

A process-oriented model of N₂O and NO emissions from forest soils

2. Sensitivity analysis and validation

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Abstract. The process-oriented model PnET-N-DNDC describing biogeochemical cycling of C- and N and N-trace gas fluxes (N₂O and NO) in forest ecosystems was tested for its sensitivity to changes in environmental factors (e.g., temperature, precipitation, solar radiation, atmospheric N-deposition, soil characteristics). Sensitivity analyses revealed that predicted N-cycling and N-trace gas emissions varied within measured ranges. For model validation, data sets of N-trace gas emissions from seven different temperate forest ecosystems in the United States, Denmark, Austria, and Germany were used. Simulations of N₂O emissions revealed that field observations and model predictions agreed well for both flux magnitude and its seasonal pattern. Differences between predicted and measured mean N₂O fluxes were <27%. An exception to this was the N-limited pine stand at Harvard Forest, where predictions of fluxes deviated by 380% from field measurements. This difference is most likely due to a missing mechanism in PnET-N-DNDC describing uptake of atmospheric N₂O by soils. PnET-N-DNDC was also validated for its capability to predict NO emission from soils. Predicted and measured mean NO fluxes at three different field sites agreed within a range of $\pm 13\%$. The correlation between modeled and predicted NO emissions from the spruce and beech stand at the Höglwald Forest was $r^2 = 0.24$ (spruce) and $r^2 = 0.35$ (beech), respectively. The results obtained from both sensitivity analyses and validations with field data sets from temperate forest soils indicate that PnET-N-DNDC can be successfully used to predict N₂O and NO emissions from a broad range of temperate forest sites.

1. Introduction

Estimates of the contribution of temperate forest ecosystems, which cover 10^7 km² of the global land surface [e.g., Steudler *et al.*, 1989; Potter *et al.*, 1996], to atmospheric nitrous oxide (N₂O) and nitric oxide (NO) have a high degree of uncertainty. The source strength of these ecosystems are estimated to be in a range of 0.05–2.0 Tg N₂O-N yr⁻¹ [e.g., Schmidt *et al.*, 1988; Davidson, 1991; Houghton *et al.*, 1992] and 0.1–0.85 Tg NO-N yr⁻¹ [Davidson, 1991; Potter *et al.*, 1996; Lee *et al.*, 1997]. These uncertainties are mainly due to (1) the limited number of field measurements; (2) the restricted temporal coverage of data sets to assess daily, seasonal, and inter-annual variations in fluxes [Papen and Butterbach-Bahl, 1999; Gasche and Papen, 1999]; (3) limited information on the impact of anthropogenic influences (e.g., enhanced atmospheric N input into these ecosystems leading to changes in source strengths) [Butterbach-Bahl *et al.*, 1998]; and (4) a lack of information about the effects of different forest types (e.g.,

coniferous, deciduous forests) on N-trace gas emissions from forest soils.

In view of the huge spatial and temporal variability of environmental conditions in forest ecosystems, it is doubtful that the uncertainties associated with global estimates of N₂O and NO source strengths of temperate forest soils will be significantly reduced by additional field measurements alone. We believe the most promising strategy to overcome these problems is the development of process-oriented models, which are able to describe the processes in forest soils involved in N-trace gas production and emission (e.g., mineralization, nitrification, denitrification, plant-microbe competition for inorganic nitrogen) and their dependency on changing environmental conditions. Such models could be used to quantify N-trace gas flux rates from temperate forest soils on a regional and global scale, as has been already demonstrated for agricultural ecosystems of the United States [Li *et al.*, 1996]. In addition, the process of model development highlights data gaps and can suggest areas where field and laboratory studies can focus.

In a companion paper [Li *et al.*, this issue] the development and structure of the process-oriented model PnET-N-DNDC is described in detail. This model simulates the cycling of C and

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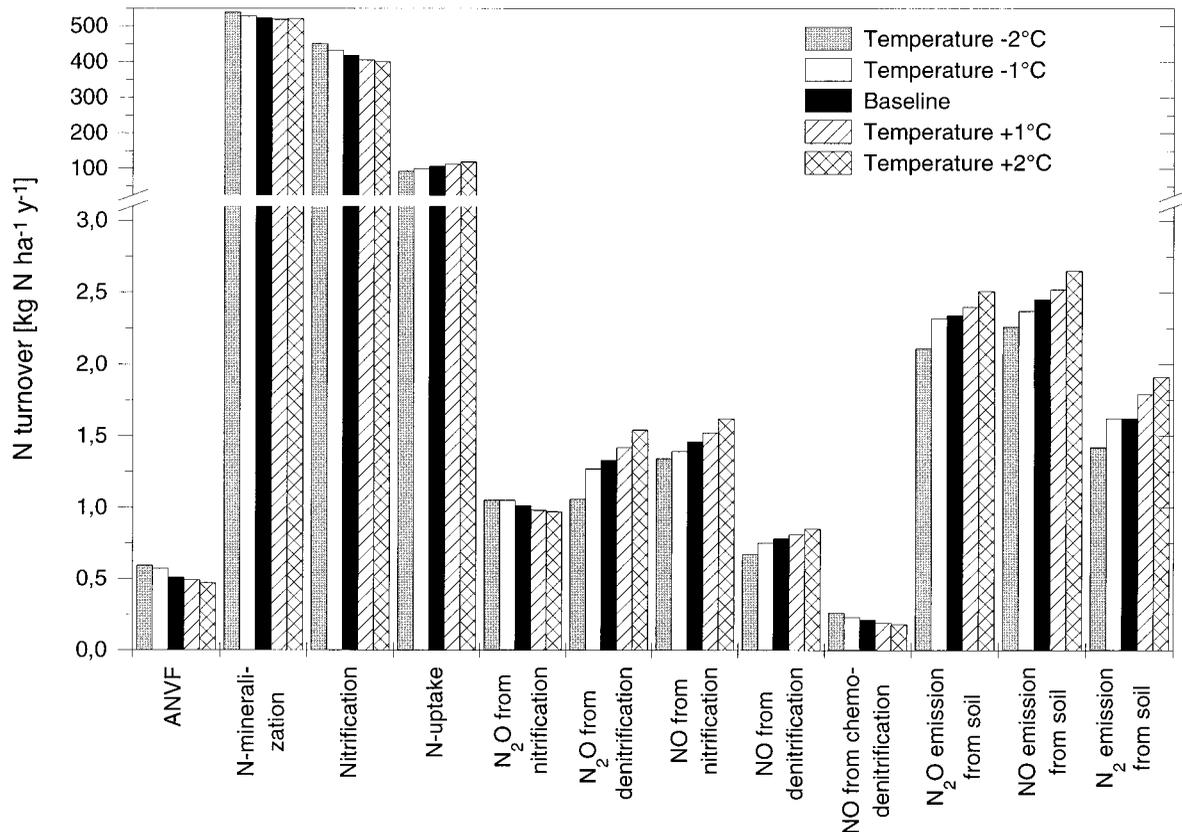


Figure 1. Sensitivity of the anaerobic volume fraction (ANVF) of the soil, the N-turnover rates, and the N-gas emissions to changes in air temperature.

N in temperate forest ecosystems and the production and emission of N-trace gases by the microbial processes of nitrification and denitrification and the physicochemical process of chemodenitrification.

In order to validate the capabilities of PnET-N-DNDC in predicting N-trace gas fluxes the model was applied to seven deciduous and coniferous forest sites in the United States and Europe, and the results were compared with field measurements. These comparisons as well as a sensitivity analysis for the environmental factors used as drivers or input parameters to run PnET-N-DNDC are presented in this paper.

2. Results and Discussion

2.1. Model Sensitivity

Within PnET-N-DNDC, three different processes can contribute to N-trace gas production in the soil. Two of them are microbiological (nitrification and denitrification) and one is physicochemical (chemodenitrification). As has been already described by other authors [e.g., *Firestone and Davidson, 1989; Conrad, 1996*], the magnitude of these processes and thus the magnitude of N-trace gas production in the field strongly depends on environmental conditions (e.g., soil temperature, soil moisture, pH value, O₂ concentration, size of anaerobic microsites, NH₄⁺ and NO₃⁻ concentrations in the soil). A variety of equations have been used within PnET-N-DNDC to numerically describe processes involved in N-cycling and N-trace gas production in forest ecosystems and to quantify their sensitivity to environmental factors [*Li et al., this issue*]. Because the cycling of nitrogen within the ecosystem (e.g., mineralization,

nitrification, denitrification, immobilization, plant uptake, N-leaching) and the processes involved in N-trace gas production are closely linked in PnET-N-DNDC, a sensitivity analysis was performed to study the impact of changes in environmental conditions on model predictions of N-trace gas production and emission. These sensitivity analyses demonstrate the basic behavior of the model.

As a baseline scenario, a 90-year-old beech stand on a loamy soil with a pH value of 3.6 in the uppermost mineral soil and a soil organic carbon content (SOC) of 5.1% was assumed. Meteorological data for 1995 from the Höglwald field site, Germany (48°30'N, 11°19'E), were used as climate drivers in the exercise. Rainfall N-concentration was set at 2.5 ppm in the baseline scenario. This scenario is in accordance with current parameters at the beech site at the Höglwald Forest [*Papen and Butterbach-Bahl, 1999*]. Model sensitivity was tested for model drivers (temperature, precipitation, photosynthetically active radiation (PAR)) and model input parameters (N-concentration in precipitation, litter mass of the forest floor, soil organic carbon content (SOC), pH, soil texture, and dominant tree species) by varying one factor and keeping all others constant.

We found in our study that even for the baseline scenario gross nitrification rates were above 400 kg N ha⁻¹ yr⁻¹. It is worthwhile to acknowledge that this figure is in good agreement with estimates of *Ingersen et al. [1999]*, *Davidson et al. [1990, 1992]*, *Zak et al. [1990]*, and *Stark and Hart [1997]*, who showed that gross nitrification rates in temperate forest soils are in a range of 73–1142 kg N ha⁻¹ yr⁻¹. These high values for

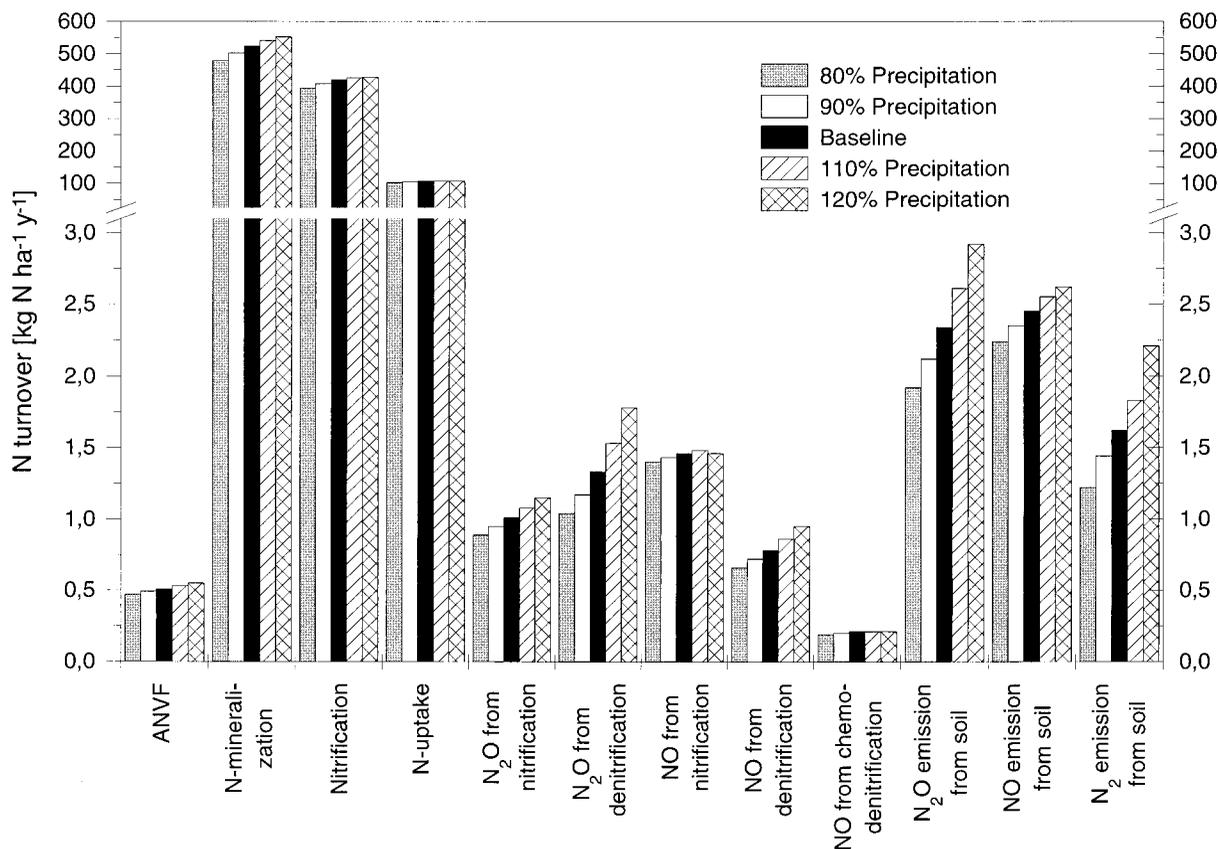


Figure 2. Sensitivity of the anaerobic volume fraction (ANVF) of the soil, the N-turnover rates, and the N-gas emissions to changes in precipitation.

gross nitrification rates were explained by the internal cycling of nitrate in forest soils [e.g., Davidson *et al.*, 1992; Stark and Hart, 1997].

One of the major factors controlling N-turnover and N-trace gas production in forest ecosystems is temperature. Figure 1 summarizes model outputs for key variables (anaerobic volume fraction (ANVF) of the soil or anaerobic balloon) and processes (N-mineralization, nitrification, plant N-uptake, and N₂O, NO, and N₂ emission) involved in N-cycling if the baseline temperature is varied from -2°C to $+2^{\circ}\text{C}$. Changes in average annual air temperature from 5.9°C (2°C lower than baseline) to 9.9°C (2°C higher than baseline) resulted in decreases in the volumetric fraction of the anaerobic balloon and N-mineralization and increases in plant-N-uptake. The latter finding is in agreement with field measurements performed by Geßler *et al.* [1998], who found that the uptake of NH_4^+ and NO_3^- by spruce and beech roots at the Höglwald Forest site was positively correlated with soil temperature.

Model predictions of decreasing nitrification rates with increasing temperatures are at a first glance somewhat surprising, but can be explained by the reduced availability of NH_4^+ for nitrification at higher temperatures due to higher N-uptake rates by plants (Figure 1) and increased microbial immobilization (e.g., at 2°C higher than baseline microbial biomass increased by 3%). The consequences of lower nitrification rates on N-trace gas emissions are at least partially compensated for by increased emission of N₂O and NO during nitrification at higher temperatures [Li *et al.*, this issue] (Figure 1), so that nitrification-related N-trace gas emissions were fairly constant

(N₂O) or increased (NO) in the temperature range tested. A similar statement holds for the contribution of denitrification to N-trace gas emission. Although the volume of anaerobic fraction decreases with increasing temperature due to increased evapotranspiration and decreased soil moisture, the increase in unfavorable conditions for denitrification is more than compensated for by the temperature effects on rates of N-trace gas production by denitrification (Figure 1).

Precipitation has a major impact on biogeochemical cycling of nitrogen in forest soils. Changes in the amount of precipitation and its temporal distribution directly influence the soil moisture regime and, consequently, the water availability for plant production and soil microbial processes. The sensitivity of PnET-N-DNDC was tested for changes in total annual precipitation amount of up to 20% (Figure 2). It is obvious that all of the parameters tested, that is, size of the anaerobic balloon, N-mineralization, nitrification, and denitrification, as well as N-gas production and emission, increased with increasing precipitation. N₂O and N₂ emissions due to denitrification were most sensitive to increasing precipitation (in comparison to the baseline scenario: decreases of 78% (N₂O) and 75% (N₂) for a scenario with 20% lower precipitation rates, increases of 134% (N₂O) and 136% (N₂) for a scenario with 20% higher precipitation rates) since this depends on the size of the “anaerobic balloon” [Li *et al.*, this issue], which strongly increases at higher precipitation rates. The increase in mineralization, nitrification, and nitrification-related production of N-trace gases with increasing precipitation is due to the fact that under low-precipitation scenarios these processes are limited by low

Table 1. Results of the Sensitivity Study for the Impact of Changes in Photosynthetic Active Radiation (PAR), N-Concentration in Rainfall, Litter Mass of the Forest Floor, Soil Organic Carbon Content (SOC), Soil pH, Soil Texture, and Tree Species on Predictions of PhET-N-DNDC for the Anaerobic Volume Fraction of the Soil (ANVF), N-Mineralization, Nitrification, N-Uptake by Plants and Emission of N-Gases (NO, N₂O, N₂)

Change	ANVF	N Mineralization	N Nitrification	N Uptake	N ₂ O From Nitrification	N ₂ O From Denitrification	NO From Nitrification	NO From Denitrification	NO From Chemodenitrification	N ₂ O	NO	N ₂
Baseline, kg N ha ⁻¹ yr ⁻¹	0.506	211.0	419	106.5	1.01	1.33	1.46	0.78	0.21	2.34	2.45	1.62
PAR												
-20%	2.0	0.8	8.2	-6.5	8.2	10.9	9.2	14.7	0.0	9.8	10.2	-8.1
-10%	0.4	0.1	3.2	-2.9	2.1	1.6	3.5	4.0	0.0	1.8	3.4	-5.4
+10%	-0.4	-0.1	-3.0	2.3	-2.1	-2.3	-3.5	-2.7	-5.0	-2.2	-3.4	0.7
+20%	-0.4	-0.1	-5.0	4.1	-3.1	-3.1	-5.7	-5.3	-5.0	-3.1	-5.5	0.7
N concentration in rainfall												
-1.0 ppm	-0.6	-1.5	-6.7	-2.3	-8.2	-5.5	-5.0	-8.0	-25.0	-6.7	-7.6	4.7
-0.5 ppm	-0.2	-0.7	-3.5	-1.1	-4.1	-3.1	-2.1	-4.0	-15.0	-3.6	-3.8	3.4
+0.5 ppm	0.4	0.7	3.5	1.1	4.1	2.3	2.1	4.0	10.0	3.1	3.4	-3.4
+1.5 ppm	1.0	2.0	11.2	3.0	13.4	4.7	7.8	10.7	40.0	8.4	11.5	-10.7
Litter mass												
-20%	-1.6	-8.7	-3.2	-3.5	-4.1	-7.8	-2.8	-6.7	-10.0	-6.2	-4.7	-13.4
-10%	-0.8	-4.3	-1.7	-1.7	-2.1	-4.7	-1.4	-4.0	-5.0	-3.6	-2.5	-4.7
+10%	1.0	4.2	1.7	1.5	2.1	4.7	1.4	4.0	5.0	3.6	2.5	6.0
+20%	1.8	8.5	3.5	2.9	4.1	8.6	2.8	9.3	10.0	6.7	5.5	11.4
SOC												
-20%	-5.4	-4.1	1.6	-0.4	-8.6	-19.2	3.0	-2.2	0.0	-14.7	1.1	-19.6
-10%	-2.4	-1.7	1.4	-0.3	-3.6	-9.6	2.1	0.0	0.0	-7.0	1.3	-10.3
+10%	2.2	1.9	-0.2	0.0	5.0	8.7	-0.4	2.2	0.0	7.1	0.4	9.2
+20%	4.2	3.3	-1.4	0.3	8.6	16.3	-2.1	2.2	0.0	13.0	-0.6	19.6
Soil pH												
-0.5	-0.2	-0.2	-20.3	0.1	-18.6	-22.7	-17.6	-18.7	695.0	-20.9	324.7	-31.5
-0.3	0.0	-0.1	-10.2	0.2	-14.4	-26.6	-12.2	-11.0	260.0	-21.3	126.7	-23.5
+0.4	0.0	0.1	6.9	-0.9	35.1	91.4	5.1	66.7	-100.0	67.1	-25.0	47.0
+0.9	-0.4	0.2	8.9	-2.5	105.2	282.8	10.2	196.0	-100.0	206.1	20.0	139.6
Texture												
sand	-67.0	-38.6	-44.9	-18.0	-68.0	-84.4	-50.4	-82.7	0.0	-77.3	-56.3	-64.4
sandy loam	-56.0	-15.4	-16.4	-5.8	-46.4	-76.6	-14.2	-69.3	0.0	-63.5	-30.5	-55.7
sandy clay	73.6	-2.6	-32.3	-2.0	47.4	64.1	-35.5	29.3	-10.0	56.9	-12.7	163.8
loam.												
sandy clay	156.8	2.6	-36.0	-2.5	112.4	146.1	-56.0	30.7	-15.0	131.5	-24.9	875.2
birch	1.7	19.8	26.6	-22.3	15.8	10.6	26.6	34.8	37.5	12.8	30.1	-26.6
hardwood	1.2	18.4	21.2	-17.6	12.9	9.6	21.0	28.3	25.0	11.1	23.7	-22.8
oak	-0.7	40.4	54.6	-55.3	46.0	92.3	52.4	65.2	262.5	72.3	74.5	-35.9
spruce	-40.7	4.9	41.4	-16.5	-2.9	-48.1	54.9	-6.5	56.3	-28.6	35.5	-69.6
fir	-41.1	9.3	51.8	-26.0	2.2	-37.5	64.8	0.0	106.3	-20.4	47.7	-71.7
hemlock	-41.1	8.3	50.3	-24.6	2.2	-41.3	63.5	0.0	93.8	-22.6	45.9	-71.2
pine	-46.6	10.1	57.5	-28.7	5.0	-51.0	74.2	-8.7	100.0	-26.8	50.0	-79.9

Values given represent percent of change compared to the baseline scenario (first line in table).

Table 2. Site Characteristics of the Different Temperate Forest Sites Used for Validation of PnET-N-DNDC

	Höglwald ^{a,b} Germany 48°N		Harvard ^{c,d,e} United States 42°N	Copenhagen ^f Denmark 55°N	Klausen- Leopoldsdorf ^g Austria 48°N	Schottenwald ^h Austria 48°N	Oak Ridge ⁱ United States 36°N
	Spruce	Beech	Pine/Hardwood	Spruce	Beech	Beech	Oak
Forest age	90	94	62/80	31	55	135	70
Soil							
Texture	loam	loam	sandy loam	loamy sand	loamy silt	loamy silt	silt loam
Clay fraction	0.1	0.1	0.1	0.09	0.29	0.19	0.14
pH (litter layer)	3.2	4.0	3.2/3.3	3.7	5.2	5.0	4.8
pH (mineral soil)	3.2	3.6	3.8	3.7	4.5	4.2	4.8
SOC at top mineral soil	0.029	0.051	0.058/0.076	0.061	0.064	0.038	0.053
Climate				j	k	l	m
Annual mean temperature, °C	7.3	7.3	7.4	7.3	8.9	10.1	14.2
Annual precipitation, mm	800	800	1120	800	1036	973	860
N in precipitation, ppm	2.5	2.5	0.2	1.5	1.0	4.2	0.5

^aRothe [1997].^bKreutzer [1995].^cBowden *et al.* [1991].^dAber *et al.* [1993].^eMagill *et al.* [1997].^fAmbus and Christensen [1995].^gDaten der FBVA.^hJandl *et al.* [1997].ⁱWilliams and Fehsenfeld [1991].^jDanish Meteorological Institut.^kHydrographischer Dienst Niederösterreich.^lZentralanstalt für Meteorologie.^mNational Oceanic and Atmospheric Administration (NOAA).

soil moisture values during summer. The impact of changes in precipitation on plant uptake of nitrogen from the soil was negligible, indicating that forest growth was not limited by soil water shortages (Figure 2).

Changes of the intensity of photosynthetically active radiation (PAR) in a range of $\pm 20\%$ of the baseline had significant consequences on the N-uptake of plants. PnET-N-DNDC predicts a reduction of plant nitrogen uptake of 6.5% under 20% reduced PAR. As a result of increased N-availability in the soil, both nitrification and denitrification increased, although mineralization did not change (Table 1). It must be noted, however, that the sensitivity study was done for only a 1-year time period and that for longer model runs predictions of this parameter may change significantly, since N input by litter fall will decrease markedly with time.

The sensitivity of PnET-N-DNDC to changes in input parameters required to run the model are summarized in Table 1. Processes involved in N-cycling and N-trace gas production within PnET-N-DNDC were most sensitive to changes in soil pH and texture and to changes in dominant tree species. Over a 1-year time frame at least, the model was less sensitive to changes in rainfall N-concentration, soil organic carbon (SOC), and forest floor litter mass (Table 1). These results are discussed in more detail below.

Soil pH is especially important for N-trace gas production by the microbial processes of nitrification and denitrification and also by the physicochemical process of chemodenitrification [Li *et al.*, this issue]. Therefore, for example, an increase in soil pH by +0.4 units (referenced to the baseline) resulted in an increase in N₂O emission by 67.1%, while a pH increase of +0.9 resulted in an increase in N₂O emission by 206.1%. Rates of NO production by chemodenitrification are most sensitive to changes in soil pH. Reducing soil pH by -0.5 units resulted in an increase in NO-production by chemodenitrification by a factor of approximately 7, whereas an increase in soil pH by

+0.4 units reduced NO-production via chemodenitrification to 0 (Table 1).

Soil microbial processes modeled within PnET-N-DNDC were sensitive to changes in soil texture (Table 1). This is largely due to the importance of soil texture in the soil water regime, which directly influences the diffusion of gases within the soil and the availability of O₂ within the soil profile. Because of this, soil texture has a major impact on the size of the “anaerobic balloon” within the different soil layers [Li *et al.*, this issue]. Changes in soil water regime and in the size of the anaerobic balloon directly feed back to N-trace gas production and emission within PnET-N-DNDC since (1) rates of N₂O emission by nitrification are positively linked to soil moisture [Ingwersen *et al.*, 1999] and (2) denitrification activity is strictly coupled to the size and occurrence of anaerobic sites [Li *et al.*, this issue]. Therefore changing the soil texture in PnET-N-DNDC from sand to sandy clay resulted in N₂O emissions from the soil ranging from 0.5 kg N ha⁻¹ yr⁻¹ (-77.3% referenced to baseline) to 5.4 kg N ha⁻¹ yr⁻¹ (+131.5% referenced to baseline) (Table 1).

PnET-N-DNDC models several forest types, such as pine, spruce, fir, hemlock, mixed hardwoods, oak, birch, and beech. The effect of different tree species on N-cycling and N-trace gas emission from soil was also investigated (Table 1). Beech showed the highest N demand due to its distinctly low C/N ratio in leaves and roots. As a consequence of high N-uptake by beech, less available nitrogen is left in the soil to support microbial N-turnover (nitrification and denitrification). The model results indicate that (1) beech had the lowest nitrification rate, and (2) total N gas emission (e.g., NO + N₂O + N₂) from beech was lower than that from other forest types. Owing to the prediction that the beech forest had a relatively high fraction of anaerobic volume in the soil (ANFV), a consequence of leaf geometry since beech leaves on the forest floor can create a gas diffusion barrier and of an intense O₂-

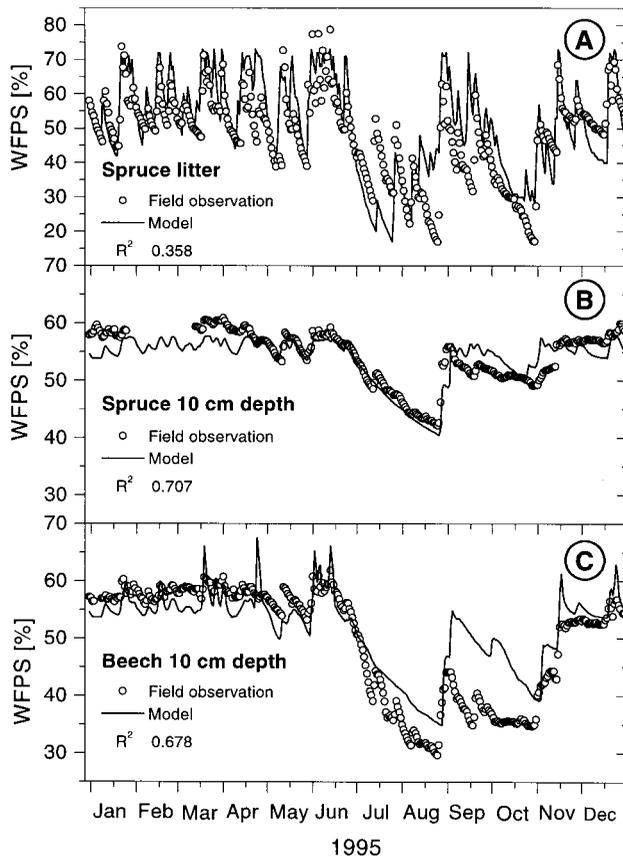


Figure 3. Comparison of measured and simulated values of percent water-filled pore space (WFPS) of the spruce ((a) litter layer and (b) mineral soil 10 cm depth) and (c) beech site at the Höglwald Forest (Germany) for the year 1995. For data on precipitation and air temperature, see Figure 4. Soil moisture data were provided by Rothe [1997] and used for calculation of percent WFPS as described by Papen and Butterbach-Bahl [1999].

consumption in the soil due to enhanced mineralization of the relatively easily decomposed litter, the probability that nitrification-produced NO and N₂O will be further involved in denitrification is higher than for the other forest types (Table 1). Therefore beech soil favors the emission of more reduced N-gases such as N₂O and N₂, rather than NO. In contrast, the model predicts relatively low N₂O emissions from coniferous forests, although they had higher total N gas emissions as compared to the beech forest scenario. Because of the relatively low ANVF of the spruce forest, NO emissions by nitrification in particular are enhanced. Only limited information is available in the literature about the effects of tree species on N-trace gas emissions from soils. Butterbach-Bahl *et al.* [1998], Papen and Butterbach-Bahl [1999], and Gasche and Papen [1999] showed for the Höglwald Forest that the primary N-trace gas emitted from the beech soil was N₂O, whereas NO emissions were quantitatively more important at the spruce site. The model predictions thus are in agreement with the field observations.

2.2. Model Validation at Different Field Sites

2.2.1. Site descriptions. For model validation, PnET-N-DNDC was applied to seven different temperate forest ecosystems in Europe and the United States. These sites are Höglwald Forest, Germany (spruce and beech); Harvard

Forest, United States (pine); Copenhagen, Denmark (spruce); Klausen-Leopoldsdorf, Austria (beech); Schottenwald, Austria (beech); Oak Ridge, United States (oak). With the exception of the site at Oak Ridge, measurements of N-trace gas emissions (N₂O and/or NO emissions) covered approximately an entire year. Site characteristics, required as input parameters for PnET-N-DNDC, are listed in Table 2. More specific information about the sites and about methods used for measurements of N-trace gas emissions can be found in the relevant literature (Höglwald Forest [e.g., Kreuzer, 1995; Rothe, 1997; Butterbach-Bahl *et al.*, 1997; Papen and Butterbach-Bahl, 1999; Gasche and Papen, 1999]; Harvard Forest [Aber *et al.*, 1993; Bowden *et al.*, 1991; Magill *et al.*, 1997]; Copenhagen [Ambus and Christensen, 1995]; Klausen-Leopoldsdorf and Schottenwald [Zechmeister-Boltenstern and Meger, 1997; Jandl *et al.*, 1997]; and Oak Ridge [Williams and Fehsenfeld, 1991]). Meteorological input data, required as model drivers, that is, minimum and maximum daily temperature as well as the sum of daily precipitation, were either obtained from continuous measurements at an open site close to forest stands (Höglwald Forest) or were supplied by the meteorological services of the various countries for weather stations closest to the sites (see Table 2).

For documentation of model performance and for comparison between measured and simulated values, r^2 values were calculated by use of the following equation:

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

where x_{mod} is the value obtained from simulation runs using PnET-N-DNDC, x_{meas} is the value obtained from the measured field data, and \bar{x}_{meas} is the average of measured field data.

2.2.2. Soil moisture. All processes related to C- and N-cycling in forest ecosystems are strongly dependent on water availability of soils. Therefore successful modeling of soil hydrology in forest ecosystems is a prerequisite in order to exactly model C- and N-cycling in forest soils. In order to validate the soil hydrology submodule in PnET-N-DNDC we compared measured and simulated values of water-filled pore space (WFPS) for the Höglwald Forest site (Figure 3), for which data of WFPS values (calculated from continuous measurements of soil moisture) exist for the entire year 1995. For the litter layer of the spruce forest, PnET-N-DNDC was able to capture the seasonal trend of changes in WFPS as well as the magnitude of WFPS with high accuracy (Figure 3a).

Also for the mineral soil (10 cm depth) a good agreement between measured and simulated values of WFPS was found, though WFPS was underestimated by approximately 5% in winter and spring (Figure 3b). In Figure 3c, measured and simulated values for WFPS in 10 cm soil depth for the beech stand are compared. Also for the beech site, WFPS was slightly underestimated during winter and spring by approximately 5%; however, in summer and, especially, in early autumn the model overestimated measured values of WFPS up to approximately 10%. This discrepancy between measured and simulated values of WFPS at the beech site is mainly due to an underestimation of evapotranspiration by the beech stand. Future work will concentrate on further improvement of the soil hydrology submodule of PnET-N-DNDC especially for deciduous forest sites.

2.2.3. N₂O emissions. For all sites except Oak Ridge, field measurements of N₂O emissions were available and could be used for model validation. For the Höglwald Forest site,

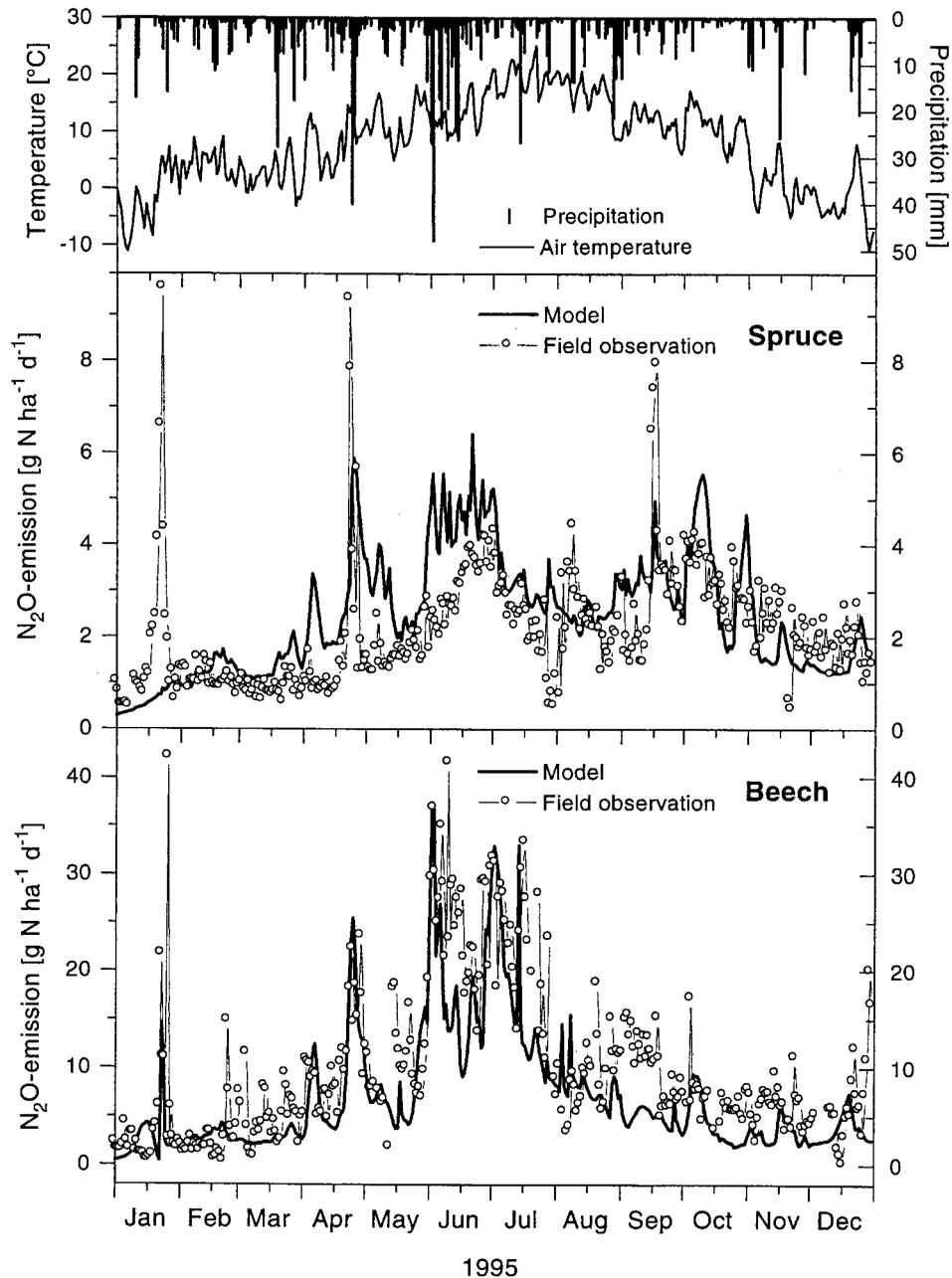


Figure 4. Precipitation, air temperature, and measured and simulated N_2O emission rates from soil of the spruce and the beech stands at the Höglwald Forest (Germany) for the year 1995. Field data represent daily means of N_2O emission rates. Field data from Papen and Butterbach-Bahl [1999].

which is strongly influenced by atmospheric N-deposition [Göttlein and Kreutzer, 1991], we used the 1995 data set published by Papen and Butterbach-Bahl [1999] (Figure 4). For both the spruce and beech stands, modeled and measured emissions were in general agreement in terms of magnitude and seasonal pattern of emission rates (Figure 4 and Table 3). Averaged daily N_2O -emission rates from field measurements at the spruce and the beech site were $2.1 \pm 1.3 \text{ g N ha}^{-1} \text{ d}^{-1}$ and $9.9 \pm 8.3 \text{ g N ha}^{-1} \text{ d}^{-1}$, respectively (Table 3). PnET-N-DNDC overestimated the N_2O -emission rate from the spruce soil by 15% ($2.4 \pm 1.3 \text{ g N ha}^{-1} \text{ d}^{-1}$) and underestimated it by 26% at the beech site ($7.3 \pm 6.6 \text{ g N ha}^{-1} \text{ d}^{-1}$). For the spruce site, differences between measured and predicted N_2O fluxes

are largely due to an overestimation of N_2O -fluxes during spring (April–June); modeled N_2O fluxes for all other periods of the year are in general agreement with field measurements (Figure 4). The overestimation of N_2O fluxes in spring by PnET-N-DNDC may result from underestimating N-uptake by plants in this season, thereby reducing the competition for inorganic nitrogen between microorganisms and plants and favoring microbial N-turnover. Underestimation of N_2O fluxes from the beech site at the Höglwald Forest by PnET-N-DNDC occurred mainly in autumn. During this season, measured N_2O emissions in the field are approximately twice as high as predictions by PnET-N-DNDC (Figure 4). The reason for this discrepancy may be an underestimation of fresh litter miner-

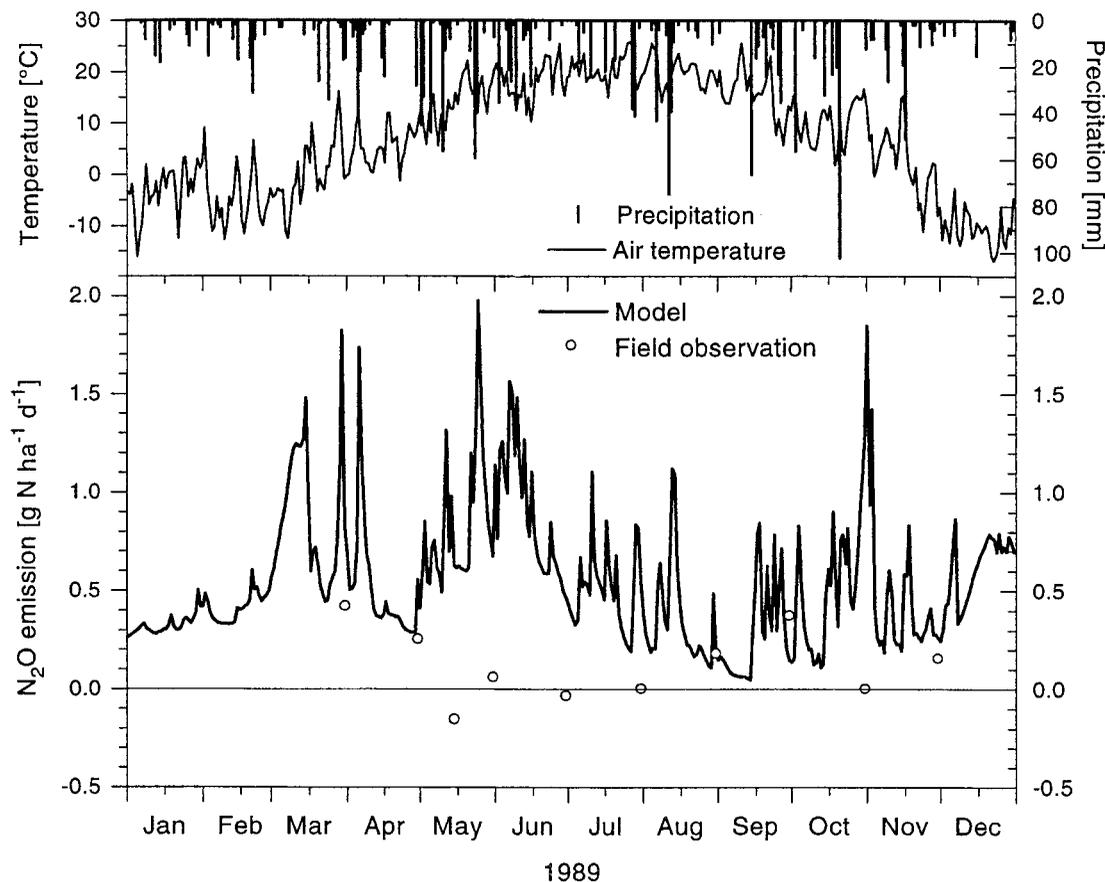
Table 3. Compilation of Results for N₂O-Emissions From the Different Field Sites as Derived From Model Runs With PnET-N-DNDC and From Field Measurements

	Mean N ₂ O Emission Rate, g N ha ⁻¹ d ⁻¹		Model Accuracy, % of measured flux	Modeling Efficiency, <i>r</i> ²
	Measured	Modeled		
Höglwald spruce	2.1 ± 1.3	2.4 ± 1.3	115	0.08
Höglwald beech	9.9 ± 8.3	7.3 ± 6.6	74	0.45
Harvard Forest	0.1 ± 0.2	0.6 ± 0.4	481	...
Copenhagen	2.3 ± 2.2	1.7 ± 1.0	73	0.17
Klausen-Leopoldsdorf	5.2 ± 5.2	5.5 ± 4.5	105	0.08
Schottenwald	13.4 ± 15.2	12.8 ± 17.0	96	0.79

alization in autumn, thereby underestimating in particular nitrification in the soil. Furthermore, PnET-N-DNDC underestimated N₂O emissions during periods of frost and soil thaw at the spruce site by 100% and the beech site by approximately 50% (Figure 4) indicating that some processes involved in N₂O emission during these periods are at present not sufficiently described in the model. In view of the quantitative importance of frost periods and of soil thaw for annual rates of N₂O emissions from temperate forest sites [Papen and Butterbach-Bahl, 1999], future work will concentrate on a better implementation of these processes in the model in order to further improve the performance of PnET-N-DNDC.

The Harvard Forest represents a temperate forest ecosystem with low atmospheric N-deposition and low rates of N cycling.

For model validation, measurements of N₂O emissions from a pine stand were used [Bowden *et al.*, 1991]. These authors observed a maximum in N₂O emissions (approximately 0.4 g N₂O-N ha⁻¹ d⁻¹) in March and N₂O fluxes close to zero or even an uptake of atmospheric N₂O in late spring and summer. Although the modeled N₂O-emissions for this site were lowest in comparison with other sites, the prediction of N₂O fluxes by PnET-N-DNDC were still too high (0.6 ± 0.4 g N ha⁻¹ d⁻¹) as compared to the field measurements (0.1 ± 0.2 g N ha⁻¹ d⁻¹) for the Harvard Forest pine stand (Table 3 and Figure 5). Bowden *et al.* [1991] clearly show that uptake of atmospheric N₂O does occur in N-limited forest soils at certain times. At present, this observation can only be explained by a further reduction of N₂O to N₂ by the enzyme N₂O-reductase (deni-

**Figure 5.** Precipitation, air temperature, and measured and simulated N₂O emission rates from soil of the pine stands at the Harvard Forest (United States). Field data from Bowden *et al.* [1991].

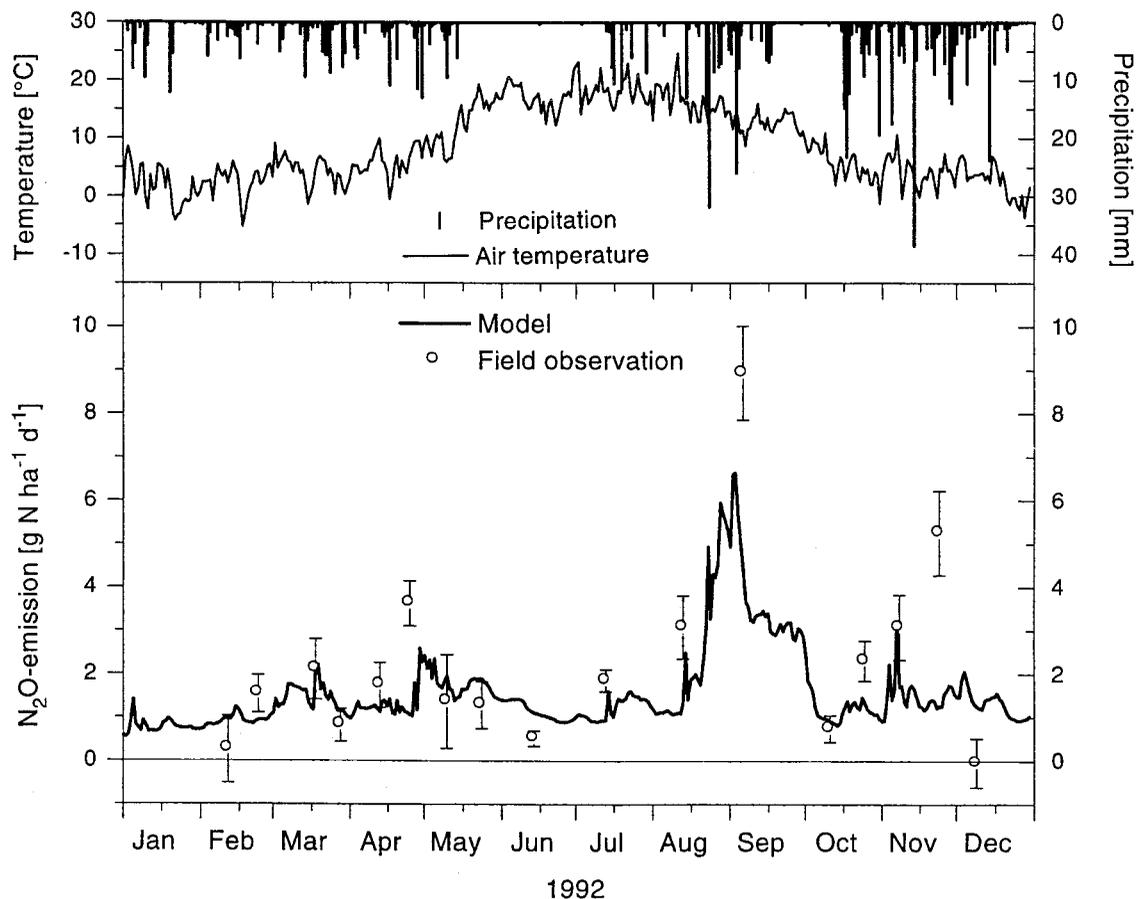


Figure 6. Precipitation, air temperature, and measured and simulated N_2O emission rates from soil of the spruce stands at a forest in the near of Copenhagen (Denmark). Field data from *Ambus and Christensen* [1995].

trifying pathway). The kinetic characteristics of this atmospheric N_2O -uptake by soils is not known and therefore could not be considered in PnET-N-DNDC. As a consequence of neglecting atmospheric N_2O -uptake, PnET-N-DNDC can only predict net emission of N_2O from soils, either produced by nitrification or denitrification.

A further validation study was performed for a spruce forest site in Denmark (Table 2) for which biweekly N_2O emissions during 1992 have been published by *Ambus and Christensen* [1995]. Figure 6 shows that the seasonal trends of measured and predicted N_2O emissions are in good agreement; that is, model predictions are confirmed by field measurements. Low N_2O fluxes, for example, during a dry period in June and high fluxes of N_2O after rewetting of the soil in August and September are well simulated. In general, PnET-N-DNDC underestimated N_2O -emissions at this site, especially in summer and late autumn (Figure 6). The predicted mean N_2O -emission rate is 27% lower than the mean N_2O emission rate calculated from the field data (Table 3). Further model studies revealed that the underestimation of N-turnover rates for this site was most likely due to a general moisture limitation. If soil moisture was increased by initializing the model with a higher clay content, that is, choosing a soil texture of silty loam (clay content: 14%) instead of loamy sand (clay content: 9%), the model performance was improved significantly from r^2 values of 0.17 to $r^2 = 0.55$. This underestimation of soil moisture may be due to special site characteristics (e.g., additional water

supply by slope water) or to the model's weakness in capturing effects of high organic carbon content on the hydrology in sandy soils.

Figure 7 shows the results of model application to the field site of Klausen-Leopoldsdorf, a 55-year-old beech forest stand in Austria, for which biweekly N_2O -emissions covering the entire year of 1997 are available (site characteristics are shown in Table 2). The model captured the general seasonal trend and magnitude of N_2O emissions, although the correlation between the modeled and measured results was rather low ($r^2 = 0.08$) (Table 3). During summer the model underestimated N_2O emissions, whereas in late spring and autumn N_2O fluxes were overestimated. We hypothesize that the modeled N-availability in the soil during the period of vegetation growth was poorly simulated due to an inaccurate estimation (1) of plant N-uptake in late spring (underestimation) and summer (overestimation) and (2) of mineralization activity of fresh litter in autumn (overestimation). More complete field data on N-cycling within forest ecosystems (e.g., mineralization, gross nitrification and denitrification activity, and plant uptake) are required to further validate this hypothesis and to improve the model. Nevertheless, it must be stressed that model prediction of the annual mean N_2O -emission rate ($5.5 \pm 4.5 \text{ g N}_2\text{O-N ha}^{-1} \text{ d}^{-1}$) was in very good agreement with field measurements ($5.2 \pm 5.2 \text{ g N}_2\text{O-N ha}^{-1} \text{ d}^{-1}$) (Table 3).

Predicted and measured N_2O -emissions for the Schottenwald, another beech forest stand in Austria (age: 135 years) for

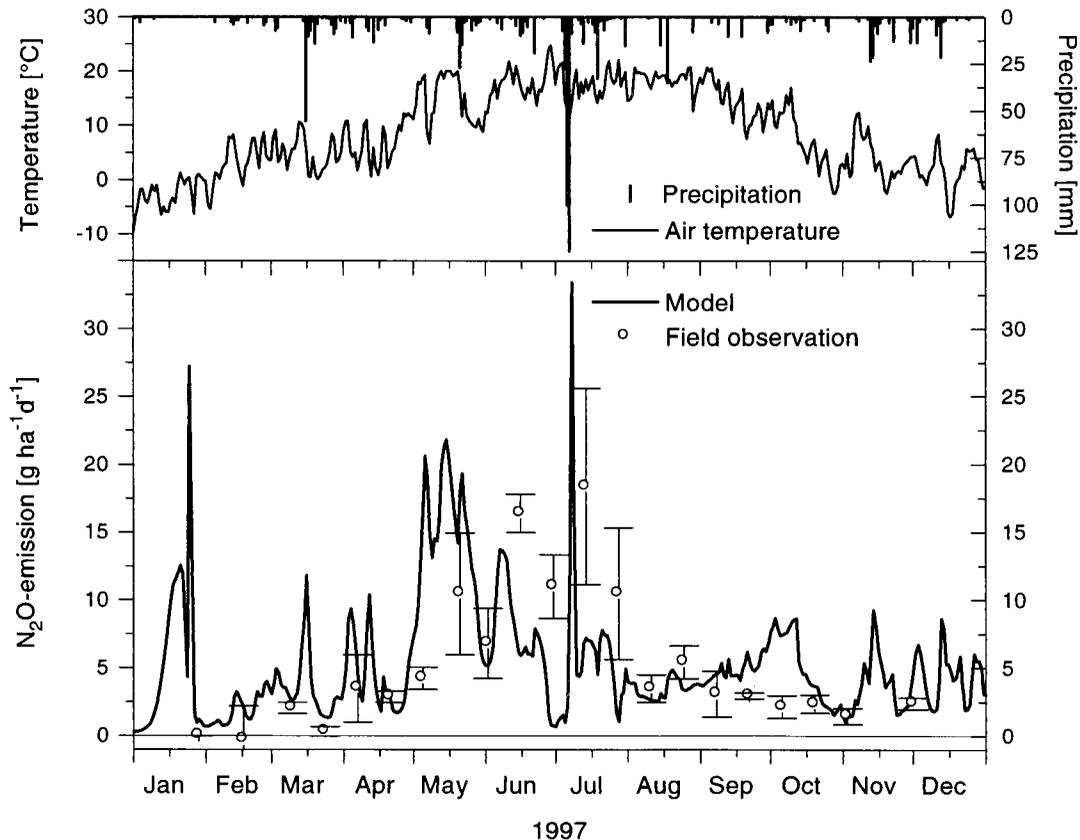


Figure 7. Precipitation, air temperature, and measured and simulated N_2O emission rates from soil of the beech forest at Klausen-Leopoldsdorf (Austria). Field data from S. Zechmeister-Boltenstern and S. Meger (personal communication, 1997).

which N_2O -emissions for 1997 are available, were in excellent agreement (Figure 8). Correlation between predicted and measured results for the Schottenwald was highest ($r^2 = 0.79$) among the sites; the predicted average daily N_2O emission rate differed only by 4% from the average daily N_2O emission as calculated from field measurements (Table 3). In view of the similarity in climatic background and soil characteristics for both stands in Austria (Schottenwald and Klausen-Leopoldsdorf), one may ask why N_2O emissions are roughly a factor of 3 higher for the Schottenwald site. Model results suggest that the likely reason for this difference in emissions is due to pronounced differences in amount of atmospheric N-input; the Schottenwald site receives approximately $35 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, whereas the site at Klausen-Leopoldsdorf receives only approximately $10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. This additional N stimulates microbial N-turnover and hence N_2O -production by nitrification and denitrification. Furthermore, higher N-demand of the younger beech forest at Klausen-Leopoldsdorf is an additional factor which contributes to differences in N-availability between the sites.

2.2.4. NO emission. PnET-N-DNDC is designed to predict both N_2O and NO emissions from temperate forest soils. Owing to sparse data of NO -emissions from temperate forest soils in the literature, we focused model validation on only three field sites. For the Höglwald spruce and beech sites, complete annual cycles of NO -emissions are available [Gasche and Papen, 1999], while for the Oak Ridge site (United States)

measurements of NO -emissions from an oak forest only covered an 18-day period [Williams and Fehsenfeld, 1991].

For the spruce forest stand at the Höglwald Forest, prediction of NO -emissions by PnET-N-DNDC were in general agreement with field observations in terms of flux magnitude and seasonal pattern (Figure 9). Predictions of NO emissions by the model are high as compared to measured NO -emissions only during a rainy period in June 1995 (Figure 9). Gasche and Papen [1999] have hypothesized that during this period the forest floor, the horizon in which most of the emitted NO is produced, was close to water saturation, and therefore NO diffusion in this layer was decreased. Consequently, the sharp decrease in NO -emission observed in the field could be explained by increased NO consumption, for example, by denitrification [Gasche and Papen, 1999]. PnET-N-DNDC failed to predict high NO consumption rates by denitrification during high soil moisture contents in the forest floor since the model assumes that all NO produced by nitrification in the forest floor is immediately emitted to the atmosphere [Li et al., this issue], in contrast to the mineral layer, where consumption of NO can occur. Further model development is required to improve the NO diffusion mechanisms from the forest floor into the atmosphere. The correlation between the predicted and measured NO emissions for the spruce forest stand was low ($r^2 = 0.24$). However, mean daily NO emission rates, calculated from field measurements and predicted by PnET-N-DNDC, were identical ($23.6 \text{ g NO-N ha}^{-1} \text{ d}^{-1}$, see Table 4).

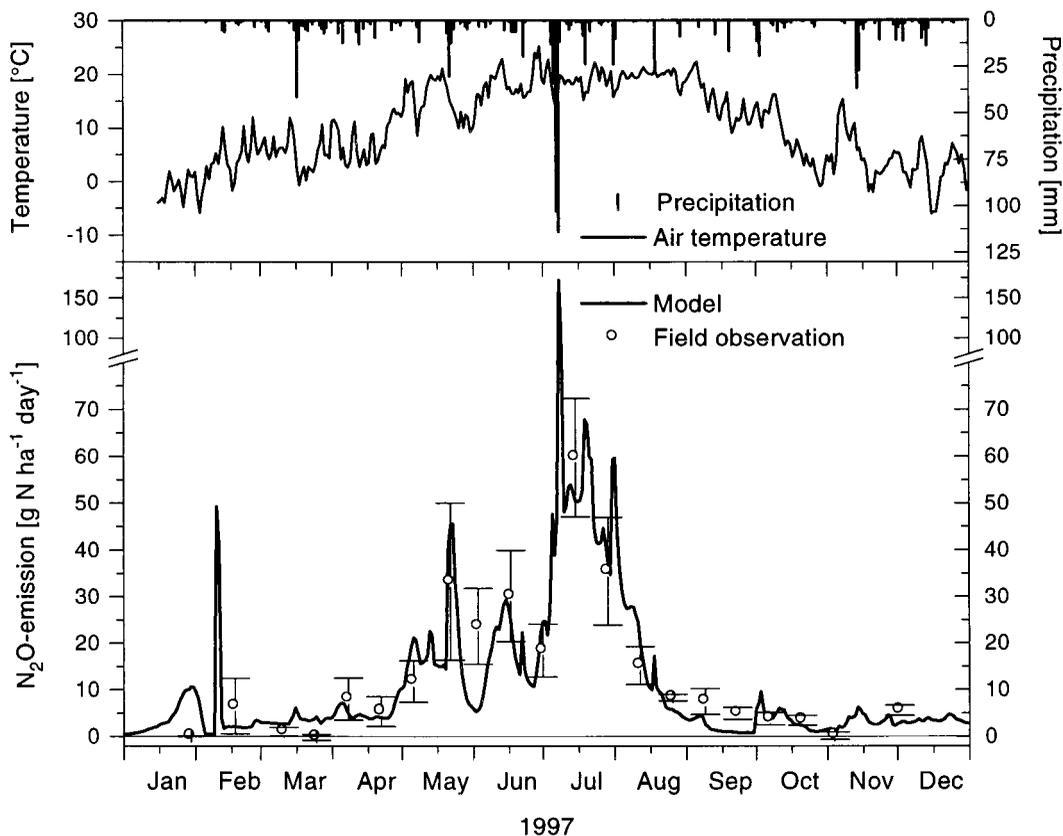


Figure 8. Precipitation, air temperature, and measured and simulated N_2O emission rates from soil of the beech forest at Schottenwald (Austria). Field data from S. Zechmeister-Boltenstern and S. Meger (personal communication, 1997).

The correlation between predicted and measured NO emission for the beech forest stand at the Höglwald site was improved over that of the spruce stand ($r^2 = 0.35$). However, especially during summer (July and August 1995), the model did not capture the extremely high short-term temporal variability of NO fluxes measured in the field (e.g., Figure 9: beech). The more “smoothed” picture given by the model is most likely related to the fact that as a climatic driver in the model daily rainfall amount with a fixed intensity is used [Li *et al.*, 1992] and not with the actual real intensity: however, short-term rainfall of high intensity (as was the case during summer 1995) will have dramatic short-term effects on those soil processes, which quickly react to sudden changes in soil water availability (e.g., microbial activity, diffusion of gases). Nevertheless, both the seasonal pattern and the magnitude of NO emissions were captured by the model, and the mean daily NO emissions were in good agreement with field measurements (model: $7.0 \text{ g NO-N ha}^{-1} \text{ d}^{-1}$; field: $6.2 \text{ g NO-N ha}^{-1} \text{ d}^{-1}$, see Table 4). NO emissions were approximately a factor of 4 lower than at the spruce site, largely due to three factors: (1) the higher soil pH value of the beech site decreased NO production from chemodenitrification markedly. At the spruce site, approximately 30% of NO emissions were due to chemodenitrification, whereas for the beech site chemodenitrification contributed only approximately 9%; (2) based on lower C/N ratios in the litter, PnET-N-DNDC predicts enhanced mineralization and higher nutrient allocation from the forest floor to the uppermost mineral layer, thereby increasing the impor-

tance of the uppermost mineral layer at the beech site for N- and C-turnover. Since NO produced by nitrification in this layer can be consumed during denitrification, rates of NO emitted to the atmosphere will decrease, and emissions of N_2O and N_2 will be favored; and (3) the increased N-demand of beech as compared to spruce limits N-availability in the soil for microbial processes.

Owing to the brief period of NO measurements from the oak forest soils at Oak Ridge (September/October 1988), the extent of model validation for this site is limited. Model simulation for this site over the period for which measurements of NO emission are available revealed a general agreement between model and field observations with regard to the magnitude of NO emissions (field: $0.2 \text{ g NO-N ha}^{-1} \text{ d}^{-1}$; model: $0.3 \text{ g NO-N ha}^{-1} \text{ d}^{-1}$; see Table 4). For further model validation, year-round measurements of NO emissions would be desired.

3. Conclusion

The results obtained from validation studies indicate that PnET-N-DNDC can be used to predict N_2O as well as NO emission rates from temperate forest soils with reasonable accuracy since measured and predicted values of N gas emissions from a wide range of temperate forest ecosystems are fairly comparable (Figure 10). Under conditions of considerable atmospheric N input, PnET-N-DNDC appears to slightly underestimate N_2O emissions from the soil (e.g., Höglwald:

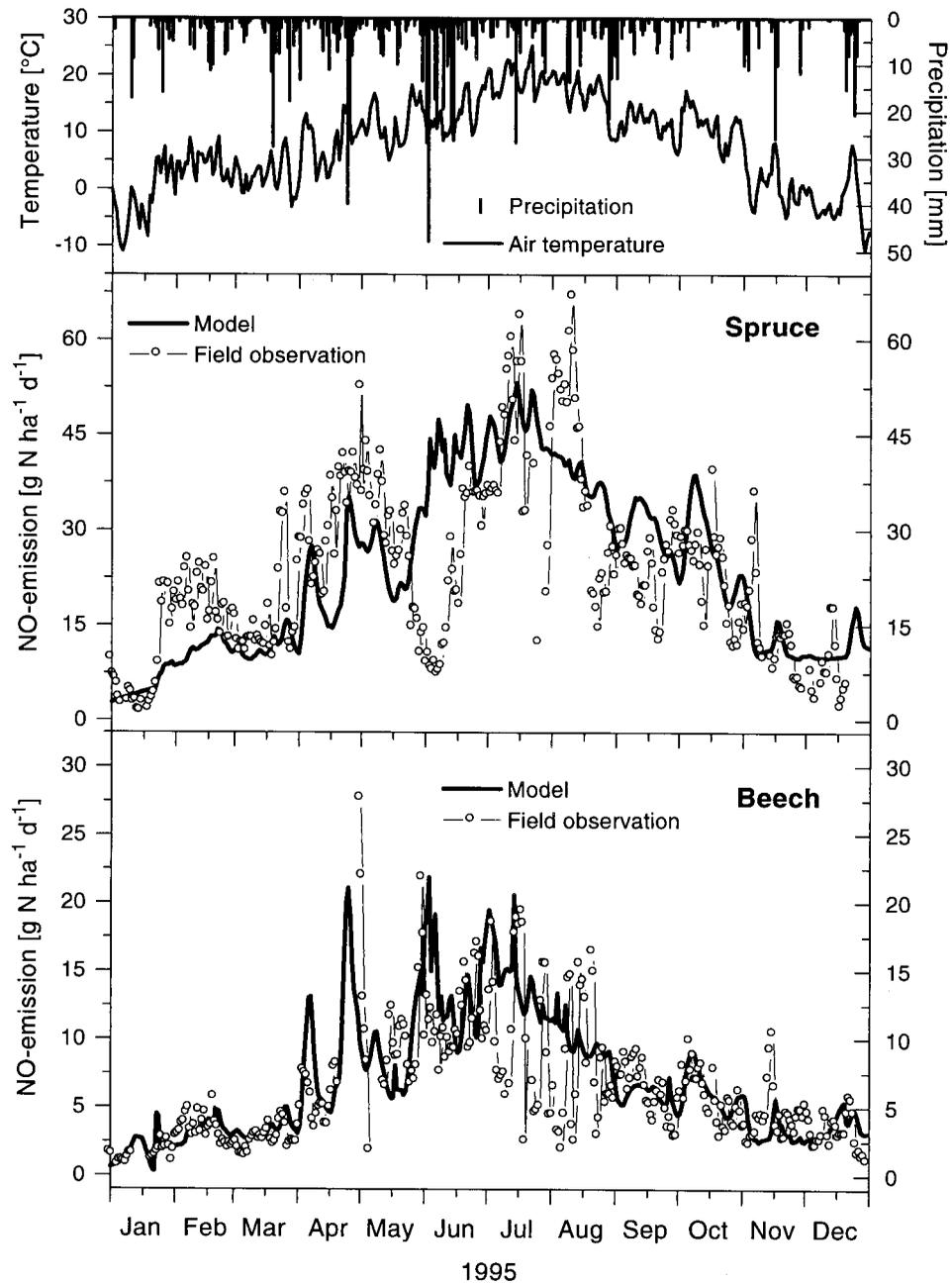


Figure 9. Precipitation, air temperature, and measured and simulated NO-emission rates from soil of the spruce and the beech stands at the Högwald Forest (Germany) for the year 1995. Field data from *Gasche and Papen* [1999].

Table 4. Compilation of Results for NO-Emissions From the Different Field Sites as Derived From Model Runs With PnET-N-DNDC and From Field Measurements

	Mean N ₂ O Emission Rate, g N ha ⁻¹ d ⁻¹		Model Accuracy, % of measured flux	Modeling Efficiency, <i>r</i> ²
	Measured	Modeled		
Högwald spruce	23.6 ± 13.5	23.6 ± 13.6	100	0.24
Högwald beech	6.2 ± 4.4	7.0 ± 4.6	113	0.35
Oak Ridge	0.20 ± 0.00	0.33 ± 0.03	95	...

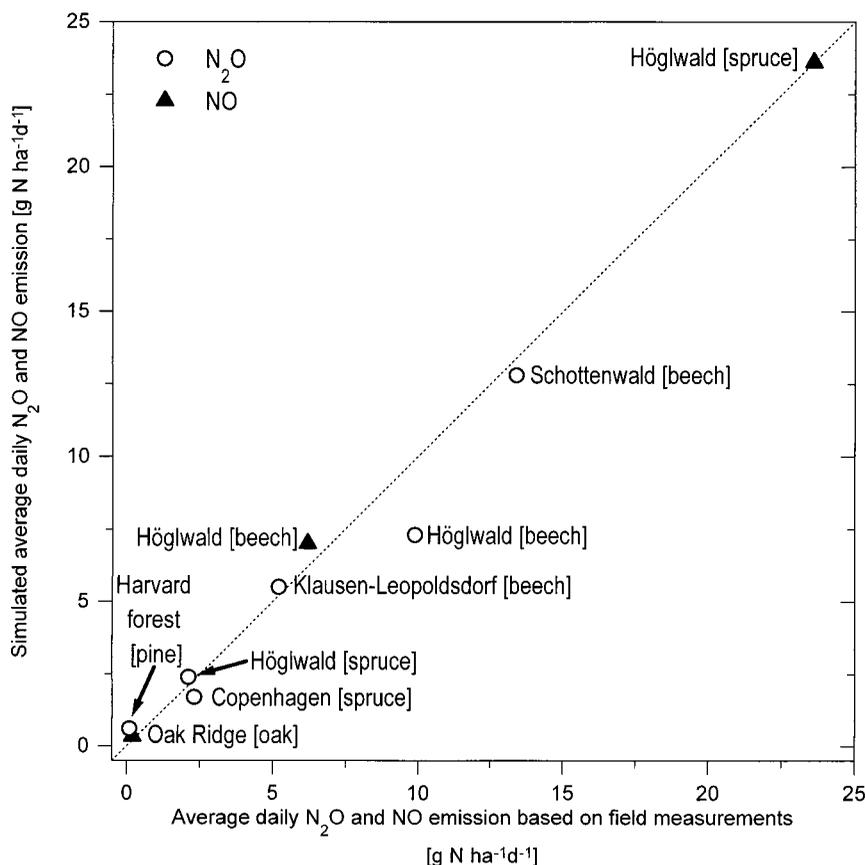


Figure 10. Comparison of measured versus simulated N-gas emission for the different field sites used for model validation.

beech, Figure 10). For the Höglwald Forest, at which data sets on N₂O as well as NO emissions are available for both a beech and spruce site, the impact of forest type on the magnitude of N-trace gas emission was well described by PnET-N-DNDC.

This validation study suggests that PnET-N-DNDC needs further improvement, especially with regard to seasonal changes in N-uptake by plants and to atmospheric N₂O uptake by N-limited forest soils. In addition, modules need to be adapted/developed and implemented in PnET-N-DNDC to simulate high N₂O emissions during extended period of frost and freezing/thawing cycles of soils, which field measurements have shown to make significant contributions to annual emission rates from forest soils [Papen and Butterbach-Bahl, 1999].

We anticipate that PnET-N-DNDC may prove to be a useful tool in improving the estimations of regional and global N₂O and NO emissions from forest soils. This will require a coupling of PnET-N-DNDC to a Geographic Information System (GIS) containing a detailed database on the regional distribution of soil (e.g., soil organic matter) and climate characteristics and land use patterns (e.g., forest type).

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References

- Aber, J. D., A. Magill, R. Boone, J. M. Melillo, P. Steudler, and R. Bowden, Plant and soil response to chronic nitrogen additions at the Harvard Forest, Massachusetts, *Ecol. Appl.*, 3, 156–166, 1993.
- Ambus, P., and S. Christensen, Spatial and seasonal nitrous oxide and methane fluxes in Danish forest-, grassland-, and agroecosystems, *J. Environ. Qual.*, 24, 993–1001, 1995.
- Bowden, R. D., J. M. Melillo, P. A. Steudler, and J. D. Aber, Effects of nitrogen additions on annual nitrous oxide fluxes from temperate forest soils in the northeastern United States, *J. Geophys. Res.*, 96, 9321–9328, 1991.
- Butterbach-Bahl, K., R. Gasche, L. Breuer, and H. Papen, Fluxes of NO and N₂O from temperate forest soils: Impact of forest type, N deposition and of liming on the NO and N₂O emissions, *Nutr. Cycling Agroecosyst.*, 48, 79–90, 1997.
- Butterbach-Bahl, K., R. Gasche, C. Huber, K. Kreutzer, and H. Papen, Impact of N-input by wet deposition on N-trace gas fluxes and CH₄-oxidation in spruce forest ecosystems of the temperate zone in Europe, *Atmos. Environ.*, 32, 559–564, 1998.
- Conrad, R., Soil microorganisms as controllers of atmospheric trace gases (H₂, CO, CH₄, OCS, N₂O, and NO), *Microbiol. Rev.*, 60, 609–640, 1996.
- Davidson, E. A., Fluxes of nitrous oxide and nitric oxide from terrestrial ecosystems, in *Microbial Production and Consumption of Greenhouse Gases: Methane, Nitrogen Oxides, and Halomethanes*, edited by J. E. Rogers and W. B. Whitman, pp. 219–235, Am. Soc. for Microbiol., Washington, D. C., 1991.
- Davidson, E. A., J. M. Stark, and M. K. Firestone, Microbial produc-

- tion and consumption of nitrate in an annual grassland, *Ecology*, *71*, 1968–1975, 1990.
- Davidson, E. A., S. C. Hart, and M. K. Firestone, Internal cycling of nitrate in soil of mature coniferous forest, *Ecology*, *73*, 1148–1156, 1992.
- Firestone, M. K., and E. A. Davidson, Microbiological basis of NO and N₂O production and consumption in soil, in *Exchange of Trace Gases Between Terrestrial Ecosystems and the Atmosphere*, edited by M. O. Andreae and D. S. Schimel, pp. 7–21, John Wiley, New York, 1989.
- Gasche, R., and H. Papen, A three-year continuous record of nitrogen trace gas fluxes from untreated and limed soil of a N-saturated spruce and beech forest ecosystem in Germany, *2*, NO and NO₂ fluxes, *J. Geophys. Res.*, *104*, 18,505–18,520, 1999.
- Geßler, A., S. Schneider, D. von Sengbusch, P. Weber, U. Hanemann, C. Huber, A. Rothe, K. Kreutzer, and H. Rennenberg, Field and laboratory experiments on net uptake of nitrate and ammonium by the roots of spruce (*Picea abies*) and beech (*Fagus sylvatica*) trees, *New Phytol.*, *138*, 275–285, 1998.
- Göttlein, A., and K. Kreutzer, The Höglwald experimental site as compared to other ecological field studies, *Forstwiss. Forsch.*, *39*, 22–29, 1991.
- Houghton, J. T., B. A. Callander, and S. K. Verney, *Climate Change 1992: The IPCC Assessment*, Cambridge Univ. Press, New York, 1992.
- Ingwersen, J., K. Butterbach-Bahl, R. Gasche, O. Richter, and H. Papen, Barometric Process Separation: New method for quantifying nitrification, denitrification, and nitrous oxide sources in soils, *Soil Sci. Soc. Am. J.*, *63*, 117–128, 1999.
- Jandl, R., H. Kopecki, and G. Glatzel, Effect of a dense *Allium ursinum* (L.) ground cover on nutrient dynamics and mesofauna of *Fagus sylvatica* (L.) woodland, *Plant Soil*, *189*, 245–255, 1997.
- Kreutzer, K., Effects of forest liming on soil processes, *Plant Soil*, *168–169*, 447–470, 1995.
- Lee, D. S., I. Köhler, E. Grobler, F. Rohrer, R. Sausen, L. Gallardo-Klenner, J. G. J. Olivier, F. J. Dentener, and A. F. Bouwman, Estimation of global NO_x emissions and their uncertainties, *Atmos. Environ.*, *31*, 1735–1749, 1997.
- Li, C., S. Frolking, and T. A. Frolking, A model of nitrous oxide evolution from soil driven by rainfall events, 1, Model structure and sensitivity, *J. Geophys. Res.*, *97*, 9759–9776, 1992.
- Li, C., V. Narayanan, and R. C. Harriss, Model estimates of nitrous oxide emissions from agricultural lands in the United States, *Global Biogeochem. Cycles*, *10*, 297–306, 1996.
- Li, C., J. D. Aber, F. Stange, K. Butterbach-Bahl, and H. Papen, A process-oriented model of N₂O and NO emissions from forest soils, 1, Model development, *J. Geophys. Res.*, this issue.
- Magill, A. H., J. D. Aber, J. J. Hendricks, and R. D. Bowden, Biogeochemical response of forest ecosystems to simulated chronic nitrogen deposition, *Ecol. Appl.*, *7*, 402–415, 1997.
- Papen, H., and K. Butterbach-Bahl, A three-year continuous record of nitrogen trace gas fluxes from untreated and limed soil of a N-saturated spruce and beech forest ecosystem in Germany, 1, N₂O emissions, *J. Geophys. Res.*, *104*, 18,487–18,503, 1999.
- Potter, C. S., P. A. Matson, P. M. Vitousek, and E. A. Davidson, Process modeling of controls on nitrogen trace gas emissions from soils worldwide, *J. Geophys. Res.*, *101*, 1361–1377, 1996.
- Rothe, A., Einfluß des Baumartenanteils auf Durchwurzelung, Wasserhaushalt, Stoffhaushalt und Zuwachsleistung eines Fichten-Buchen-Mischbestandes am Standort Höglwald, *Forstl. Forschungsber.*, *163*, 174 pp., 1997.
- Schmidt, J., W. Seiler, and R. Conrad, Emission of nitrous oxide from temperate forest soils into the atmosphere, *J. Atmos. Chem.*, *6*, 95–115, 1988.
- Stark, J. M., and S. C. Hart, High rates of nitrification and nitrate turnover in undisturbed coniferous forests, *Nature*, *385*, 61–64, 1997.
- Stuedler, P. A., R. D. Bowden, J. M. Melillo, and J. D. Aber, Factors controlling methane uptake in acidic temperate forest soils, *Nature*, *341*, 314–316, 1989.
- Williams, E. J., and F. C. Fehsenfeld, Measurement of soil nitrogen oxide emissions at three North American ecosystems, *J. Geophys. Res.*, *96*, 1033–1042, 1991.
- Zak, D. R., P. M. Groffmann, K. S. Pregitzer, S. Christensen, and J. M. Tiedje, The vernal dam: Plant-microbe competition for nitrogen in norther hardwood forests, *Ecology*, *71*, 651–656, 1990.
- Zechmeister-Boltenstern, S., and S. Meger, Nitrous oxide emissions from two beech forests near Vienna, Austria, paper presented at the 7th International Workshop on Nitrous Oxide Emissions, Cologne, Germany, April 21–23, 1997.

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