

Simulation of nitrous oxide and nitric oxide emissions from tropical primary forests in the Costa Rican Atlantic Zone

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Abstract

Nitrous oxide (N₂O) and nitric oxide (NO) are important atmospheric trace gases participating in the regulation of global climate and environment. Predictive models on the emissions of N₂O and NO emissions from soil into the atmosphere are required. We modified the CENTURY model (Soil Sci. Soc. Am. J., 51 (1987) 1173) to simulate the emissions of N₂O and NO from tropical primary forests in the Atlantic Zone of Costa Rica at a monthly time step. Combined fluxes of N₂O and NO were simulated as a function of gross N mineralization and water-filled pore space (WFPS). The coefficients for partitioning N₂O from NO were derived from field measurements (Global Biogeochem. Cycles, 8 (1994) 399). The modified CENTURY was calibrated against observations of carbon stocks in various pools of forest ecosystems of the region, and measured WFPS and emission rates of N₂O and NO from soil to the atmosphere.

WFPS is an important factor regulating nutrient cycling and emissions of N₂O and NO from soils making the accuracy of the WFPS prediction central to the modeling process. To do this, we modified the hydrologic submodel and developed a new method for the prediction of WFPS at the monthly scale from daily rainfall information. The new method is based on: (1) the relationship between monthly rainfall and the number of rainfall events, and (2) the relative cumulative frequency distribution of ranked daily rainfall events. The method is generic and should be applicable to other areas.

Simulated monthly average WFPS was 0.68±0.02 — identical with the field measurement average of 0.68±0.02 from the annual cycle observed by Keller and Reiners (Global Biogeochem. Cycles, 8 (1994) 399). Simulated fluxes of N₂O and NO were 52.0±9.4 mg-N m⁻² month⁻¹ and 6.5±0.7 mg-N m⁻² month⁻¹, respectively, compared with measured averages of 48.2±11.0 mg-N m⁻² month⁻¹ and 7.1±1.1 mg-N m⁻² month⁻¹. The simulated N₂O/NO ratio was 11.2±1.9 compared with the measured value of 10.9±4.7.

WFPS is the dominant determinant of the fraction of gross N mineralization that is emitted from the soil as N₂O and NO. If WFPS were not limiting during part of the year, this fraction would be 4.2%. With some periods of lower WFPS, the realized fraction is 2.2%. Because of the strong relationships between N₂O and NO emission rates and rainfall and its derivative, WFPS, these moisture variables can be used to scale up nitrogen trace gas fluxes from sites to larger spatial scales. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: CENTURY; Nitrogen; Mineralization; Modeling; Rainfall; WFPS

Software availability

Name: CENTURY

Developer: The CENTURY crew, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, USA.

Tel.: +1-970-491-1982

Fax: +1-970-491-1965

Email: century@nrel.colostate.edu

Year first available: 1988. The modified version was available in 1998.

Hardware required: Sun workstations

Software specifications: Languages Fortran and C/C++, Unix Operating System

Cost: Free on request

* Corresponding author. Current address Raytheon Systems Company, EROS Data Center, Sioux Falls, SD 57198, USA. Tel.: +1-605-594-6168; fax: +1-605-594-6529.

E-mail address: sliu@edcmail.cr.usgs.gov (S. Liu).

1. Introduction

1.1. Nitrogen oxide fluxes from tropical ecosystems

Nitrous oxide (N_2O) is an important greenhouse gas (Ramanathan, 1988) and participates in reactions leading to depletion of the stratospheric ozone (Crutzen, 1970; Cicerone, 1989). Nitric oxide (NO) participates in numerous reactions affecting acid deposition (Calvert and Stockwell, 1983) and photochemical production of tropospheric ozone (Logan, 1983; Thompson, 1992).

The N_2O budget is not clearly understood (Nevison and Holland, 1997) but wet tropical forest soils are estimated to be the largest single global source of N_2O , producing about 2.4 Tg N_2O -N yr^{-1} or about 30% of the global production (Matson and Vitousek, 1990; Davidson, 1991; Bouwman et al., 1995). Wet tropical forest soils also emit NO at a rate of 2.2 Tg NO-N each year (Davidson, 1991). The emissions of N_2O and NO from soil into the atmosphere are byproducts of nitrification and denitrification (Firestone and Davidson, 1989; Granli and Bockman, 1994), which are controlled, in turn, by many factors including N availability, the quality and quantity of soil organic matter (which serves as energy source for most microbial processes), soil texture, pH, soil microbial activity, soil moisture, soil aeration and soil temperature. These soil variables are proximal controls of the processes which, in turn, are affected by management practices such as fertilization, cultivation and shifting land use (Robertson, 1989; Keller et al., 1993).

Numerous field measurements on the emission rates of N_2O and NO from various soils consistently demonstrate strong spatial and temporal variabilities (Keller et al. 1986, 1988; Matson and Vitousek, 1987; Livingston et al., 1988; Parton et al., 1988; Luizao et al., 1989; Davidson, 1991; Granli and Bockman, 1994; Keller and Reinert, 1994; Mosier et al. 1996, 1997). Even the most extensive and long-term of these studies involved limited time and range of environmental conditions. Continuous monitoring of these trace gas emissions in the field is expensive and technologically difficult at present. In addition, both land cover and land use management practices are changing rapidly. As a result of both spatial/temporal variability in emission rates, and the fast rate of land use change, predictive models on the production of nitrogen trace gases from various ecosystems are necessary for scaling up field measurements to regional and global scales, and for predicting future changes in emission rates of these gases.

1.2. Modeling approaches for estimating nitrogen oxide emissions

Several modeling approaches have been proposed for estimating the emission of nitrogen trace gases from

various ecosystems at different temporal and spatial scales (Matson and Vitousek, 1990; Li et al., 1992a,b; Bouwman et al., 1993; Bouwman and Taylor, 1996; Parton et al., 1996; Potter et al. 1996, 1997). The CENTURY model simulates emissions of total nitrogen gases as fractions of gross and net N mineralization (Metherall et al., 1993). The CASA model, which is based in part on the soil organic matter submodel of CENTURY, simulates the total emission of nitrogen trace gases from soils as a fraction of gross N mineralization, and partitions N_2O , NO and N_2 from the total flux by hypothesized relations drawn from laboratory studies (Potter et al. 1996, 1997). The DNDC model simulates N_2O and NO fluxes at a daily time step by explicitly considering the physical, chemical and biological controls on the nitrification and denitrification processes (Li et al., 1992a,b). The NGAS model (Parton et al., 1996) simulates N_2O and N_2 emissions from soils in the Great Plains based on soil texture, soil NH_4^+ , soil WFPS, soil N turnover rate, and soil temperature. To date, the only effort to model the nitrogen trace gas emissions specifically from tropical forest soils at the field scale has been made by Potter et al. (1997) with CASA. However, CASA's performance to date produces differences between predicted and measured N_2O fluxes on a daily basis of about one order of magnitude.

1.3. The CENTURY model

We have selected the CENTURY model (Parton et al., 1987; Metherall et al., 1993; Parton et al., 1994a,b) for modification and development as a part of a larger study dedicated to the scaling up of nitrogen trace gas emission estimates from sites to regions in the Costa Rican Atlantic Zone. CENTURY simulates the long-term dynamics of carbon, nitrogen, phosphorus and sulfur for different plant-soil systems. Specific plant production submodels (e.g. grassland, forest and crop) are linked to a common soil organic matter (SOM) submodel. The SOM submodel simulates the flows of selected elements through the different inorganic and organic pools in the top 20 cm of the soil, running on a monthly time step. CENTURY includes a simplified water budget submodel which calculates monthly evapotranspiration, water content of the soil, and saturated flow between soil layers. The CENTURY model obtains input values through twelve data files, each containing a certain subset of variables describing characteristics of crop/tree, soil, and management practices. For the purpose of our larger study, CENTURY must be modified and parameterized for major ecosystems of the Atlantic Zone. One of these is the tropical primary forest.

1.4. Requirements for modifying CENTURY for tropical wet forests

Although CENTURY has successfully simulated carbon dynamics and plant production in various ecosys-

tems around the world (e.g., Parton et al. 1987, 1993; Schimel et al., 1994), some difficulties have been experienced in application to wet tropical areas (Vitousek et al., 1994; Motavalli et al. 1994, 1995). One of the reasons might be the disjunction between the relatively long monthly time step used in CENTURY compared with the high frequency dynamics of precipitation and soil moisture content. It is assumed originally in the CENTURY model that total monthly rainfall is precipitated in one single event with soil being wetted once. Soil moisture content is calculated as the difference between rainfall and potential evapotranspiration (PET) if rainfall is larger than the PET. If the difference is larger than field capacity of the soil, soil moisture equals field capacity; the rest of the water goes to deep percolation. If PET is higher than rainfall, there is no recharge to the soil water pool. Evapotranspiration (ET) depletes the soil available water, which varies between field capacity and wilting point, to either meet the PET requirement until soil moisture content reaches the wilting point of the soil. Soil moisture is determined according to water storage in previous month, net rainfall input, and the amount of water being withdrawn by ET. Using this scheme, soil moisture remains at field capacity in areas with abundant rainfall such as moist tropical areas, and it remains at the wilting point in areas where PET is larger than rainfall. In reality, this is not the case. Soil moisture seldom reaches the wilting point at the monthly scale in wet tropical regions.

Time step is an important factor for model selection and development. The time step chosen depends on research purposes, data availability, our understanding of the problem, and requirements on computational efficiency. For the estimation of seasonal and annual fluxes of nitrogen trace gases at the regional or global scale, a model with a monthly time step is generally sufficient as long as it adequately integrates conditions over the desired time scale in a manner representing outcomes from models having shorter time steps. One of the short-term driving variables for nitrogen trace gas emissions from soils is the soil wetting–draining dynamic associated with rainfall events. This short-term dynamic can be addressed with a short-term time step like a day as done by Li et al. (1992a, 1992b) with DNDC, or NGAS by Parton et al. (1996). But, short time step models require equivalent weather data or their facsimiles to simulate the effects of rainfall events. In fact, daily weather data are neither easy to obtain in many tropical regions, nor easy to simulate for future conditions. If rain event frequencies, along with monthly precipitation, can be properly represented in the hydrology submodels of monthly time step models, they would have the advantages of fewer weather data requirements (monthly precipitation, maximum and minimum temperatures are easier to get and often demonstrate less spatial variability in time and space than do daily/hourly data), and they would cost

less computationally because of their higher speed and lesser memory requirements.

1.5. Objectives

The objectives of this research were to: 1) modify the hydrologic submodel of the CENTURY, due to its importance in regulating biogeochemical processes in general and nitrogen trace gas emission rates from soils in particular, (2) to develop methods for modeling the emissions of nitrogen trace gases from soils at the monthly time step scale, (3) to independently parameterize the modified CENTURY model with data about moist tropical primary forests, (4) to calibrate the modified CENTURY with field measurements of water-filled pore space (WFSP), N_2O and NO fluxes, and (5) to predict N_2O and NO emissions from a tropical moist primary forest at a monthly time step.

2. Methods

2.1. The study area

Field measurements of nitrous oxide, nitric oxide, and soil moisture were obtained from three primary forest sites at the La Selva Biological Station (10°26'N, 84°0'W) in the Costa Rican Atlantic Zone over an annual cycle (Keller and Reiners, 1994). This station is one of the last places in that region in which upland primary rain forests can be studied as representatives of other remaining forest tracts and of areas now deforested. General information about La Selva and the region can be found in McDade et al. (1994); detailed information about the sites is given by Reiners et al. (1994) and Keller and Reiners (1994). Mean annual rainfall between 1984 and 1996 at La Selva was 3516 mm (Fig. 1). Mean monthly maximum and minimum air temperatures during the same period were 30.6 and 21.0°C, respectively. Each of the three forest sites was sampled in replicate monthly from October 1990 to December 1992 (Keller and Reiners, 1994).

2.2. Model modification

2.2.1. The hydrologic submodel

A new hydrologic submodel was developed to replace the original CENTURY version. The new submodel uses data related to total monthly rainfall, the number of rainy days, and the frequency distribution of the daily rainfall classes. The hydrologic submodel was modified from the original format described in the introduction by combining the relationship between monthly rainfall and the number of rainy days with the relative frequency distribution of ranked daily rainfall classes. The following statistical relationships were first developed based on

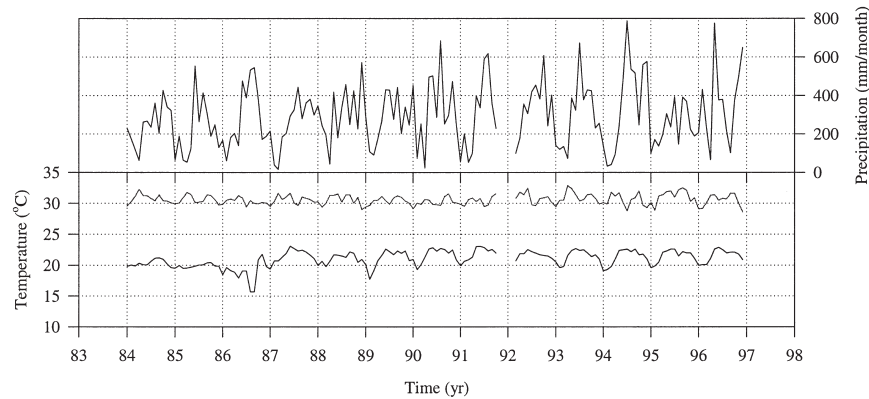


Fig. 1. Monthly precipitation, maximum and minimum temperatures as measured at the weather station at the La Selva Biological Station, Costa Rica, from 1984 to 1996.

historical daily rainfall information from La Selva (Fig. 1):

1. The association of the number of monthly rainy days with monthly rainfall, and
2. The relative frequency distribution of ranked daily rainfall amounts.

Fig. 2 illustrates the relationship between the number of rainy days in a month and monthly rainfall for La Selva Biological Station. These data show that the number of monthly rainy days varies from about 10 to 25 and is quite closely related to total monthly rainfall amount. By sorting daily rainfall amounts in descending order, the relationship between the normalized cumulative rainy

days and the normalized cumulative rainfall as observed at La Selva was developed (Fig. 3).

Fig. 3 suggested that daily rainfall varied greatly during the course of the year. Large daily rainfall events accounted for about 55% of the total annual precipitation although they only happened on 20% of the rainy days. If we assume all the rainy days are evenly distributed in time, the rest of the rainy days (80%) will certainly play a more important role in determining the regime of monthly soil moisture because they cover 80% of the time. Due to the importance of bypass flow in the soil hydrologic regime in the study area (Radulovich et al., 1992), large daily rainfall events (particularly if they are brief) may play a limited role in regulating mean monthly soil moisture content compared to the more fre-

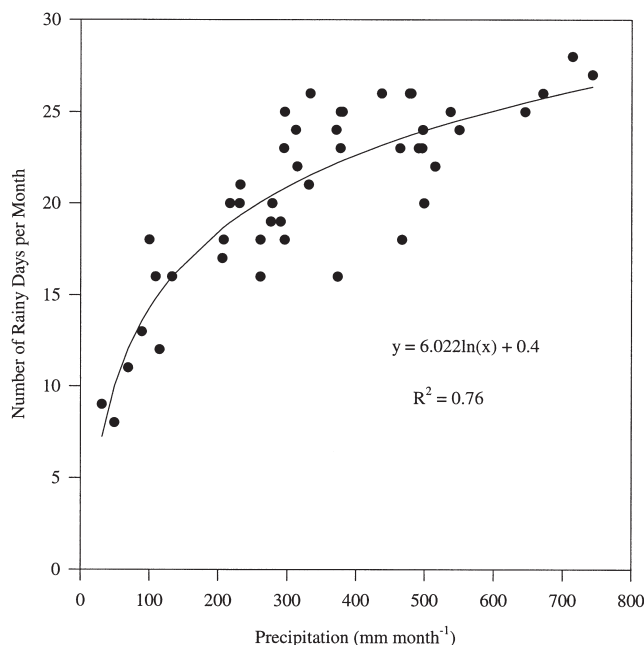


Fig. 2. Relationship between monthly rainfall and the number of rainfall events at La Selva, Costa Rica, from 1984 to 1991.

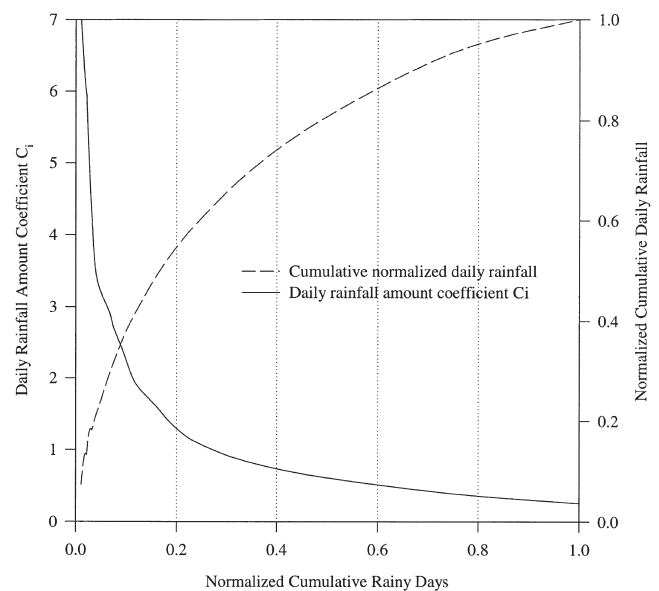


Fig. 3. Relationships between normalized cumulative daily rainfall, daily rainfall amount coefficient C_i (see text for details) and normalized cumulative rainy days at La Selva, Costa Rica, from 1984 to 1991. Daily rainfall values were sorted in descending order.

quent small ones. Large rainfall events may essentially run quickly through the macropores, therefore, separation of the total rainfall into various rainfall classes may be helpful in the simulation of monthly soil moisture dynamics.

In order to capture the impact of small but frequent daily rainfall events in the simulation of monthly soil moisture, five rainfall classes with an equal frequency were used in this study (Fig. 3). The average amount of daily rainfall in each class was determined using the following procedures:

1. Develop the relationship between cumulative normalized rainy days and the cumulative, ordered, normalized daily rainfall (Fig. 3);
2. Calculate the average daily rainfall amount coefficient (C_i) for each class. The rainfall amount coefficient is the slope of the curve developed in step 1;
3. Calculate the average amount of daily rainfall for class i (R_i) by using the following formula:

$$R_i = C_i \frac{P}{n} \quad (1)$$

where P and n are monthly total rainfall and its corresponding number of events, respectively. The number of rainfall events is calculated based on monthly rainfall using the relationship developed before (Fig. 2).

In the model, it was assumed that rainy days were evenly distributed in time over the course of the month and that rainfall for any given rainy day can be the daily rainfall associated with any of the five classes, with the same probability of 0.2. The average monthly soil moisture for each soil layer k was approximated as:

$$\bar{\theta}_k = \frac{1}{5} \sum_{j=1}^5 \frac{\theta_{k,0} + \theta_{k,j,1}}{2} \quad (2)$$

where $\theta_{k,0}$ and $\theta_{k,j,1}$ are soil moisture contents at the beginning and end of the month, respectively, for soil layer k and rainfall class j . Soil moisture content at the end of the month was calculated using the following mass conservation equation:

$$\theta_{k,j,1} = \theta_{k,0} + \sum_{i=1}^n (I_{k,j} - O_{k,j,i} - E_{k,j,i}) \quad (3)$$

where n is the number of rainy days in a month, $I_{k,j}$ is average net daily rainfall (i.e., gross mean daily rainfall R_i minus interception) for the first soil layer ($k=1$) or the amount of water input from the upper layer through percolation ($k>1$) for rainfall class j , $O_{k,j,i}$ is the amount of water in layer k that is percolated to the deeper layer,

and $E_{k,j,i}$ is the evapotranspiration loss from layer k during a wet–dry cycle (i.e., from the beginning of a rainy day to the beginning of the next rainy day). In the model, net rainfall was routed through the top soil layer by simply filling up soil moisture content to its field capacity and the excess, if any, was routed through the lower layers in a similar way. No soil hydraulic properties were used in the routing process due to the coarse time step used in the model. In reality, rainy days rarely distributed evenly over time. They might be clustered (e.g., a large daily rainfall event followed by a series of small daily rainfall events). Therefore, the current hydrological sub-model might be improved by including the simulation of the distribution of rainy days in time (i.e., sequence of rainy days) rather than using the assumption of even distribution.

2.2.2. The N_2O and NO emission submodel

The combined flux of N_2O and NO is assumed to be a function of gross nitrogen mineralized and water-filled pore space (WFPS):

$$F_{N_2O+NO} = a * N_{min}^* f_{WFPS} \quad (4)$$

where F_{N_2O+NO} is the combined flux of nitrous oxide and nitric oxide, N_{min} is the gross nitrogen mineralized, a is the fraction of N_{min} emitted at optimal WFPS, and f_{WFPS} (ranged from 0 to 1) is the regulation of WFPS on the combined flux. The rationale behind Eq. (4) is based on: 1) N_2O flux is proportional to nitrogen mineralization potential at the regional scale (Matson and Vitousek, 1987), 2) N_2O flux is proportional to nitrification rate (Maag and Vinther, 1996) which in turn is a function of soil moisture (Keller and Reiners, 1994; Maag and Vinther, 1996) and nitrogen mineralization (Adams and Attiwill, 1982), and 3) NO and N_2O fluxes are dependent on soil moisture (Parton et al., 1988; Luizao et al., 1989; Drury et al., 1992; Parsons et al., 1993; Keller and Reiners, 1994).

According to field measurements obtained from primary forests in Costa Rica (Keller and Reiners, 1994), the relationship between monthly N_2O/NO and WFPS can be described by:

$$R_{N_2O/NO} = a_1^* e^{b_1 WFPS} \quad (5)$$

where a_1 and b_1 are coefficients. Therefore, nitrous oxide flux is:

$$F_{N_2O} = \frac{F_{N_2O}}{F_{N_2O} + F_{NO}} F_{N_2O+NO} = \frac{1}{1 + \frac{1}{a_1} e^{-b_1 WFPS}} F_{N_2O+NO} \quad (6)$$

and nitric oxide flux is:

$$F_{NO} = F_{N_2O+NO} - F_{N_2O} \quad (7)$$

2.3. Model parameterization

Parameterization of a generic model is essential for simulating the dynamics of a specific ecosystem type like the the tropical primary forest in the Costa Rican Atlantic Zone. Values for more than 100 variables relevant to the characteristics of trees and site were obtained or estimated. The values assigned to these variables were selected from data available in the literature from wet tropical regions, but derived from studies carried out in Costa Rica as much as possible. Some of the parameter values are listed in Table 1. Other parameters for the tropical moist primary forest ecosystems are described below:

1. The C/N ratios of active soil organic matter (SOM), slow SOM and passive SOM were assigned values of 13, 25 and 10, respectively (Schimel et al., 1994). The C/N ratio of newly formed slow SOM produced from active SOM was assigned 15 (Parton et al., 1993).
2. Assigned values for nitrogen concentrations (% of dry weight) in live leaves, fine branches, large wood, coarse root and fine root were 1.55 (Scatena et al.,

1993), 1.42 (Heaney and Proctor, 1989; Schimel et al., 1994), 0.45, 0.19, 0.28 and 1.57 (Scatena et al., 1993), respectively. The corresponding C/N ratios were 29, 111, 263, 178 and 31 for live leaves, fine branches, large wood, coarse root and fine root, respectively.

3. Theoretical maximum gross production was placed at $600 \text{ g C m}^{-2} \text{ month}^{-1}$. Maximum net primary production (NPP) of the ecosystem was $275 \text{ g C m}^{-2} \text{ month}^{-1}$, based on biomass and litterfall information (Table 1).
4. Forest production allocation coefficients were estimated based on production of each part (Golley et al., 1975; Raich, 1983; Jordan, 1989) as follows: 0.460, 0.160, 0.168, 0.130 and 0.082 for leaves, fine branches, large wood, coarse root and fine root, respectively.
5. Monthly leaf litterfall rate was assumed to be constant based on the observation of Heaney and Proctor (1989) and Wieder and Wright (1995). Monthly death rates of other parts ((production or litterfall)/biomass/12) were estimated based on production or litterfall and their corresponding standing biomass, assuming the primary forests are under

Table 1
Parameterization of CENTURY for a tropical primary forest in Costa Rica

Category	Variable	Initial Value	Simulated	References ^a
Soil	bulk density (g cm^{-3})	0.7		1, 2, 3, 4
	sand content	0.12		5, 2, 3
	silt content	0.15		5, 2, 3
	clay content	0.73		5, 2, 3
	porosity (g cm^{-3})	0.75		1
	pH	4.5		6, 1, 3, 4
	rooting depth (cm)	50		2
	soil C (g C m^{-2})	5560	5848	2, 7
	SOM C/N ratio	10		1, 8, 9
Forest floor	total C (g C m^{-2})	2000		2, 7
	C in non-woody debris (g m^{-2})	122		2
Live biomass	Leaves (g C m^{-2})	364	330	10
	Fine branches (g C m^{-2})	5000 ^b	4847	
	Large wood (g C m^{-2})	10000 ^b	10148	
	Total above-ground wood	15000	15021	10
	Coarse root (g C m^{-2})	2640 ^c	2624	
	Fine root (g C m^{-2})	145	139	2
	Total root (g C m^{-2})	2785	2763	10, 11
	Leaves (g C m^{-2})	342		8
Litter	Small woody debris	113	125	2, 8
	Large woody debris	1641 ^d	1578	
	Above-ground woody debris	1754	1703	2
	Coarse root debris	528 ^e	548	
	Fine root debris	289 ^f		

^a Reiniers et al. (1994); 2: Raich (1983); 3: Werner (1984); 4: Vitousek and Denslow (1986); 5: Fernandes and Sanford (1995); 6: Gower (1987); 7: Veldkamp (1994); 8: Marrs et al. (1988); 9: Heaney and Proctor (1989); 10: Golley et al. (1975); 11: Jordan (1989).

^b Based on total above-ground biomass and assume 0.5 to be the ratio of fine branches (diameter >10 cm) and large wood.

^c Total root biomass minus fine root biomass.

^d Total above-ground woody debris minus small woody debris.

^e Assuming equal to 20% of coarse root biomass.

^f Assuming equal to fine root biomass.

quasi-steady state conditions. The monthly death rates assigned were 0.0352, 0.0018, 0.0012 and 0.0032 for fine root, fine branches, large wood and coarse root, respectively.

6. The decomposition rates of fine branches, large wood and below-ground woody tissue were assigned 5.0, 0.4 and 0.9, respectively, based on the turnover rate of each part and assuming the ecosystem has reached steady state conditions.
7. Specific leaf area was given a value of $0.00667 \text{ m}^2 \text{ g}^{-1}$ (Vitousek et al., 1994). Maximum sapwood biomass was designated as 9950 g m^{-2} (Jordan, 1989).
8. Soil organic carbon was partitioned into active, slow and passive pools according to Veldkamp (1994) and assuming the active pool accounts for 3% of the total SOC. As a result, the active, slow and passive SOC pools were 184, 2550 and 2650 g C m^{-2} , respectively.
9. Based on the average annual energy balance equation, Sellers (1965) recommended the following equation to estimate annual potential ET (PET in mm year^{-1}):

$$\text{PET} \approx 1000 \frac{(1-\alpha)R_0}{L} \quad (8)$$

where α is albedo of the surface, R_0 is the annual incident radiation ($\text{J m}^{-2} \text{ year}^{-1}$), and L is the latent heat of vaporization (J m^{-3}). There are no radiation data available at the La Selva weather station. However, based on radiation measurements from Los Diamantes ($83^\circ 46' \text{W}$ and $10^\circ 13' \text{N}$) and a value of 0.12 for albedo (Shuttleworth, 1989), the PET was estimated to be 1538 mm yr^{-1} .

10. According to Eklund et al. (1997), nitrogen deposition (N_{dep} in $\text{g N m}^{-2} \text{ yr}^{-1}$) from the atmosphere is closely related to annual precipitation (P in cm):

$$N_{\text{dep}} = -3.515 + 0.0114P \quad (9)$$

11. No experimental data were available on the value of the coefficient a in Eq. (4). However, a value of 0.02 was used by Potter et al. (1996) to estimate the emissions of nitrogen trace gases from various ecosystems including tropical moist forests. Model simulation of N_2O and NO emissions from pastures in the same region indicated an emission value of 0.05 (Liu et al., 1999). We have initially adopted Potter's value and the applicability of this value to our system will be further evaluated.
12. According to field measurements (Keller and Reiners, 1994), the regulatory influence of WFPS on the

total flux of N_2O and NO is illustrated in Fig. 4 and described by the following equation:

$$f_{\text{WFPS}} = \frac{0.0137 e^{9.1287 \text{WFPS}}}{M_{\text{N}_2\text{O}+\text{NO}}} \text{ for WFPS} < \text{WFPS}(M_{\text{N}_2\text{O}+\text{NO}}) \quad (10)$$

where $M_{\text{N}_2\text{O}+\text{NO}}$ and $\text{WFPS}(M_{\text{N}_2\text{O}+\text{NO}})$ is the maximum measured total flux of N_2O and NO and its corresponding WFPS, respectively. The maximum flux $M_{\text{N}_2\text{O}+\text{NO}}$ is $16 \text{ ng cm}^{-2} \text{ hr}^{-1}$ as measured by Keller and Reiners (1994) (Fig. 4). For con-

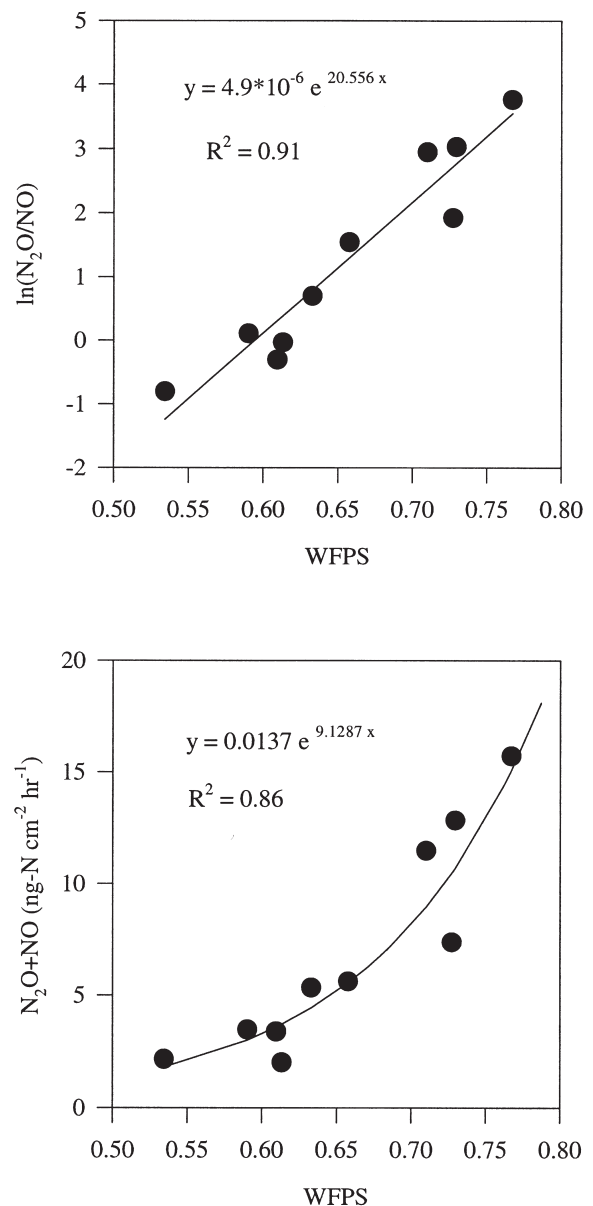


Fig. 4. The $\text{N}_2\text{O}+\text{NO}$ ~WFPS and $\text{N}_2\text{O}:\text{NO}$ ~WFPS relationships as measured by Keller and Reiners (1994) from three tropical primary forests in Costa Rica.

venience, the f_{WFPS} is assumed to be 1 when WFPS exceeded $WFPS(M_{N_2O+NO})$. In reality, the total flux of N_2O and NO would decline as WFPS approaches 100% from $WFPS(M_{N_2O+NO})$, with N_2 as becoming the dominant N gas emitted. However, this may not actually occur in the model as monthly mean WFPS values are probably never near 100% at uplands.

13. The ratio of nitrous oxide to nitric oxide is described by the following equation based on the data presented by Keller and Reiners (1994) (Fig. 4):

$$R_{N_2O/NO} = 4.9 \cdot 10^{-6} \cdot e^{20.556 WFPS} \quad (11)$$

2.4. Model calibration

The model was run for a 3000 year simulation to reach “quasi-steady state” conditions in order to calibrate ecosystem dynamics. Monthly precipitation, maximum and minimum temperatures collected from 1984 to 1996 at La Selva Biological Station (Fig. 1) was used to run the model. The climatic records during this 13 year period were repeated for the simulation period of 3000 years (when a “quasi-steady state” has been reached). The missing values at the end of 1991 and beginning of 1992 were filled with the records of the previous year.

The model was first calibrated with observations of (1) live biomass of leaves, fine branches, stems, coarse roots and fine roots, (2) soil organic carbon (SOC) in the top 20 cm of the soil, (3) active, slow and passive pools of SOC, and (4) woody debris on the forest floor, to make sure that the model was parameterized correctly to simulate the carbon dynamics and forest production. Then, the simulated results of WFPS, and fluxes of N_2O and NO corresponding to the climate conditions when the field measurements were taken (Keller and Reiners, 1994) were calibrated in terms of its ability to predict nitrogen trace fluxes at the monthly time scale. During the calibration period, decomposition rates of SOC in various pools and field capacity of the soil, were adjusted until the differences between simulated results and the field-based estimates of the above mentioned ecosystem characteristics were within 10% of error. While, theoretically, the relative predictive errors on these characteristics could be minimized by searching through many iterative simulations, it was impossible in our case to reach a solution within a reasonable amount of time, given the amount of time required to finish a 3000-year run and the large number of runs. Therefore, our calibration method was empirical and based on our previous knowledge about the systems. It is possible to calibrate the model within 5% error limit if only one single characteristic of the system such as leaf biomass was used. Many calibration runs indicated that the minimal

error limit was 10% if the model were calibrated against all the above-mentioned ecosystem characteristics simultaneously.

2.5. Model validation

The WFPS, N_2O and NO field data collected from another forest site near Guacimo ($10^{\circ}12'N$, $83^{\circ}32'W$), also located in the Atlantic lowlands of Costa Rica (Keller et al., 1993), was used for validation. This site was sampled eight times during the period February to November 1992 for N_2O fluxes. Because no site-specific field measurements were available about the characteristics (e.g., biomass, net primary production, SOC) of the forest, we applied the La Selva forest parameterization, as accomplished in the calibration phase, to the Guacimo forest. Climate data, including monthly rainfall, monthly maximum and minimum air temperatures, was obtained from Guacimo Weather Station.

2.6. Model predictions

The long-term dynamics of the N_2O and NO emissions from the ecosystem were analyzed based on the simulated results of a 13 year period under “quasi-steady state” conditions. The number of years included in the analysis corresponded to the time period for which we had meteorological observations. Finally, the relationships between nitrogen trace gas emission rates and WFPS and rainfall were analyzed based on the 13 year simulation to see if simple relationships could be obtained to facilitate the scaling-up of nitrogen trace gases from sites to regions.

3. Results and discussion

3.1. Model calibration

The calibrated carbon in live biomass of leaves, fine branches, large stem wood, coarse root and fine root at the quasi steady state conditions were 330, 4847, 10184, 2624 and 139 g C m^{-2} , respectively close to their initial values (Table 1). The simulated SOC was 5828 g C m^{-2} , which was close to the initial value of 5560 g C m^{-2} . The simulated small, large woody debris and coarse root debris were 152, 1752, and 608 g C m^{-2} , respectively, close to the initial values (Table 1). The simulated active, slow and passive SOC pools were 178, 2582 and 2688 g C m^{-2} , respectively, which were in accordance with their initial values of 184, 2550 and 2650 g C m^{-2} . Not surprisingly, we found that the default maximum decomposition rates of 0.2 and 0.0045 yr^{-1} for the slow and passive SOC in CENTURY (Parton et al., 1993; Parton et al., 1994a,b), which was originally parameterized for the Great Plains, were too low for the tropical moist

primary forest ecosystem. Values of 0.28 and 0.0080 yr^{-1} were used in our simulation to reach the above better agreement of simulated and observed slow and passive SOC pools and total SOC. All these agreements between simulated and observed carbon stocks in different parts of the ecosystem (differences were within 10%) indicated that our parameterization of CENTURY to the tropical primary forest in Costa Rica was successful for simulating steady-state simulations.

The temporal fluctuation and the magnitude of WFPS as observed in the three primary forest plots were well-simulated by the modified CENTURY (Fig. 5a). The model successfully captured the seasonal pattern of WFPS observations, based on the information given in Table 2: the slope and intercept were not significantly different from 1 and 0, respectively. The model also explained 62% of the variation of monthly WFPS observations (Table 2). We noticed that the use of field capacity (defined as the soil moisture content at -0.1 to -0.3 bar soil matric potential) to specify the upper limit of soil moisture content was not practical in moist tropical areas, where more than 20 rainy days in a month are common (Fig. 2). Soils usually require two or three days to reach field capacity after rainfall (Brady, 1990). Soils have few opportunities to dry for two or three days to reach their field capacities in those areas because of recurring rainfall. In reality, soil moisture contents are frequently higher than the field capacity. We have used the average of the four highest daily moisture contents measured during the wetter season to represent the possible highest monthly moisture content of the ecosystem and replaced the field capacity with this maximum monthly moisture content.

The value 0.02 assigned to the emission coefficient a in Eq. (4) was too small, which means that a potentially larger fraction of gross mineralized N could be emitted from the soil in the forms of N_2O and NO. The coefficient a was adjusted to 0.042, which gave a better agreement in magnitude between the predictions and measurements of the fluxes of N_2O and NO (Fig. 5b and c). Numerically, doubling $N_{\min}$ could have the same effect as doubling the emission coefficient a on the predicted N_2O and NO (see Eq. (4)). However, doubling $N_{\min}$ would result in a totally different system that would have different biomass pools, C and nutrient fluxes than the one that has been calibrated in this study. The seasonal pattern of N_2O emissions from the ecosystem were well captured by the modified CENTURY ($a \approx 1$ and $b \approx 0$) (Table 2). NO fluxes were generally underestimated during dry months (when NO fluxes were high) and overestimated during wet months (when NO fluxes were low) (Table 2 Fig. 5c). The model accounted for 67% and 74% of the variations in N_2O and NO flux measurements, respectively.

In total, the simulated average fluxes of N_2O and NO were 52.0 ± 9.4 and $6.5 \pm 0.7 \text{ mg-N m}^{-2} \text{ month}^{-1}$, respectively,

corresponding well with the measurements of 48.2 ± 11.0 and $7.1 \pm 1.1 \text{ mg-N m}^{-2} \text{ month}^{-1}$. The simulated WFPS (0.68 ± 0.02) and $\text{N}_2\text{O}/\text{NO}$ ratio (11.2 ± 1.9) also agreed well with field measurements of 0.68 ± 0.02 and 10.9 ± 4.7 , respectively. The combined flux of N_2O and NO accounted for 2.2% of the gross N mineralization ($2.65 \text{ gN m}^{-2} \text{ month}^{-1}$), was close to the value of 2% used by Potter et al. (1996). The dependence of the fraction of gross N mineralization emitted from soils as either N_2O or NO on WFPS has important implications on the estimation of the emissions of nitrogen trace gases at the regional and global scales. If the dependence were ignored or a constant fraction were used (e.g., Potter et al., 1996), errors could be introduced in the prediction of N_2O emissions from various ecosystems: emission rates would be under-estimated in wetter regions/seasons and over-estimated in drier regions/seasons.

3.2. Model validation

The model under-estimated WFPS during the wet season ($a < 1$ and $a > 0$) and over-estimated WFPS during the dry season ($b > 0$) at the Guacimo forest site (Table 2 and Fig. 5d). But the model still accounted for 58% of the variation of monthly WFPS measurements ($R^2 = 0.58$). The seasonal pattern of N_2O fluxes was well simulated by the model ($a \approx 1$ and $b \approx 0$) (Table 2). The coefficient of determination of the model (R^2) was 0.37, lower than that from the calibration run (Table 2). The lower R^2 value may be attributed to the smaller range of WFPS fluctuation at the Guacimo site during the observation period, compared to that at the La Selva sites (Fig. 5a and d). There was no relation between simulated and measured NO fluxes at Guacimo site ($a \approx 0$). The NO fluxes were underestimated by a factor of two (Fig. 5f). In fact, the NO fluxes observed at this site increased with the increase of WFPS, which was the opposite as observed at other sites in the region (e.g., Keller and Reinert, 1994). The causes for the discrepancy between simulated and observed NO fluxes at this site are unknown.

It should be noticed that field data (i.e., WFPS, N_2O and NO fluxes) for each month were estimates based on measurements collected on several days (Keller et al., 1993; Keller and Reinert, 1994). Although each monthly field-data-based estimate was likely different from its truth, the collection of all the estimates would reflect the general temporal patterns of the variables investigated. This is supported by the agreement between field estimates and simulated results in forests (this study) and seven pastures (Liu et al., 1999). Because of the time and labor involved in field measurements of N_2O and NO fluxes, it is difficult to improve N_2O and NO flux estimates over long-time periods, through increasing sample points and frequency. However, the scaling-up of daily field measurements of N_2O and NO to monthly

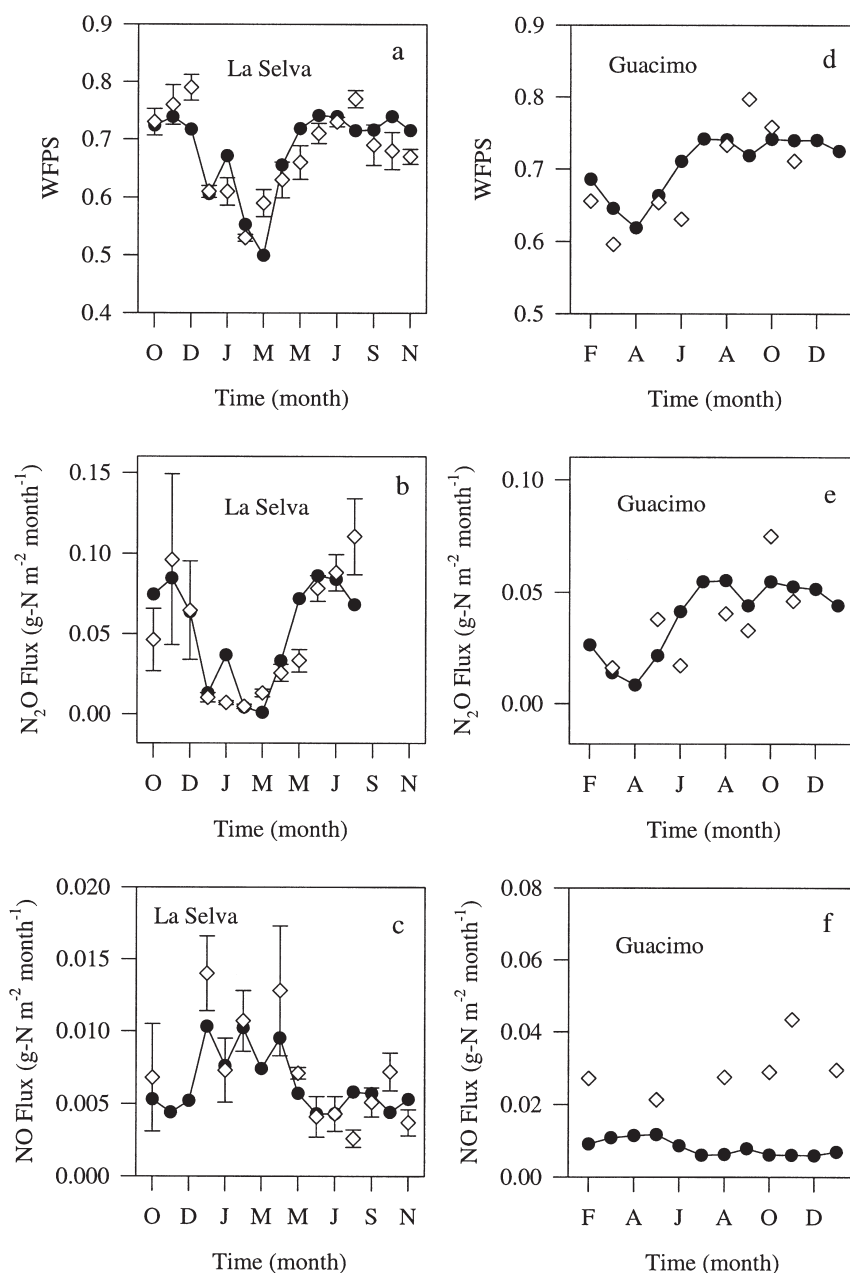


Fig. 5. Comparison of predicted (solid circles) and measured (diamonds) water-filled pore space (WFPS), N_2O and NO fluxes from tropical primary forests. Measurements taken from three forests near La Selva during October 1990 to December 1992 were used in model calibration, while those taken from a Guacimo forest during February 1992 to January 1993 were used for model validation. See Table 2 for a statistical evaluation of the model performance.

and annual time scales could be improved by using WFPS measurements, which can be monitored continuously in the field. Current field-based N_2O and NO flux estimates are generally based on time, which should be abandoned. N_2O and NO fluxes are more closely related to the dynamics of WFPS than the change or length of time.

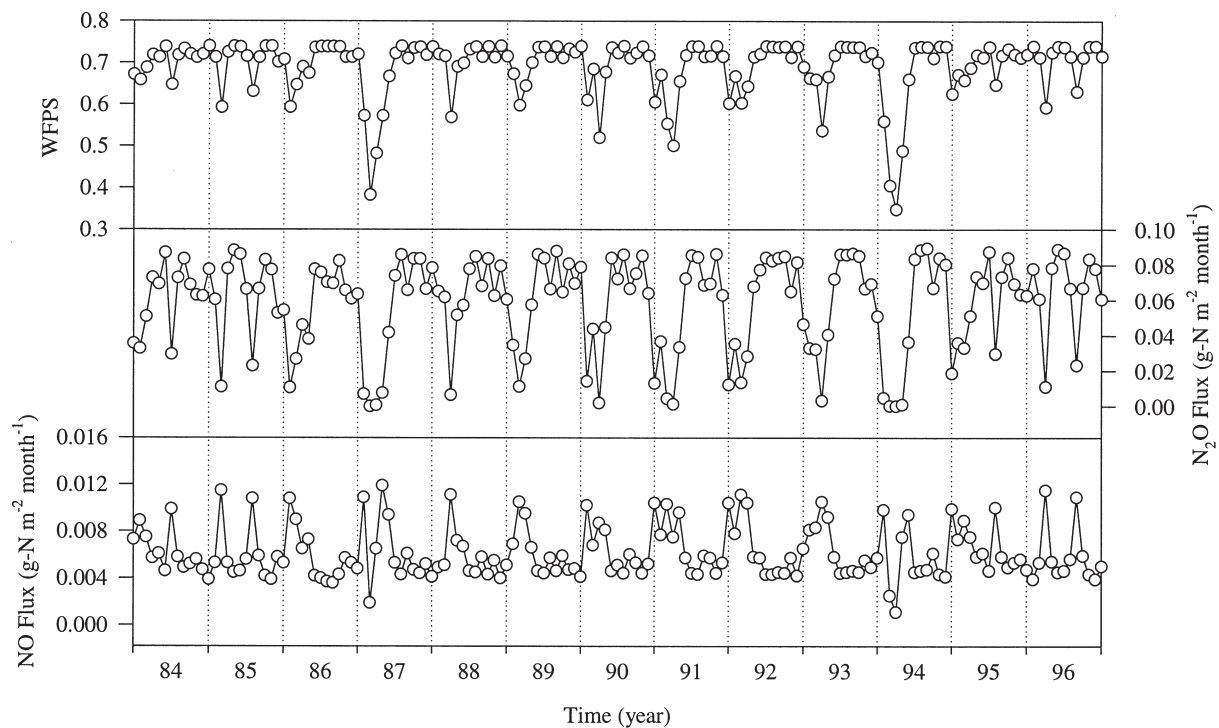
3.3. Long-term dynamics of N_2O and NO emissions from the ecosystem

Seasonal fluctuations and interannual variation of WFPS, and fluxes of N_2O and NO were apparent in the simulation for 1984 to 1996 (Fig. 6). The seasonal pattern of WFPS, mainly determined by that of rainfall (see Fig. 1), dictated the seasonal patterns of both N_2O and

Table 2

Results of linear regression of simulated N₂O, NO fluxes and WFPS on observed values: simulated= a *observed+ b

Parameter	Coefficient	Values	Lower limit (95%)	Higher limit (95%)	Conclusion ^a
Calibration (La Selva)					
N ₂ O	a	0.700	0.392	1.008	$a \approx 1$
	b	0.018	−0.001	0.037	$b \approx 0$
	R^2	0.67			
NO	a	0.539	0.338	0.740	$a \neq 0, a \neq 1$
	b	0.003	0.001	0.004	$b > 0$
	R^2	0.74			
WFPS	a	0.798	0.454	1.142	$a \approx 1$
	b	0.143	−0.091	0.377	$b \approx 0$
	R^2	0.62			
Validation (Guacimo)					
N ₂ O	a	0.510	−0.008	1.004	$a \approx 1$
	b	0.021	−0.004	0.046	$b \approx 0$
	R^2	0.37			
NO	a	−0.206	−0.440	0.028	$a \approx 0$
	b	0.013	0.007	0.028	$b > 0$
	R^2	0.44			
WFPS	a	0.410	0.124	0.695	$a \neq 0, a \neq 1$
	b	0.422	0.224	0.621	$b > 0$
	R^2	0.58			

^a $\approx$ means “not significantly different from”, and $\neq$ means “significantly different from” at $\alpha=0.05$.Fig. 6. Seasonal and interannual variations of predicted WFPS, and fluxes of N₂O and NO from 1984 to 1996.

NO fluxes. The emission rates of N₂O from the ecosystems were higher in the wetter season, when WFPS was higher, while those of NO demonstrated a reverse pattern. The combined fluxes of N₂O and NO were much smaller in the drier season compared to those in the wetter season. All these simulated results were consistent with field observations by Keller and Reiners (1994).

The inter-annual variabilities (reflected by the standard errors in Table 3) of monthly N₂O and NO emissions from tropical primary forests were higher in the drier season, which corresponded to the higher variability of monthly rainfall, and lower in the wetter season. Based on the predicted maximum N₂O fluxes, it can be seen the seasonality of N₂O emission may not exist in

Table 3

Monthly means, standard errors, maximum and minimum values of the simulated fluxes of N₂O and NO, and WFPS from 1984 to 1996

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
N ₂ O flux (mg-N m ⁻² month ⁻¹)												
Mean	47.5	34.9	25.6	13.9	40.3	65.4	78.6	76.5	70.4	76.3	74.2	69.5
Std. Err.	6.7	6.3	6.0	5.0	7.2	5.4	2.4	4.2	4.7	2.4	2.6	2.4
Minimum	12.2	4.7	0	0	0.2	28.8	59.2	29.6	23.2	63.8	62.6	52.9
Maximum	78.8	77.9	61.8	51.2	78.3	88.6	87.3	88.4	89.3	84.9	86.0	81.4
NO flux (mg-N m ⁻² month ⁻¹)												
Mean	6.6	7.8	7.6	8.1	7.5	6.3	4.7	5.0	5.7	5.1	4.9	4.8
Std. Err.	0.7	0.6	0.8	0.8	0.6	0.5	0.1	0.4	0.5	0.2	0.2	0.2
Minimum	4.1	3.9	1.9	1.1	4.3	4.2	4.0	3.7	3.6	4.3	4.3	3.9
Maximum	10.4	10.9	11.1	11.5	11.9	9.4	5.7	10.0	10.9	6.1	5.7	5.8
Water-filled pore space (WFPS)												
Mean	0.68	0.66	0.61	0.55	0.65	0.71	0.73	0.73	0.72	0.73	0.73	0.72
Std. Err.	0.01	0.02	0.03	0.03	0.02	0.01	0.01	0.01	0.01	0.00	0.00	0.00
Minimum	0.60	0.56	0.38	0.35	0.45	0.65	0.71	-0.65	0.63	0.71	0.71	0.70
Maximum	0.74	0.74	0.72	0.69	0.73	0.74	0.74	0.74	0.74	0.74	0.74	0.74
N ₂ O/NO												
Mean	9.3	5.8	3.7	1.7	6.0	11.9	17.0	16.8	13.7	15.5	15.3	14.9
Std. Err.	1.8	1.6	1.1	0.7	1.3	1.6	0.9	1.4	1.4	1.0	1.0	1.1
Minimum	1.2	0.5	0.0	0.0	0.0	3.2	10.3	3.0	2.1	10.9	11.3	9.0
Maximum	19.4	19.8	12.1	7.1	14.6	19.5	19.6	19.8	19.4	19.4	19.7	19.9

this kind of ecosystem in some years, depending on the seasonality of rainfall. The higher variability of monthly N₂O and NO fluxes during the drier season was probably caused by the higher variability of WFPS during the same period (Table 3).

The predicted monthly mean N₂O flux from 1984 to 1997 was 56.1±2.2 (i.e., mean±standard error) mg-N m⁻² month⁻¹, quite comparable to field measurements of 52.0±9.4 mg-N m⁻² month⁻¹, but much higher than the predicted value of 11.37 mg-N m⁻² month⁻¹ for global-scale tropical rain forests by Potter et al. (1996). Field measurements did indicate that the lowland tropical forests in Costa Rica were “hot spots” for the emissions of N₂O due to its high rainfall and high nitrogen availability (Keller et al. 1986, 1988; Matson and Vitousek, 1987; Livingston et al., 1988; Robertson and Tiedje, 1988; Luizao et al., 1989; Steudler et al., 1991; Keller and Reiners, 1994).

The predicted average NO emission rate during the 13 year period was 6.2±0.2 mg-N m⁻² month⁻¹, which was close to the measurements of 6.5±0.7 mg-N m⁻² month⁻¹ observed during 1991 (Keller and Reiners, 1994) but lower than the predicted rate of 9.87 mg-N m⁻² month⁻¹ for tropical rain forest by Potter et al. (1996). It is important to keep in mind that NO fluxes are soil emissions but not necessarily ecosystem emissions. In tropical forest settings NO reacts with ozone to form NO₂ and the resulted NO₂ deposits on the vegetation and soil. Therefore, much of the NO release simply goes to internal cycling (Kaplan et al., 1988; Bakwin et al., 1990).

The predicted mean monthly ratios of N₂O to NO varied from 1.7 to 17.0 (Table 3), which was higher than

1.2 as predicted by Potter et al. (1996). The shape of our partitioning curve of N₂O and NO was similar to the hypothesized curve used by Potter et al. (1996, 1997). However, our WFPS is lower at the half-N₂O point, and N₂O has a smaller fractional value when WFPS<0.5 than values used in Potter et al. (1996, 1997). Potter et al. (1997) realized the hypothesized curve was not general and should be modified for the prediction of the emissions of nitrogen trace gases from tropical forest soils in Hawaii.

3.4. Environmental controls on the emissions of nitrogen trace gases

WFPS has long been found to be an important controlling factor on the emissions of nitrogen trace gases from soils (e.g., Davidson, 1991; Keller and Reiners, 1994). It affects the decomposition processes of organic matter (thus the N mineralization and immobilization), nitrification rates, denitrification rates, and the emission pathways of these gases. In the modified CENTURY model presented here, WFPS influences the decomposition processes which controls the amount of gross N mineralized, regulates the fraction of gross mineralized N that is emitted from the soils in the forms of N₂O and NO, and controls the partitioning of N₂O and NO. The second effect of WFPS was not employed in CASA (Potter et al., 1996), even though CASA uses the CENTURY soil organic matter submodel. It would be impossible to catch the seasonal patterns of N₂O and NO emissions from the tropical primary forests if the second effect of the WFPS were not considered in our case.

Monthly N₂O emission rates increased exponentially

with monthly WFPS (Fig. 7). The sensitive range of WFPS for N_2O emission for tropical moist primary forest ecosystems in this area was from 0.5 to 0.74. N_2O emission rates became very small with WFPS lower than 0.5. The maximum emission rate of N_2O was $89.3 \text{ mg-N m}^{-2} \text{ month}^{-1}$ (Fig. 7 and Table 3), which corresponded the highest realizable WFPS of the ecosystems at the monthly time scale. The strong relationship between WFPS and N_2O flux suggests that N was not a limiting factor for the production of nitrogen trace gases in this forest ecosystem although it may be so in other ecosystems of the same region (see Eq. (4)).

The maximum NO emission rate was 11.9 mg-N m^{-2}

month^{-1} (Table 3) corresponding to a WFPS of 0.58 (Fig. 7). NO was further reduced to N_2O at higher WFPS, while it increased with WFPS below 0.58. This relationship was determined by the control of WFPS on the combined flux of N_2O and NO (see Eq. (10)) when WFPS was lower than 0.59, and by the increased reduction of NO to N_2O at higher WFPS reflected in the partitioning curve (Fig. 4). The control of WFPS on the combined flux of N_2O and NO was realized through its control on the mineralization of N (Fig. 7) and then by its control on the fraction of gross mineralized N which would emit as N_2O and NO.

Predicted monthly WFPS increased asymptotically

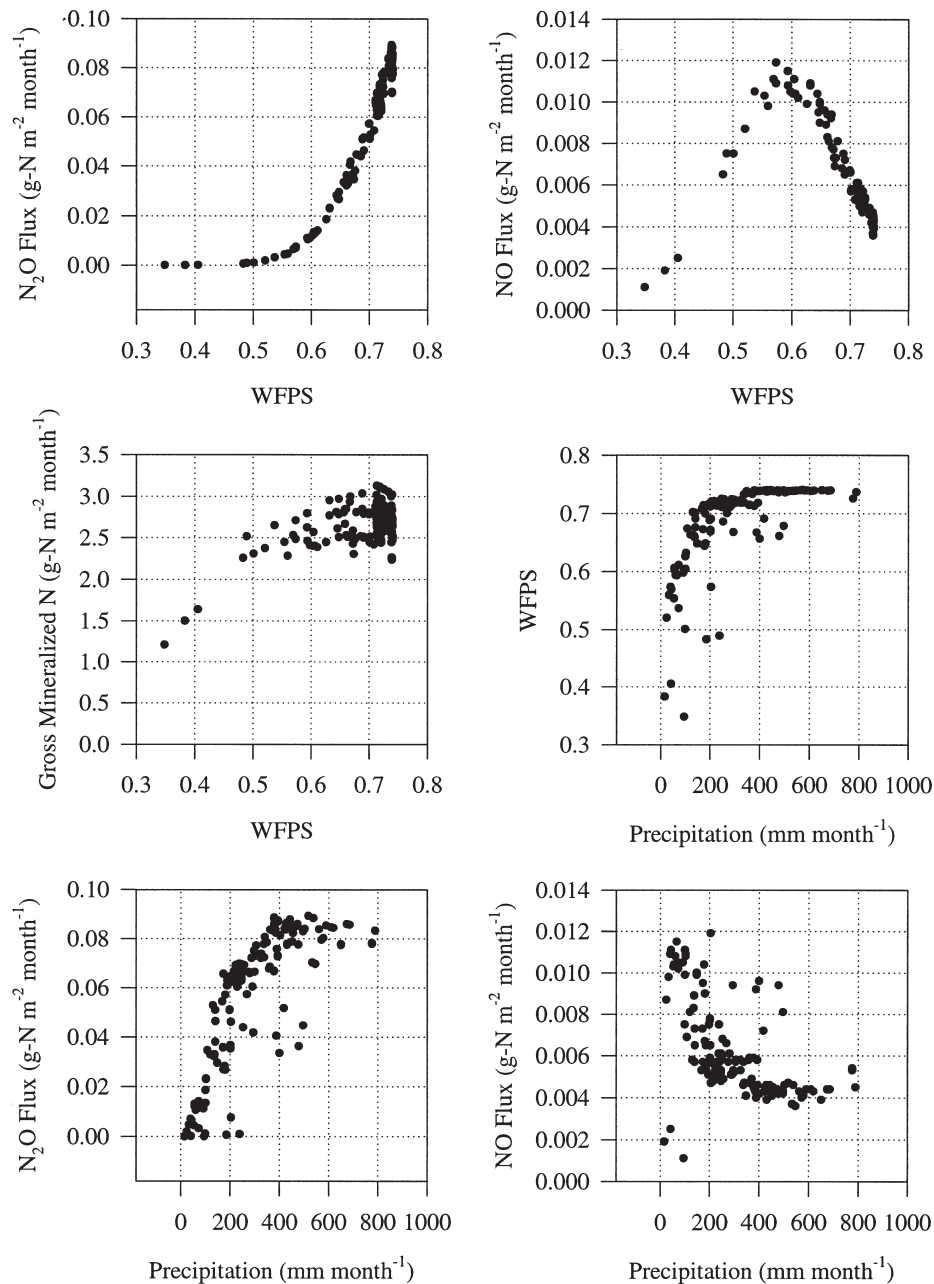


Fig. 7. The relationships between predicted monthly nitrogen trace gas emission rates, WFPS, and precipitation in tropical primary forests.

with monthly rainfall (Fig. 7). Monthly WFPS reached its maximum after monthly rainfall exceeded 300 mm, which corresponded to more than 20 rainy days in a month (Fig. 2). N_2O flux increased linearly before reaching its maximum when monthly rainfall exceeded 400 mm (Fig. 7). On the other hand, NO fluxes decreased exponentially with rainfall to a more or less constant

rate of $4.3 \text{ mg-N m}^{-2} \text{ month}^{-1}$ (Fig. 7). In general, the relationships between nitrogen trace gas fluxes and rainfall were more variable than those between nitrogen trace gas fluxes and WFPS. However, those results did indicate that N_2O and NO emissions were still somehow driven by rainfall events (which was closely related to rainfall amount (Fig. 2)) even at a monthly time step,

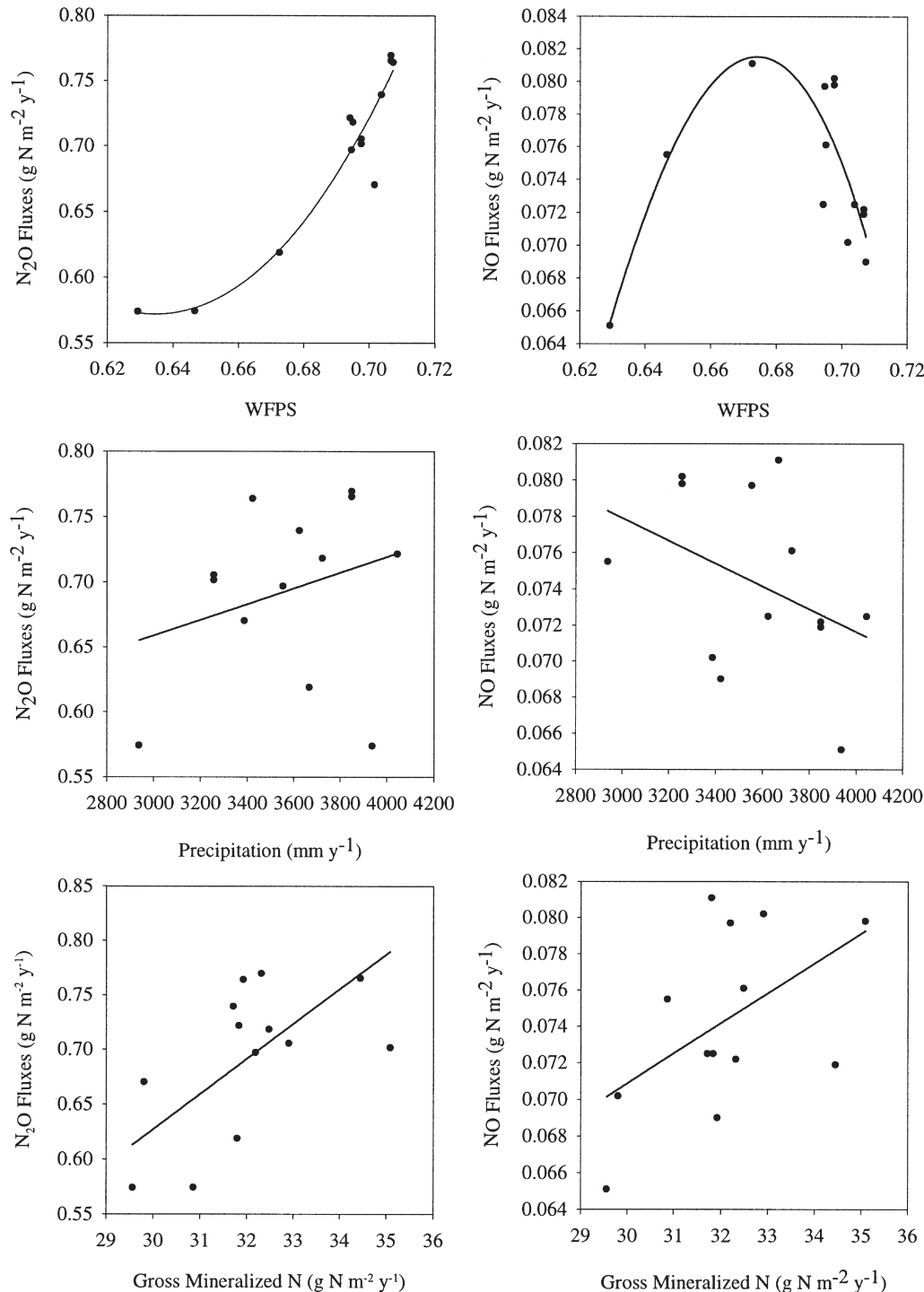


Fig. 8. The relationships between predicted yearly nitrogen trace gas emission rates, WFPS, precipitation and gross nitrogen mineralization rate in tropical primary forests.

which is logically similar to the theoretical basis of DND model (Li et al., 1992a,b), although the latter is operated on a daily time scale.

Annual N_2O and NO fluxes were 673.2 ± 18.6 and $74.2 \pm 1.3 \text{ mg N m}^{-2} \text{ y}^{-1}$, respectively, based on 13 years of simulations, indicating that the inter-annual variability of N_2O and NO fluxes was small. Annual N_2O and NO fluxes were closely related to annual mean WFPS (Fig. 8). The relationships between nitrogen trace gas fluxes and annual precipitation and gross N mineralization rate were weak. Because there is no field data to confirm or contradict the simulated results on the inter-annual variability of N_2O and NO fluxes and their relationships with environmental variables, we presented these as a model hypothesis, which could be tested in the field.

Because WFPS plays a central role on regulating the N_2O and NO emissions from primary forest soils, the successful prediction of WFPS is essential to the prediction of the fluxes of N_2O and NO and their seasonalities. The method developed for the prediction of WFPS, with considering the variabilities (magnitude and frequency) of daily rainfall events, was successful in this moist tropical area. Theoretically, we cannot see any reasons which prevent this method being able to be applied to other areas and other models.

4. Summary and conclusions

For environments having frequent precipitation events, it is apparent that emissions of N_2O and NO from soils would be better modeled if a shorter time step were used, because nitrogen trace gases emissions are largely controlled by soil moisture conditions which, themselves, vary considerably with rainfall events (Li et al., 1992a,b). On the other hand, daily weather data are usually difficult to obtain, particularly for studies directed to regional or global scales, and require considerably more computation. Our results indicated that a monthly time step is usable if it incorporates sufficient information representing the patterns of daily precipitation events of the modeled area. A monthly time step model enjoys the advantage of the fact that monthly climate data are usually easier to get or to simulate than are daily data, and such data have less variability in time and space. With the attributes described in this paper, the modified CENTURY successfully simulated carbon pools of the tropical primary forest ecosystem, WFPS, and emission rates of N_2O and NO from the soil into the atmosphere with a monthly time step.

The simulation of soil moisture content or WFPS is critical for the modeling of the emissions of N_2O and NO from tropical primary forests. WFPS affects the decomposition processes of soil organic matter, thus influencing the mineralization of nitrogen. Our study indicated that the combined flux of N_2O and NO was

not a constant fraction of the gross mineralized nitrogen, as hypothesized by Potter et al. (1996, 1997), but rather is a function of both gross mineralized N and WFPS. Finally, WFPS affects the partitioning of the N_2O and NO or more directly the microbial activities which generates the two trace gases in soils (Davidson, 1991). Representation of this functional relationship contributed to the successful simulations of modified CENTURY as well.

Emissions of nitrogen trace gases from tropical primary forests demonstrate strong seasonal patterns and interannual variability. This variability is mainly determined by the temporal variabilities of rainfall as it affects WFPS. In the particular ecosystem modeled here, nitrogen was not a limiting factor in the production of nitrogen trace gases from the ecosystems. The relationships between nitrogen trace gas emissions and WFPS or rainfall presented in this paper may be used to scale nitrogen trace gas emission rates up from sites to regions.

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