BIOSPHERE-ATMOSPHERE EXCHANGE OF TRACE GASES IN THE TROPICS: EVALUATING THE EFFECTS OF LAND USE CHANGES

Michael Keller[1] and Pamela A. Matson[2]

[1]International Institute of Tropical Forestry
Rio Piedras, Puerto Rico
[2]NASA Ames Research Center
Moffett Field, California

ABSTRACT

Tropical soils and vegetation represent globally significant sources of a range of atmospheric gases, including CO_2, CO, N_2O, NO, CH_4, and volatile organic compounds. Conversion of tropical forests to agriculture and other uses, and intensification of agricultural practices in both forest and savanna areas are occurring very rapidly; yet the impacts of these land use practices on biogeochemical cycles, trace gas emissions, and atmospheric chemistry are not well understood. We present early results of IGAC's Biosphere-Atmosphere Trace Gas Exchange in the Tropics (BATGE) Activity that evaluate the importance of tropical land use change on fluxes of a number of gases.

Soils are important sources and sinks for trace gases, especially for oxides of nitrogen. On-going studies in Brazil, Costa Rica, Puerto Rico, and Mexico suggest that conversion of forest to pasture results in elevated soil emissions of nitrogen oxides in the first decade or less after clearing, but that older pastures, unless intensively managed, have lower fluxes than forests. Forest conversion to pasture also diminishes the soil sink strength for methane; in some cases the direction of the flux is reversed and pasture soils become methane sources. Likewise, results from a number of tropical regions suggest that agricultural sites recently converted from native vegetation have elevated fluxes of nitrogen and carbon gases, but that high emissions of nitrogen oxides and reduced uptake of methane in older agricultural systems are maintained only with intensive management and fertilizer use. Moreover, the magnitude of fluxes occurring in response to fertilization depends on soil type and management considerations such as crop type, fertilizer type, application rate, and application methods. The great spatial and temporal variability in trace gas responses to tropical agricultural practices complicates estimates of their importance at regional and global scales.

Few attempts have been made to study vegetation sources and sinks for trace gases in the tropics. It is clear that tropical vegetation can produce large quantities of volatile

Global Atmospheric-Biospheric Chemistry
Edited by R.G. Prinn, Plenum Press, New York, 1994

organic compounds. Forests may be strong sinks for oxidants and odd-nitrogen compounds. Changes in the species composition and structure of vegetation will almost certainly change these system properties; but our ability to predict the magnitude of these changes is severely hampered by a dearth of relevant data.

INTRODUCTION

Tropical terrestrial ecosystems cover approximately 42% of global land area. This region supports lush tropical rain forests with the highest levels of biological diversity on earth as well as a variety of other important terrestrial ecosystems with markedly different characteristics. Tropical forests and woodlands cover 25×10^6 km^2, 17% of earth's land surface, and account for over 40% of terrestrial net primary production (Rodin *et al.*, 1975). Tropical wetlands cover nearly 2×10^6 km^2, representing 36% of global wetlands (Matthews and Fung, 1987). Tropical savannas cover 19×10^6 km^2 (Bolin *et al.*, 1979).

Within these broad vegetation categories, there is great variation. Wet and humid tropical forests (rain forests) account for nearly 50% of all tropical forests and are among the most productive terrestrial systems with net primary production (NPP) in these systems of 13 to 28 Mg ha^{-1}yr^{-1}) (Murphy and Lugo, 1986). Seasonally dry tropical forests and woodlands receive far less attention than rain forests, but they once covered approximately 40% of the original forest area in the tropics. They are less productive systems (NPP ranging from 8 to 21 Mg ha^{-1}yr^{-1} (Murphy and Lugo, 1986) than are the humid forests, but they have been much more intensively cleared and managed (Janzen, 1988). These different tropical forest types are defined by the amount of precipitation, evapotranspiration, and the length of the dry season they experience. Within each climatic zone there are important variations in soil chemical and physical characteristics that lead to enormous differences in productivity and biogeochemical characteristics (Richter and Babbar, 1991; Vitousek and Sanford, 1986; Sanchez, 1981). Similarly, tropical wetlands and tropical savannas also differ in well-characterized ways as functions of climate and soils (Gore, 1983; Huntley and Walker, 1982). Such variations in climate and soil result in major variations in ecosystem biogeochemical cycling (Vitousek and Sanford, 1986). A growing number of studies suggest that these variations also affect the exchange of trace gases between terrestrial ecosystems and the atmosphere. Ecological variations have been used as the basis for regional and global extrapolations of trace gas fluxes (e.g., Matson and Vitousek, 1990; Sanhueza *et al.*, 1990; Bartlett *et al.*, 1988; Bartlett and Harriss, 1993).

In addition to the naturally occurring components of variation, land use changes resulting from human activity have become an increasingly important force in the tropics. Large areas of the humid tropics are being converted from forest to pasture, agriculture, or other land uses. The FAO estimates that an average of 1.7×10^5 km^2 of tropical closed and open forest were cleared annually from 1980 to 1990 (FAO, 1991). A greater proportion of the dry tropical forests has undergone conversion to human-dominated systems already (Janzen, 1988). Savanna ecosystems are widely managed for grazing (especially by regular burning) and are increasingly being converted to more intensive agricultural use. Given that the human population is likely to double by 2100 (with nearly all growth occurring in the developing world) and that a significant proportion of existing cropland is already subject to degradation due to erosion, salinization, and desertification in dryland areas (Crosson and Rosenberg, 1990), the demand for conversion of natural tropical systems to agricultural land will increase (Meyer and Turner, 1992). At the same time, intensification of tropical agriculture through the use of fertilizers, irrigation, herbicides, and other management practices is inevitable (Meyer and Turner, 1992; Naylor and Matson, 1993).

The effects of tropical land conversions on the biogeochemical cycling of carbon and in particular on carbon dioxide (CO_2) exchange between terrestrial ecosystems and the atmosphere have been the subject of intense analysis (e.g., Houghton *et al.*, 1987, 1991; Detwiler and Hall, 1988; Crutzen and Andreae, 1990). The effects of these conversions on cycling and emissions of other gases have received much less attention (Keller *et al.*, 1991). Likewise, the effects of tropical agricultural practices on trace gas fluxes have been largely unstudied (Vitousek and Matson, 1993), with the exception of rice agriculture, which has received considerable attention with respect to methane emissions (see Neue and Sass, this volume).

Because of the increasing importance of tropical land use change, including both conversion of natural to managed lands and intensification of managed land use, IGAC's Biosphere-Atmosphere Trace Gas Exchange in the Tropics (BATGE) Activity focuses on the exchanges of gases and the physical and biological factors that control them both in undisturbed ecosystems and in those undergoing change. The goals of BATGE are to:

- determine the fluxes of trace gases between tropical biomes and the atmosphere,
- determine the factors that control these fluxes,
- assess the effects of land use change on the exchange of trace gases, and
- develop the ability to predict the impact of both climate and land use changes on these fluxes.

The BATGE Activity excludes from its scope studies of wetland rice agriculture, carbon storage in tropical soils and vegetation and the direct effects of biomass burning. These problems are covered by the IGAC-RICE and BIBEX Activities and the IGBP-GCTE Core Project, but with appropriate communication with BATGE. In the following sections, we discuss the state of knowledge regarding tropical contributions to the budgets of the long-lived trace gases methane (CH_4) and nitrous oxide (N_2O) and the biological sources and sinks of short-lived trace gases such as nitric oxide (NO), ozone (O_3) and volatile organic carbon compounds (VOC). We present early data from several BATGE studies that address the importance of land use change in forested systems and describe a study illustrating the importance of 40 years of land use change in a tropical forest region.

LONG LIVED GASES

Methane

Natural tropical wetlands are a globally significant source of methane. In a recent review of methane emissions from natural wetlands, Bartlett and Harriss (1993) estimated that tropical wetlands (20°N to 30°S) emit 66 Tg yr^{-1} versus total releases from natural wetlands of 109 Tg yr^{-1} or the total source of 400 to 500 Tg yr^{-1} (1 Tg = 10^{12} g) (Cicerone and Oremland, 1988; Vaghjiani and Ravishankara, 1991; Fung *et al.*, 1991). Natural tropical wetland area is relatively limited, accounting for about 1.9×10^6 km^2 (Matthews and Fung, 1987). However, average methane fluxes from these areas are very high, 148 to 233 mg CH_4 m^{-2} d^{-1} (Bartlett and Harriss 1993). High fluxes of methane from sediments to the atmosphere are especially common in tropical areas. High temperatures and biological productivity promote the formation of methane bubbles in sediments. Bubbles may escape directly to the atmosphere bypassing oxidation at the sediment water interface (Keller and Stallard, 1993; Martens and Klump, 1980). Plants that inhabit permanently or seasonally inundated areas possess adaptations to bring oxygen to their roots. These structures and associated active and passive transport mechanisms also serve as efficient conduits for methane emissions to the atmosphere (Dacey, 1981; Chanton and Dacey, 1991).

Knowledge of methane emissions from tropical wetlands has been increasing rapidly through field studies in the basins of the worlds largest rivers, the Amazon and Congo (e.g., Bartlett *et al.*, 1988; Tathy *et al.*, 1992). Other important wetland habitats in the tropics have received little or no study. These include some of the world's most extensive wetlands such as the Pantanal of South America, the Okavango and Sudd of Africa and the peat-forming swamp-forests of Malaysia and Indonesia (Thompson and Hamilton, 1983; Breunig, 1990). The latter areas with an extent of 2×10^5 km^2 are under considerable pressure for timber extraction.

As with other tropical habitats, wetland areas are subject to pressure from development. Wetland areas are being created, destroyed and modified. In densely populated South Asia and South East Asia (mainly tropical) over 8×10^5 km^2 are planted to wetland rice. While much of this area may result from conversion of natural wetland habitats, over 35% is irrigated (Neue, 1992). The methane source from rice is discussed in an accompanying paper in this volume (Neue and Sass). Drainage of wetlands for agriculture or flooding of large areas due to hydroelectric projects and other water management schemes may provoke considerable changes in wetland areas and hence methane emissions. The trend towards increased hydroelectric development appears to be accelerating. For example, Brazil's hydroelectric capacity increased by 57% from 1980 to 1985 (Shea, 1988). In dams planned for areas of low relief such as the Amazon Basin, large areas may be flooded for small power returns. The Balbina dam alone floods over 1,500 km^2 even though it yields only 85 megawatts of power (Fearnside, 1989). Shallow waters of tropical reservoirs can emit large amounts of methane. In Gatun Lake, Panama, the reservoir that forms the Panama Canal, methane emissions from shallow waters (<6 m) average 195 to 1302 mg CH_4 m^{-2} d^{-1} (Keller and Stallard, 1993). Average emissions from deeper waters are an order of magnitude lower. An estimate of the current and future methane sources from tropical reservoirs requires information regarding their hypsography.

There is little information regarding the effects of human disturbance and water management from tropical wetlands. Some examples from the temperate and sub-tropical areas point to important considerations for future studies. Wetland methane emissions can correlate with primary productivity as demonstrated for South Florida marshlands by Whiting *et al.* (1991). The productivity effect on methane emissions may explain why methane emissions from flooded forests in the South East U.S. increase at sites receiving sewage effluents (Harriss and Sebacher, 1981). The effects of water management may be complex. Harriss *et al.* (1989) evaluated the effect of drainage and agricultural and urban development for the Everglades wetland area of South Florida. Surprisingly, they found that although large areas of the wetland were drained, overall annual methane emissions for the region increased. A major cause for this increase was the creation of high biological productivity water impoundments that remained flooded permanently.

Well-drained soils typically consume methane. In most upland environments, methane consumption is limited by rates of diffusion of atmospheric methane into the soil. The best global estimate for soil methane consumption based on diffusivities for soils classified in a digitized global soil database is 29 Tg CH_4 yr^{-1}, about 7% of the current estimates of the annual methane source (Dörr *et al.*, 1993). Methane uptake, about 1 mg CH_4 m^{-2} d^{-1}, has been found in a range of tropical forest and savanna habitats (e.g., Seiler *et al.*, 1984; Keller *et al.*, 1986; Delmas *et al.*, 1992). A number of measurements of dry soils from Venezuelan savanna sites have shown small methane emissions (Hao *et al.*, 1988) The source of these emissions remains mysterious.

The conversion of natural soils to agricultural use generally results in a diminished capacity of these soils to consume methane (Mosier *et al.*, 1991). The conversion of tropical forest to pasture and agriculture in Panama resulted in a 3-fold decrease in soil methane consumption (Keller *et al.*, 1990). In pastures, soil compaction impedes drainage.

Wetter soils have lower gas diffusivities and hence lower methane uptake. Unpublished studies in Costa Rica (Keller, private communication) show that conversion of forest to pasture may even reverse the direction of methane flux, i.e. a small sink becomes a small source. Fertilization also diminishes methane consumption in temperature environments (Steudler *et al.*, 1989; Mosier *et al.*, 1991). The mechanism for this inhibition has not been unambiguously identified for any site nor has this fertilization effect been observed at tropical field sites.

Nitrous Oxide

Early budgets for nitrous oxide (McElroy and Wofsy, 1986; Keller *et al.*, 1986) concluded that tropical forest soils (as they were prior to human disturbance) are the single most important source of nitrous oxide to the atmosphere. Since then, many more flux measurements (e.g., Goreau and de Mello, 1988; Matson and Vitousek, 1987; Keller *et al.*, 1988; Matson *et al.*, 1990) and alternative regional budgets (e.g., Matson and Vitousek, 1990; Sanhueza *et al.*, 1990) have generally supported the early conclusions, although in later budgets the magnitude of the tropical forest source has been reduced. The importance of the undisturbed tropical forest source for nitrous oxide can be explained in the context of nitrogen biogeochemistry. In most lowland tropical forests, rates of nitrogen transformations in the soil and cycling through the vegetation are much greater than in most temperate or boreal forests (Vitousek and Sanford, 1986; Vitousek and Matson, 1988). Nitrogen functions as an excess nutrient, and losses via gas flux appear to be quantitatively and proportionally larger than in higher latitude forests.

We have found that while tropical forests as a whole may be the most important source of nitrous oxide, fluxes vary significantly among tropical forest types. Matson and Vitousek (1987) and Matson *et al.* (1990) reported a strong positive relationship between soil nitrogen cycling rates and nitrous oxide fluxes across a range of tropical soil types; they used the areal extent and distribution of those soil types to develop a tropical budget for nitrous oxide (Matson and Vitousek, 1990). Seasonally dry tropical forests have significantly lower annual fluxes than humid forests (Garcia-Mendez *et al.*, 1991; Matson and Vitousek, 1993), and exhibit variation within the climatic type as well (Vitousek *et al.*, 1989).

The early McElroy and Wofsy (1986) budget was essentially a balanced budget; in it, N_2O from fossil fuel combustion accounted for the annual atmospheric increment of 3.5 Tg. It is now clear that combustion accounts for less than 10% of the annual increase in tropospheric nitrous oxide (Watson *et al.*, 1990). A number of other possible sources for the increase have been identified, including biomass burning, degassing of irrigation water, agricultural activity, emissions from natural systems receiving large inputs of anthropogenic nitrogen deposition, and specialized industrial processes (cf., Vitousek and Matson, 1993). Even assuming the upper limits on the ranges of each of these sources, it is difficult to account for the global sink and accumulation (Watson, 1990). There are a number of reasons why tropical land use change and intensification of tropical agriculture may be significant contributors to the missing source.

While most soils lose carbon and nitrogen after conversion from natural vegetation to agriculture, loss rates in tropical soils are particularly rapid. Matson *et al.* (1987) estimated that 20 to 25 Tg of nitrogen are lost annually by tropical land-clearing, not including the amount lost in biomass burning. There are relatively few studies on the pathways by which this nitrogen is lost, but some have reported increased nitrous oxide emissions following disturbance (Keller *et al.*, 1986; Matson *et al.*, 1990). Luizão *et al.* (1989) reported elevated nitrous oxide fluxes from tropical pastures ranging in age from 3 to 10 years following forest clearance and estimated a 3-fold greater annual flux from pastures than forests. Assuming that all tropical pastures of all ages had similar increases over forest fluxes, Matson and Vitousek (1990) estimated that tropical forest conversion could account for one-fourth to one-half of the annual global increase in N_2O.

In a more recent study of forest lands converted to pasture in Costa Rica, Keller *et al.* (1993) found that young pastures (under 10 years old) had significantly elevated fluxes over forests, but that fluxes in older pastures were lower than those in forests. Luizão *et al.* and Keller *et al.*'s studies were both done in humid tropical areas on relatively fertile soils. Garcia-Mendez *et al.* (1991) measured N_2O fluxes in pastures converted from seasonally dry tropical forest, and found that upland pastures did not have elevated fluxes. More research spanning the range of climate and soils in the tropics will be necessary to accurately estimate the global importance of forest conversion to pasture.

The effects of agricultural practices (especially nitrogen fertilization) on nitrous oxide emissions has received considerable attention, but only in the temperate zone (Eichner, 1991). The concentration of studies in the temperate zone is not surprising, considering that less than 20 years ago nearly all fertilizer N was applied in temperate zone agriculture. Now, however, nearly half of the approximately 80 Tg N applied each year is used in the developing world, including most of the tropics. This trend of increasing use in the developing world and stable use in the developed world is projected to continue (FAO, 1985; EPA, 1990). As Vitousek and Matson (1993) point out, even the current amount of fertilizer N nearly doubles the amount added to terrestrial ecosystems via natural processes. Such an alteration of the global budget of nitrogen is likely to affect all the fluxes of the nitrogen cycle, including fluxes out of terrestrial systems to the atmosphere.

Current estimates based on temperate zone data suggest that direct losses of N_2O related to fertilization may account for 0.5 to 1.0 Tg N_2O–N yr^{-1}. If tropical agricultural systems function as tropical forests do, then a greater proportion of the total quantity of N cycled between soil and plants (and applied in fertilizer) is likely to be emitted as N_2O in tropical systems than is measured in temperate systems (Vitousek and Matson, 1993). There have been very few studies of nitrogen gas flux from tropical agricultural systems. Garcia-Mendez *et al.* (1991) measured N_2O fluxes from maize and sorghum and from a managed pasture; they found fluxes elevated over forest both in maize (in the first season after forest clearing) and in fertilized pastures, but lower fluxes in sorghum that had not received fertilizer or organic matter inputs for many years. Matson (private communication) measured large pulses of nitrous oxide immediately after fertilization events in tropical sugar cane systems; the proportion of the fertilizer N lost as N_2O was very small (<1%) in fields using sub-surface irrigation/fertilization, but much higher in fields receiving broadcast applications of nitrogen. Keller (private communication) measured N_2O losses of as great as 20% of the applied N in palm plantations in Costa Rica where ammonium nitrate fertilizer was broadcast. However, N_2O losses varied greatly among fields. It appears that management practices (and not just quantity or type of N applied) are critical to the control of nitrous oxide flux. Clearly, there is need for more research on trace gas fluxes in tropical agriculture before conclusions can be drawn concerning the importance of the tropical agricultural systems as sources of N_2O.

REACTIVE GASES

Nitric oxide

Nitric oxide (NO) is a short-lived, reactive gas; thus, its global budget is not well constrained by atmospheric measurements, in contrast to the budgets for nitrous oxide, methane or carbon dioxide. Moreover, estimates of NO flux at the soil-air interface do not necessarily equate to inputs to the atmosphere because NO can react and be deposited in plant canopies. Internal deposition within the forest was the fate of about 80% of the soil NO emission observed in forests during the wet season in forest near Manaus, Brazil (Bakwin *et al.*, 1990a, b). Despite the uncertainties in the global budget of NO, it does appear that undisturbed tropical forests and savannas are stronger sources than are temperate systems (Johansson *et al.*, 1988; Johansson and Sanhueza, 1988; Kaplan *et al.*, 1988; Sanhueza *et al.*, 1990; Williams *et al.*, 1992; Müller, 1992).

In temperate systems, NO flux is positively correlated with inorganic nitrogen concentrations in the soil (Williams and Fehsenfeld, 1991), and agricultural systems tend to have higher fluxes than do undisturbed ecosystems (Williams *et al.*, 1992). Data on flux of NO from managed tropical soils, whether in pasture or agriculture, are extremely limited. Davidson *et al.* (1991) reported elevated NO fluxes from a fertilized pasture and maize field in Mexico where Garcia-Mendez *et al.* (1991) also found elevated N_2O fluxes. Likewise, Matson (private communication) found concomitant increases in NO and N_2O after fertilization of sugar cane fields, although the proportional increase in NO was less than that of N_2O. Because the plant canopy is at times absent or limited in agricultural systems, it is likely that a larger fraction of emitted NO reaches the atmosphere in agricultural systems than in forests. Thus, it is probable that the increase of nitrogen fertilization in the tropics will increase nitric oxide fluxes. Likewise, the biomass burning associated with tropical land clearing represents a very significant source of NO, and represents one of the important ways tropical land use change effects a whole range of reactive gases (Crutzen and Andreae, 1990; Lobert *et al.*, 1990).

Vegetation Emissions of Reactive Gases

Terrestrial vegetation emits more volatile organic carbon compounds (VOC) to the atmosphere than industrial processes (Müller, 1992). These compounds are important to regulating atmospheric oxidants at global and regional levels, balancing the global carbon cycle, and producing organic acids that contribute to acidic deposition in remote areas (Fehsenfeld *et al.*, 1992). Isoprene and the monoterpene compounds have been investigated most extensively and a variety of emission algorithms have been developed to relate fluxes to environmental conditions, the most critical being light intensity and temperature (Guenther *et al.*, 1991). Both temperature and light intensity are higher in the tropics versus the temperate and boreal zones. Accordingly, tropical emissions probably account for more than half of global emissions of isoprene (Rasmussen and Khalil, 1988). Oxygenated hydrocarbons are also found in abundance in rural air; their sources, which may be biogenic, are poorly understood (Fehsenfeld *et al.*, 1992).

Investigation of the vegetation emissions of VOC to the atmosphere in the tropics is exceedingly limited. Data collected as part of the Brazilian-American Amazon Boundary Layer Expedition (ABLE-2A) in forest outside Manaus, Brazil may be the only measurements of VOC emissions that permit area flux estimation. Based on data collected at the ABLE experimental sites, isoprene emissions are estimated in the range of 25 to 38 mg m^{-2} d^{-1} and monoterpenes at about 6 mg m^{-2} d^{-1} (Zimmerman *et al.*, 1988; Jacob and Wofsy, 1988). We do not know of published estimates for vegetation VOC emissions from tropical dry forests or tropical savannas.

We cannot estimate the effects of land use change in the tropics on vegetation emissions of VOC. Replacement of natural vegetation with pastures and crops certainly leads to lower leaf areas. Taken alone, the reduction of leaf area would lead to lower fluxes were VOC emissions independent of species. However, VOC emissions are highly species dependent and may vary within species depending upon growing conditions such as nutrient availability or herbivory by insects (Lerdau, 1991).

Vegetation also emits carbon monoxide through light dependent and light-independent pathways (Lüttge and Fischer, 1980; Siegel and Siegel, 1987). The importance of this emission from tropical vegetation is unknown. Measurements of boundary layer CO concentrations in tropical forest as part of ABLE-2B indicate the presence of a strong source, 4×10^{11} molecules cm^{-2} s^{-1}, for this gas (Kirchhoff and Marinho, 1990). This CO source cannot be explained by hydrocarbon oxidation in the model of Jacob and Wofsy (1990). The effects of land use change on the vegetation source of CO is unknown.

Deposition of Reactive Gases

Although there are few measurements, it appears that tropical forests may be strong sinks for ozone. A summary of measurements of canopy-level ozone deposition for tropical forests is given in Table 1. The measured deposition velocities are at the high end of the range of deposition velocities measured for O_3 over vegetation surfaces (Finlayson-Pitts and Pitts, 1986). Given the expression for deposition velocity recommended by Baldocchi *et al.* (1987),

$$V_d = 1/(r_a + r_b + r_c) \tag{1}$$

we recognize three "resistances" to trace gas deposition: the aerodynamic resistance (r_a), the boundary layer resistance (r_b), and the net-canopy resistance (r_c). Two of these terms, r_a and r_c, are likely to change both from day to night and from wet season to dry season. Fan *et al.* (1990) showed that changes in stomatal resistance (part of the term r_c) could explain the day to night differences in O_3 deposition observed at the Ducke tower site outside of Manaus Brazil. In comparison to the wet season results, dry season nighttime O_3 deposition velocities measured at a nearby site by Kaplan *et al.* (1988) are quite large. Andreae *et al.* (1992) found a similar deposition velocity for nighttime measurements over forest in the Congo Basin. These results cannot be explained by changes in stomatal resistance; stomata close at night increasing stomatal resistance. Greater nighttime deposition velocities for O_3 in the dry season probably results a from smaller aerodynamic resistance (r_a), a function of wind speed, atmospheric stability, and surface roughness.

Deforestation would change the resistance to O_3 deposition through changes to r_a and r_c. Leaf area would decrease as a result of deforestation leading to a greater canopy resistance term. Using the boundary-layer model of Jacob and Wofsy (1990), Fan *et al.* (1990) calculated that halving the leaf area index leads to a 16% decrease in O_3 flux to the canopy. Changes in aerodynamic resistance had a proportionally greater effect. Doubling r_a resulted in a 30% decrease in O_3 flux while halving r_a caused a 40% increase in O_3 flux. The effect of deforestation on r_a is an open question.

Table 1. A summary of mean values for canopy level ozone deposition velocities (V_d) and fluxes (F) at a given reference height (z_r) at tropical forest sites.

Location	Time (Day/Night)	Season (Wet/Dry)	V_d $cm\ s^{-1}$	z_r m	F molec. $cm^{-2}\ s^{-1}$	Source
Brazil	Night	Dry	1.8	6	5.6×10^{11}	Kaplan *et al.* (1988)
Brazil	Day	Wet	1.8	39	2.3×10^{11}	Fan *et al.* (1990)
Brazil	Night	Wet	0.3	39	2.2×10^{10}	Fan *et al.* (1990)
Congo	Night	Dry	1.2	n.s.	1.5×10^{11}	Andreae *et al.* (1992)

n.s. = Reference height is not specified.

One study indicates that tropical forests may also be a strong sink for reactive nitrogen compounds. Bakwin *et al.* (1990b) observed that the forest outside of Manaus, Brazil was a net sink for NO_y (8×10^9 molecules $cm^{-2}\ s^{-1}$). Deposition was greater during the daytime than at night. It is unclear whether stomatal or aerodynamic resistance has the greater effect on this diel pattern.

TROPICAL LAND USE CHANGE AT A REGIONAL SCALE: A CASE STUDY

For long-lived trace gases such as methane and nitrous oxide, soil-atmosphere fluxes are often not sufficiently large to cause measurable perturbations in local and regional atmospheric concentrations. Therefore it is difficult to make areal or regional estimates for fluxes of these gases without resorting to some extrapolation scheme (Stewart *et al.*, 1989). Generally, small scale chamber measurements (<1 m^2) are used to quantify soil-atmosphere flux (Mosier, 1989). The simplest approach may be to sample an area randomly and to estimate the areal flux based upon the random sample. Because trace gas fluxes can be highly variable in space and time, a large numbers of samples may be required to achieve an estimate with an acceptable level of error (Folorunso and Rolston, 1984). A modification of this approach requires stratifying the study area according to parameters that control trace gas fluxes (Matson *et al.*, 1989). The resulting sub-units may then be sampled randomly and greatest effort may be placed in sub-units of greatest flux or greatest variability in order to reduce the absolute error of the areal flux estimate. Areal flux (F) is then estimated as

$$F = \sum A_i f_i \qquad (2)$$

where A_i represent the areas of sub-units and f_i are the flux estimates for those areas. Land cover may be an appropriate criterion for choosing areal sub-units since controlling variables such as soil moisture or soil fertility will be associated with a land cover class. Remote sensing provides a technique for classifying land cover (Matson *et al.*, 1990).

We apply the approach described above to the Sarapiqui Canton of Costa Rica, a rain forest area subject to rapid development. We use data from the Costa Rican agricultural census (Censo Agropecuario, 1983) for classification of the Sarapiqui Canton according to land use. Available data span three decades, from 1963 through 1983. Sarapiqui was almost entirely forested prior to colonization in the 1950s (Hall, 1984). We have extrapolated land use trends to the present decade. The agricultural census divides land use according to three categories: forest, pasture, and crops. We sub-divided the pasture category into young and old pastures. Young pastures are those that have been converted from forest use less than 10 years prior to a given date. Old pastures were converted more than 10 years ago. To simplify our analysis further, we assume that the use of land passes from forest directly to pasture and that old pastures are converted to crop land (Figure 1). Except in limited cases such as the banana expansion of the 1960s (cf., Veldkamp *et al.*, 1992), capital requirements limited the pace of agricultural development. In the Sarapiqui Canton, as in other parts of Latin America, cattle raising is a preferred economic activity as a result of a complex of factors including cultural heritage, government incentives, land tenure requirements, and low capital and labor requirements (Hecht, 1992). Land use distributions for five decades based upon census data and our assumptions are presented in Table 2.

Fluxes for given land uses were determined using chamber techniques. For forest and pasture we conducted monthly surveys of flux over at least one year at four forest sites and 10 pastures covering a range of ages from 2 to 35 years. All sites were on similar inceptisols, which cover most of the Sarapiqui Canton. Details of sampling and analysis are described by Keller *et al.* (1993). We use unpublished data based on 8 crop sites (bananas, palms, manioc) on inceptisols and andisols to estimate flux from the crop category. These sites are heavily fertilized; these crops generally receive more than 200 kg-N annually in the form of ammonium nitrate and urea. Farmers apply fertilizer 4 to 6 times per year. Average annual fluxes for methane and nitrous oxide according to land use type are compiled in Table 3.

Figure 2 presents the results of this flux × area extrapolation. In the first decade of colonization, nitrous oxide emissions for the Canton jump to 3 times forest levels. By 1993, emissions of nitrous oxide are still double pre-development levels owing to the substantial areas of crops and a small area of new pastures. In the case of nitrous oxide, fluxes from young pastures dominate the balance. For methane, a weak soil sink is converted to a nearly negligible level as pasture areas become predominant.

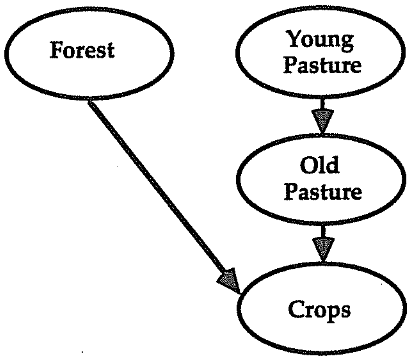

Figure 1. The pattern of land use change observed in the Sarapiqui Canton of Costa Rica from 1953 to 1993.

Table 2. Land use in Sarapiqui Canton of Costa Rica from 1953 to 1993. Percentage of area is shown for each land use category.

Year	Forest	Young Pasture	Old Pasture	Crops
1953	100	0	0	0
1963	70	24	0	6
1973	50	20	22	8
1983	32	18	38	12
1993	24	8	52	16

Table 3. Estimates of methane and nitrous oxide fluxes from soil to the atmosphere from four land use categories in Sarapiqui Canton of Costa Rica. Positive fluxes indicate net transfer of a gas from the soil to the atmosphere (emission from soil). Negative fluxes indicate net transfer of a gas from the atmosphere to the soil (consumption by soil).

Land use	CH_4 Flux (mg m^{-2} d^{-1})	N_2O Flux (ng-N m^{-2} h^{-1})
Forest	−1.22	6.78
Young Pasture	+0.65	48.95
Old Pasture	+0.65	2.20
Crops	−1.22	29.00

This preliminary analysis of land use change is necessarily simplistic. A more comprehensive analysis would use process-based models to estimate fluxes from a database of soil and management characteristics. Soil-atmosphere exchange of methane and nitrous oxide also represents a simple case because these long-lived gases are not lost rapidly by atmospheric reaction or uptake on vegetation surfaces. However, even from this preliminary regional analysis we learn that we must take a dynamic view of the role of land use change in atmospheric processes. In the near-term, and even in the long-term, tropical land use change will contribute significantly to changing the composition of the atmosphere.

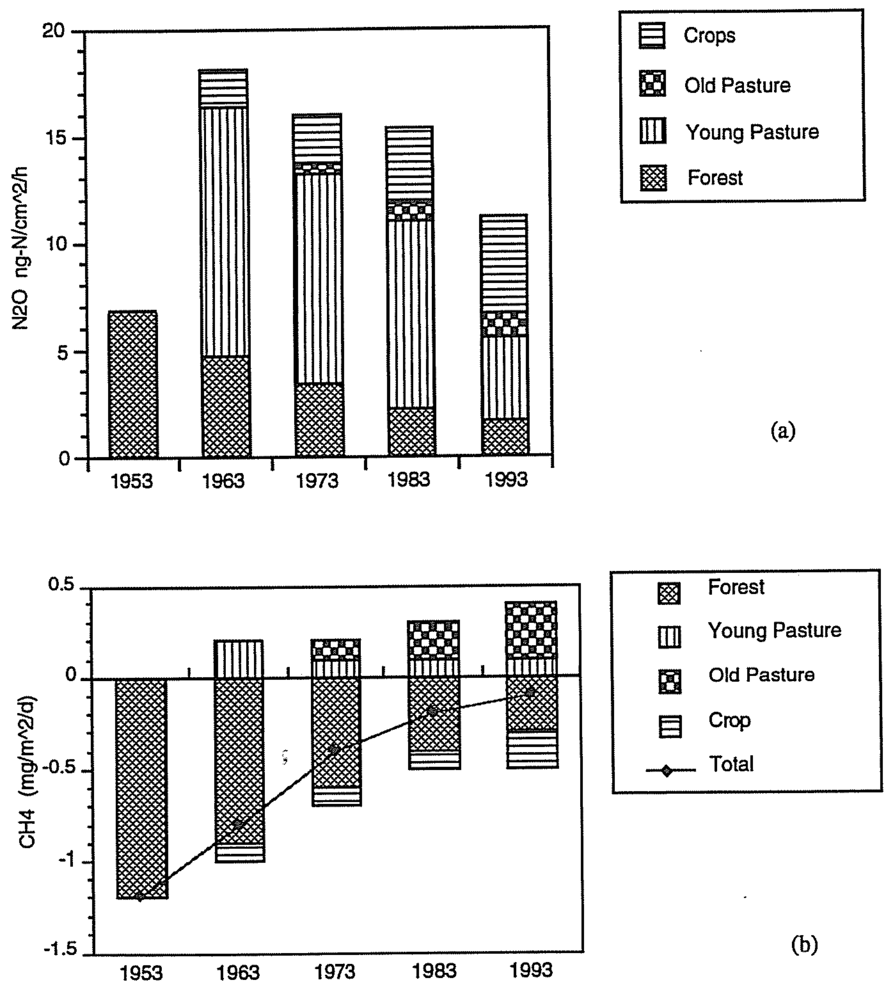

Figure 2. Fluxes of **(a, upper panel)** N_2O (ng–N cm^{-2} h^{-1}) and **(b, lower panel)** CH_4 (mg m^{-2} d^{-1}) for the Sarapiqui Canton of Costa Rica from 1953 through 1993. Net transfers of a gas from soil to the atmosphere are indicated as positive fluxes. Net transfers of a gas from the atmosphere to the soil are indicated as negative fluxes.

REFERENCES

Andreae, M.O., A. Chapuis, B. Cros, J. Fontan, G. Helas, C. Justice, Y.J. Kaufman, A. Minga, and D. Nganga, 1992, Ozone and aitken nuclei over equatorial Africa: Airborne observations during DECAFE 88, *J. Geophys. Res.*, 97:6137-6148.

Bakwin, P.S., S.C. Wofsy, S.-M. Fan, M. Keller, S.E. Trumbore and J.M. da Costa, 1990a, Emission of nitric oxide from tropical forest soils and exchange of NO between the forest canopy and atmospheric boundary layers, *J. Geophys. Res.*, 95:16,755-16,764.

Bakwin, P.S., S.C. Wofsy and S.-M. Fan, 1990b, Measurements of reactive nitrogen oxides (NO_y) within and above a tropical forest canopy in the wet season, *J. Geophys. Res.*, 95:16,765-16,772.

Baldocchi, D.D., B.B. Hicks, and P. Camara, 1987, A canopy stomatal resistance model for gaseous depostion to vegetated surfaces, *Atmos. Environ.*, 22:869-884.

Bartlett, K.B., P.M. Crill, D.I. Sebacher, R.C. Harriss, J.O. Wilson, and J.M. Melack, 1988, Methane flux from the Central Amazonian floodplain, *J. Geophys. Res.*, 93:1571-1581.

Bartlett, K.B. and R.C. Harriss, 1993, Review and assessment of methane emissions from wetlands, *Chemosphere*, 26:261-320.

Bolin, B., E.T. Degens, P. Duvignaud, and S. Kempe, 1979, *in* "The Global Carbon Cycle," B. Bolin, E.T. Degens, S. Kempe, and S. Kertner (eds.),Wiley, Chichester.

Bruenig, E.F., 1990, Oligotrphic forested wetlands in Borneo, *in:* "Ecosystems of the World 15: Forested Wetlands," A.E. Lugo, M. Brinson, and S. Brown (eds.), Elsevier, Amsterdam.

Censo Agropecuario, 1983.

Chanton, J.P. and J.W. Dacey, 1991, Effects of vegetation on methane flux, reservoirs, and carbon isotopic composition, *in:* "Environmental and Metabolic Controls on Trace Gas Emissions from Plants," T. Sharkey, E. Holland, and H. Mooney (eds.), Academic Press, New York.

Cicerone, R. and R. Oremland, 1988, Biogeochemical aspects of atmospheric methane, *Global Biogeochem. Cycles*, 2:299-327.

Crosson, P.R. and N.J. Rosenberg, 1990, Strategies for Agriculture, *in:* "Managing Planet Earth. Readings from Scientific American Magazine," Freeman and Co., New York.

Crutzen, P.J. and M.O. Andreae, 1990, Biomass burning in the tropics: Impact on atmospheric chemistry and biogeochemical cycles, *Science*, 250:1669-1678.

Dacey, J.W., 1981, Pressurized ventilation in the yellow waterlilly, *Ecology*, 62:1137-1147.

Davidson, E.A., P.M. Vitousek, P.A. Matson, R. Riley, G. Garcia-Mendez and J.M. Maass, 1991, Soil emissions of nitric oxide in a seasonally dry tropical forest of Mexico, *J. Geophys. Res.*, 96:15,439-15,445.

Delmas, R.A., J. Servant, J.P. Tathy, B. Cros, and M. Labat, 1992, Sources and sinks of methane and carbon dioxide exchanges in the mountain forest in Equatorial Africa, *J. Geophys. Res.*, 97:6169-6179.

Detwiler, R.P. and C.A.S. Hall, 1988, Tropical forests and the global carbon cycle, *Science*, 239:42-47.

Dörr, H., L. Katruff, and I. Levin, 1993, Soil texture parameterization of the methane uptake in aerated soils, *Chemosphere*, 26:697-713.

EPA, 1990, "Greenhouse gas emissions from agricultural ecosystems," United States Environmental Protection Agency Report, Washington, D.C.

Eichner, M.J., 1990, Nitrous oxide emissions from fertilized soils: Summary of the available data, *J. Env. Qual.*, 19:272-280.

FAO, 1985, "FAO Fertilizer Yearbook," United Nations Food and Agriculture Organization, Rome.

FAO, 1991, "Forest Resources Assessment 1990 Project," Forestry N.7, United Nations Food and Agriculture Organization, Rome.

Fan, S.M., S.C. Wofsy, P.S. Bakwin, D.J. Jacob, and D.R. Fitzjarrald, 1990, Atmosphere-biosphere exchange of CO_2 and O_3 in the Central Amazon forest, *J. Geophys. Res.*, 95:16,851-16,864.

Fearnside, P.M., 1989, Brazil's Balbina Dam: Environment versus the legacy of the pharoahs in Amazonia, *Environm. Mgt.*, 13:401-423.

Fehsenfeld, F. and 10 others, 1992, Emissions of volatile organic compounds from vegetation and the implications for atmospheric chemistry, *Global Biogeochem. Cycles*, 6:351-388.

Finlayson-Pitts, B.J. and J.N. Pitts, 1986, "Atmospheric Chemistry: Fundamentals and Experimental Techniques," John Wiley and Sons, New York.

Folorunso, O.A. and D.E. Rolston, 1984, Spatial variablity of field-measured denitrification gas fluxes, *Soil Sci. Soc. Am. J.*, 48:1214-1219.

Fung, I., J. John, J. Lerner, E. Matthews, M. Prather, L.P. Steele, and P.J. Fraser, 1991, Three-dimensional model synthesis of the global methane cycle, *J. Geophys. Res.*, 96:13,033-13,065.

Garcia-Mendez, G., J.M. Maass, P.A. Matson and P.M. Vitousek, 1991, Nitrogen transformations and nitrous oxide flux in a tropical deciduous forest in Mexico, *Oecologia*, 88:362-366.

Gore, A.J.P. (ed.), 1983, "Mires: Swamp, Bog, Fen, and Moo," Elsevier, Amsterdam.

Goreau, T.J. and W.Z. de Mello, 1988, Tropical deforestation: Some effect on atmospheric chemistry, *Ambio*, 17:275-281.

Guenther, A.B., R.K. Monson, and R. Fall, 1991, Isoprene and monoterpene emission rate variability: Observations with eucalyptus and emission rate algorithm development, *J. Geophys. Res.*, 96:10,799-10,808.

Hao, W.M., D. Scharffe, and P.J. Crutzen, 1988, Production of N_2O, CH_4, and CO_2 from soils in the tropical savanna during the dry season, *J. Atm. Chem.*, 7:93-105.

Harriss, R.C. and D.I. Sebacher, 1981, Methane flux in forested swamps of the southeastern United States, *Geophys. Res. Lett.*, 8:1002-1004.

Harriss, R.C., D.I. Sebacher, K.B. Bartlett, D.S. Bartlett, and P.M. Crill, 1989, Sources of atmospheric methane in the South Florida environment, *Global Biogeochem. Cycles*, 2:231-243.

Hecht, S.B., 1992, Logics of livestock and deforestation: The case of Amazonia, *in:* "Development or Destruction: The Conversion of Tropical Forest to Pasture in Latin America," T.E. Downing, S.B. Hecht, H.A. Pearson, and Carmen Garcia-Downing, (eds.), Westview Press, Boulder, Colorado.

Houghton, R.A., R.D. Boone, J.R. Fruci, J.E. Hobbie, J.M. Melillo, C.A. Palm, B.J. Peterson, G.R. Shaver, G.M. Woodwell, B. Moore, D. Skole and N. Meyers, 1987, The flux of carbon from terrestrial ecosystems to the atmosphere in 1980 due to changes in land use: geographic distribution of the global flux, *Tellus*, 39B:122-139.

Houghton, R.A., D.L. Sklole and D.S. Lefkowitz, 1991, Changes in the landscape of Latin America between 1950 and 1985. II. Net release of CO_2 to the atmosphere, *Forest Ecol. and Mgt.*, 38:173-199.

Janzen, D.H., 1988, Tropical dry forests: The most endangered major tropical ecosystem, *in:* "Biodiversity," E.O. Wilson (ed.), National Academy Press, Washington, D.C.

Jacob, D.J. and S.C. Wofsy, 1988, Photochemistry of biogenic emissions over the Amzon forest, *J. Geophys. Res.*, 93:1477-1486.

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.

Johansson, C., H. Rodhe and E. Sanhueza, 1988, Emission of NO in a tropical savanna and cloud forest during the dry season, *J. Geophys. Res.*, 93:7180-7192.

Johansson, C. and E. Sanhueza, 1988, Emission of NO from savanna soils during the rainy season, *J. Geophys. Res.*, 93:14,193-14,198.

Kaplan, W.A., S.C. Wofsy, M. Keller, and J.M. da Costa, 1988, Emission of NO and depostion of O_3 in a tropical forest system, *J. Geophys. Res.*, 93:1389-1395.

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., W. Kaplan, S.C. Wofsy and J.M. da Costa, 1988, Emissions of N_2O from tropical forest soils: Response to fertilization with NH_4^+, NO_3^- and PO_4^{-3}, *J. Geophys. Res.*, 93:1600-1604.

Keller, M. and R.F. Stallard, 1993, Methane emission by bubbling from Gatun Lake, Panama, *J. Geophys. Res.*, in press.

Keller, M. D.J. Jacob, S.C. Wofsy and R.C. Harriss, 1991, Effects of tropical deforestation on global and regional atmospheric chemistry, *Climatic Change*, 19:139-158.

Keller, M., E. Veldkamp, A.M. Weitz, and W.A. Reiners, 1993, Pasture age effects on soil-atmosphere trace gas exchange in a deforested area of Costa Rica, submitted.

Kirchhoff, V.W.J.H. and E.V.A. Marinho, 1990, Surface carbon monoxide measurements in Amazonia, *J. Geophys. Res.*, 95:16,933-16,943.

Lerdau, M., 1991, Plant function and biogenic terpene emissions, *in:* "Environmental and Metabolic Controls on Trace Gas Emissions from Plants," T. Sharkey, E. Holland, and H. Mooney (eds.), Academic Press, New York.

Lobert, J.M., D.H. Scharffe, W.M. Hao and P.J. Crutzen, 1990, Importance of biomass burning in the atmospheric budget of nitrogen-containing trace gases, *Nature*, 346:552-554.

Luizão, F., P. Matson, G. Livingston, R. Luizão and P.M. Vitousek, 1989, Nitrous oxide flux following tropical land clearing, *Global Biogeochem. Cycles*, 3:281-285.

Lüttge, U. and K. Fischer, 1980, Light-dependent net CO-evolution by C_3 and C_4 plants, *Planta*, 149:59-63.

Martens, C.S. and J.V. Klump, 1980, Biogeochemical cycling in an organic-rich coastal marine basin. 1. Methane sediment-water exchange processes, *Geochim. et Cosmoch. Acta*, 44:471-490.

Matson, P.A. and P.M. Vitousek, 1987, Cross-system comparisons of soil nitrogen transformations and nitrous oxide flux in tropical forest ecosystems, *Global Biogoechem. Cycles*, 1:163-170.

Matson, P.A., P.M. Vitousek, J.J. Ewel, M.J. Mazzarino and G.P. Robertson, 1987, Nitrogen transformations following tropical forest felling and burning on a volcanic soil, *Ecology*, 68:491-502.

Matson, P.A., P.M. Vitousek, and D.S. Schimel, 1989, Regional extrapolation of trace gas flux based on soils and ecosystems, *in:* "Exchange of Trace Gases Between Terrestrial Ecosystems and the Atmosphere," M.O Andreae and D.S. Schimel (eds.), John Wiley and Sons, New York.

Matson, P.A., P.M. Vitousek, G.P. Livingston, and N.A. Swanberg, 1990, Sources of variation in nitrous oxide flux from Amazonian ecosystems, *J. Geophys. Res.*, 95:16,789-16,798.

Matson, P.A. and P.M. Vitousek, 1990, Ecosystem approach to a global nitrous oxide budget, *Bioscience*, 40(9):667-672.

Matson, P.A. and P.M. Vitousek, 1993, Biosphere-atmosphere interactions in a tropical deciduous forest ecosystem, *in:* "The Tropical Deciduous Forest Ecosystem," H.A. Mooney, E. Medina and S.H. Bullock (eds.), Springer-Verlag, New York, in press.

Matthews, E. and I. Fung, 1987, Methane emissions from natural wetlands: Global distribution, area, and environmental characteristics of sources, *Global Biogeocheem. Cycles*, 1:61-86.

McElroy, M.B. and S.C. Wofsy, 1986, Tropical forests: Interaction with the atmosphere, *in:* "Tropical Rain Forests and the World Atmosphere," G.T. Prance (ed.), Westview Press, Boulder, Colorado.

Meyer, W.B. and B.L. Turner, II., 1992, Human population growth and global land use/cover change, *Annual Rev. of Ecol. and Systemat.*, 23:39-61.

Mosier, A., 1989, Chamber and isotope techniques, *in:* "Exchange of Trace Gases between Terrestrial Ecosystems and the Atmosphere," M.O Andreae and D.S. Schimel (eds.), John Wiley and Sons, New York.

Mosier, A., D. Schimel, D. Valentine, K. Bronson, and W. Parton, 1991, Methane and nitrous oxide fluxes in native, fertilized, and cultivated grasslands, *Nature*, 350:330-332.

Müller, J.-F., 1992, Geographical distribution and seasonal variation of surface emissions and deposition velocities of atmospheric trace gases, *J. Geophys. Res.*, 97:3787-3804.

Murphy, P.G. and A.E. Lugo, 1986, Ecology of tropical dry forest, *Annual Rev. of Ecol. and Systemat.*, 17:67-88.

Naylor, R. and P.A. Matson, 1993, Environmental Impact of Population Growth, *EOS*, 74:178-179.

Neue, H.-U., 1992, Agronomic practices affecting methane fluxes from rice cultivation, *Ecolog. Bull. (Copenhagen)*, 42:174-182.

Rasmussen, R.A. and M.A.K. Khalil, 1988, Isoprene over the Amazon Basin, *J. Geophys. Res.*, 93:1417-1421.

Richter, D.D. and I. Babbar, 1991, Soil diversity in the tropics, *Adv. in Ecol. Res.*, 21:315-389.

Rodin, L.E., N.I. Bazilevich and N.N. Rogov, 1975, The productivity of the world's main ecosystem, *in:* "Productivity of World Ecosystem," W. National Academy Press, Washington, D.C.

Sanchez, P.A., 1981, Soils of the humid tropics, *in:* "Blowing in the Wind: Deforestation and Long-Range Implications," Department of Anthropology (ed.), College of William and Mary, Williamsburg, VA.

Sanhueza, E., W.M. Hao, D. Scharffe, L. Donoso and P.J. Crutzen, 1990, N_2O and NO emissions from soils of the northern part of the Guayana Shield, Venezuela, *J. Geophys. Res.*, 95:22,481-22,488.

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. Atm. Chem.*, 1:171-186.

Shea, C.P., 1988, Shifting to renewable energy, *in:* "The State of the World 1988," World Watch Institute, W.W. Norton & Company, New York.

Siegel, S.M. and B.Z. Siegel, 1987, Biogenesis of carbon monoxide: Production by fungi and seed plants in the dark, *Phytochem.*, 26:3117-3119.

Steudler, P., R.D. Bowden, J.M. Mellilo, and J.D. Aber, 1989, Influence of nitrogen fertilization on methane uptake in temperate forest soils, *Nature*, 341:314-316.

Stewart, J.W.B., and 11 others, 1989, Extrapolation of flux measurements to regional and global scales, *in:* "Exchange of Trace Gases between Terrestrial Ecosystems and the Atmosphere," M.O Andreae and D.S. Schimel (eds.), John Wiley and Sons, New York.

Tathy, J.P., B.Cros, R.A. Delmas, A. Marenco, J. Servant, and M. Labat, 1992, Methane emission from flooded forest in Central Africa, *J. Geophys. Res.*, 97:6159-6168.

Thompson, K. and A.C. Hamilton, 1983, Peatlands and swamps of the African continent, *in:* "Mires: Swamp, Bog, Fen, and Moor," Gore, A.J.P. (ed.), Elsevier, Amsterdam.

Vaghjiani, G.L. and A.R. Ravishankara, 1991, New measurement of the rate coefficient for the reaction of OH with methane, *Nature*, 350:406-409.

Veldkamp, E., A.M. Weitz, I.G. Staritsky, and E.J. Huising, 1992, Deforestation trends in the Atlantic zone of Costa Rica: A case study, *Land Degrad. and Rehab.*, 3:71-84.

Vitousek, P.M. and R.L. Sanford, Jr., 1986, Nutrient cycling in moist tropical forest, *Annual Rev. of Ecol. and Systemat.*, 17:137-167.

Vitousek, P.M. and P.A. Matson, 1988, Nitrogen transformations in tropical forest soils, *Soil Biol. Biochem.*, 20:361-367.

Vitousek, P.M., P.A. Matson, C. Volkmann, J.M. Maass and G. Garcia-Mendez, 1989, Nitrous oxide flux from seasonally-dry tropical forests: A survey, *Global Biogeochem. Cycles*, 3:375-382.

Vitousek, P.M. and P.A. Matson, 1993, Agriculture, the global nitrogen cycle, and trace gas flux, "Proceedings of the 10th International Symposium on Environmental Biogeochemistry," August 19-23, 1991, in press.

Watson, R.T., H. Rodhe, H. Oeschger and U. Siegenthaler, 1990, Greenhouse gases and aerosols, *in:* "Climate Change: The IPCC Scientific Assessment," J.T. Houghton, G.J. Jenkins and J.J. Ephrams (eds.), Cambridge University Press, Cambridge.

Williams, E.J. and F.C. Fehsenfeld, 1991, Measurement of soil nitrogen oxide emissions in three north American ecosystems, *J. Geophys. Res.*, 96:1033-1042.

Williams, E.J., G.L. Hutchinson and F.C. Fehsenfeld, 1992, NO_x and N_2O emissions from soil, *Global Biogeochem. Cycles*, 6:351-388.

Whiting, G.J., J.P. Chanton, D.S. Bartlett, J.D. Happell, 1991, Relationships between CH_4 emission, biomass, and CO_2 exchange in a subtropical grassland, *J. Geophys. Res.*, 96:13,067-13,071.

Zimmerman, P.R., J.P. Greenberg, and C.E. Westberg, 1988, Measurments of atmospheric hydrocarbons and biogenic emission fluxes in the Amazon boundary layer, *J. Geophys. Res.*, 93:1407-1416.