture experiments have demonstrated that NH_4^+ and NO_2^- reduce the activity of methanotrophic enzymes and inhibit growth of methanotrophs (for example, O'Neill and Wilkinson 1977; Schnell and King 1994; Gulledge and others 1997).

Conversion of tropical forests to pastures often results in temporarily increased inorganic N pools in superficial soil horizons (Piccolo and others 1994; Reiners and others 1994; Neill and others 1995). Keller and others (1990) suggested that this inhibition by soil inorganic N may explain decreases in CH_4 uptake after land clearing and pasture formation in the humid tropics.

The first objective of this study was to quantify the effects of land-use change on the soil sink for atmospheric CH_4 in eastern Amazonia, where seasonality of precipitation and soil water content is pronounced. The second objective of this study was to investigate several possible controlling mechanisms of CH_4 fluxes from these tropical soils:

1. Conversion of primary forest to pastures results in decreased N availability in pastures that are several years old, which in turn results in increased CH_4 uptake by pasture soils.
2. Gas-phase transport limits soil uptake of CH_4, and the rate of transport in a given soil is a function of soil water content. Therefore, there will be a negative relationship between CH_4 flux and soil water content.
3. Root and microbial respiration are needed to maintain anaerobic microsites for CH_4 production. Therefore, soils will consume less or emit more CH_4 when their productivity, and hence their rate of respiration, is high.

We recognize that these mechanisms are not mutually exclusive; therefore, our final objective is to explore how these potential controlling mechanisms interact with land-use change and climate to affect CH_4 fluxes.

METHODS

Site Description

We conducted these studies at two ranches, Fazenda Vitória (Victory Ranch) and Fazenda Agua Parada (Stopped Water Ranch) near the eastern Amazonian town of Paragominas (2°59'S, 47°31'W) in the Brazilian state of Pará. These study sites are located in the Tocantins subbasin of the Amazon basin. Mean annual rainfall in this region is 1850 mm, distributed in a distinctly seasonal pattern, with less than 20% of the annual total falling between June and December (Jipp and others 1998). Despite seasonal water stress, deep penetrating roots (greater than 8 m) allow the forests of this region to retain their leaf canopy year-round (Nepstad and others 1994).

Soils in the region developed on Pleistocene terraces cut into the Belterra clay and Tertiary Barreiras formations (Sombroek 1966; Clapperton 1993). These sediments consist primarily of kaolinite, quartz, and hematite and are widespread at elevations below 200 m in the Amazon basin (Clapperton 1993). Sombroek (1966) classified these soils as Kaolinitic Yellow Latosols (Haplustox according to USDA taxonomy). Oxisols cover approximately 40% of the Amazon basin (Richter and Babar 1991) and are concentrated in eastern and southern Amazonia, where rainfall is seasonal and where most of the land-use change is occurring.

Fazenda Vitória. We established two permanent measurement areas in each of the following ecosystems: primary forest, secondary forest, active pasture, and degraded pasture. Most primary forest stands in this region are remnant stands that have experienced influences of human activities, such as hunting and harvesting of single trees. Human influences before 1960 are not known. Whereas human influences are pervasive, our primary forest site had the complex floristic structure of a forest that probably had not undergone major disturbance (that is, clearing or fire) during the last few centuries. An inventory of a 5-ha plot of primary forest at Fazenda Vitória by Nepstad (1989) identified 171 species with diameter at breast height greater than 20 cm and aboveground biomass in the forest was 264 Mg ha^{-1}.

The secondary forest was a naturally regenerating forest from a pasture that had been abandoned in 1976. The area had been used with moderate intensity during the 1970s as a pasture (one to three head of cattle per hectare) and was burned periodically. At the time of measurement, stand height was patchy, with some areas as high as 13–16 m, and the aboveground biomass was 50 Mg ha^{-1}. This forest is floristically much simpler than the primary forest with 75 tree species found on 12 10 m × 10–m plots (W. Stanley personal communication).

The degraded pasture was first cleared in 1969 and had been planted to *Panicum maximum* and later to *Brachiaria humidicola.* The pasture was heavily grazed until the early 1980s (two to three head per hectare) and then grazed only intermittently until it was abandoned in 1990. Currently, there is some remaining grass cover, but much of the area is covered with woody invaders, distributed in a patchy manner. Fires frequently escape into this pasture, and it burns almost annually. The active pasture had been through a similar land-use history to that of the degraded pasture until 1987, when it was cleared, burned, disked, fertilized with phosphorous, and planted to the forage grass *B. brizantha.* The active pasture had few woody invaders.

Fazenda Agua Parada. This ranch is located approximately 20 km north of Fazenda Vitória, on the Belém-Brasília highway. This site is located in the same geologic formation, but at a lower elevation, and it appears that soils were formed directly on the Barreiras formation, although red clays of the Belterra formation were observed at some sites. Rainfall depth and seasonality were similar to Fazenda Vitória.

We located five pastures of different ages that were on their first pasture cycle after clearing, that had not been reformed after an initial degradation in forage quality. Pastures at the beginning of the study were 0, 1, 3, 6, and 13 years old. The 0-year pasture had been cut and burned approximately 6 months before measurements began, but pasture grasses were seeded only 3 months before the first measurement. For comparison, we measured fluxes at one forest site that had been selectively logged 6–9 months before we began measurements, and we measured in an area with no down or broken trees. There were no unlogged forests accessible to us at this ranch. All pastures and the logged forest were located on relatively flat land (less than 2% slope) except for the 3-year pasture, which had a steeper slope (6%–10%) and was drained by a stream. Soils on this pasture generally had a wetter appearance in the rainy season, and the pasture was dissected by ephemeral channels. On this site, our sampling was done on a relatively flat surface near the top of the slope.

CH_4 Fluxes

CH_4 surface fluxes were measured using a static chamber technique (Matson and others 1990). Chambers consisted of a polyvinyl chloride (PVC) ring (20-cm diameter × 10-cm height) and a vented PVC cover made from an end-cap of a 20-cm

diameter PVC pipe. PVC rings were pushed into the soil to a depth of 2–3 cm to make the base of the chamber. At the time of measurement, the cover was placed over the base, making a chamber with approximately a 5.5-L head-space volume. The head space was sampled by withdrawing 20 mL of gas from the chamber through a rubber septum at 30 sec, 10 min, 20 min, and 30 min using nylon syringes fitted with stopcocks. Samples were returned to the laboratory, and CH_4 analysis was done with a gas chromatograph fitted with a flame ionization detector.

CH_4 fluxes were calculated from the rate of concentration change in the chamber during the incubation, determined by linear regression based on the four samples. Occasionally, and particularly for very high fluxes, the rate of change in concentration within the chamber decreased over the course of the incubation, probably due to the reduction in the concentration gradient between the soil atmosphere and the chamber head space (Hutchinson and Livingston 1993). In these cases, only points representing the linear portion of the accumulation curve were used in the regression.

Sampling Design

Fazenda Vitória. Eight chamber bases were placed in each of two study sites in each land use and measured monthly from April 1995 to May 1996. Each study site was located in the vicinity of a soil pit instrumented with time domain reflectometry (TDR) probes (Nepstad and others 1994; Jipp and others 1998) and soil gas sampling tubes (Davidson and Trumbore 1995). Chamber bases were left in place throughout the course of the experiment on all sites except the active cattle pastures. Because these sites were actively grazed, rings were withdrawn at the end of each sampling and replaced in the same general area for the following sampling. Occasionally, because of use or root ingrowth, a permanently installed ring in one of the other ecosystems would become loose. In this case, the ring was removed and reset within 2–3 m of its original placement.

Intensive Sampling. To determine the adequacy of using eight chamber measurements per site for estimating the mean flux of each site, we sampled gas fluxes more intensively in primary forests and active pastures, once in the wet season (April) and once in the dry season (November). In the primary forest, we chose an area with no apparent human disturbance. In the pasture, we chose an area that was actively grazed. In each area, we sampled 36 chambers on a 5 m $\times$ 6–m grid in a 750-m^2 area, by using the measurement techniques cited above.

Fazenda Agua Parada. We identified a general sampling area in each pasture and in the logged forest and returned to these areas each time for measurement. These sites were sampled four times between June 1995 and May 1996; however, the last sampling was incomplete because several sites were isolated due to heavy rainfall and flooding. For each sampling, eight chambers were measured per site.

CH_4 Profiles in the Soil Atmosphere at Fazenda Vitória

Soil gases were sampled from stainless steel tubes (3 mm outside diameter) previously installed into the walls of each pit at approximately 25, 50, 75, 100, 300, 500, and 800-cm depth (for details see Davidson and Trumbore 1995). Samples were collected twice during the course of the study: once during the wet season (May 1995) and once during the dry season (September 1995).

Ancillary Measurements

CO_2 Fluxes. Fluxes of CO_2 from the soil were measured using a dynamic chamber technique (Davidson and Trumbore 1995). At the time of measurement, a vented PVC cover (20-cm PVC end-cap) was placed over the same PVC rings that were used as chamber bases for the CH_4 measurements, making a chamber with a head-space volume of approximately 4 L. Air was circulated between a LiCor 6252 infrared CO_2 analyzer and the chamber through Teflon tubing by using a battery operated pump, at a rate of 0.5 L min^{-1}. CO_2 concentrations were recorded at 5-sec intervals over a period of 3–4 min using a data logger. Fluxes were calculated from the rate of CO_2 concentration increase by using the steepest linear portion of the accumulation curve where the linear nature of the accumulation was sustained for at least 20 sec. The instrument was calibrated two to three times daily in the field using a portable standard. In almost all cases, CH_4 and CO_2 flux measurements for a particular site were made on the same day and within 90 min of each other.

Soil Temperature and Soil Water Content. Soil temperature was measured at 10-cm depth with a portable temperature probe, at the same time that gas flux measurements were made. Soil water content was measured in association with each flux measurement using TDR. TDR probes (30 cm long) were inserted vertically into the soil surface to measure the dielectric constant of the soil. The dielectric constant was converted to volumetric soil water content using calibration curves derived from laboratory analysis of intact soil cores (Jipp

and others 1998). Then, using average bulk density values for soils at each site the known particle density for the surface soils of 2.5 (J.E.M. Carvalho personal communication) and field measurements of volumetric soil water content, the percentage of water-filled pore space (%WFPS) was calculated (see Davidson 1993). All measures of soil water content are expressed as %WFPS in this article.

Inorganic N Pool Sizes. We collected eight soil samples per site, once in the dry season (July 1995) and once in the wet season (January 1996). After returning to the lab we thoroughly mixed all soil samples; coarse roots and coarse organic matter were removed. We extracted inorganic N from 15-g subsamples of field-moist soil using 100 mL of 2 M KCl. The soil–KCl solution was shaken for 1 hour on an orbital shaker and allowed to settle overnight. A 20 mL aliquot supernatant then was pipetted into sample vials and frozen for later analysis. Analysis was done on an Alpkem autoanalyzer (Wilsonville, OR, USA) by using a modified Griess-Illosvay procedure for determination of NO_3-N + NO_2-N, which was reported as NO_3-N (Bundy and Meisinger 1994) and a salicylate–hypochlorite procedure for NH_4-N (Kemper and Zweers 1986).

N-Cycling Indices. Net mineralization and net nitrification were determined using the aerobic incubation procedure of Hart and others (1994). For each sample described above, a 15-g subsample of field-moist soil was placed in a 120-mL specimen cup, which then was closed with a perforated plastic cap to allow gas exchange while minimizing evaporation loss. These subsamples were incubated for 7 days at room temperature (approximately 24°C). NH_4-N and NO_3-N concentrations were determined by extracting inorganic N from subsamples with 100 mL of 2 M KCl solution before and after incubation and analyzed as described above. Net mineralization rates were determined from the difference between inorganic N at the beginning and end of the incubation, and results were expressed on a basis of mean daily inorganic N production. Likewise, net nitrification was determined from the difference in NO_3-N at the beginning and end of the incubation, and results were expressed in similar units.

Statistics and Data Analysis

Normality was determined by a goodness of fit test using the Kolomogorov-Smirnov *D* statistic (Sokal and Rohlf 1981). CH_4 flux data were not normally distributed, but soil respiration data were log-normally distributed. We used the Box-Cox procedure (Sokal and Rohlf 1981) for estimating the best transformation to normality within the family of power transformations for CH_4 and did not find a transformation that provided a satisfactory distribution. Therefore, all statistical tests were made using nonparametric procedures. We used the NPAR1WAY procedure in SAS (SAS Institute 1992) to calculate Wilcoxon scores for the Mann-Whitney *U* test to compare two means or for the Kruskal-Wallis test to compare more than two means. Because of unequal observations among categories, no separation tests were performed. Standard errors are used to indicate probable significant differences.

To evaluate the intensive measurement results, we used a resampling procedure to determine the probability that a sample with $n = 8$ would estimate the true mean, using Resampling Stats software (Simon 1992). We drew 1000 random samples of eight, with replacement, from the full data set of 36 observations and tallied the mean of each sample to determine the probability that a random sample of eight fell within a certain distance of the mean, based upon this frequency distribution.

Table 1. Soil Characteristics for the Different Ecosystems Studied at Fazenda Vitória[a]

Ecosystem	Bulk Density (kg m^{-3})	Total Porosity[b] (m^3 m^{-3})	Macro Porosity[b] (m^3 m^{-3})	pH H_2O[c]
Primary forest	0.90	0.63	0.26	4.4
Secondary forest	0.93	0.64	—	5.5
Active pasture	1.18	0.53	0.14	5.7
Degraded pasture	1.15	0.54	0.16	5.4

[a] *Soil characteristics determined for 0–10-cm layer.*
[b] *Porosity data from Davidson and Trumbore (1995).*
[c] *pH determined in a mixture of 2.5:1 H_2O:soil.*

Results

Fazenda Vitória Land-Use Measurements

General Soil Characteristics. A summary of physical and chemical characteristics of the surface 10 cm of soils in each ecosystem is presented in Table 1. Pasture soils had higher bulk densities than the primary forest soils, but the secondary forest soils had returned to a bulk density in the surface 10 cm that was similar to that of the primary forest. Increased bulk density, by definition resulted in lower total pore space, but there was also a shift in the size distribution of pore spaces, resulting in a relative decrease in macropore space in the pasture soils. Soil pH was 4.4 in the primary forest and greater than 5.4 in the pastures and secondary forest.

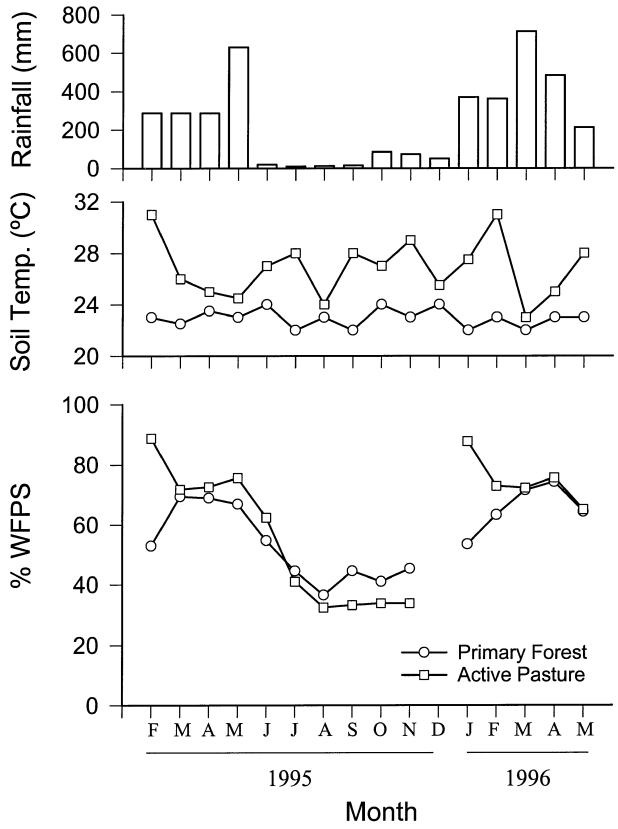

Figure 1. Monthly rainfall (**top**) for the study period, soil temperature (**middle**), and soil water content (expressed as %WFPS) in the top 30 cm of the soil profile (**bottom**).

Precipitation, Soil Temperature, and Soil Moisture. Annual rainfall was greater than the 22-year mean during this study; rainfall depths were 1905 mm and 2380 mm for 1995 and 1996, respectively. A distinct dry season can be observed from June to December (Figure 1) where precipitation made up less than 15% of the annual total for 1995.

Soil temperature was generally lower in the forest than in the pasture (Figure 1). There was no apparent seasonal variation in temperature of either the forest or pasture soils, but we note that soil temperature was measured in association with flux measurements, and no effort was made to ensure consistency with respect to time of day or meteorological conditions. Soil temperature variation was more closely associated with time of day of measurement and cloud cover.

Soil water content varied in phase with rainfall (Figure 1). Following cessation of the rains in June, WFPS in the surface 30 cm of soil declined until reaching more or less constant levels in August. Forest soils had consistently higher WFPS than pasture soils during the dry season. WFPS increased more rapidly in pasture soils after the onset of the rains in January, due to a delay in development of transpiration capacity in the pasture grasses. By the middle of the wet season, WFPS in the pastures was similar to that in the forests.

CH_4 Fluxes. During the majority of the flux measurements in 1995–96, we observed uptake (negative fluxes) of CH_4 by soils in both the forest and pasture ecosystems (Figure 2). We found no diel fluctuations in uptake rates during a test in forest and pasture soils where measurements were made at 0600, 1000, 1500, and 1800 h (data not shown). Fluxes were most negative in the dry season (June to December), and some emissions (positive fluxes) were observed during the wet season (December to May). In two instances in the primary forest, we observed extremely high emissions from a chamber in the dry season. In one instance, the flux was 28 mg m^{-2} d^{-1}, and in the other the flux was 42 mg m^{-2} d^{-1}. These fluxes were unlike any of the other 110 fluxes observed during this season in primary forests, so we excluded them from site mean calculations. The high positive flux observed in one of the active pastures in May 1995 was the result of several chambers with high fluxes during the sampling, as indicated by the relatively small standard error.

Differences in CH_4 fluxes among ecosystems were highly significant (Kruskal-Wallis test, $P = 0.0001$) in both seasons. As we noted earlier, standard errors must be used to indicate probable significant differences in pairwise comparisons (Table 2). During the dry season, uptake was similar between pastures and the primary forest, but uptake was significantly lower in the secondary forest. Wet season results showed similar flux magnitudes between the forest ecosystems and the degraded pasture, and significantly higher emissions in the active pasture, owing largely to the May 1995 observation. Seasonal differences were observed in all ecosystems and were highly significant (Mann-Whitney U test, $P = 0.0001$). The dry season was characterized by strong to moderate uptake and the wet season by low uptake or emission.

We calculated annual fluxes by stratifying the year into wet season (January to May) and dry season (June to December) and calculating the mean flux for each season. We then extrapolated that mean flux to the entire season and summed the seasonal estimates (Table 2). Strongest uptake was observed in the degraded pastures, followed by primary forests, active pastures, and then secondary forests.

Negative fluxes (soil oxidation of CH_4) were observed in 85%–95% of the individual chamber measurements in each ecosystem during the dry

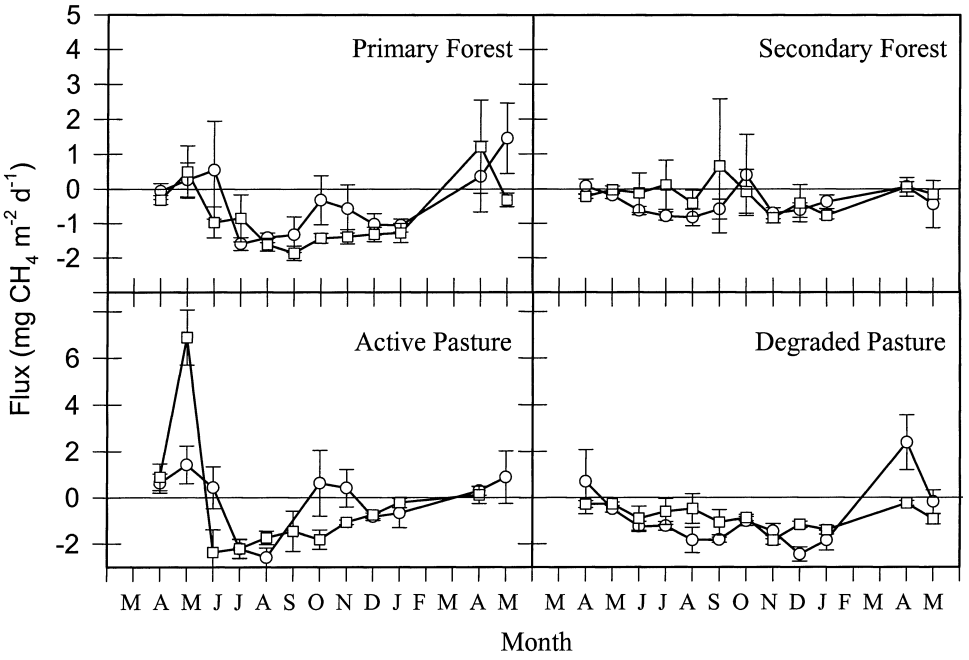

Figure 2. Monthly flux rates of CH_4 (squares, study site 1; circles, study site 2) in the different ecosystems at Fazenda Vitória. Error bars are ±1 SE.

season and in 40%–80% of the observations during the wet season. Of these negative fluxes, 50%–70% of the individual dry season flux measurements among the four land uses were significantly different from zero ($P = 0.05$), and 15%–45% of the wet season measurements were significantly different from zero. Positive flux measurements had similar incidences of significance in each season.

We calculated the minimum detectable flux following Hutchinson and Livingston (1993). For each individual chamber measurement, we computed the 95% confidence interval of the flux estimate based on the linear regression of increasing chamber concentration with time. We grouped the flux observations by increments of 0.1 mg m^{-2} d^{-1} and for each group, we calculated the percentage of observations for which the 95% confidence interval included zero. We then defined the minimum detectable flux as that flux at which greater than 67% of the confidence intervals of the individual flux observations did not include 0 (a 2:1 signal to noise ratio). The minimum detectable uptake flux was −0.5 mg m^{-2} d^{-1}, and the minimum detectable emission flux was 0.8 mg m^{-2} d^{-1}.

Intensive Sampling Results. To determine the adequacy of using eight chamber flux measurements to estimate the mean flux per site, and to understand the nature of spatial variability of fluxes, we conducted two intensive sampling campaigns in active pasture and primary forest: one in the dry season (November 1995) and one in the wet season (April 1996). Mean fluxes from the intensive sampling were generally similar to typical fluxes during the respective seasons (compare Figure 2 and Table 3).

A mean based on eight chamber measurements has a 95% probability of being ±300% of the true mean in the wet season and ±200%–400% of the true mean during the dry season (Table 3). This large degree of error was due to high relative spatial variability. Coefficients of variation for these sites ranged from 435% to 1030%.

N Availability. Inorganic N pools were dominated by NO_3^- in the primary forest, while NH_4^+ predominated in all other ecosystems (Table 4). The secondary forest showed marked seasonality in the NO_3^- pools (*t* test, $P = 0.0581$), with relatively large pools in the dry season and smaller pools in the wet season. Pastures had small NO_3^- pools relative to the primary forest, but NH_4^+ pools were not significantly different from that of the primary forest ($P = 0.05$).

Results of the net mineralization assay showed higher net ammonification and net mineralization in the forest ecosystems compared to the pasture ecosystems ($P = 0.05$) in the dry season. We measured significant NO_3^- loss during the incubation of the wet season primary forest soils and attribute this to denitrification. This NO_3^- loss is reflected in the highly negative estimate of net mineralization and

Table 2. Seasonal and Annual Summary of Fazenda Vitória CH_4 Fluxes[a]

Ecosystem	Wet Season (mg CH_4 m^{-2} d^{-1})	Dry Season (mg CH_4 m^{-2} d^{-1})	Annual Total[b] (kg CH_4 ha^{-1} y^{-1})
Primary forest	0.03 (0.21)	−0.98 (0.21)	−2.1
	88	*119*	
Secondary forest	−0.20 (0.08)	−0.34 (0.18)	−1.0
	80	*128*	
Active pasture	1.13 (0.34)	−1.42 (0.16)	−1.3
	72	*103*	
Degraded pasture	−0.26 (0.22)	−1.29 (0.11)	−3.1
	80	*112*	

[a]Values are mean (SE), and the number of observation is in italics below the mean. Negative values indicate uptake, and positive values indicate emission.
[b]Annual totals were calculated by stratifying the year into wet season (Jan–May) and dry season (Jun–Dec) and multiplying the mean flux for the season by the number of days in the respective season.

Table 3. Results of Resampling from Intensive Sampling Campaigns in the Primary Forest and Active Pasture

Percentage of True Mean	Wet Season		Dry Season	
	Primary Forest	Active Pasture	Primary Forest	Active Pasture
±50	0.318	0.388	0.126	0.353
±100	0.485	0.538	0.287	0.648
±200	0.855	0.856	0.509	0.921
±300	0.959	0.958	0.667	0.995
±400	0.988	0.994	0.845	>0.999
Mean	0.23	0.57	−0.29	−0.75
SD	1.29	2.49	2.94	2.54

Values are probabilities that a sample of eight, drawn at random and with replacement, from the population of 36 measurements fall within the given interval of the "true" mean as defined by the universe of 36 samples. Means and the SDs of the 36 chambers are reported in the lower section of the table in mg CH_4 m^{-2} h^{-1}.

net nitrification. The degraded pasture showed net immobilization from the NH_4^+ pool and a loss of NO_3^- during the incubation, which also could be due to denitrification. No consistent seasonal trend was apparent in either the inorganic N pools or the mineralization assay results.

Soil Respiration. Soil respiration (Table 5) was greater in the wet season than in the dry season for all ecosystems (*t* test, $P = 0.0001$). For both wet and dry seasons, respiration was greatest in the primary forest and lowest in the degraded pasture (ANOVA, $P = 0.0001$). Respiration rates were intermediate in the secondary forest and active pasture, although the secondary forest had significantly higher respiration during the dry season, whereas the active pasture had higher rates during the wet season.

CH_4 Concentrations in the Soil Profile. CH_4 concentrations in the soil profile were measured in two pits in each ecosystem, in the middle of the dry season when WFPS was at its lowest point and at the end of the wet season when WFPS was elevated. Concentrations were consistently below atmospheric concentrations to a depth of 800 cm (Figure 3). Subatmospheric concentrations at 30-cm depth indicated that consumption of atmospheric CH_4 occurred in the superficial soil layers. In several instances, we observed sharp concentration spikes within the profile, indicating that CH_4 production occurs at various depths within the profile.

Fazenda Agua Parada Chronosequence Measurements

Results from the chronosequence measurement show no significant trend in CH_4 fluxes with pasture age (Figure 4). Statistical analysis showed no significant differences among the sites during the wet season. During the dry season, the only significant difference was between the 3-year-old pasture, where the flux was positive, and the 0-year-old pasture where uptake was greatest. The aggregated annual flux for the pastures was −2.5 kg ha^{-1} y^{-1}, which was equal to the annual flux from the forest site.

Soil respiration also showed no significant trend with pasture age (Figure 4). Most of the pastures had significantly higher wet season respiration than the logged forest, which resulted in higher total annual soil respiration. Dry season respiration was similar among all sites, with the exception of the 3-year-old pasture. Wetter conditions in this pasture probably explained the elevated dry season respiration.

Relationship between Environmental Factors and CH_4 Fluxes

We found no significant correlations ($P = 0.05$) between CH_4 fluxes and either the individual NO_3^- and NH_4^+ pools ($R^2 = 0.027$ and 0.068, respectively) or the total inorganic N pool ($R^2 = 0.088$). We also found no significant relationship ($P = 0.05$) between net nitrification, net ammonification, or net mineralization and CH_4 fluxes ($R^2 = 0.0001$, 0.213, and 0.047, respectively). We did find a significant correlation between CH_4 fluxes and WFPS ($R^2 = 0.294$, $P = 0.0001$), and, as expected, the correlation was positive. There was also a significant correlation between soil temperature and CH_4 flux in pasture ecosystems only, but the correlation coefficient was low ($R^2 = -0.11$, $P = 0.05$).

To examine the relationship between soil respiration and CH_4 fluxes, we used the combined data sets

Table 4. Inorganic N Stocks and Results of Aerobic N Availability Assays for the Different Ecosystems of Fazenda Vitória

	NH_4-N (µg-N g-soil^{-1})	NO_3-N (µg-N g-soil^{-1})	Net Ammonification (µg-N g-soil^{-1} d^{-1})	Net Nitrification (µg-N g-soil^{-1} d^{-1})	Net Mineralization (µg-N g-soil^{-1} d^{-1})
Dry Season–July 1995					
Primary forest	14.14 a	18.64 a	0.14 a	2.25 a	2.39 a
Secondary forest	26.28 b	18.92 a	1.63 b	−0.21 b	1.42 ab
Active pasture	8.54 a	1.76 b	−0.13 a	0.40 b	0.33 b
Degraded pasture	5.58 a	3.00 b	0.58 ab	0.30 b	0.88 b
Wet Season–January 1996					
Primary forest	8.16 a	26.48 a	0.20 a	−2.48 a	−2.28 a
Secondary forest	15.04 a	5.77 b	0.38 a	0.78 b	1.16 b
Active pasture	12.70 a	3.35 b	0.08 a	0.67 b	0.75 b
Degraded pasture	15.81 a	6.17 b	−0.38 a	−0.47 c	−0.85 c

For each season, means within a column followed by the same letter are not significantly different from each other (Student-Neuman-Keuhls multiple range test, P = 0.05). Values are means of 16 observations for each ecosystem.

Table 5. Seasonal and Annual Summary of Fazenda Vitória CO_2 Fluxes

Ecosystem	Wet Season[a] (g C m^{-2} hr^{-1})	Dry Season (g C m^{-2} hr^{-1})	Annual Total[b] (Mg C ha^{-1} y^{-1})
Primary forest	0.299 a (0.014) *136*	0.181 a (0.009) *95*	20.0
Secondary forest	0.245 b (0.010) *137*	0.174 a (0.010) *94*	17.9
Active pasture	0.280 ab (0.017) *136*	0.126 b (0.008) *72*	15.3
Degraded pasture	0.222 c (0.017) *117*	0.077 c (0.004) *78*	10.4

Values are mean (SE), and the number of observations associated with each mean is shown in italics. Means in a column followed by the same letter were not significantly different from each other (ANOVA, P = 0.0001). From Davidson and others (1999).
[a]Dry season means for all ecosystems were significantly lower than wet season means (t test, P = 0.0001).
[b]Annual totals were calculated using monthly estimates of CO_2 flux.

from Agua Parada and Vitória. We eliminated observations from January 1996 to avoid the effects of early wet-up, which resulted in high CO_2 fluxes due to high respiration in superficial soil layers. The correlation between soil respiration was positive and significant ($R^2 = 0.251$, $P = 0.0001$).

Discussion

Detection Limits and Sampling Adequacy

Although few studies rigorously evaluate their spatial sampling scheme and the detection limits for their chamber measurements, it is important to ask whether the methods used to measure the fluxes and the sampling frequency were adequate to detect differences among ecosystems. The analysis of standard errors of the mean showed that the lowest detectable uptake flux was 0.5 mg m^{-2} d^{-1} and the lowest detectable emission flux was 0.8 mg m^{-2} d^{-1}. Despite this relatively high detection limit, the majority of the individual fluxes measured during the dry season in each ecosystem was significantly different from zero. We can therefore have confidence in our ability to adequately measure a mean site flux during this season. During the wet season, less than 50% of the individual chamber fluxes were significantly different from 0; thus, we have much less confidence in the absolute values of these measurements, but we can have confidence in the fact that fluxes during this season were low.

The more serious question appears to be associated with our ability to detect differences among sites due to the high degree of spatial variation. Results from the intensive sampling showed that spatial variability was high in these soils and that the mean based upon eight measurements per site had a 95% probability of being within approximately ±300% of the true mean. Detecting significant differences among sites would therefore be difficult based on a monthly sampling. To overcome this, we aggregated the 16 individual observations in the two sites per ecosystem, combined the data from all months within a season, and analyzed seasonal differences among ecosystems on this basis. Annual fluxes were calculated based on seasonal means. The large degree of spatial variability underscores the necessity of repeated measurements and sam-

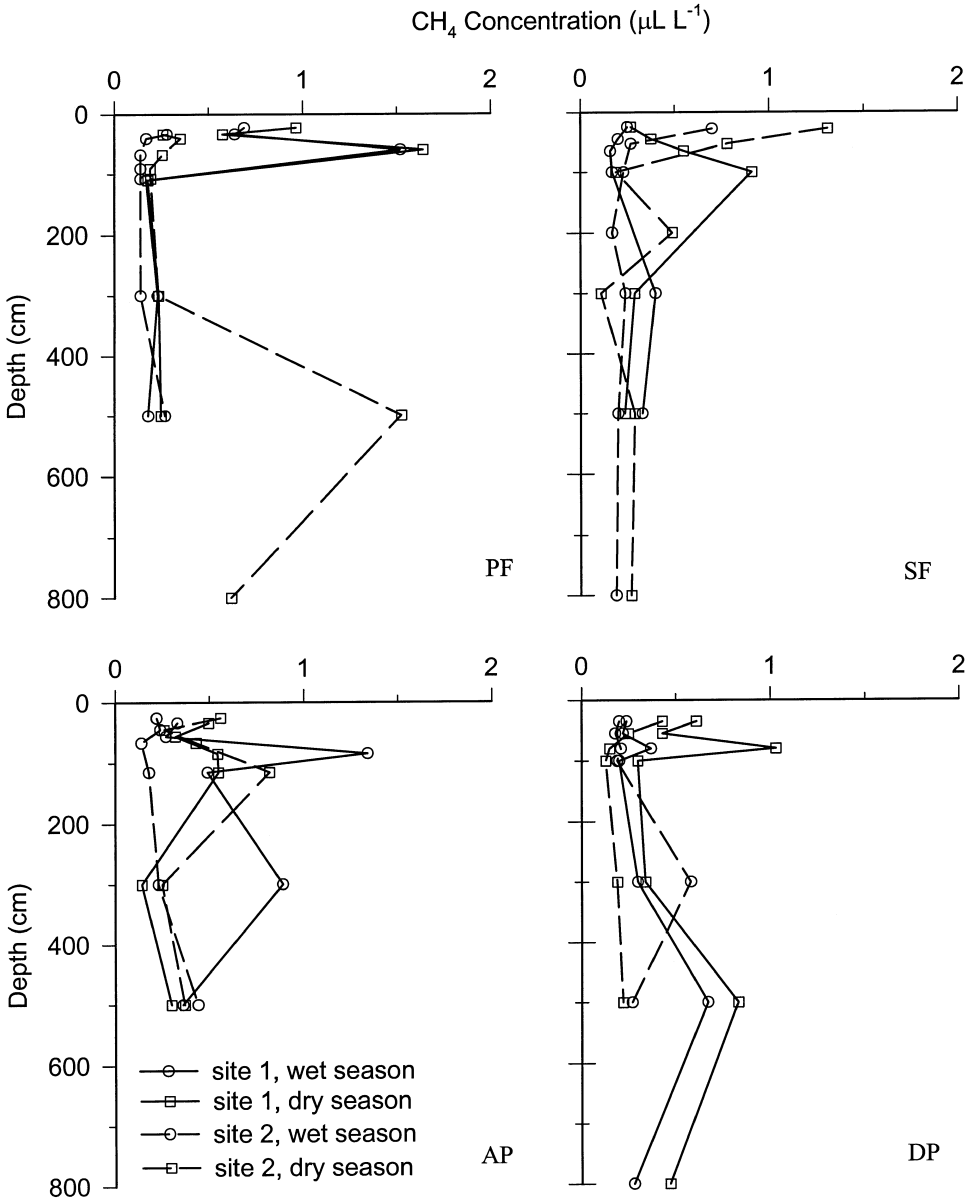

Figure 3. CH_4 profiles in soils of different ecosystems at Fazenda Vitória. Four lines in each panel indicate concentrations at two sites in each land use (PF, primary forest; SF, secondary forest; AP, active pasture; DP, degraded pasture) and two measurements (one in the late wet season and one in the mid dry season).

pling from several sites on the landscape to properly quantify the flux from these ecosystems.

Biogeochemical Controls of CH_4 Fluxes

Significant relationships have been reported between inorganic N stocks, N availability indices or rates of nitrification and CH_4 flux rates in agriculture (Hütsch 1996), fertilized forests (Steudler and others, 1989; Castro and others 1994), and fertilized grasslands (Mosier and others 1991, 1996). It has also been suggested that pulses of N availability after deforestation could inhibit CH_4 oxidation (Keller and others 1990). If N availability affected CH_4 oxidation in these forest and pasture soils of eastern Amazonia, then one might expect lower CH_4 uptake in the primary forest soils, which was not the case. We found no significant correlation between any of the measures of soil inorganic N stocks.

Another way of testing this hypothesis would be to compare net rates of mineralization and nitrification with rates and CH_4 fluxes. Net ammonification or net mineralization are thought to be indices of rates of inorganic N production. Also, just as net nitrification is used as an index of NH_4^+ availability

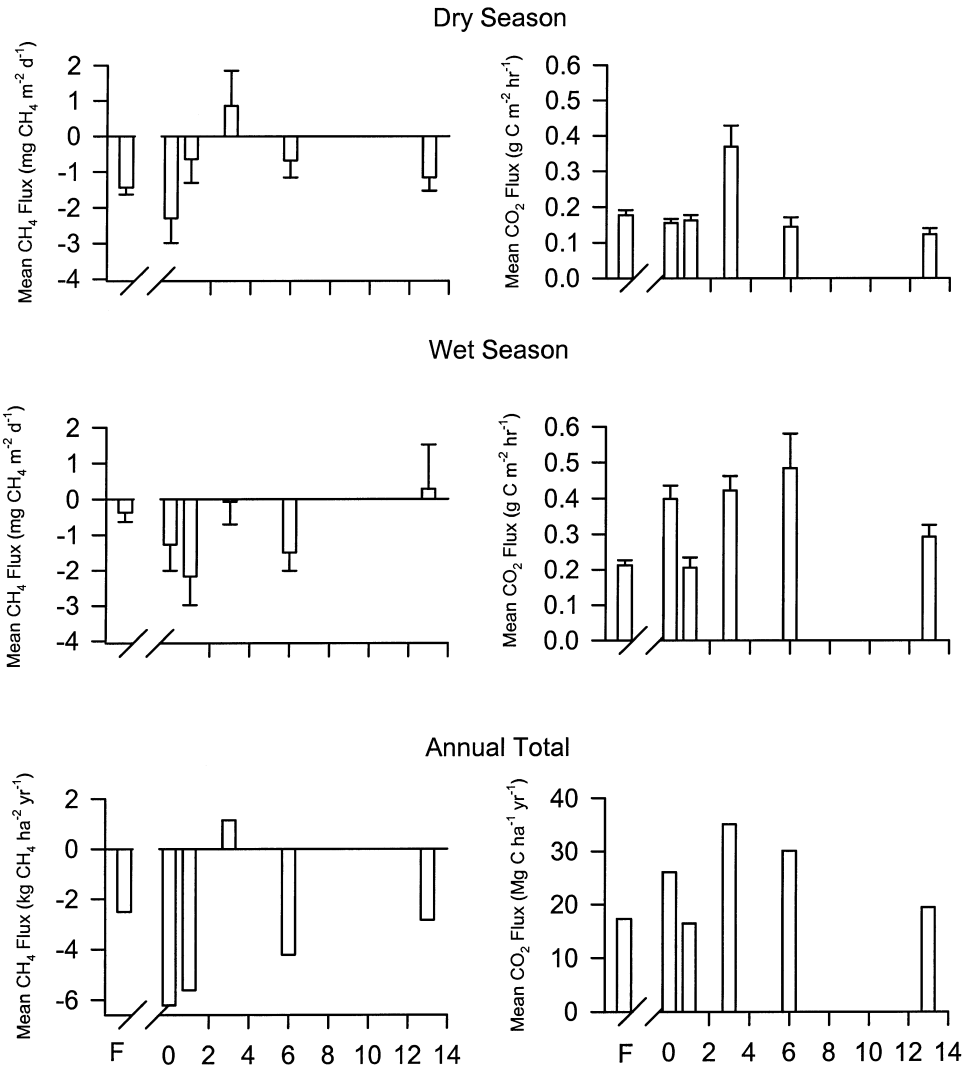

Figure 4. CH_4 and CO_2 fluxes from Agua Parada chronosequence, by season and annual extrapolation. F indicates the selectively logged forest.

to nitrifying bacteria, it can also indicate "availability" of potentially inhibiting NH_4^+ to CH_4 oxidizers. We found no significant relationships between CH_4 fluxes and any of the indices of N cycling rates. Thus, we conclude that N availability does not appear to control variation of CH_4 flux rates between these ecosystems. We did not measure N availability at Fazenda Agua Parada, but if the young pastures there had enhanced N availability, it did not appear to affect CH_4 fluxes. This is not to say that very high NH_4 levels would not inhibit CH_4 uptake in these soils; rather, we find that the ranges of variation of either extractable NH_4^+ or other indices of N availability do not explain spatial or temporal variation in CH_4 oxidation at the landscape scale.

The second hypothesized mechanism stated that gas-phase transport of CH_4 would limit soil uptake. At a given site, the rate of diffusion of a gas into the soil profile is an inverse function of soil water content. We found that CH_4 fluxes were positively correlated with %WFPS and therefore would be negatively correlated with the diffusion rate, which is consistent with this mechanism. The importance of gas-phase transport within the soil is also revealed by seasonality of CH_4 fluxes. At both Fazenda Vitória and Fazenda Agua Parada, soils were generally a strong to moderate sink in the dry season, whereas they were a weak sink or a source during the wet season.

It would be more satisfying to use the data on soil water content to calculate effective diffusivity within the soil and relate diffusivity estimates to CH_4 fluxes directly. However, the various models used to calculate diffusivity require information on total porosity and, in some cases, tortuosity or the distribution of macropores and micropores (see review by David-

son and Trumbore 1995), which are difficult to measure with confidence. When the simple model of Millington and Quirk (1961) is used, which does not distinguish among pore sizes, the correlation between calculated diffusivity and CH_4 flux is significant ($R^2 = 0.246$, $P = 0.0001$), albeit less strong than the correlation between WFPS and CH_4 flux. Keller and Reiners (1994) also found a good correlation between diffusivity estimated with a similar simple model and CH_4 fluxes measured in forests and pastures of Costa Rica. However, using the more complicated model of Millington and Shearer (1971) and the approach of Davidson and Trumbore (1995) for estimating microporosity from field observations of water content at field capacity (Table 1), we calculated that the macropores of the Fazenda Vitoria soils were nearly always air filled, even during the rainy season. Because this model assumes that most gas transport occurs within the macropores, our estimates of diffusivity from this second model varied little between seasons and were not significantly correlated with CH_4 flux. In contrast, Weitz and others (1998) found a good correlation using their assumptions of macroporosity and microporosity for soils of forests and clearings at La Selva, Costa Rica. This site receives 4000 mm of mean annual precipitation, which appears to result in frequent events of reduced air-filled macroporosity and reduced diffusivity. The difference between our results and those of Weitz and others (1998) could also be due to differences in assumptions about macroporosity. In agreement with Keller and Reiners (1994) and Weitz and others (1998), we conclude that the effect of diffusion on gas-phase transport is the most likely mechanistic explanation for the effect of varying water content on CH_4 fluxes, but that uncertainties in parameterization of diffusivity models degrades the predictive capacity of the regression models based on diffusivity estimates, especially where the complexity of the diffusivity models requires information on pore size distribution that is difficult to acquire with confidence.

The third mechanism states that high rates of soil respiration can create anaerobic microsites as O_2 is consumed, resulting in CH_4 production in the soil. Therefore, soils should consume less or emit more CH_4 when CO_2 production by root and microbial respiration is high. The relationship between soil respiration and CH_4 flux was positive and highly significant, which is consistent with this mechanism. Soil respiration has been interpreted as a good measure of total C allocation to roots and litter, and it correlates well with ecosystem productivity (Raich and Nadlehoffer 1989). Therefore the correlation between soil respiration and CH_4 fluxes observed in this study is comparable to a similar relationship between net ecosystem productivity and CH_4 fluxes found by Whiting and Chanton (1993) across a range of wetland types. We suggest that a common process is at work in both upland soils and wetlands: as productivity increases and the C flux through upland soils or wetlands increases, the probability of microsites of CH_4 production also increases, causing a shift along the continuum from high rates of CH_4 uptake, to low net CH_4 uptake, to low net CH_4 emission, to high CH_4 emissions.

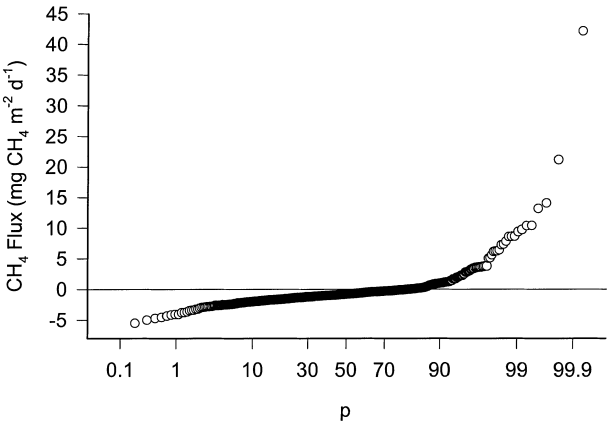

Figure 5. Probability plot of CH_4 flux observations from individual chambers for all ecosystems at Fazenda Vitória. Probability was calculated as $P = [(i - 0.5)/n]$, where i is the rank of the individual observation, and n is the total number of observations.

Production Hot Spots

Many of our observations indicated that there is a source of CH_4 in these soils. In each data set (Fazenda Vitória, Fazenda Agua Parada, intensive sampling data), approximately 20% of the fluxes were positive, and 10% were greater than 1.0 mg m^{-2} h^{-1} (Figure 5). We also encountered zones of relatively high CH_4 concentrations in the soil profile. Most of the positive flux measurements were observed during the wet season, resulting in estimates of net positive fluxes from several ecosystems for this season. We cannot be certain of the source of CH_4 in the soil profile that gave rise to these positive fluxes, but two mechanisms appear to be worth considering. First, termites are a well-known source of CH_4 in soils (Seiler and others 1984), and they are common in the forests and pastures of eastern Amazonia (Bandeira 1979; Bandeira and Torres 1985). The second mechanism worth considering is that high rates of respiration in the soil profile may have depleted oxygen in the soil atmosphere locally and produced anaerobic microsites where CH_4 was

Table 6. Summary of Interactions of CO_2 and CH_4 Fluxes by Land Use and Season

		Season			
		Wet[a]		Dry[b]	
	Land Use	CO_2 Flux	CH_4 Flux	CO_2 Flux	CH_4 Flux
Decreasing annual respiration ↓	Primary forest	High	Net emission	Moderate	Low net uptake
	Secondary forest	Moderate	Low net uptake	Moderate	Low net uptake
	Active pasture	High	Net emission	Low	High uptake
	Degraded pasture	Moderate	Low net uptake	Low	High uptake

[a] *High WFPS; low diffusivity.*
[b] *Low WFPS; high diffusivity.*

generated. As we saw above, most of the positive fluxes were observed during the wet season when soil WFPS exceeded 60% (Figure 1), a condition that would limit O_2 diffusion into the soil. Since most of the positive fluxes were also associated with high rates of respiration, this mechanism appears to be a plausible explanation for at least part of the positive flux observations.

Interactions of Land-Use Change, Soil Water Content, and Soil Respiration

The patterns of seasonal emissions of CO_2 and CH_4 fluxes were linked as they varied between seasons and across land uses. Whenever soil respiration rates were high, as in the primary forest and active pasture during the wet season, net positive emissions of CH_4 from the soil were also observed (Table 6). When soil respiration rates were moderate, CH_4 consumption apparently slightly exceeded production, resulting in low net uptake of atmospheric CH_4 by the soils. When soil respiration rates were low, as in both pastures during the dry season, rates of uptake of atmospheric CH_4 were high (Table 6). These patterns indicate that root and microbial respiration may affect the balance of CH_4 production and consumption, and hence CH_4 fluxes.

A plausible mechanism to explain linkage between CO_2 and CH_4 fluxes is that O_2 consumption during microbial and root respiration affects the availability of O_2 to methanotrophs and methanogens in some fraction of the microsites within the soil. Hence, the availability of O_2 is affected by both physical restraints on diffusion, which are determined by soil water content and soil texture, and by biological processes of O_2 consumption. Thus, the effect of high rates of soil respiration reinforces the effect of restricted diffusivity during the wet season by increasing the probability of occurrence of anaerobic microsites where methanogenesis can occur and by reducing the probability of well-aerated microsites of CH_4 consumption. The combined effect either reduces the sink strength of CH_4 or results in the soil becoming a net source.

The significance of this finding is that seasonality of precipitation must be interpreted in terms of its effects both on diffusivity and on plant phenology and microbial activity. Furthermore, responses of plant communities to seasonal patterns of precipitation vary depending upon the land use and ecosystem type within the same climatic regime. Where exotic grasses are very productive during the wet season and senescent during the dry season, CH_4 fluxes can vary from net emission to relatively high rates of uptake (Figure 1 and Table 6). The deeper-rooted forest ecosystems, in contrast, maintain modest rates of soil respiration during the dry season, which results in lower rates of net CH_4 uptake. Finally, the degraded pasture, which has the lowest annual soil respiration, and hence the lowest demand for O_2 by plant roots and soil microorganisms, had the highest rate of annual uptake of atmospheric CH_4.

This interaction of WFPS and soil respiration can be expressed quantitatively as a multiple linear regression by using the data from this study (Figure 6). We discarded one late wet season observation from a secondary forest where CH_4 uptake was low despite a high respiration rate and high WFPS [this observation was flagged by a DFFITS analysis (Rawlings 1988) as being an influential point and met the criteria for exclusion]. The relationship was highly significant ($P = 0.0001$, $R^2 = 0.43$). This two-factor model explains a much greater percentage of the variability than either of the single-factor relationships.

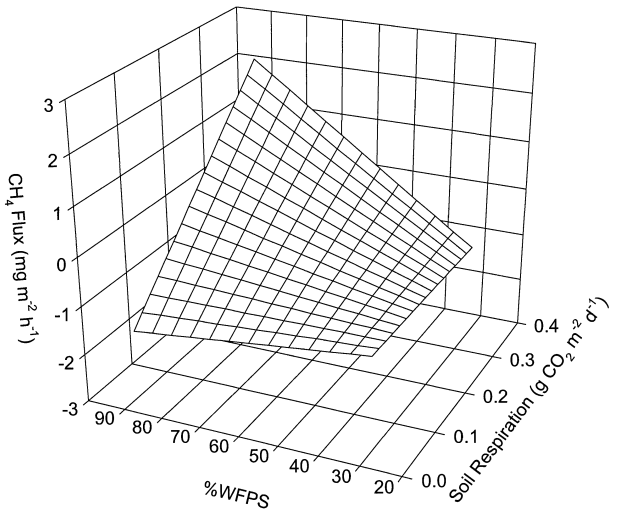

Figure 6. Response surface model explaining how soil respiration and WFPS control the soil–atmosphere CH_4 flux. Model parameters are $CH_4 = -1.502(WFPS) - 6.265(CO_2) + 20.065(WFPS \cdot CO_2) - 0.567$.

Effect of Land-Use Change on the Annual CH_4 Flux

At Fazenda Vitória, conversion of primary forest to pasture resulted in decreased annual CH_4 consumption in the active pastures, but the degraded pastures consumed more CH_4 than the primary forest during the study period. These results for the active pasture are generally consistent with other studies that have shown decreased consumption or conversion to a net source following deforestation and pasture establishment in tropical soils (Keller and others 1993; Keller and Reiners 1994; Steudler and others 1996). These previous studies, however, did not consider degraded or abandoned pastures. Our finding that annual net CH_4 consumption was higher in the degraded pasture is new, and it appears to be related to decreased soil respiration that may have led to fewer microsites of methanogenesis. Steudler and others (1996) and Fearnside (1996) have calculated that biomass burning and cattle emissions have a much larger effect on the CH_4 budget of the Amazon basin than does the change in soil fluxes due to forest-to-pasture conversion of land use. Our results showing that degraded pasture soils consume as much atmospheric CH_4 as forest soils reinforce this conclusion.

The results from the Agua Parada ranch chronosequence showed no difference in CH_4 fluxes between young pastures and the primary forest. We did observe somewhat increased soil respiration in most pastures during the wet season, but only in the 3-year-old pasture where the largest increase in annual soil respiration was observed, did high soil respiration result in decreased CH_4 sink strength. One problem in interpreting these results is that infrequent sampling (only four times in a year) may have been inadequate to quantify the CH_4 flux and detect real differences among forests and pastures. Results from our intensive sampling suggested that the power to accurately measure a flux from a site based on eight chambers was low. Aggregation of observations from two sites and several dates within a season was required to calculate reliable seasonal means for each land-use type at Fazenda Vitória.

Comparisons with Other Studies

Globally, tropical ecosystems are considered to be significant sinks for atmospheric CH_4 (Dörr and others 1993; Potter and others 1996; Mosier and others 1997). Consumption of atmospheric CH_4 has been observed in upland soils of many humid tropical forests (Table 7). Our estimate of the annual CH_4 flux in eastern Amazonian forest soils is among the lowest observed in these ecosystems, but is consistent with observations on other fine-textured Oxisols near Manaus (Keller and others 1986). Medium-textured Inceptisols of central Africa and Central America and coarse-textured Ultisols in western Amazonia consume atmospheric CH_4 at much higher rates than fine-textured Amazonian Oxisols. No data are available for coarse-textured Oxisols, but we would expect that the texture class is more important than the soil order, because gas transport of O_2 and CH_4 are the most important factors affecting CH_4 fluxes, and soil texture strongly affects diffusivity of gases within soils. Based on three published studies (Keller and others 1986; Steudler and others 1996; this study), it appears that variability of CH_4 consumption in upland soils of Amazonian forests is equal to the variability encountered in humid tropical forests worldwide. Stratification of the data presented in Table 7 by soil texture appears to explain a significant portion of this variability. Fine-textured soils in humid tropical forests consume 1.5–2.0 kg ha^{-1} y^{-1}, while medium- and coarse-textured soils consume greater than 4.0 kg ha^{-1} y^{-1}.

The importance of soil texture, water content, and diffusivity observed in this study and as suggested by the summary in Table 7 provides support for the modeling approach of Potter and others (1996), which calculated CH_4 fluxes based on soil texture, a dynamic model of soil water content, and calculations of diffusivity and CH_4 concentration gradients. The results of this study, however, suggest that an additional important factor in the balance between CH_4 production and oxidation within the soil is rate of microbial and root respiration, which is related to plant phenology and site productivity.

Table 7. Tabulation of CH_4 Flux Measurements in Upland Humid Tropical Forests

Location	CH_4 Uptake (kg CH_4 ha^{-1} y^{-1})	Soil Type	Texture Class	Rainfall (mm y^{-1})	Author
Rondônia, Brazil	6.3	Ultisol	Coarse	2200	Steudler and others (1996)
La Selva, Costa Rica	5.8	Inceptisol	Medium	4000	Keller and others (1993)
Guacimo, Costa Rica	5.6	Inceptisol	Medium	4000	Keller and others (1993)
La Selva, Costa Rica	4.6	Inceptisol	Medium	4000	Keller and Reiners (1994)
Rio deJaneiro, Brazil	6.8	Inceptisol	Medium	2100	Dos Santos (1997)
Impfondo, Congo	7.0	Inceptisol	Not reported	1500	Tathy and others (1992)
Southwestern Congo	4.1	Inceptisol	Not reported	1500	Delmas and others (1992)
Barro Colorado, Panama	2.1	Oxisol	Fine	2600	Keller and others (1990)
Manaus, Brazil	1.4	Oxisol	Fine	2000	Keller and others (1986)
Paragominas, Brazil	1.9	Oxisol	Fine	1800	This study

ACKNOWLEDGMENTS

Partial support for this research was provided by NSF Atmospheric Chemistry Program under National Science Foundation grant ATM-9410759. Funding for L.V.V. was supplied in part by an appointment to the Global Change Distinguished Postdoctoral Fellowships sponsored by the US Department of Energy, Office of Health and Environmental Research and administered by the Oak Ridge Institute for Science and Education. Logistical support in Brazil was supplied by the Universidade Federal do Pará, the Empresa Brasileira de Pesquisa Agropecuária/ Centro de Pesquisa Agropecuária do Trópico Úmido, and the Instituto de Pesquisa Ambiental da Amazônia. We thank Fazenda Agua Parada for access to forest and pasture sites on their ranch. We also thank Edivan da Costa Oliveira, Ciro Campos da Sousa, João Batista Souza, and Denis Nascimento for their contributions in the field and in the laboratory.

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