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Historical and future land use effects on N_2O and NO emissions using an ensemble modeling approach: Costa Rica's Caribbean lowlands as an example

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[1] The humid tropical zone is a major source area for N_2O and NO emissions to the atmosphere. Local emission rates vary widely with local conditions, particularly land use practices which swiftly change with expanding settlement and changing market conditions. The combination of wide variation in emission rates and rapidly changing land use make regional estimation and future prediction of biogenic trace gas emission particularly difficult. This study estimates contemporary, historical, and future N_2O and NO emissions from 0.5 million ha of northeastern Costa Rica, a well-documented region in the wet tropics undergoing rapid agricultural development. Estimates were derived by linking spatially distributed environmental data with an ecosystem simulation model in an ensemble estimation approach that incorporates the variance and covariance of spatially distributed driving variables. Results include measures of variance for regional emissions. The formation and aging of pastures from forest provided most of the past temporal change in N_2O and NO flux in this region; future changes will be controlled by the degree of nitrogen fertilizer application and extent of intensively managed croplands. *INDEX TERMS:* 0315 Atmospheric Composition and Structure: Biosphere/atmosphere interactions; 1610 Global Change: Atmosphere (0315, 0325); 1615 Global Change: Biogeochemical processes (4805); *KEYWORDS:* land use change, nitrous oxide, nitric oxide, Costa Rica, greenhouse gases, scaling up

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1. Introduction

1.1. Land Cover Change and Biogenic Trace Gas Emissions in the Tropics

[2] A central issue of Earth system science is the accumulation of radiatively active gases in the atmosphere and the likelihood that absorption of infra-red radiation by these gases will lead to an increase in average atmospheric temperature [*Houghton*, 1997]. Gases of principal concern are CO_2, CH_4, N_2O, chlorofluorocarbons, and O_3 [*Houghton et al.*, 1996]. Each of these gases has different sources, spectral behavior, atmospheric lifetimes and sinks [*Andreae and Schimel*, 1989; *Cicerone*, 1989; *Bouwman*, 1998; *Khalil and Rasmussen*, 1992; *Houghton et al.*, 1996; *Volk et al.*, 1996].

[3] Nitrous oxide (N_2O) is ranked third in importance as a greenhouse gas on a molar basis when taking into account concentration and atmospheric turnover rate, while it is ranked fifth in terms of total contribution [*Rodhe*, 1990]. Nitrous oxide is also globally important in its role in decreasing stratospheric ozone levels [*Crutzen*, 1970; *Nevison and Holland*, 1997]. The atmospheric concentration of N_2O is increasing by about 0.25% yr^{-1} [*Prinn et al.*, 2000] for reasons that are not completely clear [*Khalil and Rasmussen*, 1992; *Nevison and Holland*, 1997] but are thought to be largely due to expansion and intensification of agriculture [*Kroeze et al.*, 1999]. Nitrous oxide is produced from a variety of sources but wet tropical soils are one of the primary sources, amounting to 25–40% of total emissions [*Matson and Vitousek*, 1990; *Davidson*, 1991; *Bouwman et al.*, 1995; *Nevison and Holland*, 1997].

[4] Nitric oxide (NO), also emitted from soils, is not a greenhouse gas as it is a short-lived, reactive species. However, NO is important in tropospheric chemical interactions including production of ozone, itself a potent greenhouse gas [*Logan*, 1983; *Thompson*, 1992]. *Davidson and Kingerlee* [1997] calculated global emissions from soils to be about 21×10^{12} g yr^{-1} with highest flux rates coming from temperate and tropical cultivated land, thorn forests

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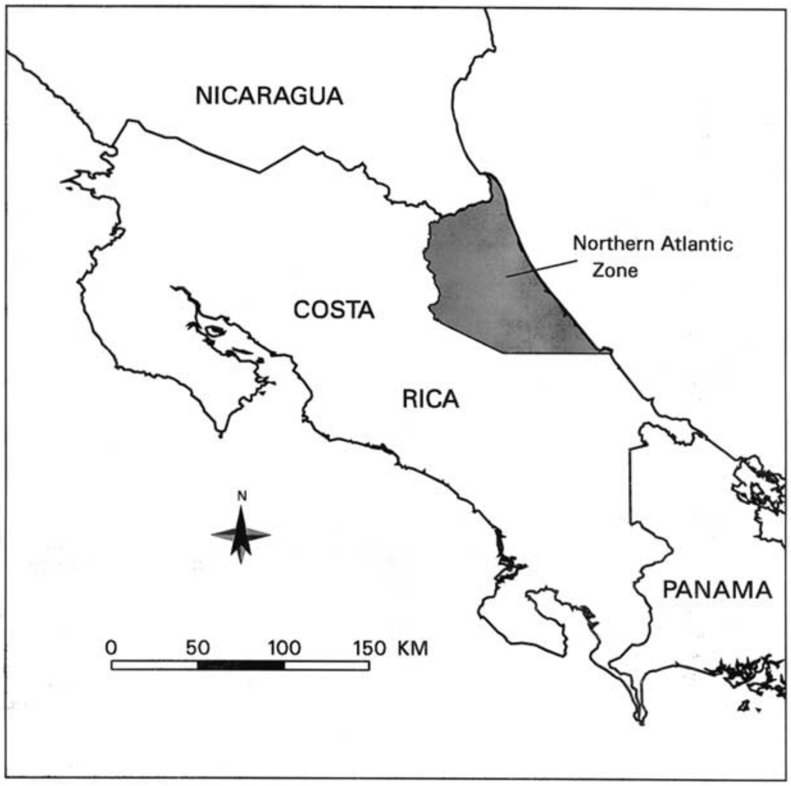

Figure 1. Map of Costa Rica and the Northern Atlantic Zone (NAZ).

and tropical savanna/woodlands. *Chameides et al.* [1994] estimated that fertilizer-induced soil emissions of NO_x represented about 13% of present-day totals for gases but could represent 22% in a slowly developing world and 18% of a rapidly developing world by 2025. They pointed out that especially when productive agricultural areas are spatially associated with strong sources of NO_x emissions, the resulting enhancement of ozone by NO_x and its deleterious effects on crops would create a growing cost to crop production and resulting increase in the prices of agricultural commodities.

[5] Increased rates of N_2O emissions are implicated as the sources underlying increasing atmospheric concentrations [*Andreae and Schimel*, 1989; *Bouwman*, 1998; *Nevison and Holland*, 1997; *Veldkamp et al.*, 1998]. One possible factor leading to increasing emissions is land use change in the humid tropics, a major source area [*Bouwman*, 1998]. Some undisturbed forests throughout the humid tropics have high background rates, but rates can become even temporarily higher when forests are cut and converted to pasture [*Luizao et al.*, 1989; *Keller et al.*, 1993, 1997; *Keller and Reiners*, 1994; *Veldkamp et al.*, 1999; *Verchot et al.*, 1999], or tillage agriculture [*Mosier et al.*, 1996a; *Crill et al.*, 2000]. Nitrogen and other chemical applications may be heavy in tillage agriculture and some plantation agriculture. It is evident that application of nitrogen fertilizer to soils increases fluxes of both N_2O and NO [*Eichner*, 1990; *Mosier et al.*, 1991, 1996b; *Matthews*, 1994; *Granli and Bockman*, 1994; *Yienger and Levy*, 1995; *Davidson et al.*, 1996; *Keller and Matson*, 1994; *Matson et al.*, 1996, 1998; *Mosier et al.*, 1996b, 1997; *Veldkamp and Keller*, 1997a, 1997b].

[6] The northern Atlantic Zone of Costa Rica (NAZ) is an example of a humid tropical region undergoing rapid change in land use (Figure 1). This area is climatically representative of other wet tropical areas of the world that occur at low elevation (minimum monthly temperature of about 20°C) [*Lauer*, 1983] but is a region of relatively fertile soils [*Nieuwenhuyse*, 1996]. The NAZ falls primarily in Costa Rica's Limon Province in which agricultural development has been a fairly recent phenomenon. The population of this 0.919 million ha Province around the turn of the century (1892) was only 7500 and then grew from about 33,750 in 1927 to 114,178 in 1973 [*Instituto de Investagaciones Sociales*, 1976] to 285,101 in 1997. Earlier in the 20th century, the population was concentrated around the coastal city of Limon and along the railroad line between Limon and San Jose [*Nunley*, 1960] so that most of the Province remained forested until after the 1940s.

[7] The typical pattern of agricultural development in the NAZ following deforestation is conversion to pasture followed by crops or abandonment depending on the quality of soils. Pastures on less fertile soils may be abandoned to secondary forests or planted to tree plantations. Pastures on more fertile soils, usually on recent alluvium, are often converted to banana plantations. Soils of intermediate quality are converted to heart-of-palm (palmito), pineapple, cassava, beans, taro, maize, other annual crops or floricultural species. Corporate agriculture

has become widespread in the NAZ and reacts quickly to changes in markets and agricultural technology. Thus, the pattern of land use can change rapidly. For example, between 1960 and 1984 the area under forest cover in the central part of the NAZ was reduced from 73% to 6% [*Veldkamp et al.*, 1992].

1.2. Objectives of This Research

[8] Given the relative importance of the humid tropics to the N_2O and NO global budgets, given the sensitivity of emissions of these gases to land use, and given the complex changes in land use taking place in the humid tropics today, the linkage between land use change and trace gas emissions becomes an important scientific question. The goal of this research is to define linkage in a rapidly developing area in the humid tropics, the Northern Atlantic Zone of Costa Rica (NAZ). The specific objective of this paper is to estimate contemporary, historical and future N_2O and NO emissions over the 0.5 million ha NAZ with measures of variance.

[9] Most estimates of emissions for a defined geographic domain are based upon the simple multiplication of site values times the area the site represents [*Schimel et al.*, 1997a; *Burke*, 2000]. The availability of spatial data for the principal drivers and of measures of temporal variation is usually limited, or not seriously considered, a general "scaling up" problem thoroughly addressed by *Rastetter et al.* [1992]. In this research, we sought to develop a method that takes into account both spatial and temporal variation to provide measures of variance for the region as a whole.

[10] Defining the relationship between land cover/land use change and regional emissions of N_2O and NO requires a synthesis of several scientific methodologies. This paper reports on how extensive field measurements of gas emissions have been used to develop simulation models of the emission processes, how the models have been linked to GIS representations of the NAZ, and how an ensemble of model runs for regional conditions have led to a conditional probability distribution for past, present, and possible future emissions.

2. Data and Methods

2.1. Field Measurements

[11] Field measurements of gas emission rates along with ancillary environmental data used to parameterize models were available from several earlier studies in the NAZ. Such data were published for primary (old growth) and secondary wet tropical forests, active pastures of 25–30 years of age, abandoned pastures, and secondary forests by *Keller et al.* [1993], *Parsons et al.* [1993], *Reiners et al.* [1994, 1998], *Keller and Reiners* [1994], and *Parsons and Keller* [1995]. Analogous data were published for banana, and several varieties of pasture management including pastures of younger ages by *Veldkamp and Keller* [1997a, 1997b] and *Veldkamp et al.* [1998, 1999]. Although more recent data [*Crill et al.*, 2000] are continuing to emerge, they were not available in time to be used in this study for parameterizing a crop model. The seriousness of this unavailability will be evaluated in terms of the differences between the rates of known land cover types, and the areas involved in the crops.

2.2. Field-Scale Modeling Methods

[12] In cooperation with the originators and developers of CENTURY at the Natural Resources Ecology Laboratory at Colorado State University (W. Parton, D. Schimel, D. Ojima, we have modified the widely-used ecosystem simulation model CENTURY to simulate N_2O and NO emissions at the monthly time step). CENTURY is an ecosystem simulation model centered on carbon and nitrogen dynamics in soils [*Parton et al.*, 1987, 1993, 1994]. It has been adapted to a wide range of ecosystem types and has been used for biogeochemical purposes at the regional [*Parton et al.*, 1989, 1996a]; continental [*VEMAP Participants*, 1995; *Schimel et al.*, 1997b]; and global scales [*Schimel et al.*, 1994, 1997a; *Parton et al.*, 1996a, 1996b]. *Parton et al.* [1996b] adapted CENTURY for direct simulation of N_2O and NO production with a daily time step but this adaptation requires input variables not available for this present study. We have adapted CENTURY for three ecosystem types: forest, pasture and banana plantation and further modified these adaptations of CENTURY to simulate secondary as well as primary forest, forest plantations, pastures receiving different levels of grazing and forage management, and miscellaneous crops such as pineapple and heart-of-palm. Details on these model adaptations can be found in the works of *Liu et al.* [1999, 2000]. In brief, these modifications involved development of a realistic soil hydrology routine that would represent the kinds of frequent storm events encountered in the NAZ and routines for linking nitrogen mineralization to both nitrification and denitrification and separating denitrification products based primarily on water-filled pore space of soils.

[13] This research is related to an analogous modeling and regional extrapolation project for a subsection of the NAZ for the year 1992 by *Plant* [1998, 2000] using the DNDC model [*Li et al.*, 1992a, 1992b]. *Plant and Bouman* [1999] also modeled alternative pasture management approaches for the NAZ. Direct comparisons of areal emissions are not possible between those products and the results given here because of the different land areas and mix of land cover types involved in each study.

2.3. Spatial Databases

[14] As described above, CENTURY is a point, or field-scale model. In order to deploy it over heterogeneous space, it must be linked with spatial data to estimate emissions over a geographic domain, the NAZ. This section describes preparation of land cover/land use data for 1996 (the contemporary date for this research) analogous data for earlier years and for future scenarios.

2.3.1. Land Cover 1996

[15] A classified image was produced from the 11 November 1996 (path 15/row53) Thematic Mapper scene aided by hydrography, soil drainage and banana plantation GIS digital map layers, and by extensive ground truthing in the NAZ. A small part of another scene (16 June 1992; path 14/row 53) was treated the same way to complete the southeastern corner of the NAZ. The resulting classified image was a full resolution (30 m raster) product showing

Table 1. Changes in Land Use From the 1996 Distribution Dictated for Future Scenarios[a]

Landuse Type	Growth Scenario	Decline Scenario
Pasture	increase on forest land below 1550 m elevation by 33%	convert 30% on poorer soils to secondary forest
	convert 30% on better soils to legume/grass pasture	
	convert 20% on better soils to palmito	
Crops		convert 10% on poorer soils to pasture
		Convert 10% on poorer soils to secondary forest
Banana	leave unchanged	leave unchanged

[a] The changes are dictated, nominally for the year 2010, based on suggestions by Bas Bouwman, REPOSA staff.

the distribution of 20 land cover classes [*Driese et al.*, 2001].

[16] One of these cover classes was cloud cover and cloud shadow, defined by a spectral class selection process followed by hand editing. This class covered 5.6% of the NAZ. Cells in this class were converted to other land cover classes for emission estimation purposes by a statistical approximation process that permitted assignment of all cells to noncloud cover classes. This modified image was resampled to 1 ha raster format and converted to an ArcGrid (ESRI©) coverage to be added to the GIS data set.

[17] Of the original 545,579 1 ha cells representing the entire NAZ, 154,579 cells were classified as forested swamp. Because no N_2O or NO emission field data exist for this land cover type, it was eliminated from the region of estimation by masking out that cover type. This reduced the area for which emissions could be estimated to 391,000 1 ha cells, 72% of the total NAZ area.

2.3.2. Historical Spatial Databases for Land Cover/Land Use

[18] For historical land cover data, we used data mapped at 1:200,000 scale in the Atlas del Cambio de Cobertura de la Tierra en Costa Rica 1979–1992 [*Instituto Meteorologico Nacional*, 1996]. Atlas data had been created digitally with GIS methods from MSS satellite-derived data. Although produced digitally, data in digital format were not available to us so we were forced to scan the map sheets covering the NAZ from the hard copy maps. The maps provided by this atlas included only eight land cover classes for the NAZ region compared with the 20 classes extracted from the 1996 TM image. To make sequential comparisons, the 1996 data had to be simplified and cross-walked with the Atlas data to produce common land cover/land use digital maps.

2.3.3. Future Spatial Databases for Land Cover/Land Use

[19] In the time frame of the next few decades, changing soil properties associated with land use change will be primary to furthering changes in regional N_2O and NO emissions. The nature of further land use change is difficult to predict because of the complex interplay between technological innovations, global economic and trade conditions and Costa Rica's domestic policies. Therefore, we offer two contrasting scenarios for the near future we nominally date as 2010.

[20] The best authorities for such scenarios were agricultural scientists associated with the Dutch–Costa Rican REPOSA project. These scientists had completed a full regional land use model built upon crop models for pastures, bananas and other crops coupled into a linear programming system. The scenarios used in this research are relatively simple alterations of present land cover/land use provided by Bas Bouman, formerly with REPOSA, now with the International Rice Institute.

[21] Two contrasting future scenarios were devised, one for further agricultural development, the other for economic stagnation, both derived from the 1996 coverage produced from TM imagery. In both cases, the area occupied by forested swamp (primarily along the Caribbean coast) was left unchanged (Table 1). Drainage and cutting proceeding from west to east have decreased the swamp area of the NAZ over the last two decades but further development in that direction will slow down as the drainage projects encounter the progressively higher water table near the coast. Development of this kind, should it occur, will lead to pasture establishment which will, in the early stages, lead to high rates of nitrogen oxide emissions.

[22] With an expansion in the regional agricultural economy, more upland forest might be cut. However, most of the remaining forest is in the foothills of the mountains so that expansion of better land for grazing or other purposes will also be limited by soil quality and steep terrain. Nevertheless, the expansion scenario included a conversion of 33% of the remaining forests on better remaining soils to pastures (Table 1). These would, by definition, be young pastures with high rates of emission. With the economic stagnation scenario there was no change in upland forest area.

[23] With economic growth, 30% of the pastures on better soils were converted to improved pastures with leguminous mixtures planted along with more productive grasses [*Veldkamp et al.*, 1998], and 20% of pastures on better soils were converted to heart-of-palm plantation (Table 1). Both of these alterations lead to higher gas emission rates. For the economic stagnation scenario, 30% of pastures on poorer soils were abandoned and become converted to secondary forest through normal successional processes. No modification in

gas emission rate for these young forests [*Keller and Reiners*, 1994] was made in the regional estimate under this scenario.

[24] The area devoted to crops (pineapple, cassava, ornamentals, maize, taro) was left the same for the economic growth scenario (Table 1). According to Bouman, a change in the mixture of crops grown might be expected but not an increase in crop area. For economic stagnation, we reduced 10% of crops on less fertile soils to pasture, and converted another 10% to secondary forest through abandonment.

[25] The area in banana plantation, the principal cash crop of the NAZ, was left unchanged in both scenarios. The area in banana is presently set by artificial import regulations by the European community, so that expansion or diminution in banana plantations are not related to normal market forces.

2.3.4. Determination of Pasture Age

[26] Assigning pasture age was one of the most crucial steps for realistically determining N_2O fluxes for the region [*Keller et al.*, 1993]. Pasture age cannot be determined with TM data from a single date and recorded information at the parcel level is non-existent. Consequently, we established a set of age assignment rules for determining the relative ages of pastures for each of the simulated time intervals. This assignment was based, in part, on presence or absence of pastures in the land cover data for the different time frames. Pastures occurring at a point in time where they did not occur at an earlier point in time had to have been established between those two times.

[27] For cases in which historical spatial comparisons were inadequate, we based assignment rules on observations and model rules by *Hall et al.* [1995] and on statistical results by *Veldkamp and Fresco* [1997]. Combining these generalizations, our pasture age assignment rules for each time frame were as follows.

[28] For the 1979 data, which had no precedent data with which to compare, we assumed that half the pastures occurring in the land cover/land use database were young pastures. The half of all pastures located on poorly drained soils (as defined by the REPOSA GIS database) and those most distal from existing pastures, rivers, roads and the rivers, were assigned to the young category in that order of properties. For 1992, all pastures occurring in the 1992 land cover/land use data that did not occur on the 1979 coverage were defined as young pastures. The remainder were defined as old pastures. For 1996, all pastures appearing in the 1996 land cover data occupying cells defined as forest in the 1992 land cover data were defined as young pastures. The remainder were defined as old pastures. For both of the 2010 scenarios all pastures were old except for those virtually converted from forest to pasture in the GIS for the scenario for economic growth. All pastures in the economic stagnation scenario are defined as old.

[29] Given assignment to young and old classes, the output years for young and old pastures were randomly generated within 1–15 years and 16–60 years, respectively, following their establishment.

2.3.5. Fertilization and Leguminous Nitrogen Fixation

[30] Emissions of N_2O and NO vary with pasture management (i.e., natural, leguminous and fertilized pastures) [*Veldkamp et al.*, 1998]. However, no database exists to characterize the spatial distribution of these pastures in the region. We set a distribution of 5%, 5% and 90% of fertilized, legume-improved and traditional pastures, respectively, for the contemporary and past pastures. Estimates for legume-improved and especially, fertilized pastures, are possibly too high but there are no data for improving these values.

[31] The compositions for the future scenarios were specified as described in section 2.3.3. These pasture types were allocated randomly in space. The fertilization rate was 300 kg N ha^{-1} yr^{-1}. This rate was assumed to be applicable to fertilized pastures, crops and banana plantations [*Veldkamp et al.*, 1998]. Legume-based N-fixation rate was estimated to vary from 100 kg N ha^{-1} yr^{-1} on the infertile soils to 150 kg N ha^{-1} yr^{-1} on the fertile soils [*Ibrahim*, 1994].

2.3.6. Temperature and Precipitation Data

[32] Our adaptation of CENTURY operated on a monthly time step requiring monthly precipitation and mean maximum and minimum air temperatures. We acquired monthly mean precipitation and maximum and minimum temperatures along with their standard deviations for 21 stations in the NAZ from the Instituto Meteorologico Nacional in San Jose, Costa Rica. Because the soil wetting cycle is critical to gas emission rates, it was important to account for storm frequencies. The frequency distribution of rainy days within months and the distribution's effect on soil moisture were calculated from daily weather data from weather stations and incorporated into the hydrology submodel as described by *Liu et al.* [2000]. Thiessen polygons were created in ArcInfo based on geographic coordinates of these 21 stations (Figure 2). All climate data were placed in a separate data file linked with the Thiessen polygon coverage through the polygon ID. During modeling simulations, polygon-specific climate data were retrieved by polygon ID to generate time series of monthly precipitation, maximum and minimum temperatures to run the simulations. Nitrogen input rates via precipitation were taken from *Ecklund et al.* [1997].

2.3.7. Soils Data

[33] We obtained spatial data on soil texture, soil fertility class and drainage class from a GIS database created by Research Program on Sustainability in Agriculture (REPOSA) [*Krabbe*, 1993; *Stoorvogel and Eppink*, 1995]. Texture was represented in the database as categorical classes such as "fine sandy loam" (Figure 2). Because CENTURY requires numerical values for sand, silt and clay fractions, we randomly selected numerical values for each of these fractions (adding to 100%) from the range of these values falling within the quantitative limits of the defined class boundaries denoted by the USDA triangular classification system of soil texture. In selecting values, we assumed uniform distributions within the textural classes. Initial soil organic carbon (SOC) values are required to run CENTURY. Initial SOC is stochastically generated from the "fertility" categorical classes (four) derived from the REPOSA GIS database. To link the fertility classes with SOC concentrations, we calculated the averages and standard deviations of SOC within each fertility class based on data collected by Dutch scientists from 99 soil profile data sets [*Stoorvogel and Eppink*, 1995]. Initial SOC content for each model run was randomly generated from the mean and standard deviation of SOC within the fertility class, assuming a normal distribution.

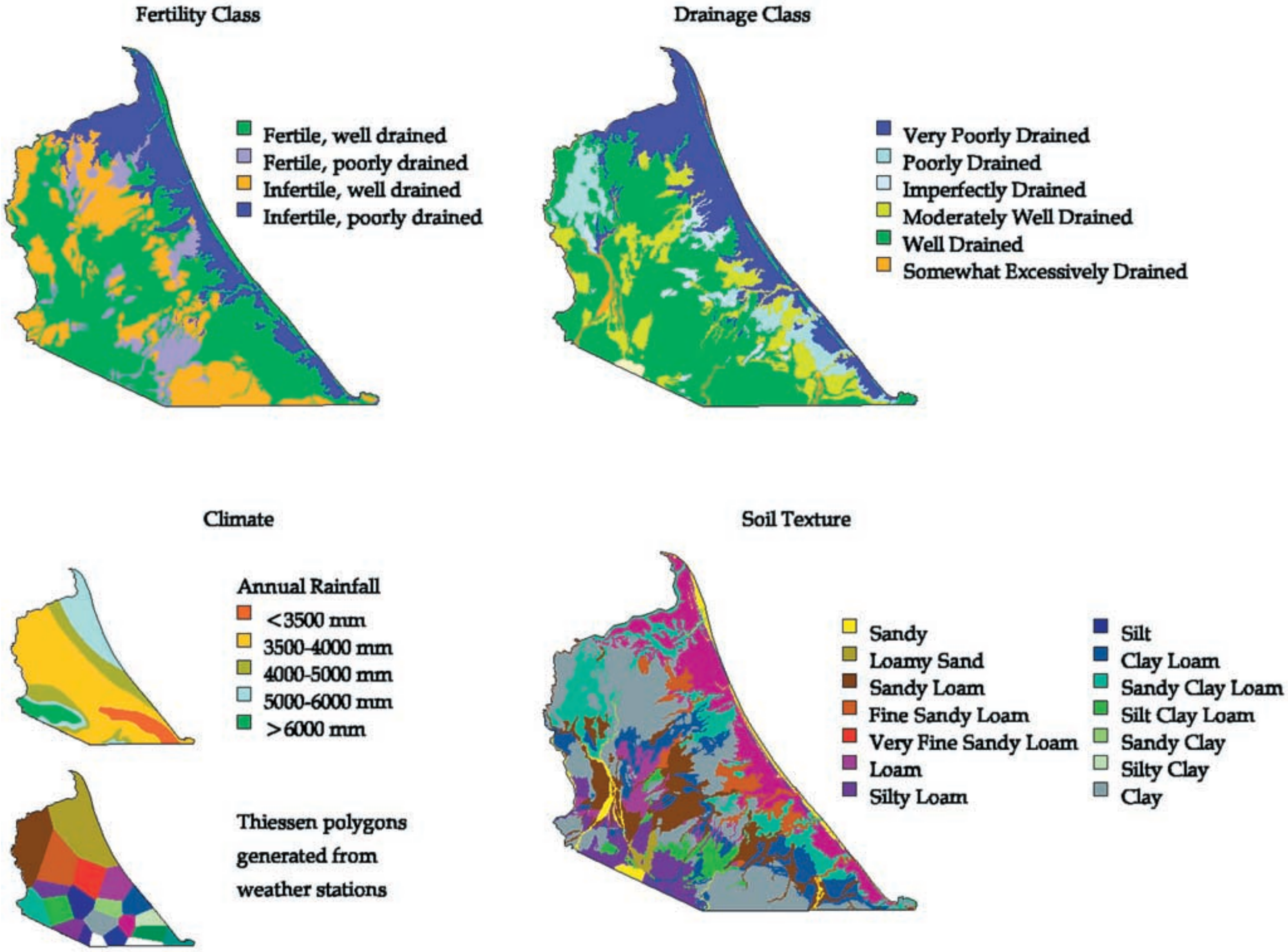

Figure 2. Spatial distribution of geographic variables in the NAZ used as model drivers for CENTURY.

[34] Soil drainage values were taken directly from the REPOSA GIS layer as six classes based on FAO definitions of soil drainage and were used directly in the model.

[35] All of these spatial data except land cover/land use were originally organized in vector format data sets. The vector data were converted to 1 ha raster format within ArcGrid. Low resolution maps of the drivers are illustrated in Figure 2.

2.4. Computing Emissions With Century and the Spatial/Historical Data

2.4.1. Categorical Versus Continuous Spatial Data

[36] The land cover/land use assignments to grid units are categorical and furthermore, were developed at relatively fine scale of 30 m pixel units. In contrast, climate variables change continuously over scales of kilometers and years while soil variables change continuously in space over scales of tens of meters and over times of years. Even the best regional GIS databases must generalize information like this for realistically sized map units. Inasmuch as GIS map units are typically represented as categorical divisions of continuous variables, one cannot assume that a numerical value for an environmental variable is the true estimate for every discrete point within that polygon [*Burrough*, 1991; *Lathrop et al.*, 1995]. As with most other GIS-based spatial data, our sources of climate and soils data are lumped into categorical classes and represented as polygons. One of the tasks of this research was to generate statistical estimates of continuous variables for these categorical map units. A further task was to generate a joint frequency distribution (JFD) for the variables taking into account their intrinsic patterns of variability and their co-distribution in space. The following sections explain how categorical data were acquired and how statistical distributions generated to form JFDs from which to run CENTURY.

2.4.2. Incorporating Variance and Covariance of Model Variables for Computation

[37] As noted above in the description of the spatial distribution of driving variables, map units such as polygons or tessellations of pixels are generalizations for statistically distributed site characteristics. Simply driving the model with crude means for each variable from each overlapping thematic coverage would not take into account the variance within each variable and the covariance between them. It is necessary to sample from the statistical distributions in a way that effectively captures the covariance of the variables with one another. In the absence of knowledge that responses are linear, it is prudent to assume that the combination of

independently varying driving variables will produce nonlinear responses. Because of the generalization of spatial representations of driving variables, it is not feasible to define exact values for particular locations of large areas. The spatial resolution of map units sets the limit to the locational accuracy of the major model variables as a definable area, within which a distribution of the variable distribution can be estimated and assigned.

[38] The direct approach of incorporating variance and covariance of input variables in the simulation process can be expressed as:

$$E(p) = \int E[p(\mathbf{X})]f(\mathbf{X})dX \qquad (1)$$

where p is the process-based environmental model, $\mathbf{X}$ is a vector of model variables, and f is the JFD of $\mathbf{X}$. Generally, it is impossible to analytically integrate (1) because the models are usually complex. Therefore, (1) is often modified as a summation over a JFD table of the major input variables $\mathbf{X}$. To do this, the major input variables can be partitioned in space into discrete, homogeneous regions using GIS techniques:

$$E(p) = \sum_{i=1}^{n} E[p(\mathbf{X}_i)]F(\mathbf{X}_i) \qquad (2)$$

where n is the number of strata or unique homogeneous regions as defined by the GIS overlays of the major input variables, and F is the frequency of cells or the total area of strata i as defined by the vector of $\mathbf{X}_i$. We refer to the cells occurring in each homogeneous region as a simulation cohort because all the simulation cells within the cohort fall within the same, unique combination of generalized map classes for all of the driving variables.

2.4.3. Generating JFD of Input Variables

[39] Five GIS coverages were used to generate the JFD of the major input variables: land cover classes, climate Thiessen polygons, soil texture classes, soil fertility, and soil drainage classes. The original land cover grid at 30 m resolution was resampled to 100 m resolution. Other vector-based GIS coverages were converted to grids with 100 m cell size. By combining these five grids, a grid representing the JFD of these variables was generated. The number of cohorts varied by year but, as an example, 1100 simulations cohorts were formed for 1996 from the 328,000 cells (1 cell = 1 ha).

2.4.4. Flow of Model Execution

[40] The model ran for 2000 years for each forest simulation after which a quasi-steady state condition was insured. All nonforest simulations started from the conversion of forest (age = 0 year) to 60 years of age, considering the fact that N_2O and NO emissions reach quasi-steady state conditions after about 15 years since conversion. Twenty stochastic simulations were performed for each simulation cohort. Twenty simulations were judged to be adequate based on the acceptable standard errors associated with the means of these runs balanced by consideration for the considerable computation time required by simulations, particularly for members of forest cohorts. All members of a cohort belonged to the same land cover class but varied in terms of climate, soil texture, soil fertility, and soil drainage within the bounds established for the cohort. The output year for each nonforest simulation was randomly generated, ranging from year 1 to year 60 except for young and old pastures. These operations were run for the entire region via a graphical user interface (GUI) that facilitated the complex interactions between the GIS database, the model and statistical calculations.

[41] The CENTURY model was run for the entire region via a graphic user interface (GUI). Steps outlined below are diagrammed in Figure 3.

1. Select an existing JFD grid.
2. Specify the meaning of each column in the attribute table of the JFD grid. In the JFD table, the first two columns are cohort index and frequency, respectively. The meanings of other columns could be land cover type, climate region as defined by Thiessen polygon, soil texture, drainage class and soil fertility. The order of these variables is not predefined.
3. Specify the number of stochastic model simulations for each simulation cohort.
4. Start the model run.

[42] With initiation of the program, the attribute table of the JFD along with information about the meaning of each variable in the table was passed from ARC/INFO to Unix environment. Within the Unix environment, the program proceeded through the following steps iteratively until all simulation cohorts in the JFD table had been processed.

1. Read simulation cohort ID, frequency, land cover, and other related information that is uniquely associated with a simulation cohort from the JFD table.
2. Copy the default input files from the default file library, according to land cover of the cohort, to a set of temporary input files.
3. Update the temporary input files by incorporating information read from the JFD table with other expert knowledge.
4. Run CENTURY using the updated input files.
5. Write the simulation cohort ID and simulated results into designated output files.
6. Return to step c until the number of stochastic model simulations is finished.
7. Read the next simulation cohort or a line in the JFD table and go to step b until there is no more simulation cohort left in the JFD table.

[43] It is in step 3 that the stochastic parameterization is implemented. The statistical distributions described with respect to the quantitative spatial variables are searched and random samples selected for input to CENTURY.

2.4.5. Calculating Means and Weighted Standard Deviations for the NAZ

[44] Averages and standard deviations for each of the cohorts were calculated from outputs of their respective 20 simulation runs. These statistics were used to calculate emissions for the entire NAZ. The weighted average gas emission rate R_t (kg N yr^{-1}) for the entire NAZ was calculated according to equation (3)

$$R_t = \sum_{i=1}^{m} \overline{R}_i A_i \qquad (3)$$

where m is the total number of simulation cohorts in the region, $\overline{R}_i$ and A_i are the mean flux (kg N ha^{-1} yr^{-1}) and the total area (ha) of cohort i, respectively.

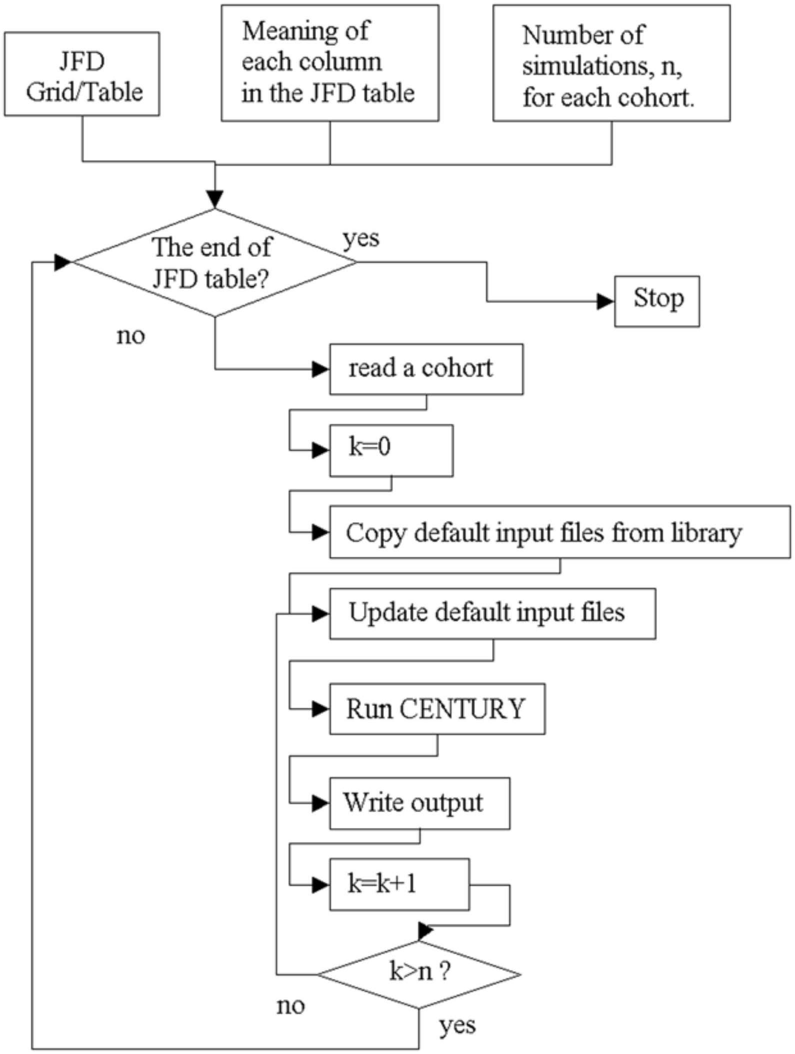

Figure 3. Diagram of information flow linking the CENTURY model with GIS data to produce estimates of regional emissions.

[45] The weighted standard deviation for this estimate of regional emission (δ_t) was calculated according to equation (4)

$$\sigma_t = \sqrt{\sum_{i=1}^{m} (\sigma_i A_i)^2} \tag{4}$$

where σ_I is the standard deviation among the $\overline{R}_{ij}$; $j = 1, 2, \ldots, 20$.

[46] Another source of error is estimation of land cover classes. No estimate of error accompanied the historical data sets in the atlas. The seven 1996 land cover classes used in this estimate were actually collapsed from 18 cover classes determined by *Driese et al.* [2001], a process that should reduce errors by combining similar cover into more general classes. Driese et al. were unable to formally calculate errors of omission and commission for the 18 original cover types because of unavailability of sufficient validation data. Had they been available, it is likely that confusion between similar physiognomic cover types would be more prevalent in the map than confusion between distinctly different physiognomic types. Forest is rarely confused with pasture but pasture may be more frequently confused with croplands. Fortunately, the total areas occupied by croplands and fincas are small as shall be seen in the results. One of the most important classifications in this process is between old and new pastures and that dichotomy was not derived from the land cover product by Dreise et al. as explained above. That dichotomy is very important but there are no field data by which to check the method used. In summary, there is no formal way to incorporate land cover designations into the error estimation process but we feel that this error is small compared with other sources of error.

3. Results and Discussion

3.1. Land Cover Change

[47] Areas occupied by the simplified land cover classes for 1979, 1992 and 1996, and two scenarios for 2010 are

Table 2. Areas, Specific N_2O and NO Flux Rates Per Unit Area, and Total Fluxes for the NAZ Modeling Domain for Five Different Time Intervals[a]

		Specific Flux Rate, kg N ha^{-1} yr^{-1}		Total Flux, Mg N yr^{-1}	
Land Cover	Area, ha	N_2O	NO	N_2O	NO
		1979 Simulations			
Forest	273,138	6.0 (0.4)	1.1 (0.1)	1,650 (102)	295 (35)
Banana	32,406	9.0 (1.2)	15.1 (1.6)	293 (38)	488 (54)
Crops	5,152	9.6 (1.7)	14.3 (1.7)	49 (9)	74 (9)
Bare soil	0	0.0 (0.0)	0.0 (0.0)	0 (0)	0 (0)
Young pastures	37,455	21.7 (2.7)	9.8 (1.6)	814 (101)	366 (59)
Old pastures	39,486	2.2 (0.3)	0.9 (0.1)	87 (10)	35 (5)
Finca	2,165	2.0 (0.5)	1.0 (0.3)	4 (1)	2 (1)
Total/wtd. mean	389,802	7.4 (0.4)	3.2 (0.2)	2,897 (149)	1,260 (88)
		1992 Simulations			
Forest	189,192	6.1 (0.4)	1.1 (0.1)	1,150 (76)	201 (23)
Banana	48,776	9.2 (1.2)	14.9 (1.6)	447 (60)	729 (81)
Crops	22,632	9.4 (1.6)	15.4 (1.6)	212 (38)	348 (36)
Bare soil	180	2.2 (0.8)	0.8 (0.4)	<1 (<1)	<1 (<1)
Young pastures	76,358	21.8 (2.9)	9.4 (1.7)	1,661 (219)	715 (129)
Old pastures	50,997	2.2 (0.3)	0.9 (0.4)	3 (1)	1 (1)
Total/wtd. mean	389,666	9.2 (0.6)	5.2 (0.4)	3,585 (243)	2,040 (158)
		1996 Simulations			
Forest	152,887	6.0 (0.4)	1.1 (0.1)	923 (58)	171 (21)
Banana	48,662	8.9 (1.2)	15.6 (1.6)	433 (61)	758 (80)
Crops	9,291	9.7 (2.1)	17.3 (3.1)	90 (20)	161 (29)
Bare soil	14,890	2.1 (0.2)	0.8 (0.1)	31 (2)	13 (1)
Young pastures	82,330	20.8 (2.6)	8.9 (1.4)	1,717 (211)	731 (115)
Old pastures	67,393	2.1 (0.2)	0.9 (0.1)	143 (13)	59 (8)
Finca	7,929	2.1 (0.1)	0.9 (0.1)	16 (1)	7 (1)
Total	383,382	8.8 (0.6)	5.0 (0.4)	3,354 (228)	1,900 (145)
		2010 Growth Simulations			
Forest	104,124	6.3 (0.4)	1.1 (0.1)	660 (44)	112 (13)
Banana	48,662	9.2 (1.3)	15.7 (2.1)	449 (62)	763 (101)
Crops	40,036	9.9 (1.3)	16.4 (1.4)	395 (51)	656 (57)
Bare soil	14,890	2.1 (0.2)	0.9 (0.1)	31 (2)	13 (1)
Young pastures	48,763	20.2 (2.2)	8.4 (1.1)	986 (110)	412 (55)
Old pastures	118,977	2.2 (0.2)	0.7 (0.1)	259 (22)	86 (9)
Finca	7,929	2.1 (0.1)	0.9 (0.1)	16 (1)	7 (1)
Total	383,381	7.3 (0.4)	5.3 (0.4)	2,796 (145)	2,049 (130)
		2010 Stagnation Simulations			
Forest	197,927	6.0 (0.4)	1.1 (0.1)	1,182 (79)	212 (24)
Banana	48,662	9.5 (1.5)	16.4 (1.8)	461 (73)	799 (89)
Crops	8,233	9.9 (1.9)	15.8 (1.9)	81 (16)	130 (15)
Bare soil	14,890	2.0 (0.1)	0.9 (0.1)	30 (2)	13 (1)
Old pastures	105,741	2.1 (0.2)	0.8 (0.1)	225 (20)	89 (13)
Finca	7,929	2.1 (0.2)	0.9 (0.1)	17 (1)	7 (1)
Total	383,382	5.2 (0.3)	3.3 (0.3)	1,996 (111)	1,250 (95)

[a] The five different time intervals are 1979, 1992, 1996, 2010 with economic growth and 2010 with economic stagnation. Area weighted means for specific flux rates and grand totals are given for each year of simulation along with standard errors in parentheses.

listed in Table 2 and graphed in Figure 4. We assumed that the entire NAZ was forested in 1900, a nominal date for the time prior to modern agricultural development began. In fact, Native Americans practiced small scale agriculture in Pre-Columbian times, usually on the more fertile soils of river terraces of the region [*McDade and Hartshorn*, 1994] so that the NAZ was probably never entirely forested for the last 10,000 years. Nevertheless, small scale farming effects were probably trivial compared to other errors in this analysis so we assumed a fully forested condition in order to compare a pre-Euro-American state with contemporary conditions.

[48] Four salient points on land cover change emerge (Figure 4). First, there was a dramatic reduction in forest cover from 100% in 1900 to 70% in 1979 and as low as 40% in 1996, the year of best record. Without question, this is the largest change in land cover/land use in the NAZ and it has important implications for biogenic gas emissions and other ecological functions. Second, much of forest land was converted to pasture. The percentage of NAZ in pasture rose from 0% in 1900 to 39% by 1996. Conversion of 40% of the area's forest to pasture, given the very high amplitude of change in nitrogen oxide gas emission resulting from that process [*Keller et al.*, 1993; *Keller and Reiners*, 1994], had profound implications for regional emissions over that period. The percentage of land in young pasture, the most critical land cover type, rose to a peak of 21.5% of the area

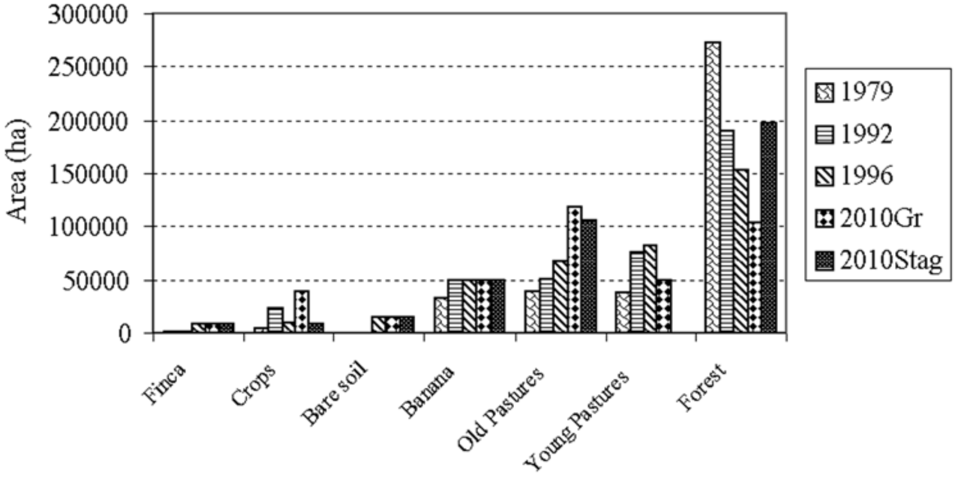

Figure 4. Composite graph of NAZ land type area in hectares for each of the time periods.

in 1996 and fell again in both scenarios. The third point is that some forest land, and later, pastureland, was converted to banana cultivation, an agricultural activity involving a significant amount of area and large chemical inputs to the system. Banana plantations occupied about 8.3% of the area in 1979 and were up to 12.7% of the area by 1996. The scenarios do not project an increase in banana plantation area in the future because of international market controls. The fourth point is that croplands and associated bare soil, together with fincas (ca. 1 ha landholdings including houses and garden plots), rose to occupy 8.4% of the area by 1996. This category will never be managed homogeneously and probably not with the same amount of nitrogen fertilizer as is practiced with bananas, but is the land sector with the greatest potential for managerial intensification and could become comparable with banana plantations in the future in terms of nitrogen oxide fluxes.

[49] Conversion of forested land to pasture or other agricultural uses is only practical where topography, soils and drainage permit. In the case of the NAZ, this constrains development to a zone between the mountains bordering the southwest and southern borders of the area (Figure 2), and the coastal swamps along the Caribbean Sea and south of the bordering San Juan River on the north. Forest cover, although mostly second growth in later years, persists in the mountainous foothills and along margins of the riverine and coastal swamps. The central band of development lying between the mountains and the swampy coastal margin consisting of banana plantations, pastures, croplands and fincas is more diversified in the 1996 image and derivative 2010 scenario images than do the Atlas-derived land cover representations because of the much finer grained land cover representation derived from the 1996 image.

3.2. Biogenic Gas Fluxes by Land Cover Types

3.2.1. Nitrous Oxide

[50] Columns 3–6 in Table 2 show the emission rates specific to land cover types plus their standard errors. These are not simply averages of field measurements in the various ecosystem types. These are simulated values from CENTURY that take into account joint distributions of climate and soil factors as well as assignations of pasture ages and fertilization rates in a stratified-random manner explained in methods. Average data are presented for each time interval but as there is little difference expected or found between intervals, we will focus only on 1996 rates.

[51] Average emission rates for N_2O varied between land cover types by a factor of 10.1, the lowest being finca, the highest being young pastures (Figure 5). Across this range, there are essentially three emission rate groups: (1) bare soil, fincas and old pastures averaging 2.1 kg N ha^{-1} yr^{-1}; (2) forest, banana and croplands with an intermediate range of 6–10 kg N ha^{-1} yr^{-1}; and young pastures with very high rates around 21 kg N ha^{-1} yr^{-1} (Figure 5). Young pastures temporarily have very high emission rates that after 15 years drop to relatively low rates. The wide dynamic range of emission rates in pastures in this area were documented by *Keller et al.* [1993], *Keller and Reiners* [1994], and *Veldkamp et al.* [1998]. After deforestation itself, this temporal change in pasture behavior is the most important determinant for estimation of regional N_2O emissions in this environment. The weighted average rate of 8.75 kg N ha^{-1} yr^{-1} for 1996 is a relatively high flux rate on a global basis, even with the area weighted inclusion of low production areas like bare soil, old pastures and fincas [*Bouwman et al.*, 1993, 1995].

[52] Standard errors for these ecosystem-specific N_2O emission rates range from 5.9% (forest in 1979 and 1996) to 38.6% (bare soil in 1992) of the means (Table 2). Variability is a product of the number of cells involved in calculations for a particular land cover type, the real variability in spatially-related drivers and the dynamic range characterizing CENTURY operation in the different ecosystem types.

[53] Comparison of mean simulation values with field measurements is problematic for two reasons. First, data in Table 2 are annual means derived from, in some cases, hundreds of cohorts, each cohort representing a different combination of land use history, management, soils and climate conditions. These values cannot represent the full range of simulation outputs. Second, field measurements are deliberately made over a wide range of conditions including

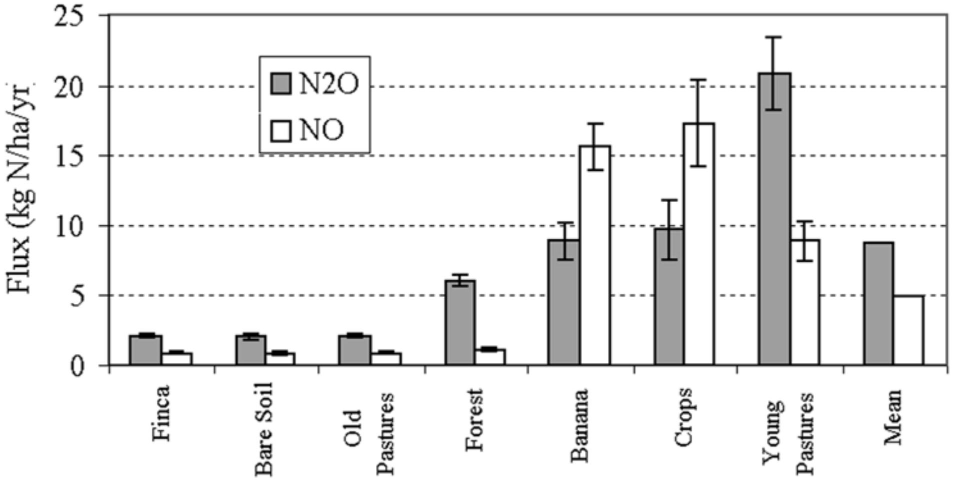

Figure 5. Land cover types-specific emission rates for 1996, a representative year for the NAZ.

full annual and management cycles. Field measurements can range over an order of magnitude. Both field and simulation results are important for their environmentally driven dynamical variation rather than their mean characteristics. Nevertheless, we can say that the mean, annual simulation values fall within the range of field measurements in all cases except simulation values for both gases are just above the range for young pastures. To make more detailed comparisons, readers can compare N_2O and NO fluxes in Table 2 with the ranges shown by *Keller and Reiners* [1994] for forests, *Keller and Veldkamp* [1997a] for banana plantations, *Mosier et al.* [1998] plus *Crill et al.* [2000], and *Weitz et al.* [2001] for crops, and *Keller and Reiners* [1994] and *Veldkamp et al.* [1998] for both young and old pastures. See also the work of *Liu et al.* [1999, 2000] for quantitative evaluations of model outputs compared with field data for forest and pasture ecosystems. There are no field data for bare soil and fincas with which to compare simulation data.

[54] Extrapolation of regional rates from the NAZ to similar areas of Earth would not be prudent. Increases in N_2O flux in young pastures following deforestation have been observed in the NAZ and outside of Manaus, Brazil [*Luizao et al.*, 1989], but there are other cases in Rondonia and Para states of Brazil where even young pastures appear to emit little N_2O relative to forests [*Keller et al.*, 1997; *Verchot et al.*, 1999]. There are few areas in the wet tropics with native soils as fertile as these and where modern agriculture is practiced with such intensive nitrogen fertilization. Thus, agricultural emission rates are comparatively high [*Matson and Vitousek*, 1990; *Bouwman et al.*, 1993] and might better be viewed as an upper limit at the regional scale in such environments.

3.2.2. Nitric Oxide

[55] Average emission rates for NO in 1996 varied between land cover types by a factor of 18.3, the lowest being bare soil, the highest being banana plantations and croplands (Table 2). Essentially there was a low emission rate set: forest, old pastures, fincas and bare soil (ca. 0.9 kg N ha^{-1} yr^{-1}); one intermediate type: young pastures (8.9); and two high types: bananas (15.6) and crops (17.3 kg N ha^{-1} yr^{-1}) (Figure 5). In contrast with N_2O, where high values were associated with the young pasture phenomenon, high NO values were associated with intensively fertilized crops like banana and all those associated with the "crops" category. Net emissions of NO for this region will continue to be related to the distribution of land in these categories. Unlike the influence of young pastures on N_2O emissions, these systems probably will not decline in their NO production over time because of presumed, continuing, nitrogenous fertilizer inputs. These emission rates, particularly of banana, crops and young pastures, are relatively high compared with published values [*Matson and Vitousek*, 1990; *Bouwman et al.*, 1993; *Davidson and Kingerlee*, 1997] as expected because of the relatively fertile soils associated with this volcanic region [*Keller and Reiners*, 1994].

[56] Standard errors for land cover type-specific NO emission rates ranged from 8.7% (crops in 2010-growth) to 42.6% (bare soil 1992) of the means, a range comparable with that of N_2O (Table 2).

3.3. Regional Emission Rates

3.3.1. Nitrous Oxide

[57] Estimates of N_2O and NO emission rates for the entire NAZ at a particular time interval are the product of the total area of land cover types and emission rates of those cover types. We reiterate, however, that this is not a matter of simply summing areas and multiplying by average rates. Rather, this calculation was done on a cell by cell basis using joint distribution table for environmental factors as explained in methods. Summations for the entire NAZ area by time interval are presented in Table 2 and Figure 6. The estimate for average total area emissions for 1900 when the area was ostensibly all forest was calculated by multiplying the entire 1979 area by the average 1979 forest emission rate. This may create a slight underestimate for 1900. The more fertile soils were occupied by agriculture in 1979, slightly reducing the average emission rate from forests in that year. The application of 1979 forest rates to the entire

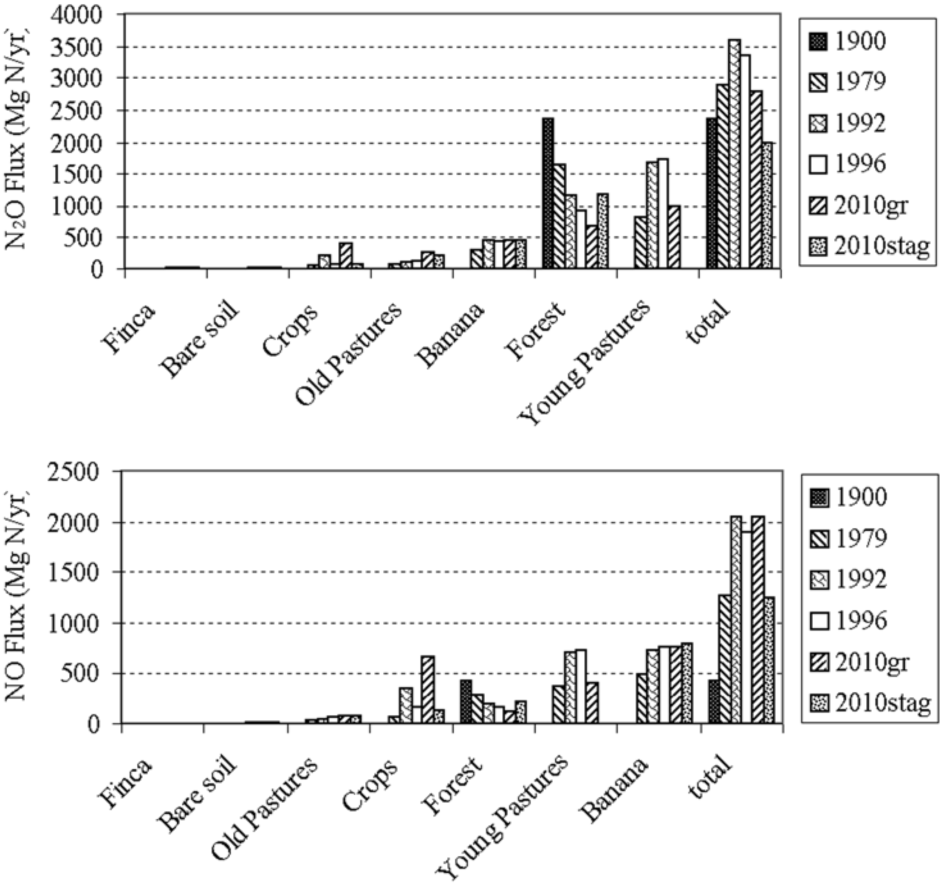

Figure 6. (a) N_2O flux rate and (b) NO flux rate for the entire NAZ with respect to land cover type and time interval.

area will therefore yield a slight underestimate for an entirely forested domain in 1900 (Table 2).

[58] The contribution of the entire NAZ to the atmospheric pool of N_2O-N during 1996, the best year of estimate, was 3354 t N yr^{-1} (Table 2) with 95% confidence range of 2907 to 3802 t N yr^{-1}. Land cover type percentage contributions toward N_2O flux in ascending order for 1996 were: finca = 0.5, bare soil = 0.9, crops = 2.7, old pastures = 4.3, bananas = 12.9, forest = 27.5 and young pastures = 51.2 (Figure 6a). Measures of variation for regional fluxes by land cover type are in the same range as for their specific emission rates (Table 2). The lowest ratio of standard error to mean in 1996 for N_2O was 6.26% (forest type in 1979), a land cover type of much area and thus, many 1 ha cells for calculating the mean and variance. The highest value was 38.49% (bare soil in 1992), a cover type of only 180 total ha in that year.

[59] It is clear from these data that the original forests were active sources of N_2O in pre-agricultural time and that changes in land use have not increased N_2O fluxes as much as might be supposed. Young pastures have the highest rates of specific N_2O production (Table 2) and are the leading source in 1996, but their overall contributions are temporary. Only if agricultural lands were abandoned to forest to subsequently recover their capacity for high N_2O production [*Reiners et al.*, 1994; *Keller and Reiners*, 1994] and were then reconverted to pasture, would young pastures continue to be the leading source areas of N_2O. Even under the growth scenario in which more forest was converted to young pasture, the percentage contribution by young pastures dropped to 35%. Under the stagnation scenario, the percentage went to zero because there was no more young pasture formation and the share of N_2O production by forests rose to 59% (Table 2). Under any probable scenario, the high rates of N_2O fluxes for the entire NAZ estimated for the late 20th century were temporary, depending on the high dynamical response of forest conversion to young pastures.

[60] The change in N_2O emissions resulting from agricultural development is a central question that stimulated this research; these results can help to set boundaries on how important such changes may have been for the lowland tropics globally. For the NAZ, the calculated 1900 regional flux rate of 2354 t N yr^{-1} is probably a reasonable estimate for a background value. Less certain is the year of maximum emissions. The year 1992, had the highest estimated emission of 3585 t N yr^{-1}, but we cannot know whether this was the peak year. The exact peak probably would have correlated with the year of maximum area in young pasture throughout the domain (Figure 6a), but without annual land cover data, that date cannot precisely be known. Given the similarity between 1992 and 1996, however, it is not

unreasonable to believe that the optimal combination of land use for maximum N_2O emission probably occurred in the early 1990s. Given these two end-points of 1900 and 1992, the difference in emission rates was 1231 t N yr^{-1}, a fractional change of only 52% over the 1900 rate. The contribution from the region increased, but the increase was limited by the considerable N_2O emitted from the original forest vegetation before development began.

[61] Regional rates from the NAZ could be extrapolated to similar climatic areas of Earth but would not be prudent. There are few areas in the wet tropics with native soils as fertile as these and where modern agriculture is practiced with such intensive nitrogen fertilization. These rates are comparatively high [*Matson and Vitousek*, 1990; *Bouwman et al.*, 1993] and might better be viewed as an upper limit at the regional scale in such environments.

3.3.2. Nitric Oxide

[62] The estimate for NO fluxes from soils to the directly overlying atmosphere in 1996 was 1899 t N yr^{-1} (Table 2) with a 95% confidence range of 1616 to 2183 kg N yr^{-1}. The relative importance of various land cover types relative to emissions of this gas were different from their ranking with respect to N_2O emissions as might be expected from the different production processes involved. Percentage contributions for 1996 in ascending order were: finca = 0.4, bare soil = 0.7, old pastures = 3.1, crops = 8.5, forest = 9.0, young pastures = 38.5, and banana = 40.0 (Figure 5b). These ascending rankings are products of land area and specific emission rates. The orders are the same for the two gases except for the top three producing areas. For N_2O, young pastures outrank forest and banana, whereas for NO, banana outranks young pastures and forest. Standard errors for NO regional fluxes were slightly higher than those for N_2O (Table 2). The lowest ratio of standard error to the mean was 8.75 for crops in the 2010 growth scenario, an area of 40,036 ha and the highest was 41.46% for bare soil in 1992, an area of only 180 ha.

[63] The effect of agricultural development led to more dramatic increases in regional NO emissions than they did for N_2O. The highest estimate for past NO emissions was for 1992, reaching 2040 t NO–N yr^{-1} (Table 2 and Figure 6b). This value was 485% higher than the estimated 1900 background level of 420 t NO–N yr^{-1}. Furthermore, the growth scenario for 2010 accelerates this rate slightly further to 2048 t NO–N yr^{-1}. This larger response is due to the role of fertilized banana plantations and crops in producing regional NO compared with the role of forests and ephemeral young pastures for N_2O (Table 2 and Figure 6b). NO flux is driven by fertilizer application so that as long as intensive agriculture persists in the NAZ, there will be higher rates of NO flux than existed in pre-development conditions. This is in contrast with N_2O where fluxes should decrease regardless of the future land use changes. The economic stagnation scenario shows how a decline in land in crops will lead to a decrease in NO flux, the result of lesser nitrogen fertilization application.

[64] Unlike N_2O, NO emissions from the soil do not necessarily lead to emissions from the ecosystem. In closed canopy tropical forests, most NO does not escape the canopy layer, particularly at night [*Bakwin et al.*, 1990; *Kaplan et al.*, 1988]. In the presence of ozone, NO reacts rapidly to form NO_2, a reactive compound that deposits on leaves and other surfaces. When the canopy is low and sparse, there is a greater likelihood that NO emitted at the soil surface will be released to the atmospheric boundary layer. For example, *Yienger and Levy* [1995] estimated canopy loss factors for NO_x gases for tropical canopy types to range from 39% for grasslands to 75% for rain forests. While we do not explore this possibility here, it is likely that the difference in the atmospheric contribution of NO from sparse canopies of developed landscapes as compared to the natural forest, is even greater than the difference resulting from the change in soil emissions [cf. *Keller et al.*, 1991].

3.4. Methodological Implications for Making Estimates for Heterogeneous Regions

3.4.1. Does an Ensemble Modeling Approach Make a Difference?

[65] The ensemble modeling approach used in this study was designed to provide a better estimate of regional fluxes for a heterogeneous region like the NAZ than could be provided by conventional methods. In this section we analyze how much difference the ensemble modeling approach makes compared with the conventional method of multiplying mean or median values for cohorts by their respective areas. First, we test the affect of multiple simulations for capturing the influences of variances and covariances of input variables in making flux estimates for single cohort. Second, we address the relationship between number of cohorts, the geographic "grain" of the regional analysis, with the final estimate. Third, we calculate the difference between the regional estimate produced by this ensemble method with the results of a straight-forward multiplication of cohort mean values by their area.

3.4.2. Effects of Taking Variance and Covariance Into Account on Individual Cohort Estimates

[66] To illustrate the importance of variances of covariance of the variables that define the individual cohorts, the leading five cohorts (in terms of making the largest contribution to regional flux of N_2O) were selected from the array of 1301 cohorts in 1996. These five were four young pasture cohorts, and one forest cohort. The land cover class, climate regime, drainage class, soil fertility class and soil texture class of these five cohorts are listed in Table 3. For each of these cohorts, N_2O and NO fluxes were calculated in two ways. The first used 20 simulations with each simulation based on statistical distributions for the variables. The second used mean values for driving variables associated with the cohorts.

[67] In about half of the cases (six of ten for both gases), the ensemble results were higher than the single simulation results (Figure 7). Differences between estimates for particular cohorts ranged from insignificant to 64% (difference/lower value) in the worst case. Clearly, there was a greater range of variation among cohorts computed by the conventional method; N_2O emissions varied from 5.1 to 32.1 kg N ha^{-1} yr^{-1} as compared with 6.1 to 20.7 kg N ha^{-1} yr^{-1} estimated by the ensemble approach. These results indicate that the ensemble approach, by incorporating variances and covariances, tends to "downweight" driving variable com-

Table 3. Major Environmental Conditions of the Five Dominant Simulation Cohorts in the JFD Table

							Ensemble			Single		
JFD-ID	Area, ha	Cover	Climate	Drainage	Fertility	Texture	N_2O	NO	stdd N_2O	stdd NO	N_2O	NO
1	7476	young pasture	3	1	1	10	20.7	10.2	3.0	2.0	16.0	6.2
2	6707	young pasture	4	4	3	14	16.8	7.0	3.2	1.2	11.5	4.7
3	5910	young pasture	3	4	3	14	16.4	6.8	1.7	1.2	20.3	7.3
4	4115	young pasture	4	3	1	9	19.5	9.5	4.0	2.4	32.1	12.6
5	10881	primary forest	18	4	3	14	6.0	1.0	0.5	0.2	5.3	0.8

binations that produce more skewed fluxes through single simulations. Consequently, the ensemble approach reduces the variability of fluxes among various cohorts in addition to providing confidence limits.

3.4.3. Effect of Number of Cohorts on the Regional Estimate

[68] Spatial data for the 1996 simulations led to 1301 cohorts, each a unique combination of land cover, soil texture, etc., and each making a different contribution to total regional flux. Here we examine the relationship between number of cohort classes, a measure of environmental variability taken into account by this study, and regional assessment accuracy. Table 4 shows the number of cohorts needed to account for different targets for total flux estimation. Half of the regional fluxes were located in just 47 and 61 cohorts, or 4% and 5% of the total number of cohorts for N_2O and NO fluxes, respectively. Clearly, the flux percentages and the area percentages were highly correlated. The more important cohorts usually had larger spatial extents rather than higher specific emission rates. Only 28% (329) and 30% (353) of the cohorts were needed to estimate 95% of the regional fluxes for N_2O and NO fluxes, respectively. Simulations performed on the remaining 70% of the smaller cohorts, which covered only about 10% of the area in the region, had little impact on regional flux estimates.

3.4.4. Conventional Method Bias Relative to the Ensemble Method

[69] The final question in this comparison is whether or not a conventional method of multiplying cohort means or medians by their areas would lead to a net underestimate, or overestimate for the region. Aggregate annual fluxes for each land cover type were calculated by the conventional method and the ensemble method and plotted as functions of one another (Figure 8). Regressions based on the land cover types were calculated and compared with a 1:1 relationship. The slopes of the linear regression of the conventional method against the ensemble method were <1 (0.89 and 0.84 for N_2O and NO fluxes, respectively), indicating that fluxes computed by the conventional method

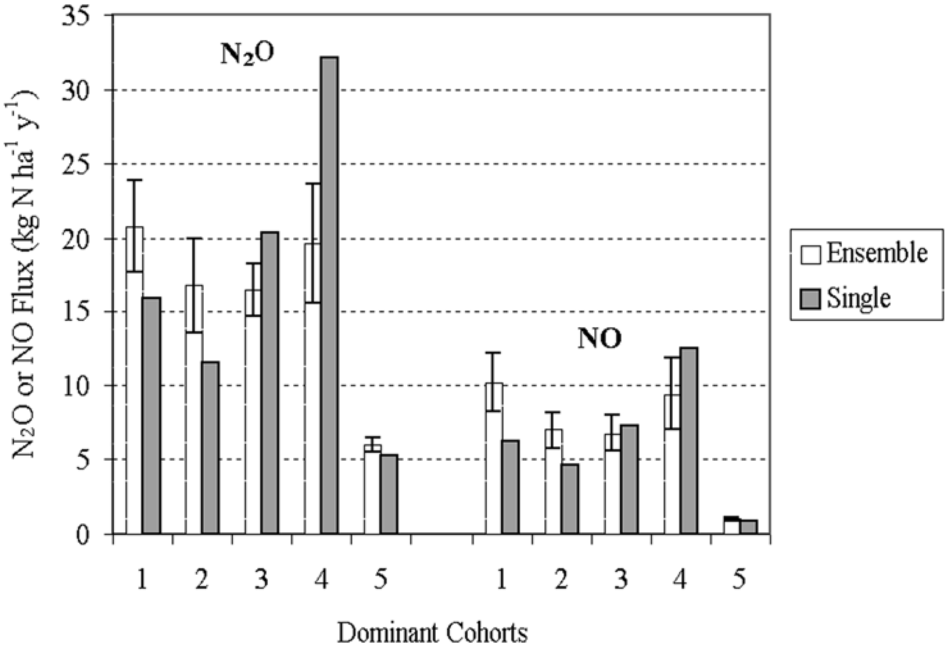

Figure 7. Estimated fluxes of N_2O and NO emissions from the five most dominant cohorts computed stochastic model simulations for each cohort versus simple multiplication of cohort areas by average emission values. The land cover for cohorts 1–4 was young pasture and that for cohort 5 was primary rain forest. One standard error is shown for the fluxes obtained by the ensemble approach (20 stochastic simulations for each cohort).

Table 4. Number of Cohorts and the Total Area Needed to Reach Prescribed Percentages of the Total Regional N_2O or NO Flux[a]

	Number of Cohorts Needed to Reach the Prescribed Percentage		Corresponding Area of Selected Cohorts	
Percentage of the Total Regional Flux	N_2O Flux	NO Flux	N_2O	NO
5	2 (0.2%)	2 (0.2%)	3.7	3.7
25	14 (1.2%)	22 (1.9%)	16.4	24.5
50	47 (4.0%)	61 (5.2%)	39.2	43.9
75	122 (10.5%)	143 (12.3%)	60.1	65.2
95	329 (28.2%)	353 (30.2%)	87.9	89.0

[a] The mean fluxes of N_2O and NO were sorted in descending order.

were systematically underestimated by 11% and 16% for these two gases, respectively. The mean regional area-weighted fluxes of N_2O and NO were 8.03 and 4.03 by the conventional method and 8.75 and 4.95 kg N ha^{-1} yr^{-1} by the ensemble approach, a difference of 8% and 18%, respectively, and an explicit measure of the downward bias by the conventional method.

[70] The power of the computational methodology used here is its capability of incorporating variances and covariances of the input variables in scaling ecological processes and phenomena from site to heterogeneous regions [*Liu et al.*, 2000]. This approach effectively addresses the impact of distributional information for input variables on the output of nonlinear ecological models at the regional scale. The conventional approach of simply multiplying the mean/mode of a cohort by its representative area and ignoring the differences among components of the cohort in parameterizing models may be biased in making regional estimates as well as prohibiting measures of variance for the regional estimate.

3.5. General Discussion

[71] This study presents a short time series and two future scenarios for N_2O and NO flux from a region representative of the wet, lowland tropics in terms of climate, soils and land use. According to these results, the regional flux rate for N_2O and NO varied over time since the development of agriculture in the 20th century although the mix of land use types had different effects on these two gas emissions. The most critical land use change for N_2O was the conversion of forest to pasture because for approximately 10 years, young pastures had extraordinary rates of flux. This means that an historic outburst of N_2O would be short-lived, however, and that the 52% increase between 1900 and the early 1990s was only temporary. Banana plantations and croplands utilizing nitrogenous fertilizers will maintain higher than preagricultural rates but not of such a dramatic level because their rates are close to the rates observed in the original forest vegetation. Scenarios of agricultural decline in the region would even lead to a lower regional flux rate than was experienced in the original forested condition.

[72] Regional NO flux was actually more highly influenced by land use change than was N_2O flux, increasing over estimated original conditions by 485%. As we note above, this considers only the flux to the atmosphere directly above the soil. Regional differences before and after development actually may be magnified by diminution in canopy absorption. Young pastures, while an important source, were less important than were banana plantations and croplands where nitrogen fertilizers vastly accelerated the rate of NO emissions. Not only are NO emissions altered more by land use change, but these elevated rates will be permanent as long as nitrogen fertilizers are added to croplands and banana plantations of the region.

[73] Perhaps more important than these results is the opportunity provided by this work to evaluate how well we can make such estimations. There are two important sources of uncertainty in our regional estimation using the modified CENTURY model. First, is the uncertainty inherent in the model; second is the uncertainty in the model inputs. In the first case, parameters of the model were calibrated to the mean conditions observed in the NAZ. Those mean observations were themselves uncertain and we have not attempted to evaluate how changes in internal model parameters would affect our regional estimations of flux. In the second case, we have exhaustively investigated variation in model response to inputs from the NAZ of Costa Rica. This region offers an unusual, if not unique, case for performing careful regional estimation because of the richness of spatial data on environmental drivers and field measurements of gas emissions. We used a statistical method for making spatial estimations that would account for internal variability of properties within GIS polygons and spatial covariance between the various drivers. Some sources of uncertainty in the land use, specifically confusion in classification of land cover types and designation of young versus old pastures could not be incorporated into an estimate of total uncertainty. Measures presented here are a lower bound to estimates of uncertainty because they did not take into account these other sources of error.

[74] If we only look at the standard error of estimate (Table 2) for the entire region in 1996, it is only 6.8% of the mean for N_2O flux and 7.2% of the mean for NO flux. That seems very good. If, however, we look at the full range of the 95% confidence interval, then the range is 27% of the N_2O mean flux and 30% of the NO mean flux for 1996. Estimates of uncertainty attributable to model performance, pasture age designation and land cover classification would raise these percentages even higher.

[75] What would it take in terms of effort and expense to reduce uncertainty further? How high must certainty be to make scientific inferences that go beyond boundary constraints on one hand, and that allow formulation of policy decisions affecting national economies and human welfare

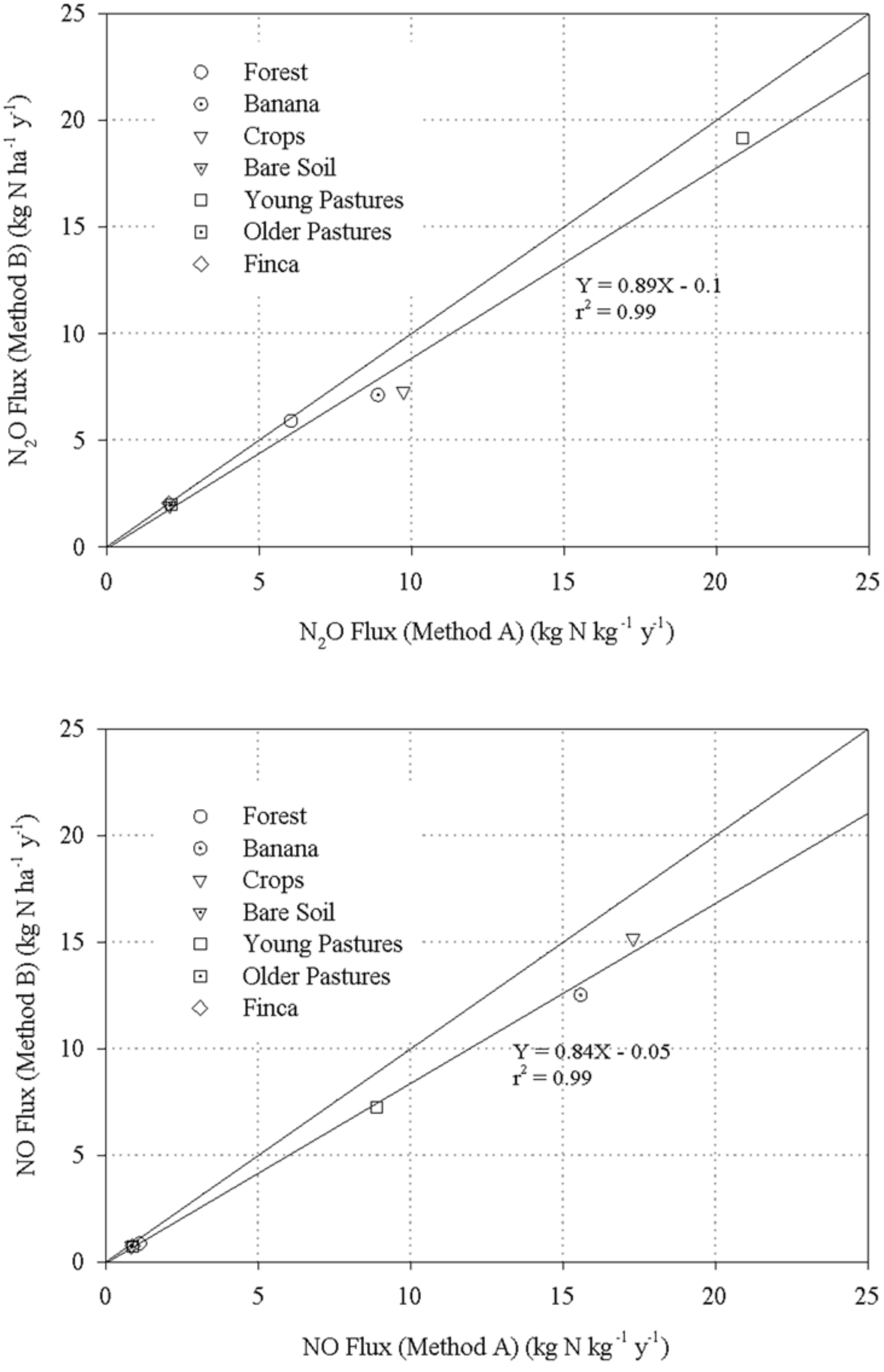

Figure 8. The difference of estimated mean fluxes of N_2O and NO using the ensemble stochastic modeling approach (abscissa) and the conventional method (ordinate). In the ensemble approach, 20 model simulations were run for each simulation cohort with values of model parameters stochastically generated from distributional information of input variables. In the conventional approach, only one model run was performed for each simulation cohort and the values for the model parameters were the "representative" values (e.g., medians or means).

on the other? Answers to these questions go beyond the proper limits of this paper, but perhaps the results of this study may aid in addressing them.

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References

Andreae, M. O., and D. S. Schimel (Eds.), *Exchange of Trace Gases Between Terrestrial Ecosystems and the Atmosphere*, 349 pp., John Wiley, New York, 1989.

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

Bouwman, A. F., Nitrogen oxides and tropical agriculture, *Nature*, *392*, 866–867, 1998.

Bouwman, A. F., I. Fung, E. Matthews, and J. John, Global analysis of the potential for N_2O production in natural soils, *Global Biogeochem. Cycles*, *7*, 557–597, 1993.

Bouwman, A. F., K. W. Van der Hoek, and J. G. J. Olivier, Uncertainties in global source distribution of nitrous oxide, *J. Geophys. Res.*, *100*, 2785–2800, 1995.

Burke, I. C., Landscape and regional biogeochemistry: Approaches, in *Methods in Ecosystem Science*, edited by O. E. Sala and H. A. Mooney, pp. 277–288, Springer-Verlag, New York, 2000.

Burrough, P. A., Soil information systems, in *Geographical Information Systems. Principles and Applications*, edited by D. J. MacGuire, M. F. Goodchild, and D. W. Rhind, pp. 153–169, John Wiley, New York, 1991.

Chameides, W. L., P. S. Kasibhatla, J. Yienger, and H. Levy II, Growth of continental-scale metro-agro-plexes, regional ozone pollution, and world food production, *Science*, *264*, 74–77, 1994.

Cicerone, R. J., Analysis of sources and sinks of atmospheric nitrous oxide (N_2O), *J. Geophys. Res.*, *94*, 18,265–18,271, 1989.

Crill, P. M., M. Keller, A. Weitz, B. Grauel, and E. Veldkamp, Intensive field measurements of nitrous oxide emissions from a tropical agricultural soil, *Global Biogeochem. Cycles*, *14*, 85–95, 2000.

Crutzen, P. J., The influence of nitrogen oxides on the atmospheric ozone content, *Q. J. R. Meteorol. Soc.*, *96*, 320–325, 1970.

Crutzen, P. J., The role of the tropics in atmospheric chemistry, in *The Geophysiology of Amazonia. Vegetation Climate Interactions*, edited by R. E. Dickinson, pp. 107–131, John Wiley, New York, 1987.

Davidson, E. A., Fluxes of nitrous oxide and nitric oxide from terrestrial ecosystems, in *Microbial Production and Consumption of Greenhouse Gases: Methane, Nitrogen Oxides, and Halomethanes*, edited by J. E. Rogers, and W. B. Whitman, pp. 219–235, Am. Soc. Microbiol., Washington, D. C., 1991.

Davidson, E. A., and W. Kingerlee, A global inventory of nitric oxide emissions from soils, *Nutr. Cycl. Agroecosyst.*, *48*, 91–104, 1997.

Davidson, E. A., P. A. Matson, and P. D. Brooks, Nitrous oxide emission controls and inorganic nitrogen dynamics in fertilized tropical agricultural soils, *Soil Sci. Soc. Am. J.*, *60*(4), 1145–1152, 1996.

Driese, K. L., W. A. Reiners, and R. C. Thurston, Rule-based integration of remotely-sensed data and GIS for landcover mapping in NE Costa Rica, *Geocarto Int.*, *16*(1), 35–44, 2001.

Ecklund, T. J., W. H. McDowell, and C. M. Pringle, Seasonal variation of tropical precipitation chemistry: La Selva, *Costa Rica, Tellus*, *31*, 3903–3910, 1997.

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

Granli, T., and O. C. Bockman, Nitrous oxide from agriculture, *Nor. J. Agric. Sci. Suppl.*, *12*, 1–128, 1994.

Hall, C. A. S., H. Tian, Y. Qi, G. Pontius, and J. Cornell, Modelling spatial and temporal patterns of tropical land use change, *J. Biogeogr.*, *22*, 753–757, 1995.

Houghton, J. T., *Global Warming. The Complete Briefing*, 2nd ed., p. 251, Cambridge Univ. Press, New York, 1997.

Houghton, J. T., L. G. Meira Filho, B. A. Callander, N. Harris, A. Kattenberg, and K. Maskell, *Climate Change. 1995. The Science of Climate Change*, p. 572, Cambridge Univ. Press, New York, 1996.

Ibrahim, M. A., Compatibility, persistence and productivity of grass-legume mixtures for sustainable animal production in the Atlantic Zone of Costa Rica, Ph.D. dissertation, Univ. of Wageningen, Wageningen, Netherlands, 1994.

Instituto de Investagaciones Sociales, La poblacion de Costa Rica, Cuidad Universitaria "Rodrigo Facio," p. 199, San Jose, Costa Rica, 1976.

Instituto Meteorologico Nacional, Programa de las Naciones Unidas para el Medio Ambiente Ministerio de Agricultura y Ganaderia, Instituto Geographico Nacional, Direccion General Forestal, Atlas del Cambio de Cobertura de la Tierra en Costa Rica, p. 32, San Jose, Costa Rica, 1996.

Kaplan, W. A., S. C. Wofsy, M. Keller, and J. M. DaCosta, Emission of NO and deposition of O_3 in a tropical forest system, *J. Geophys. Res.*, *93*, 1389–1395, 1988.

Keller, M., and P. A. Matson, Biosphere-atmosphere exchange of trace gases in the tropics: Evaluating the effects of land use changes, in *Global Atmospheric-Biospheric Chemistry*, edited by P. G. Prinn, pp. 103–117, Plenum, New York, 1994.

Keller, M., and W. A. Reiners, Soil-atmosphere exchange of nitrous oxide, nitric oxide, and methane under secondary succession of pasture to forest in the Atlantic lowlands of Costa Rica, *Global Biogeochem. Cycles*, *8*, 399–409, 1994.

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

Keller, M., E. Veldkamp, A. M. Weitz, and W. A. Reiners, Effect of pasture age on soil trace-gas emissions from a deforested area of Costa Rica, *Nature*, *365*, 244–246, 1993.

Keller, M., J. Melillo, and W. Z. de Mello, Trace gas emissions from ecosystems of the Amazon basin, *J. Br. Assoc. Advance. Sci.*, *49*, 87–97, 1997.

Khalil, M. A. K., and R. A. Rasmussen, The global sources of nitrous oxide, *J. Geophys. Res.*, *97*, 14,651–15,660, 1992.

Krabbe, W. K., The SIESTA geographic dataset: Instruction for its use and maintenance, Atlantic Zone, *Phase 2, Rep. 22b*, 53 pp., Atlantic Zone Program (Centro Agron. Tropic. de Invest. y Ensenanza (CATIE), Univ. Agric. de Wageningen (UAW) and Minist. de Agric. y Ganaderia de Costa Rica (MAG), Wageningen, Netherlands, 1993.

Kroeze, C., A. Mosier, and L. Bouwman, Closing the N_2O budget: A retrospective analysis 1500–1994, *Global Biogeochem. Cycles*, *13*, 1–8, 1999.

Lathrop, R. G., Jr., J. D. Aber, and J. A. Bognar, Spatial variability of digital soil maps and its impact on regional ecosystem modeling, *Ecol. Model.*, *82*, 1–10, 1995.

Lauer, W., Climate and weather, in *Tropical Rain Forest Ecosystems*, edited by H. Leith and M. J. A. Werger, pp. 7–53, Elsevier, New York, 1983.

Li, C., S. Frolking, and T. A. Frolking, A model of nitrous oxide evolution from soil driven by rainfall events, 1, Model structure and sensitivity, *J. Geophys. Res.*, *97*, 9759–9776, 1992a.

Li, C., S. Frolking, and T. A. Frolking, A model of nitrous oxide evolution from soil driven by rainfall events, 2, Model applications, *J. Geophys. Res.*, *97*, 9777–9797, 1992b.

Liu, S., W. A. Reiners, M. Keller, and D. S. Schimel, Model simulation of changes in N_2O and NO emissions with conversion of tropical rain forests to pastures in the Costa Rican Atlantic Zone, *Global Biogeochem. Cycles*, *13*, 663–677, 1999.

Liu, S., W. A. Reiners, M. Keller, and D. S. Schimel, Simulation of nitrous oxide and nitric oxide emissions from tropical primary forests in the Costa Rican Atlantic Zone, *Environ. Model. Software*, *15*, 727–743, 2000.

Logan, J. A., Nitrogen oxides in the troposphere: global and regional budgets, *J. Geophys. Res.*, *88*, 10,785–10,807, 1983.

Luizao, F., P. A. Matson, G. Livingston, R. Luizao, and P. M. Vitousek, Nitrous oxide flux following tropical land clearing, *Global Biogeochem. Cycles*, *1*, 163–170, 1989.

Matson, P. A., and P. M. Vitousek, Ecosystem approach to a global nitrous oxide budget, *BioScience*, *40*, 667–672, 1990.

Matson, P. A., C. Billow, S. Hall, and J. Zachariassen, Fertilization practices and soil variations control nitrogen oxide emissions from tropical sugar cane, *J. Geophys. Res.*, *101*, 18,533–18,545, 1996.

Matson, P. A., R. Naylor, and I. Ortiz-Monasterio, Integration of environmental, agronomic, and economic aspects of fertilizer management, *Science*, *280*, 112–115, 1998.

Matthews, E., Nitrogenous fertilizers: Global distribution of consumption and associated emissions of nitrous oxide and ammonia, *Global Biogeochem. Cycles*, *8*, 411–439, 1994.

McDade, L. A., and G. S. Hartshorn, La Selva Biological Station, in *La Selva. Ecology and Natural History of a Neotropical Forest*, edited by L. A. McDade et al., pp. 6–14, Univ. of Chicago Press, Chicago, Ill., 1994.

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

Mosier, A. R., J. M. Duxbury, J. R. Freney, O. Heinemeyer, and K. Minami, Nitrous oxide emissions from agricultural fields: Assessment, measurement and mitigation, *Plant Soil*, *181*, 95–108, 1996a.

Mosier, A. R., W. J. Parton, D. W. Valentine, D. S. Ojima, D. S. Schimel, and J. A. Delgado, CH_4 and N_2O fluxes in the Colorado shortgrass steppe, 1, Impact of landscape and nitrogen addition, *Global Biogeochem. Cycles*, *10*, 387–399, 1996b.

Mosier, A. R., W. J. Parton, D. W. Valentine, D. S. Ojima, D. S. Schimel, and O. Heinemeyer, CH_4 and N_2O fluxes in the Colorado shortgrass steppe, 2, Long-term impact of land use change, *Global Biogeochem. Cycles*, *11*, 29–42, 1997.

Mosier, A. R., J. A. Delgado, and M. Keller, Methane and nitrous oxide fluxes in an acid oxisol in western Puerto Rico: Effects of tillage, liming and fertilization, *Soil Biol. Biochem.*, *30*, 2087–2098, 1998.

Nevison, C., and E. Holland, A reexamination of the impact of anthropogenically fixed nitrogen on atmospheric N_2O and the stratospheric O_3 layer, *J. Geophys. Res.*, *102*, 25,519–25,536, 1997.

Nieuwenhuyse, A., Soils, geology, and soil related sustainability aspects of the perhumid tropical Limon basin, Costa Rica. Serie Technica., *Informe Technico 272*, p. 80, CATIE, Turrialba, Costa Rica, 1996.

Nunley, R. E., The distribution of population in Costa Rica, Foreign Field Research Program sponsored by Office of Naval Research, *Rep. 8*, p. 71, Natl. Acad. Sci., Natl. Res. Counc., Washington, D. C., 1960.

Parsons, W. F. J., and M. Keller, Controls on nitrate oxide emissions from tropical pasture and rain forest soils, *Biol. Fertil. Soils*, *20*, 151–156, 1995.

Parsons, W. F. J., M. E. Mitre, M. Keller, and W. A. Reiners, Nitrate limitation of N_2O production and denitrification from tropical pasture and rain forest soils, *Biogeochemistry*, *22*, 179–193, 1993.

Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima, Analysis of factors controlling soil organic matter levels in Great Plains grasslands, *Soil Sci. Soc. Am. J.*, *51*, 1173–1179, 1987.

Parton, W. J., C. V. Cole, J. W. B. Stewart, D. S. Ojima, and D. S. Schimel, Simulating regional patterns of soil C, N, and P dynamics in the central grasslands region, U.S., in *Ecology of Arable Land*, edited by M. Clarholm and L. Bergstrom, pp. 99–108, Kluwer, Norwell, Mass., 1989.

Parton, W. J., et al., Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide, *Global Biogeochem. Cycles*, *7*, 785–809, 1993.

Parton, W. J., D. S. Ojima, C. V. Cole, and D. S. Schimel, A general model for soil organic matter dynamics: Sensitivity to litter chemistry, texture and management, in *Quantitative Modeling of Soil Forming Processes*, *Spec. Publ. 39*, pp. 147–167, Soil Sci. Soc. of Am., Madison, Wis., 1994.

Parton, W. J., D. S. Ojima, and D. S. Schimel, Models to evaluate soil organic matter storage and dynamics, in *Advances in Soil Science, Structure and Organic Matter Storage in Agricultural Soils*, edited by M. R. Carter and B. A. Stewart, pp. 421–448, Lewis, Boca Raton, Fla., 1996a.

Parton, W. J., A. R. Mosier, D. S. Ojima, D. W. Valentine, D. S. Schimel, K. Weier, and A. E. Kulmala, Generalized model for N_2 and N_2O production from nitrification and denitrification, *Global Biogeochem. Cycles*, *10*, 401–412, 1996b.

Plant, R. A. J., GIS-based extrapolation of land use-related nitrous oxide flux in the Atlantic Zone of Costa Rica, *Water Air Soil Pollut.*, *105*, 131–141, 1998.

Plant, R. A. J., Regional analysis of soil-atmosphere nitrous oxide emissions in the Northern Atlantic Zone of Costa Rica, *Global Change Biol.*, *6*, 639–653, 2000.

Plant, R. A. J., and B. A. M. Bouman, Modeling nitrogen oxide emissions from current and alternative pastures in Costa Rica, *J. Environ. Qual.*, *28*(3), 866–872, 1999.

Prinn, R. G., et al., A history of chemically and radiatively important gases in air deduced from ALE/GAGE/AGAGE, *J. Geophys. Res.*, *105*, 17,751–17,792, 2000.

Rastetter, E. B., A. W. King, B. J. Cosby, G. M. Hornberger, R. V. O'Neil, and J. E. Hobbie, Aggregating fine-scale ecological knowledge to model coarser-scale attributes of ecosystems, *Ecol. Appl.*, *2*(1), 55–70, 1992.

Reiners, W. A., A. F. Bouwman, W. F. Parsons, and M. Keller, Tropical rain forest conversion to pasture: changes in vegetation and soil properties, *Ecol. Appl.*, *4*, 363–377, 1994.

Reiners, W. A., M. Keller, and K. G. Gerow, Nitrous oxide and methane fluxes across forest and pasture landscapes in Costa Rica, *Air Water Soil Pollut.*, *105*, 117–130, 1998.

Rodhe, H., A comparison of the contribution of various gases to the greenhouse effect, *Science*, *248*, 1217–1219, 1990.

Schimel, D. S., B. H. Braswell, E. A. Holland, R. McKeown, D. S. Ojima, T. H. Painter, W. J. Parton, and A. R. Townsend, Climate, edaphic, and biotic controls over storage and turnover of carbon in soils, *Global Biogeochem. Cycles*, *8*, 279–293, 1994.

Schimel, D. S., B. H. Braswell, and W. J. Parton, Equilibration of the terrestrial water, nitrogen, and carbon cycles, *Proc. Natl. Acad. Sci. U.S.A.*, *94*, 8280–8283, 1997a.

Schimel, D. S., Vemap participants, and B. H. Braswell, Continental scale variability in ecosystem processes: Models, data, and the role of disturbance, *Ecol. Monogr.*, *67*, 251–271, 1997b.

Stoorvogel, J. J., and G. P. Eppink, *Atlas de la Zona Atlantica Norte de Costa Rica: Programa Zona Atlantica*, p. 84, Cent. for Trop. Agron. Res. and Dev.-Wagen. Agric. Univ.-Costa Rican Min. of Agric. and Cattle Prod. (CATIE-UAW-MAG), Guapiles, Costa Rica, 1995.

Thompson, A. M., The oxidizing capacity of the Earth's atmosphere: Probable past and future changes, *Science*, *256*, 1157–1165, 1992.

Thompson, A. M., The oxidizing capacity of the Earth's atmosphere: Probable past and future changes, *Science*, *256*, 1157–1165, 1997.

Veldkamp, A., and L. O. Fresco, Reconstructing land use drivers and their spatial scale dependence for Costa Rica (1973–1984), *Agric. Syst.*, *55*(1), 19–43, 1997.

Veldkamp, E., and M. Keller, Nitrogen oxide emissions from a banana plantation in the humid tropics, *J. Geophys. Res.*, *102*, 15,889–15,898, 1997a.

Veldkamp, E., and M. Keller, Fertilizer induced nitric oxide emissions from agricultural soils, *Nutr. Cycling Agroecosyst.*, *48*, 69–77, 1997b.

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

Veldkamp, E., M. Keller, and M. Nunez, Effects of pasture management on N_2O and NO emissions from soils in the humid tropics of Costa Rica, *Global Biogeochem. Cycles*, *12*, 71–79, 1998.

Veldkamp, E., E. A. Davidson, H. E. Erickson, M. Keller, and A. M. Weitz, Soil nitrogen cycling and nitrogen oxide emissions along a pasture chronosequence in the humid tropics of Costa Rica, *Soil Biol. Biochem.*, *31*, 387–394, 1999.

VEMAP Participants, Vegetation/ecosystem modeling and analysis project: Comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO_2 doubling, *Global Biogeochem. Cycles*, *9*, 407–437, 1995.

Verchot, L. V., E. A. Davidson, J. H. Cattanio, I. L. Ackerman, H. E. Davidson, and M. Keller, Land use change and biogeochemical controls of nitrogen oxide emissions from soils in eastern Amazonia, *Global Biogeochem. Cycles*, *15*, 31–46, 1999.

Volk, C. M., et al., Quantifying transport between the tropical and mid-latitude lower stratosphere, *Science*, *272*, 1763–1768, 1996.

Weitz, A. M., P. M. Crill, M. Keller, E. Linder, and S. Frolking, N_2O emissions from humid tropical agricultural soils: Effects of soil moisture, texture and nitrogen availability, *Soil Biol. Biochem.*, *33*, 1077–1093, 2001.

Yienger, J. J., and H. Levy II, Empirical model of global soil-biogenic NOx emissions, *J. Geophys. Res.*, *100*, 11,447–11,464, 1995.

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