

Regional application of PnET-N-DNDC for estimating the N₂O source strength of tropical rainforests in the Wet Tropics of Australia

RALF KIESE*, CHANGSHENG LI†, DAVID W. HILBERT‡, HANS PAPAN* and KLAUS BUTTERBACH-BAHL*

*Institute for Meteorology and Climate Research, Atmospheric Environmental Research (IMK-IFU), Karlsruhe Research Centre, Kreuzackbahnstr. 19, D-82467 Garmisch-Partenkirchen, Germany, †Institute for the Study of Earth, Oceans, and Space, University of New Hampshire, Durham, NH 03824, USA, ‡CSIRO, Tropical Forest Research Centre, Maunds Rd, Atherton, QLD 4883, Australia

Abstract

In contrast to the significant importance of tropical rainforest ecosystems as one of the major sources within the global atmospheric N₂O budget (2.2–3.7 Tg N yr⁻¹), regional estimates of their N₂O source strength are still limited and highly uncertain. To contribute toward more reliable estimates of the N₂O source strength of tropical rainforest ecosystems on a regional scale, we modified a process-oriented biogeochemical model, PnET-N-DNDC, and parameterized it to simulate C and N turnover and associated N₂O emissions in and from tropical rainforest ecosystems. Model modifications included: (1) new parameterizations associated with plant physiology and soil hydrology and the addition of algorithms relating daily leaf litterfall to water stress as well as to daily rainfall to account for the effects of heavy rainfall damage; (2) the development of a denitrifier activity index that depends on soil moisture conditions and influences N turnover by denitrification; and (3) the addition of a biological N fixation algorithm. Daily simulated N₂O emissions based on site data were in good agreement (model efficiencies up to 0.83) with field observations in the Wet Tropics of Australia and Costa Rica. The model was even able to reproduce the highly dynamic pattern of N₂O emissions with short-term increases during the wet season. Sensitivity analyses demonstrated that the PnET-N-DNDC model was sensitive to changes in soil properties such as pH, clay content, soil organic carbon and climatic factors such as rainfall and temperature. By linking the PnET-N-DNDC model to a geographic information systems database, tropical rainforests in a 9000 km² area of the Wet Tropics of Australia are estimated to emit 962 t N₂O-N yr⁻¹ (2.4 kg N₂O-N ha⁻¹ yr⁻¹) between July 1997 and June 1998.

Nomenclature

PTF = pedo-transfer function
wfps = water filled pore space
SOC = soil organic carbon

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Introduction

Quantifying sources and sinks of greenhouse gases like CO₂, N₂O and CH₄ for natural, agricultural and forest

ecosystems is crucial to our understanding of land-use change effects on global climate change. Furthermore, Annex I countries ratifying the Kyoto Protocol are committed to reporting GHG sources and sinks in a transparent and verifiable manner. However, the approach that is currently suggested to provide this information – the IPCC default methodology – does not

Correspondence: Klaus Butterbach-Bahl, tel. +49 8821 183-136, fax +49 8821 183-294, e-mail: klaus.butterbach@imk.fzk.de

allow a sufficiently detailed quantification of greenhouse gases from diffuse sources like soils (Kroeze & Mosier, 2002). In addition, the IPCC N₂O assessment only accounts directly for human-influenced sources (e.g. fertilizer-induced N₂O emissions from agricultural soils). Thus, forest ecosystems, which are also a significant source for atmospheric N₂O, are not at present considered.

Because of site differences in environmental and climate conditions, reported N₂O emissions from tropical rainforest ecosystems are highly variable ranging between 0.3 and 7.5 kg N ha⁻¹ yr⁻¹ (e.g. Matson & Vitousek, 1990; Garcia-Méndez *et al.*, 1991; Steudler *et al.*, 1991; Keller & Reiners, 1994; Riley & Vitousek, 1995; Verchot *et al.*, 1999; Breuer *et al.*, 2000; Kiese & Butterbach-Bahl, 2002; Kiese *et al.*, 2003). Based on these data, tropical rainforest soils are estimated to be a major source of atmospheric N₂O contributing between 14% and 23% to the global atmospheric N₂O budget (IPCC, 1997). However, in spite of their importance, the source strength of tropical rainforest ecosystems for N₂O is still poorly characterized, due either to lack of data or their poor quality in respect to spatial and temporal considerations.

N₂O emissions from soils are the result of the complex interaction of processes involved in N₂O production, consumption and transport and their controlling biotic and abiotic factors. N₂O can be produced during the process of nitrification when ammonia is oxidized to nitrate in the presence of oxygen, as well as by the process of denitrification when nitrate, used as an alternative electron acceptor instead of oxygen, is sequentially reduced to nitrite, NO, N₂O and finally to N₂ (e.g. Firestone & Davidson, 1989; Conrad, 1996; Bremner, 1997). Therefore, the occurrence of nitrification and/or denitrification strongly depends on the presence, distribution and magnitude of oxic and anoxic microsites in the soil, which themselves are mainly influenced by soil texture and soil moisture conditions controlling soil aeration. Increasing soil moisture decreases the diffusivity of soils for gases and, thus, the diffusion of oxygen into the soil. Nitrification rates in soils are generally highest at around 60% water-filled pore space (wfps) since at this value increasing substrate availability and decreasing oxygen availability still favor the activity and substrate turnover by nitrifiers. Denitrification is increasingly dominant at values >60% wfps (i.e. at conditions where soils are becoming predominantly anaerobic) (Linn & Doran, 1984; Davidson *et al.*, 2000; Kiese & Butterbach, 2002). Both microbial processes have been shown to be dependent on soil temperature, soil texture, soil organic carbon (SOC), pH and inter- and intraspecific competition for substrates (Firestone

& Davidson, 1989; Yamulki *et al.*, 1997; Verchot *et al.*, 1999; Kiese & Butterbach-Bahl, 2002). Since both the biotic and abiotic factors are highly variable in space and time, observed N₂O emissions from rainforest soils show a substantial spatial and temporal variability (Breuer *et al.*, 2000), resulting in the above-mentioned uncertainties in relation to estimates of the N₂O source strength of tropical rainforest soils.

To improve the current estimates of N₂O emissions from tropical rainforest soils it will be necessary to follow a dual approach. On the one hand, more detailed measurements of rates of N₂O emissions from different tropical rainforest ecosystems are required. These should be both spatially representative and provide long-term coverage in order to better understand seasonal variability and to identify the major environmental drivers that control the magnitude of N₂O emissions (Kiese *et al.*, 2003). These data are also needed to further develop and validate biogeochemical models, which provide a useful instrument for integrating our knowledge of key processes and driving variables to estimate N- and C-trace gas emissions from soils. As field measurements will always be limited in space and time, process-oriented models coupled to geographic information systems (GIS) holding the spatially distributed information of all parameters needed for driving and initializing the models are at present the most promising tool for developing regional or global estimates of trace gas emissions from soils (e.g. Davidson *et al.*, 1998; Li *et al.*, 2000; Butterbach-Bahl *et al.*, 2001, 2004).

In the recent past several biogeochemical models, e.g. NGAS (Parton *et al.*, 1996), CASA (Potter *et al.*, 1996, 1997), NASA-CASA (Potter *et al.*, 2001), CENTURY (Liu *et al.*, 2000; Reiners *et al.*, 2002), DAYCENT (Parton *et al.*, 2001; Del Grosso *et al.*, 2002), ECOSYS (Grant & Pattey, 1999, 2003), DNDC (Li *et al.*, 1992) and the PnET-N-DNDC (Li *et al.*, 2000; Stange *et al.*, 2000) have been developed, which focus on simulating C and N turnover in soils and on predicting soil-atmosphere exchange of C- and N-trace gases. The PnET-N-DNDC model was developed explicitly to model biosphere-atmosphere exchange of N-trace gases based on the biogeochemical cycling of C and N in temperate forest ecosystems on a daily time step. This model describes in detail the microbial processes of nitrification and denitrification (Li *et al.*, 2000). At present it is the only model that simulates the simultaneous occurrence of oxic and anoxic sites in soils via the concept of a dynamic anaerobic balloon. The extension of anaerobic soil zones as opposed to aerobic zones is based on the calculation of O₂-diffusion rates into the soil and is recalculated at time steps of <1 h. Furthermore, the model also allows for the consumption of N oxides within the soil profile. This means that NO and N₂O

produced via nitrification can be further reduced by denitrification to N_2O or N_2 . Thus, the emission of N-trace gases is the product of simulated production, consumption and diffusion processes (Li *et al.*, 2000). Beside PnET-N-DNDC also, the ECOSYS model (Grant & Pattey, 1999, 2003) is explicitly simulating diffusion processes of gases in the soil profile and their effects on production, consumption and emission processes of N-trace gases from the soil into the atmosphere.

The intention of the present study was to further develop and validate the PnET-N-DNDC model for tropical rainforest conditions, to allow the simulation of N_2O emissions from these ecosystems. As a case study, we used the new version of the PnET-N-DNDC model to regionalize N_2O emissions from rainforest soils in the area of the Wet Tropics of Australia (9000 km²). Since this area offers huge environmental gradients with regard to climate and soil properties, it is an ideal area for testing the sensitivity of the PnET-N-DNDC model to changes in environmental factors on a regional scale. Other recent publications in which process-oriented models were used to estimate regional emissions of N-trace gas emissions from tropical soils in the Amazon basin and in Costa Rica have focused on aspects of land-use changes (Potter *et al.*, 2001; Reiners *et al.*, 2002)

Materials and methods

Adapting PnET-N-DNDC to tropical rainforests

The PnET-N-DNDC model was initially developed to predict soil carbon and nitrogen biogeochemistry, including N-trace gas emissions, in temperate forest ecosystems (Li *et al.*, 2000; Stange *et al.*, 2000; Butterbach-Bahl *et al.*, 2001). The model consists of two components (Fig. 1). The first component includes the submodels for soil climate, decomposition and forest growth. Based on daily climate data (temperature and precipitation), soil physical properties (texture) and by considering plant and microbial turnover processes of C, N and water, the soil climate submodel calculates temperature, moisture and oxygen profiles derived from one-dimensional thermal-hydraulic flow and gas diffusion equations. The forest growth submodel simulates forest growth driven by solar radiation, temperature, water and nitrogen stress, and passes the litter production, water and N demands, and root respiration to the soil climate or the decomposition submodel. The decomposition submodel quantifies the decomposition of organic matter resulting in substrate concentrations of dissolved organic carbon (DOC), NH_4^+ and CO_2 , based on decay rates (*k*-values) depending on organic matter

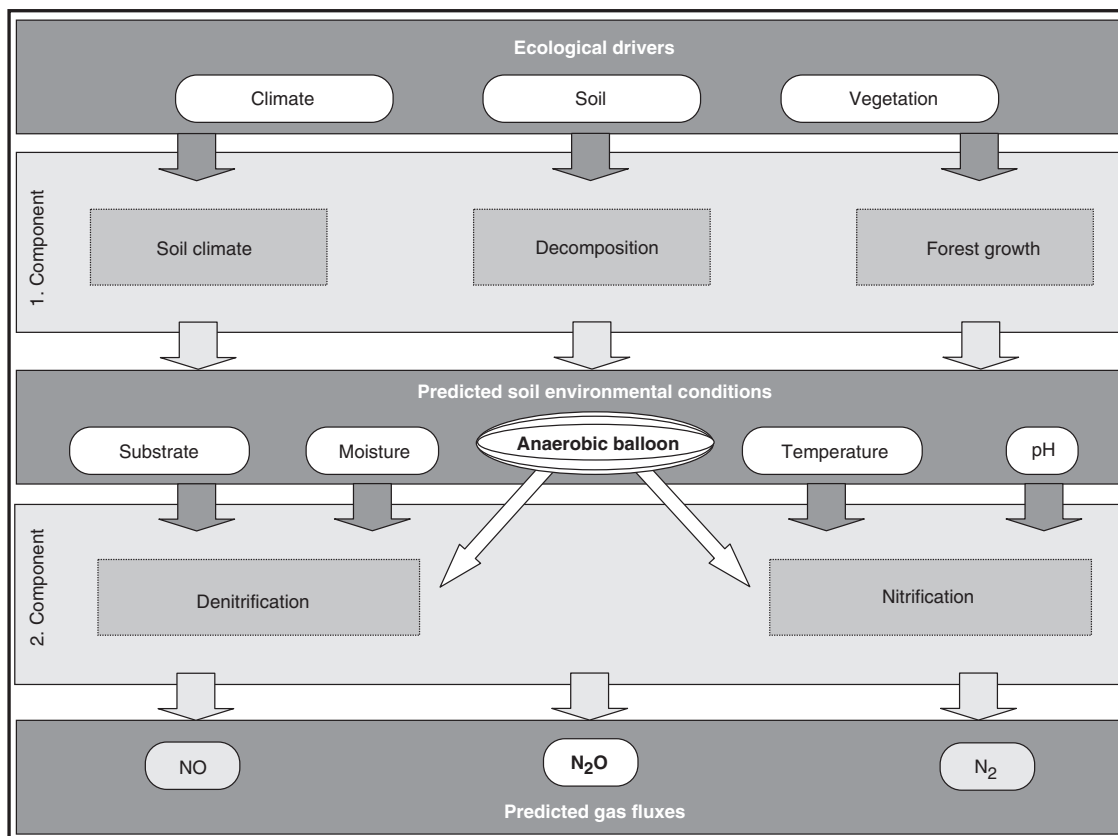


Fig. 1 Schematic overview of the PnET-N-DNDC model: components, submodels, ecological drivers and environmental conditions.

quality and soil environmental conditions. The second component includes the submodels for nitrification and denitrification. N₂O, NO and N₂ fluxes are calculated based on simulated soil microbial activities, which depend on simulated soil environmental conditions and a series of biochemical and geochemical reactions determining the transport and transformation of C and N components. To allow simultaneous occurrence of nitrification and denitrification in aerobic or anaerobic microsites, the scheme of a dynamic 'anaerobic balloon' was developed, which – based on the availability of O₂ in the respective soil layer – allocates substrates such as DOC, NH₄⁺ and NO₃⁻ into aerobic and anaerobic soil compartments (Li *et al.*, 2000).

Because of principal differences in forest growth and soil hydrological properties between tropical and temperate regions, we modified the parameterization of the original PnET-N-DNDC model to a 'tropical version', but kept the general structure of the original model. The physiological parameters for the rainforest were based on the 'Evergreen Broadleaf Forest' parameterization used in the BIOME-BGC model (Hunt *et al.*, 1996), but also on our own measurements (Kiese & Butterbach-Bahl, 2002; Kiese *et al.*, 2003). We defined leaf N retranslocation to be 0.15, wood C/N ratio = 100, leaf retention = 1.5 years, and optimum temperature of photosynthesis to be 30 °C. Leaf C/N ratio was set to 30 based on field measurements (Kiese *et al.*, 2003 and unpublished data) revealing leaf C/N ratio to be in a range of 25–44 for a variety of rainforest sites in the Wet Tropics of Australia. Since in tropical regions the vegetation period is not limited by temperature, the concept of degree days for predicting seasonality in leaf, wood and root production as well as litterfall is not appropriate to describe the growth of tropical rainforests. Therefore, we allowed forest growth throughout the entire year. As in the temperate version the magnitude of forest growth is controlled by functions for solar radiation, temperature, water and nitrogen stress. With regard to litterfall, Kiese *et al.* (2003) and Spain (1984) reported that in the study area leaf litterfall was mainly driven by soil water stress and heavy rainfall events. During the dry season, leaf litterfall increased if water stress occurred, whereas during the wet season, peaks of leaf litterfall were caused by physical damage because of heavy rainfall (Kiese *et al.*, 2003). These observations were converted, for the tropical version only, into two equations as follows:

$$\text{Daily leaf litter fall} = \text{canopy leaf mass} \times 0.003 \\ \times (1 - \text{water stress factor}),$$

$$\text{Daily leaf litter fall} = \text{canopy leaf mass} \times 0.005, \\ \text{if daily rainfall} > 100 \text{ mm.}$$

Beside physiology, new parameterizations were developed to account for the different soil hydraulic properties found in tropical rain forests. In the original version of PnET-N-DNDC, this submodel features matrix flow for 12 texture classes (Li *et al.*, 1992, 2000) based on pedo-transfer functions (PTF) derived from the Van Genuchten (1980) equation. However, these PTFs may not be appropriate for tropical soils, since aggregate structure and bioturbation, both of which affect soil hydraulic properties, can differ, especially in the heavier texture classes. Most tropical soils have a lower bulk density (0.9–1.2 g cm⁻³) than temperate soils and are highly permeable because of their microaggregated structure. To account for this phenomenon, we adjusted soil porosity, calculated as a function of bulk density and increased the saturated hydraulic conductivity for all texture classes by a factor of approximately 2. This figure is based on our own measurements and on investigations by Bonell *et al.* (1983), who showed for a catchment in the center of the study area that values for the saturated hydraulic conductivity were up to 20 m day⁻¹.

In the original PnET-N-DNDC model, biological N₂ fixation was neglected as a source of N input into forest ecosystems. This may be acceptable for temperate forest ecosystems, where biological N₂ fixation is assumed to be <2 kg N ha⁻¹ yr⁻¹ (see literature review by Cleveland *et al.*, 1999), but biological N₂ fixation cannot be neglected in tropical forests. Several investigations demonstrate that biological N₂ fixation by epiphytes, lichens, nonsymbiotic N₂-fixing bacteria in soil and litter and by symbiotic plants in tropical rainforest ecosystems can make substantial contributions to the N cycling in tropical forests and is likely to vary in a range of <2–200 kg N ha⁻¹ yr⁻¹ (Forman, 1975; Sylvester-Bradley *et al.*, 1980; Salati *et al.*, 1982; Goosem & Lamb, 1986; Vitousek *et al.*, 2002). Based on an exhaustive literature review, Cleveland *et al.* (1999) estimated the mean N₂-fixation rate of evergreen tropical rainforests to be approximately 14.7–36.1 kg N ha⁻¹ yr⁻¹. Furthermore, these authors showed that the rate of biological N₂ fixation in terrestrial ecosystems was closely related to evapotranspiration. Based on this review, we introduced a simple linear regression to PnET-N-DNDC to quantify the N₂-fixation rate:

$$N_{\text{fix}} = R_{\text{et}} \times 0.234,$$

where N_{fix} is the N₂-fixation rate (kg N ha⁻¹ day⁻¹) and R_{et} is the ecosystem evapotranspiration rate (cm water day⁻¹). The introduction of biological N₂ fixation into the model increased the simulated dynamics of C and N turnover processes in tropical rainforest ecosystems.

Previous measurements of nitrifier and denitrifier cell numbers and activities at our tropical rainforest sites in

Australia showed that denitrification activity is highest during wet season conditions (Breuer *et al.*, 2002; Kiese *et al.*, 2002). However, our results also show that at the beginning of the wet season denitrification activity and N₂O emissions are delayed by several days, although the soil has already been rewetted. Such a delay can be explained by the stepwise initialization of denitrification enzymes after the transition from aerobic (dry season conditions) to prevailing anaerobic conditions (wet season conditions), which can last from hours to days (e.g. Koerner & Zumft, 1989; Baumann *et al.*, 1996; Otte *et al.*, 1996). This finding is supported by laboratory studies with *Paracoccus denitrificans* by Waki *et al.* (1980). These authors showed that the nitrate reduction in the anaerobic period was unchanged by the length of the previous aerobic period, but that the nitrite reduction rate was significantly decreased by exposing the denitrifiers to longer aerobic periods. Based on these findings we introduced an activity index for the denitrifier population (denitrifier_activity_factor). This index was allowed to vary in a range of 0–1. Following the approaches utilized for nitrifier activity in the PnET-N-DNDC model (Stange, 2000), we calculate the denitrifier activity based on modeled soil moisture values. If soil moisture (in PnET-N-DNDC: wfps) is lower than 0.6, the denitrifier activity is reduced by 20% day⁻¹, otherwise it is increased by 10% day⁻¹. The threshold of 0.6 wfps, which determines whether denitrifier activity is increased or decreased, is derived from own measurements. These revealed that if wfps values are >60%, O₂ diffusion gets limited in the soil matrix, thus favoring N transformation by denitrification (Kiese & Butterbach-Bahl, 2002). The introduction of a denitrifier activity index certainly improved the simulation of the delayed reaction of N₂O emissions to increases in soil moisture during the transition period from dry to wet season.

The tropical version of the PnET-N-DNDC model used in this study does not account for phosphorus limitation, which might be of importance in tropical rainforest ecosystems. However, soil labile P pools, determined by the new Hedley fractionation procedure in intact highly weathered forest soils of the humid tropics, are reported to be several times larger than extractable P values resulting from mildly acidic extracting solutions that were commonly used in the past two decades (Johnson *et al.*, 2003). Studies where the Hedley fractionation method was used show that the productivity of forests in the humid tropics even growing on highly weathered soils are most likely not P limited, since available P pools in the mineral soil and organic layer exceeded the annual P requirements, which are approximately 5 kg P ha⁻¹ yr⁻¹ (Johnson *et al.*, 2003). Investigations on available P pools (acid

and bicarbonate HCO₃ extractable P) in rainforest soils throughout our study area revealed that the mean P concentration is 38.4 ± 7.9 mg P kg⁻¹ (Min: 5 mg P kg⁻¹; Max: 224 mg P kg⁻¹) (Laffan, 1988; Murtha *et al.*, 1996). Assuming a soil bulk density of 1.0 g cm³ and an effective profile depth for root P uptake of 10 cm, this results in a pool size of 38.4 ± 7.9 kg P ha⁻¹. From this, one can conclude that the growth of rainforests in our study area is most likely not P limited.

With the new parameterizations and modifications described above in the submodels of forest growth, soil climate, denitrification and the implementation of the biological N₂ fixation, the new version of PnET-N-DNDC was evaluated for its ability to simulate C and N biogeochemical cycles and associated trace gas emissions in tropical rainforest ecosystems.

Model evaluation

The tropical version of the PnET-N-DNDC model was validated against field measurements of N₂O emissions, made using the closed-chamber technique, at four tropical rainforest sites in the Wet Tropics of Australia and two sites in Costa Rica. At the Australian sites for continuous determination of N₂O emission, a mobile and fully automated measuring system was used, which consisted of a gas chromatograph equipped with a ⁶³Ni electron capture detector (ECD), an automated gas sampling system and five measuring chambers. For measurements of N₂O emission, chambers were closed automatically for 1 h (Kiese & Butterbach-Bahl 2002), respectively 100 min (Kiese *et al.*, 2003) and changes in N₂O concentrations were monitored every 15 min for each chamber. Rates of N₂O emissions were calculated from the linear increase in N₂O concentrations within the chamber air. At the Costa Rica sites measurements of N₂O emission were carried out once a month, using eight chambers. Here, at time 0, 7, 14, 21 and 28 min 20 mL gas samples were withdrawn from the chambers atmosphere and N₂O concentrations in the sample air were analyzed using ECD gas chromatography (Keller & Reiners, 1994). Mean annual temperatures ranged from 20.1 °C for the montane rainforest at Massey Creek, Australia, to 25.8 °C for the lowland rainforest sites in Costa Rica. The mean annual sum of precipitation varied between the sites: lowest rainfall occurred at the montane rainforest site at Lake Eacham, Australia (1500 mm), whereas the annual rainfall at the lowland rainforest site, Bellenden Ker, Australia, is approximately threefold higher (4395 mm) (Table 1). Soil characteristics at the six sites also differed substantially. Soil pH varied from 3.6 (sites in Costa Rica) to 5.5 (Massey Creek, Australia) and the SOC from 2.3% (Lake Eacham, Australia) to 5.2% (Massey Creek, Australia).

Table 1 Characteristics of the different tropical rainforest sites used for validation of PnET-N-DNDC

	Bellenden Ker, Australia*	Kauri Creek, Australia†	Massey Creek, Australia‡	Lake Eacham, Australia†	La Selva, Costa Rica‡,§	Guacimo, Costa Rica‡,§
Latitude	17°S	17°S	17°S	17°S	10°N	10°N
Rainforest type	Lowland	Montane	Lowland	Montane	Lowland	Lowland
<i>Soil</i>						
Type	Inceptisol	Inceptisol	Ultisol	Ultisol	Ultisol	Ultisol
Texture	Sandy clay loam	Sandy clay loam	Clay loam	Sandy clay loam	Clay	Clay
Clay fraction	0.22	0.23	0.34	0.21	0.75	0.75
pH mineral soil	4.1	5.2	5.5	4.8	3.6	3.6
SOC (%)	3.1	3.2	5.2	2.3	3.0	3.0
<i>Climate</i>						
Mean annual temperature (°C)	24.3	20.9	20.1	21.0	25.8	25.8
Annual rainfall (mm)	4395	1594	2350	1500	3962	3962
N in rainfall (ppm)	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

*Kiese & Butterbach-Bahl (2002).

†Breuer *et al.* (2000).

‡Reiners *et al.* (1994).

§Liu *et al.* (2000).

SOC, soil organic carbon.

Data sets covering longer periods of time on N₂O emissions from tropical rainforest soils are still sparse, and, at present, only the data set from Kiese *et al.* (2003) reports the seasonality of N₂O emissions in at least daily resolution for an entire year, fully covering the highly dynamic pattern of N₂O emission caused by single rainfall events during the wet season. Furthermore, the availability of daily measured meteorological input parameters was a major restriction in applying the modified PnET-N-DNDC model to other sites. For this reason, we could not evaluate the model to the data of Verchot *et al.* (1999) and Melillo *et al.* (2001) in Amazonia.

Model performance was documented using coefficient of determination (r^2), model efficiency (r_{eff}^2), logarithmic model efficiency ($\log r_{\text{eff}}^2$) and normalized root mean square prediction error (RMSPE_n) calculated using the following equations:

$$r^2 = \frac{(\sum (x_{\text{mod}} - \bar{x}_{\text{mod}})(x_{\text{meas}} - \bar{x}_{\text{meas}}))^2}{\sum (x_{\text{mod}} - \bar{x}_{\text{mod}})^2 \sum (x_{\text{meas}} - \bar{x}_{\text{meas}})^2},$$

$$r_{\text{eff}}^2 = 1 - \left(\frac{\sum (x_{\text{mod}} - x_{\text{meas}})^2}{\sum (x_{\text{meas}} - \bar{x}_{\text{meas}})^2} \right),$$

$$\log r_{\text{eff}}^2 = 1 - \left(\frac{\sum (\log x_{\text{mod}} - \log x_{\text{meas}})^2}{\sum (\log x_{\text{meas}} - \log \bar{x}_{\text{meas}})^2} \right),$$

$$\text{RMSPE}_n = \frac{\left[\sum (x_{\text{mod}} - x_{\text{meas}}) / n^2 \right]^{1/2}}{\text{SD}},$$

where x_{mod} is the simulated value, \bar{x}_{mod} is the average of all simulated values, x_{meas} is the value obtained from field data and \bar{x}_{meas} is the average and SD the standard deviation of measured field data. Since a parallel translation of measured and modeled values would still result in high values of the coefficient of determination (r^2), we also calculated other more meaningful statistical measures for model performance such as model efficiency (r_{eff}^2), $\log r_{\text{eff}}^2$, or RMSPE_n (e.g. the use of $\log r_{\text{eff}}^2$ reduce the importance of single outliers for the evaluation of model performance), whereas the RMSPE_n is a simple-to-produce measure that provides useable statistics to verify model forecasts but that conceals intensity and movement errors.

To further evaluate the modified PnET-N-DNDC, we performed a series of sensitivity tests on site and regional scales. Here, model sensitivity was calculated as variation of predicted average N₂O emissions over a 1-year simulation period in response to changes in all major input and driving parameters. Each parameter P was individually increased (P_1) or decreased (P_0) in a range that represents the site/regional uncertainty of the respective parameter ($\pm 20\%$: stand biomass, temperature, soil pH and clay content; $\pm 30\%$: leaf C/N ratio; $\pm 40\%$: rainfall; $\pm 50\%$: SOC, biological N₂ fixation and photosynthetic radiation (PAR)). The sensitive index was calculated based on the formula given by Friend *et al.* (1993):

$$\beta = \frac{(N_2O_1 - N_2O_0)N_2O_0}{(P_1 - P_0)P_0}.$$

The distance of the β value from zero is proportional to the sensitivity of a given parameter and the sign of β indicates if the correlation is positive or negative.

Regional model drivers

The study area of the 'Wet Tropics' (approximately 9000 km²) is located in the north-east of Queensland enclosing the major and most coherent area of Australian rainforest occurrence. This area includes lowland tropical rainforests along the coast as well as montane tropical rainforest on the Atherton Tablelands, an elevated plateau varying in altitude from 700 to 900 m above sea level. The Coastal Lowlands and the Atherton Tablelands are divided by the Great Escarpment with summits going up to 1600 m (e.g. Mt Bartel Frere, Queensland's highest mountain) (Fig. 2).

Climate. Data on daily rainfall and temperature for the years 1997–1998 were obtained for 61 meteorological stations within the study area from the Bureau of Meteorology, Brisbane, Australia. Because of the rough and complex topography, the spatial interpolation of precipitation data was based on the map (grid size 80 m) of mean annual rainfall within the study area, which is itself based on data from more than 400 rainfall stations and a thin plate spline interpolation using a digital terrain model (Houlder *et al.*, 1999). In the next step, this map was superimposed with the location of the available climate stations and for each of them, representative polygons of precipitation were calculated using a cost-distance approach, which considers the gradient of spatial change in annual rainfall within a given area. Since this regionalization of daily rainfall already considers topography and altitude, we used the same polygons for the spatial distribution of daily temperature values. The model was initialized with climate data prepared for the dry season (i.e. July 1997).

For all 61 climate stations, the annual sum of rainfall for the period July 1, 1997–June 30, 1998 varied within a range of 789.2–7839.6 mm (mean value: 2689.0 ± 155.3 mm). Highest rainfall values were obtained for the Bellenden Ker region (climate station at summit of Mt Bellenden Ker), which is located in the center of the study area. Significantly lower rainfall was observed for areas on the Atherton Tablelands (mean value: 1685.5 ± 226.3 mm) and in the Southern Region of the study area (mean value: 2424.1 ± 117.4 mm). Highest mean annual temperature values were observed for the tropical lowland areas close to the coast (24.2 °C), whereas records for the mean annual temperature at the Atherton Tablelands were approximately 3.5 °C lower.

Seasonal variation in rainfall was pronounced (Fig. 3). Around 80% of the annual rainfall was observed

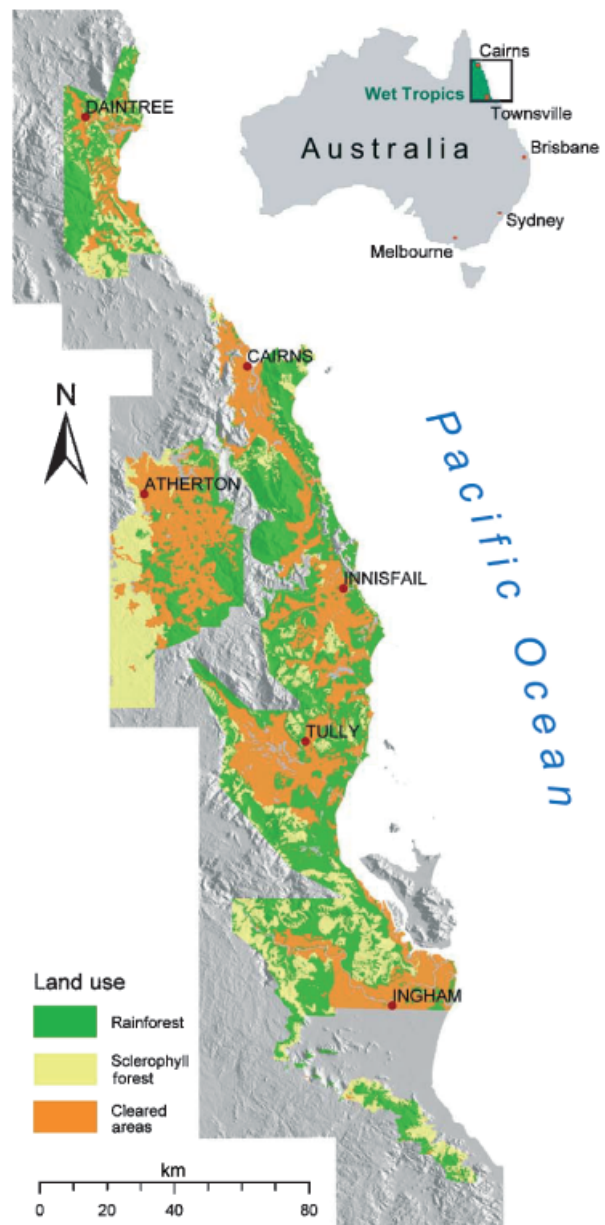


Fig. 2 Location, topography and forest distribution of the study area in north-east Queensland, Australia.

during the wet season, which lasted from December 97 to May 98, whereas less than 21% of precipitation occurred during the dry season (June 1997 to December 1997). The seasonality of temperature was less pronounced. However, during the dry season the mean temperature was approximately 4.0 °C lower than during the wet season (Fig. 3).

Soils. Digital soil series maps for specific regions of the study area, i.e. Townsville, Ingham, Cardwell-Tully, Babinda-Cairns, Mossman, Atherton and Ravenshoe,

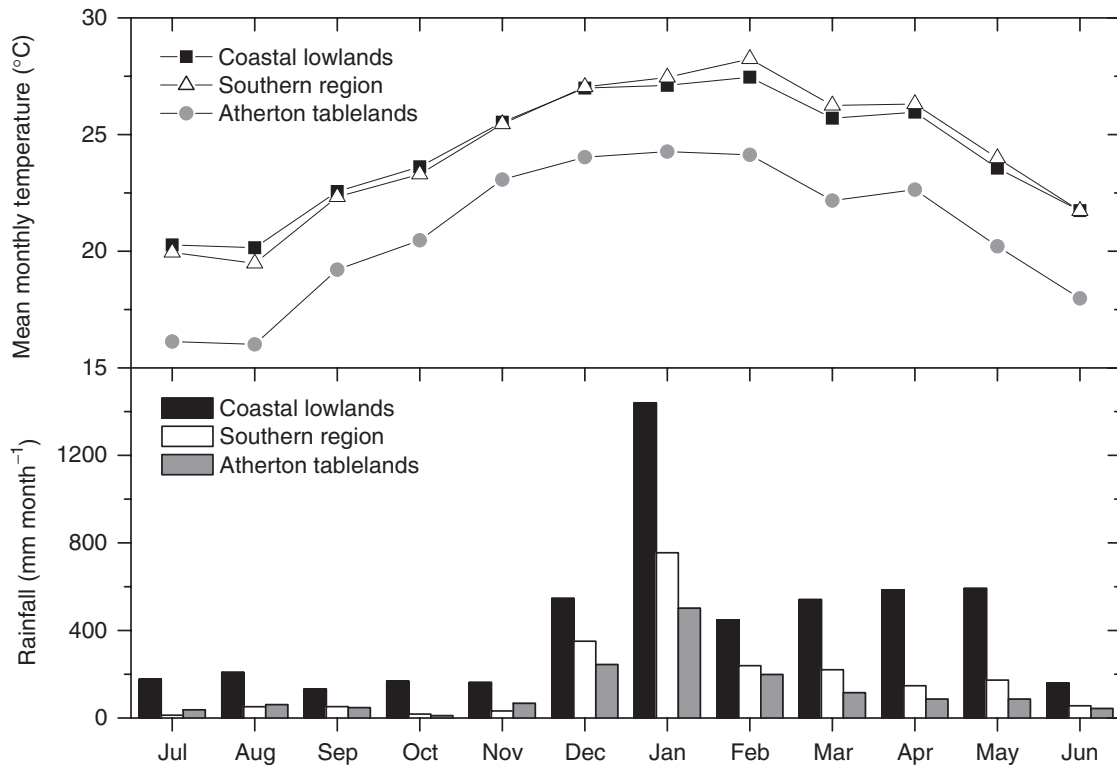


Fig. 3 Seasonality of temperature and rainfall at three representative sites in the Coastal Lowlands (Bellenden Ker), the Southern Region of the wet tropics (Cardwell) and the Atherton Tablelands (Atherton). Data presented are for the time interval July 1997 to June 1998.

Table 2 Soil characteristics of typical soil types found within the study area

Soil order	Area covered (% of study area)	Clay (%)	Stone fraction (>2 mm) (%)	SOC (%)	C/N ratio	Soil pH
Alfisols	6.1	1–35	–14	1.2–3.7	12.8–32	5.0–6.2
Inceptisols	11.2	9–60	–30	1.1–5.7	6.2–30.6	4.1–7.0
Oxisols	1.0	20–50	–15	0.7–5.9	9.1–75	4.7–6.2
Spodosols	4.4	1–24	–10	0.5–2.7	11.0–28.1	5.1–5.9
Ultisols	76.8	9–57	–50	1.1–5.3	6.7–44.5	4.2–6.6
Vertisols/entisols	<1.0					

Values given represent properties of the top soil (0–10 cm). SOC, soil organic carbon.

were provided by the Department of Primary Industries (DPI) at Mareeba, Queensland, Australia. Information on soil properties in the uppermost 10 cm of the mineral soil, i.e. SOC, C/N ratio, soil pH, stone fraction (>2 mm) and texture was derived from various reports (Murtha 1986, 1989; Laffan, 1988; Wilson *et al.*, 1990; Cannon *et al.*, 1992; Heiner *et al.*, 1994; Murtha *et al.*, 1996; Malcolm *et al.*, 1999) for each specific region. However, these reports mostly provide only one value, instead of a range, for soil properties for a given soil type within each region. We used these specific values for model initialization. Estimates of

soil fertility were based on the total N content of the soils covered by rainforests. Soils with a high fertility ($N > 0.3\%$) covered approximately an area of 28%, whereas soils with medium ($0.15\% < N < 0.3\%$) and low fertility ($N < 0.15\%$) covered an area of 42% and 30%, respectively.

According to the Australian soil classification, approximately 75 different soil series are found within the study area. Soil properties for these soil types vary significantly (e.g. pH values from 4.1 to 7.0 and SOC in a range of 0.5–5.9%). Table 2 summarizes soil characteristics of the different soil series found within

the study area grouped according to USDA Soil Taxonomy classification (USDA, 1999).

Rainforest distribution. The distribution of rainforest within the study area was derived from a digital vegetation map which was created based on the work of Tracey (1982). For the regional simulation we only considered the following forest classifications as true rainforests: complex notophyll, notophyll, simple notophyll, complex mesophyll, mesophyll, semideciduous mesophyll, simple microphyll vine forest, mesophyll vine forest with dominant palms, simple microphyll vine-fern forest, simple microphyll vine-fern thicket, deciduous microphyll vine thicket. We excluded sclerophyll forests dominated by *Eucalyptus* spp. as well as sites that were cleared since the early 20th century (Fig. 2).

For the regional application of the tropical version of the PnET-N-DNDC model, we used a polygonal data set, which was created by superimposing the digital maps of climate, soil properties and vegetation on the GIS platform ArcView. This approach resulted in 7538 different polygons covering a total area of 4011 km².

For initialization, the soil organic matter was distributed in the different pools as follows: 90% humus pool, 5% microbial biomass pool and 5% litter pool. Furthermore, the organic matter was further subdivided for its decomposability (i.e. 20% of the SOC was assumed to be very labile, 30% to be labile and 50% to be resistant) (for further details see Li *et al.*, 1992, 2000). For initialization of the vegetation pools across the study area, we used the following estimates: 380 t of wood C, 5.6 t of leaf C and 3.4 t of root C. Estimates were provided by the Tropical Forest Research Centre, Atherton, Australia.

Results and discussion

Model validation for different field sites

Simulated N₂O emissions at all sites were in good agreement with observed rates of N₂O emissions and the coefficient of determination (r^2) varied in a range of 0.36–0.83 (Table 3). At the Bellenden Ker site we found that the seasonal pattern of simulated N₂O emissions agreed closely with field observations (Fig. 4a). The model was even capable of simulating the highly dynamic changes in N₂O emissions during the wet season (November 2001 to May 2002) that were mainly caused by changes in soil moisture as a result of single rainfall events (Kiese *et al.*, 2003). However, N₂O emissions during the wet season were overestimated by a factor of up to 3. This may partly be because of an

underestimation of the soil hydraulic conductivity at the site, either caused by an underestimation of macropores or by an overestimation of the clay content. During the dry period (June 2002 to October 2002) model simulation and field results agreed closely (Fig. 4a). The overestimation of N₂O emissions during the wet season by the PnET-N-DNDC model is especially obvious for four peak events (November 2001, end of January 2002, end of February 2002 and beginning of March 2002), when heavy storms with rainfall sums of 180–300 mm per event occurred. Since the model does not simulate saturated overland flow (runoff), wfps was overestimated during these periods by approximately 15%. In consequence denitrification activity and N₂O production via denitrification were also overestimated. This result clearly shows that it will be necessary to network PnET-N-DNDC with regional hydrological models to further improve predictions of soil moisture at a given site by considering surface runoff. As a result of overestimation of N₂O emissions during the wet season simulated mean N₂O emissions for the entire observation period November 2001 to October 2002 were approximately 1.6-fold higher (4.1 ± 0.3 g N₂O-N ha⁻¹ day⁻¹) as compared with the results of field measurements (2.5 ± 0.1 g N₂O-N ha⁻¹ day⁻¹) (Fig. 4a; Table 3). The coefficient of determination r^2 equals 0.45. This shows that the model is capable of describing the dynamic changes in the magnitude of N₂O emissions during wet and dry season conditions. The more critical value for model performance, the model efficiency factor r_{eff}^2 was <0. This factor (r_{eff}^2) decreases very rapidly with increasing deviation of model predictions from field measurements. Thus, the negative value obtained for r_{eff}^2 mainly reflects the substantial overestimation of N₂O emissions during the periods of extreme rainfall events. In this case, the use of log r_{eff}^2 is probably more appropriate as a means of evaluating model performance, since periods with significant deviations are statistically less weighted. For the Bellenden Ker site and the period November 2001 to October 2002 this value was 0.39 (Table 3). Even better results were obtained for the period February to March 2000 and December 2000 to January 2001, when simulated (30.5 ± 2.9 g N₂O-N ha⁻¹ day⁻¹) and measured N₂O emissions (33.9 ± 3.9 g N₂O-N ha⁻¹ day⁻¹) were not statistically different ($P > 0.05$; Mann–Whitney test) and values for model efficiency ranged from 0.32 to 0.41 (Table 3).

A comparison of measured and simulated N₂O emissions at the Kauri Creek site (Fig. 4b) shows that the model was capable of capturing the magnitude of N₂O emissions for wet season conditions (January 2000 to February 2000) as well as for the transition period from the dry to the wet season at the end of the year

Table 3 Compilation of results for N₂O emissions from the different field sites as derived from model runs with PhET-N-DNDC and from field measurements

Site	Duration of measurements	Number of data resolution, <i>n</i>	Measured N ₂ O emission (g N ₂ O-N ha ⁻¹ day ⁻¹)			Simulated N ₂ O emission (g N ₂ O-N ha ⁻¹ day ⁻¹)			Model performance				
			Mean	Min	Max	Mean	Min	Max	RMSPE _n	<i>r</i> ²	<i>r</i> _{eff} ²	log <i>r</i> _{eff} ²	Reference for dataset
Lowland rainforest at Bellenden Ker, Australia	11/01–10/02	348/daily	2.5 ± 0.1	0.3	12.4	4.1 ± 0.3	0.3	28.6	1.99	0.45	<0	0.39	Kiese <i>et al.</i> (2003)
Lowland rainforest at Bellenden Ker, Australia	02/00–03/00 and 12/00–01/01	36/daily	33.9 ± 3.9	6.7	87.2	30.5 ± 2.9	5.2	63.4	0.81	0.36	0.32	0.41	Kiese & Butterbach-Bahl (2002)
Montane rainforest at Kauri Creek, Australia	01/00–02/00 and 11/00–12/00	44/daily	8.6 ± 1.1	1.4	31.5	9.4 ± 1.3	1.2	36.6	0.59	0.76	0.64	0.80	Kiese & Butterbach-Bahl (2002)
Montane rainforest at Kauri Creek, Australia	07/97	12/daily	3.0 ± 0.7	1.2	8.7	2.4 ± 0.2	1.6	4.0	0.79	0.56	0.32	0.51	Breuer <i>et al.</i> (2000)
Montane rainforest at Massey Creek, Australia	12/98	14/daily	15.8 ± 2.8	4.2	31.5	18.8 ± 2.2	8.5	33.3	0.59	0.71	0.62	0.44	Breuer <i>et al.</i> (2000)
Montane rainforest at Massey Creek, Australia	05/97–06/97	18/daily	4.1 ± 0.3	2.8	6.0	3.5 ± 0.3	2.0	6.6	0.85	0.73	0.23	<0	Breuer <i>et al.</i> (2000)
Montane rainforest at Lake Eacham, Australia	05/97	16/daily	2.1 ± 0.3	0.8	4.9	2.2 ± 0.2	1.3	4.0	0.52	0.74	0.71	0.71	Breuer <i>et al.</i> (2000)
Lowland rainforest at La Selva, Costa Rica	10/90–09/91	12/monthly	16.0 ± 3.7	1.2	36.6	14.4 ± 3.2	0.6	27.5	0.42	0.83	0.81	0.73	Keller & Reiners (1994)
Lowland rainforest at Guacimo, Costa Rica	03/92–11/92	7/monthly	12.4 ± 2.2	6.7	23.3	14.1 ± 3.2	2.5	27.8	0.80	0.74	0.26	<0	Liu <i>et al.</i> (2000)
Total		507	6.1 ± 0.5	0.3	87.2	7.1 ± 0.4	0.3	63.4	0.58	0.68	0.66	0.78	

RMSPE_n, normalized root mean square prediction error.

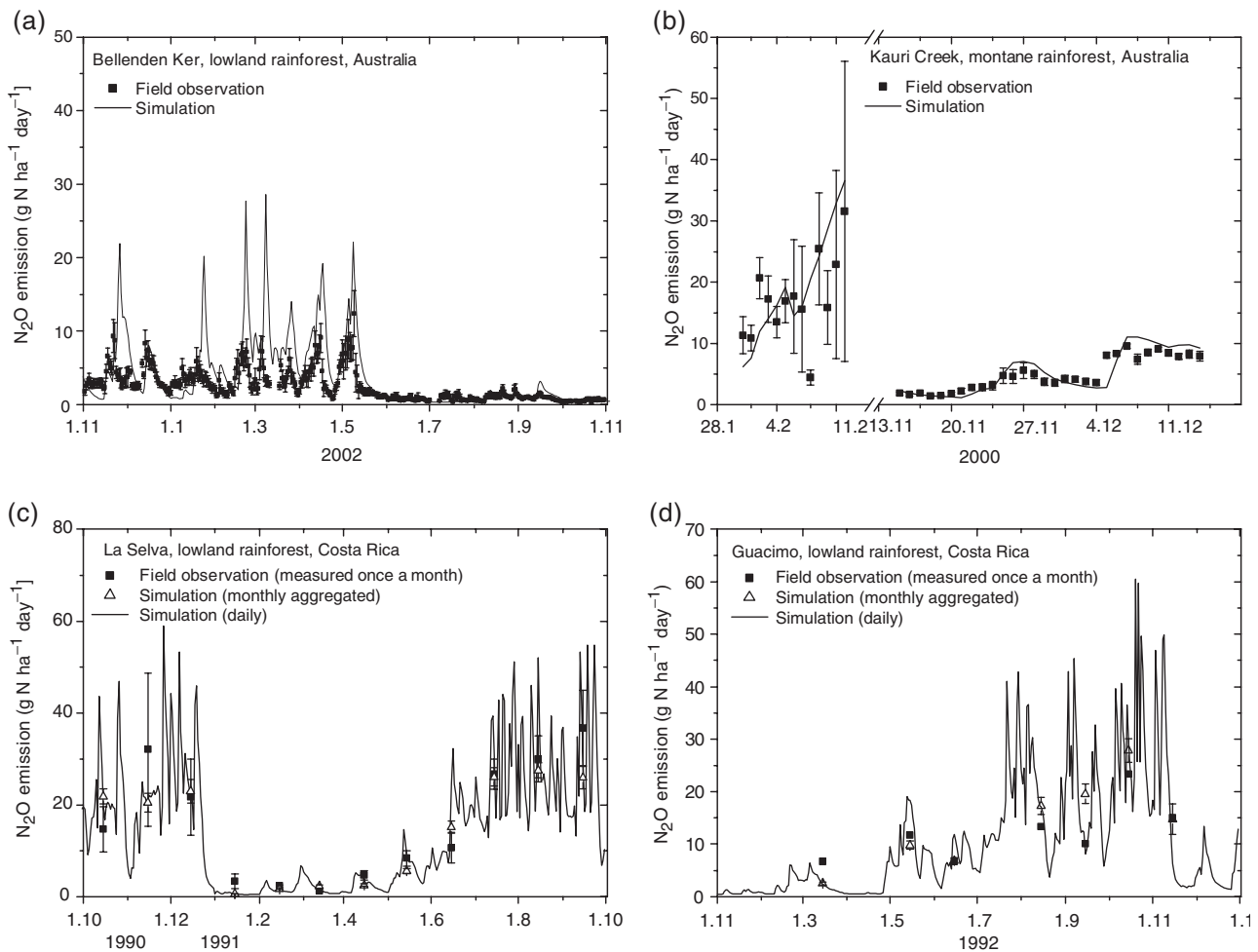


Fig. 4 Measured and simulated N_2O emissions (\pm SE, Australia sites: daily means for five chambers sampled at least in five hourly intervals; Costa Rica sites: eight chambers sampled once per month) from lowland rainforest soils at Bellenden Ker (Australia), La Selva and Guacimo (Costa Rica) and from a montane rainforest soil at Kauri Creek (Australia).

2000. The model efficiency values varied in a range of $0.8 \leq r^2 \leq 0.64$ (Table 3). For the entire period of the year 2000 for which N_2O emission measurements were available, the mean value of simulated N_2O emissions was $9.4 \pm 1.3 \text{ g N}_2\text{O-N ha}^{-1} \text{ day}^{-1}$ and, thus 9.3% higher than the calculated mean of measured N_2O emissions ($8.6 \pm 1.2 \text{ g N}_2\text{O-N ha}^{-1} \text{ day}^{-1}$) (Table 3). However, since the meteorological data for this site were obtained from a station approximately 20 km away, the deviations between the simulated and the measured N_2O fluxes may also be related to the spatial variability of rainfall within this area. This problem induced by the representativeness of meteorological input data also holds for the sites at Massey Creek and Lake Eacham, both montane rainforests sites on the Atherton Tablelands. Taking the spatial variability of rainfall into account, especially the frequent occurrence of convective rainfall events in tropical regions, simulated and

measured N_2O emissions for the Massey Creek and Lake Eacham sites were in good agreement with regard to mean, minimum and maximum values as well as with regard to the observed and simulated site and seasonal differences (Table 3). The simulated site differences in N_2O emissions are in excellent agreement with results obtained from field observations. Breuer *et al.* (2000) found significantly higher emissions at the Kauri Creek and Massey Creek site compared with the Lake Eacham site. Model results revealed that the differences in the magnitude of N_2O emissions between the Kauri Creek, Massey Creek and Lake Eacham sites are mainly attributed to differences in SOC (Tables 1 and 3).

The comparison of daily model results with monthly obtained field data is critical. For example, PnET-NDNDC predicted a huge temporal variability of N_2O fluxes from the two lowland rainforest sites in Costa

Rica, which cannot be reflected by field measurements made only once per month (Fig. 4c and d) (Keller *et al.*, 1993; Keller & Reiners, 1994). To cope with this problem, we calculated in addition mean monthly values from our model outputs and also compared these values to the results of the field measurements. The highest deviations between simulated and measured values of N₂O emission (up to 10 g N ha⁻¹ day⁻¹) occurred mainly during the wet season. For this period, the model predicts a maximum in the temporal dynamics of N₂O emissions, whereas the field measurements by Keller *et al.* (1993) and Keller & Reiners (1994) can only reflect the actual emission of N₂O at a given day. However, the mean value of simulated N₂O emissions at the La Selva site is 14.4 ± 3.2 g N₂O-N ha⁻¹ day⁻¹, and, thus, only 10% lower than the mean value that was calculated from the results of the field measurements (16.0 ± 3.7 g N₂O-N ha⁻¹ day⁻¹). The differences between monthly measured and simulated values at the Guacimo site were slightly higher resulting in a deviation of 13.7% (Fig. 4c and d; Table 2). The better agreement between simulated and measured N₂O emission for the La Selva site was also reflected by higher values of the model efficiency $r_{\text{eff}}^2 = 0.81$ at this site compared with $r_{\text{eff}}^2 = 0.26$ for simulations at the Guacimo site. Calculating the model performance across all sites ($n = 507$) resulted in $r^2 = 0.68$, $r_{\text{eff}}^2 = 0.66$ and $\log r_{\text{eff}}^2 = 0.78$ (Table 3).

To further explore the predictive capabilities of the PnET-N-DNDC model a site and regional specific

sensitivity analysis was performed. For this input parameters such as stand biomass, texture, leaf C/N ratio, SOC and soil pH as well as model drivers such as temperature, rainfall and calculated values of biological N₂-fixation rates were changed in a range that represents the uncertainty of input data for the respective sites/region (Fig. 5). Figure 5 shows that modeled N₂O emissions are most sensitive to changes in soil properties such as pH, SOC and clay content to changes in temperature and rainfall as well as to the leaf C/N ratio. Other parameters such as biomass, biological N₂ fixation and PAR are of minor importance for the magnitude of simulated N₂O emissions. In addition, N₂O emissions from different sites were most sensitive to different factors: pH for Costa Rica, clay content for Bellenden Ker, rainfall for Lake Eacham, and temperature for Massey Creek and Kauri Creek. For the Costa Rica sites the most sensitive parameter was the soil pH. This is because the soil pH at these sites is already low (pH 3.6), and that with further pH decreases microbial N turnover processes and associated N₂O emissions dropped dramatically. On the other hand, increasing the pH value for these sites shifted the value toward the optimum value for microbial N turnover processes and thus increased N₂O emissions. This effect was less pronounced at sites with pH well above 4.0 (Table 1). For the Bellenden Ker site the most sensitive factor determining the magnitude of N₂O emissions was the soil texture (Fig. 5). Although the clay content at this site is in a range

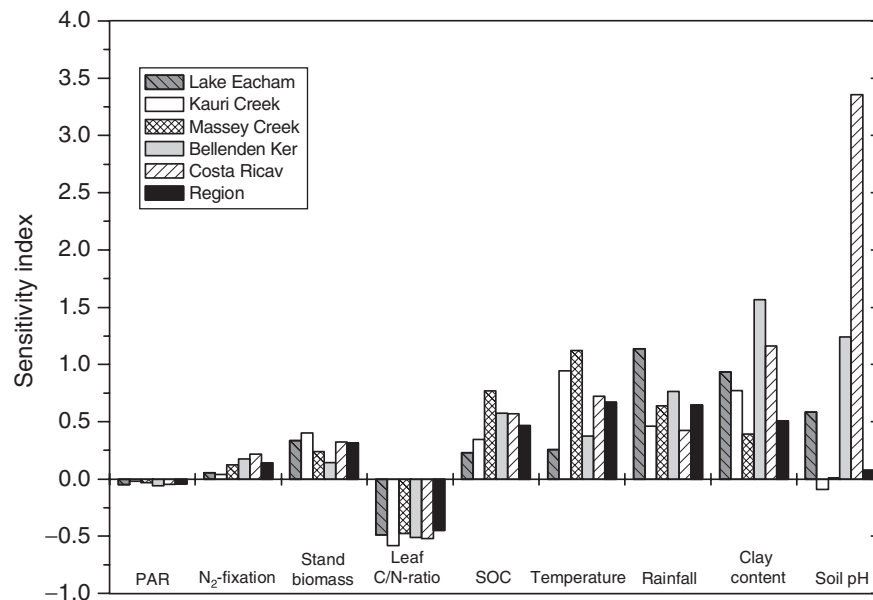


Fig. 5 Sensitivity of simulated site and regional N₂O emissions to changes in individual parameters. Details for the calculation of the sensitivity index are given in Materials and methods. The distance of the β -value from zero is proportional to the sensitivity of a given parameter. The sign of β indicates the sign of the correlation.

comparable with the Kauri Creek and the Lake Eacham sites (Table 1), the high sensitivity to changes in texture is a result of the higher rainfall at this site and the way the model couples texture properties with parameters describing soil hydraulic conductivity. Therefore, a decrease of the clay content leads to better drainage of soil water, which results in a better aeration of the soil. Consequently, the model simulates a sharp decrease of N₂O production via denitrification, which is not compensated for by a slight increase of N₂O production via nitrification. If, at the Bellenden Ker site, the clay content was higher, the processes would work in the opposite direction. The sensitivity analysis also shows that for the sites at Lake Eacham and Kauri Creek the most sensitive factors are the meteorological parameters, rainfall and temperature (Fig. 5). Of all the sites investigated, these two sites received the lowest annual rainfall (approximately 1500 mm). At the Lake Eacham site a simulated decrease in rainfall leads to a sharp decrease in N₂O emissions, since at this site the microbial N-turnover processes are already limited by water stress during the dry season. This effect is less pronounced at the Kauri Creek site, since this site has a slightly higher clay fraction, a higher SOC content and also receives approximately 100 mm more precipitation each year. Of all sites investigated, the Massey Creek site has the lowest mean annual temperature (Table 1). The sensitivity study revealed that for this site microbial N-turnover rates and associated N-trace gas production are mainly constrained by temperature. On a regional scale, the model sensitivity to changes of single parameters was less pronounced compared with results at an individual site scale. This is because most of the factors within our sensitivity analysis have a pronounced optimum with regard to N₂O emissions and, thus, varying them over the region may result in compensation effects. For example, although further increases in the clay fraction will lead to increased denitrification, this will not necessarily lead to increased N₂O production, since when anaerobic conditions are dominant, most of the N₂O produced will be further reduced to N₂, whereas under suboptimal conditions for denitrification the ratio of N₂O to N₂ production can be much higher (Li *et al.*, 2000). For the regional sensitivity analysis, this means that in some parts of the study area there is an assumption that increased clay contents of the soil will lead to an increase in N₂O emissions, whereas in other parts, where the clay content of the soil is already high, a decrease in N₂O emissions will be predicted (at the cost of an increase in N₂ emissions). This complexity of N-trace gas emissions, as realized in the PnET-N-DNDC model, is in agreement with a large number of field and laboratory studies (e.g. Linn & Doran, 1984; Firestone &

Davidson, 1989; Davidson *et al.*, 1993; Kiese & Butterbach-Bahl, 2002).

The applications of PnET-N-DNDC to the six different field sites and the sensitivity analysis provided evidence that the model is able to capture the spatial and temporal variations in soil N₂O emissions with reasonable accuracy. This result is in agreement with previous model evaluations for temperate forests (Stange *et al.*, 2000; Butterbach-Bahl *et al.*, 2001, 2004).

For further model validation we also compared predicted values of net primary productivity (NPP), soil CO₂ emissions and gross N mineralization, which were obtained for our study area of the Wet Tropics, Australia, with published values (Table 4). The mean simulated NPP values for the study area is 6451 tC ha⁻¹ yr⁻¹ (range: 2067–15 015 tC ha⁻¹ yr⁻¹) and, thus, in agreement with published values for other tropical forests (1700–21 700 tC ha⁻¹ yr⁻¹, see review by Clark *et al.*, 2001). Also, the values for soil respiration (range: 6585–16 603 tC ha⁻¹ yr⁻¹) as well as for gross N mineralization (range: 335.5–1284 kg N ha⁻¹ yr⁻¹) are in accordance with published results of field measurements (soil CO₂ emissions: e.g. Holt *et al.*, 1990; La Scala *et al.*, 2000; Kiese & Butterbach-Bahl, 2002; N mineralization: Zou *et al.*, 1992; Neill *et al.*, 1999; Breuer *et al.*, 2002).

Regional application

For the regionalization of N₂O emissions of tropical rainforests in north-east Queensland, we linked the PnET-N-DNDC model to a GIS database, which held all the relevant model drivers and input parameters (Fig. 2). The regional distribution of N₂O emissions in the study area was simulated for the time period July 1, 1997 to June 30, 1998 (Fig. 6). The annual sum of simulated N₂O emissions varied within a range of 0.5–8 kg N₂O-N ha⁻¹ yr⁻¹ (mean for the entire study area: 2.4 kg N₂O-N ha⁻¹ yr⁻¹), which is in good agreement with the reported annual N₂O-emission rates for tropical rainforest ecosystems worldwide (see overview given by Breuer *et al.*, 2000). Highest N₂O emissions were simulated for the northern region around Mossman and the Daintree National Park with N₂O-emissions rates of up to 8.0 kg N₂O-N ha⁻¹ yr⁻¹. Furthermore, high N₂O emissions (>4.0 kg N₂O-N ha⁻¹ yr⁻¹) were predicted for the mountainous Bellenden Ker and Bartel Frere region, located approximately in the center of the study area. N₂O emissions from both regions, which also receive the highest rainfall within the study area, were clearly higher than N₂O emissions from rainforest soils from the Southern Region of the study area (south of Tully down to Townsville: 0.5–2.5 kg N₂O-N ha⁻¹ yr⁻¹) and the Northern Atherton Tablelands (<3.0 kg N₂O-N ha⁻¹ yr⁻¹).

Table 4 Measured mean, minimum, and maximum values of annual rainfall and mean annual temperature as well as model predictions of PnET-N-DNDC for NPP, mean annual soil CO₂ emissions, gross N mineralization, and mean annual N₂O emission for tropical rainforest ecosystems across the study area (July 97–June 98)

Wet tropics area, July 97–June 98	Annual rainfall (mm)	Mean annual temperature (°C)	NPP (kg C ha ⁻¹ yr ⁻¹)	Mean annual soil CO ₂ emission (kg CO ₂ -C ha ⁻¹ yr ⁻¹)	Gross N mineralization (kg N ha ⁻¹ yr ⁻¹)	Mean annual N ₂ O emission (kg N ₂ O-N ha ⁻¹ yr ⁻¹)
Mean	2680	23.2	6451	11931	811.3	2.4
Minimum	789	20.1	2067	6585	335.5	0.5
Maximum	7840	25.7	15015	16603	1284.0	8.0

NPP, net primary productivity.

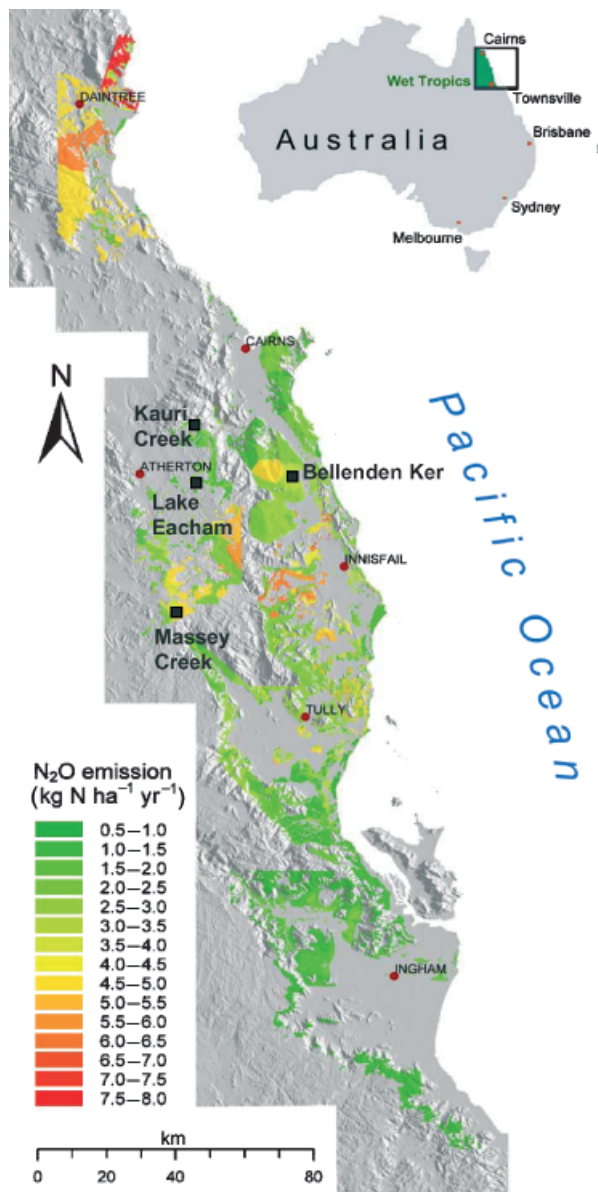


Fig. 6 Regional distribution of annual sums of N₂O emissions (kg N₂O-N ha⁻¹ yr⁻¹) from tropical rainforest in the Wet Tropics of Australia for the year July 1997 to June 1998.

However, for the Southern Atherton Tablelands, a region with higher rainfall amounts and higher SOC contents, intermediate N₂O emissions (2–6 kg N₂O-N ha⁻¹ yr⁻¹) were estimated. The significant north–south differences in N₂O emission within the study area (approximately 9000 km²) were mainly related to climate differences, e.g. precipitation and temperature. At smaller scales (e.g. Atherton Tablelands, 1000 km²), the spatial variations in N₂O emissions were triggered by both: (a) the heterogeneity of soil properties, especially SOC content and soil pH and (b) by differences in the amount of rainfall. This finding is in excellent agreement with site differences in N₂O emissions as observed by field measurements within the study area (Breuer *et al.*, 2000; Kiese & Butterbach-Bahl, 2002; Kiese *et al.*, 2003). Both predictions and measurements revealed higher annual N₂O emissions for the Coastal Lowland sites in the region of Bellenden Ker (3–7 kg N₂O-N ha⁻¹ yr⁻¹) compared with the sites on the Atherton Tablelands (Lake Eacham, Kauri Creek and Massey Creek: 1–4 kg N₂O-N ha⁻¹ yr⁻¹). The ranking of emissions as simulated by the model for sites on the Atherton Tablelands, i.e. higher emissions for the sites Kauri Creek and Massey Creek as compared with the Lake Eacham site, is in accordance with field observations.

In our model simulated nitrification was the dominant process in N₂O production during the dry season (up to 85%), whereas during the wet season N₂O production via denitrification gained significantly in importance and contributed in average 40–50% to total N₂O emissions. However, it must be pointed out that in the Pnet-N-DNDC model N₂O emissions are a result of simultaneously occurring production (nitrification and denitrification) and consumption processes (further reduction of N₂O to N₂ during denitrification) in the different soil layers (Li *et al.*, 2000) and that therefore a NO or N₂O molecule produced in a deeper soil layer may get further reduced to N₂O or N₂ during its diffusion through the soil profile into the atmosphere.

Modeled N₂O emission from rainforest soils in the study area, for which vegetation and soil type as well as climate data were available in the GIS (4011 km²), totaled in 962 t N₂O-N yr⁻¹ for the 1-year period from July 1997 to June 1998. For a comparison with figures of the Australia's National Greenhouse Gas Inventory 2002 (Australian Greenhouse Office, 2004) we converted this value to CO₂ equivalents (962 t N₂O-N = 0.486 Gg CO₂ equivalents) using the global warming potential (GWP) concept, with 100-year time horizon GWP value. In Australia's National Greenhouse Gas Inventory 2002, which was derived using guidelines provided by the Intergovernmental Panel on Climate Change, the N₂O emissions from the sector 'land-use change and forestry' are estimated to be 0.774 Gg CO₂ equivalents (0.322 Gg CO₂ equivalents from forest and grassland conversion plus 0.451 Gg CO₂ equivalents from wildfires and prescribed burning). N₂O emissions from agricultural soils in Australia are estimated to be 19.471 Gg CO₂ equivalents, i.e. 40 times higher than our estimate for tropical rainforests of the wet tropics. However, regarding the small area investigated (4011 km²) our estimate underlines the potential importance of tropical rainforest soils as a source of atmospheric N₂O on a regional, national and global scales.

Conclusions

The paper describes the development and application of a tropical version of PnET-N-DNDC in order to quantify N₂O emissions from tropical rainforest soils at both site and regional scales. The validations and sensitivity tests demonstrated that this model is capable of simulating N₂O emissions at different tropical rainforest sites with a reasonable degree of accuracy. Thus, it may be of use to scale up N₂O emissions from a site to a regional scale, e.g. to improve regional or global inventories of N₂O emissions from tropical forest soils. However, to further increase the accuracy of model predictions, we need to continuously improve and validate the model in the coming years, with regard to both (a) N turnover processes and associated trace gas fluxes and (b) soil hydrology. This will require detailed laboratory experiments on processes governing N-trace gas emissions as well as collecting of field measurements with high temporal resolution describing C and N cycling and associated N- and C-gas exchange in rainforest ecosystems across climatic zones, soil types and vegetation properties. To improve our ability to model N-trace gas emissions from tropical soils, we stress that the exclusive measurement of N₂O emissions from soils will not be sufficient in the future. Instead, it will be necessary to quantify emissions of all

N gases from soils, i.e. N₂O, NO and N₂ and to measure simultaneously the magnitude of microbial processes involved in N cycling and N-gas emissions, i.e. the processes of nitrification, denitrification, microbial immobilization of N and biological N₂ fixation. Furthermore, from the validation process for the Bellenden Ker site it became obvious that biogeochemical models such as the PnET-N-DNDC model should be networked with regional hydrological models in order to further improve soil moisture predictions, which is one of the major factor-governing processes involved in N-trace gas emissions.

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