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ORIGINAL PAPER

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Mechanisms of N_2O and NO production in the soil profile of a drained and forested peatland, as studied with acetylene, nitrapyrin and dimethyl ether

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Abstract Acetylene, dimethyl ether (DME) and 2-chloro-6-trichloromethyl pyridine (nitrapyrin) were used as inhibitors to study the contributions of nitrification and denitrification to the production of N_2O and nitric oxide (NO) in samples taken from the soil profile of a peatland drained for forestry. Acetylene and DME inhibited 60–100% of the nitrification activity in field-moist samples from the 0–5 cm and 5–10 cm peat layers, whereas nitrapyrin had no inhibitory effect. In the 0–5 cm peat layer the N_2O production could be reduced by up to 90% with inhibitors of nitrification, but in the 5–10 cm peat layer this proportion was 20–30%. All the inhibitors removed 96–100% of the nitrification potential in peat-water slurries from the 0–5 cm peat layer, but the 5–10 cm layer had a much lower nitrification activity, and here the efficiency of the inhibitors was more variable. Litter was the main net source of NO in the peat profile. NO_3^- production was lower in the litter layer than in the peat, whereas N_2O production was much higher in the litter than in the peat. Denitrification was the most probable source of N_2O and NO in the litter, which had a high availability of organic substrates.

Key words Nitrous oxide · Nitric oxide · Organic soil · Nitrification · Inhibitors

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Introduction

N_2O contributes to global warming and the destruction of O_3, whereas NO is an important component in the chemistry of the troposphere (Crutzen and Ehhalt 1977). About 70% of N_2O and 20% of NO entering the atmosphere originates from soils (Conrad 1996). Substantial emissions of N_2O and NO have been measured from boreal organic soils drained for forestry or agriculture (Lång et al. 1995; Nykänen et al. 1995; Regina et al., 1998), but there is a lack of knowledge on the proportions of N_2O and NO produced as a consequence of nitrification and denitrification in boreal peat soils. As concern about global change has grown, organic soils have attracted more interest as retainers of N and possible sources of N oxides (Öquist et al. 1996). Peatlands at northern latitudes are highly susceptible to changes in temperature and hydrology, and therefore knowledge of the microbial processes responsible for N_2O and NO production in peat would be of particular importance.

Chemical compounds which specifically inhibit autotrophic nitrification have been used to distinguish between nitrification and denitrification as sources of N oxides. Acetylene, the most frequently used inhibitor, blocks autotrophic NH_4^+ oxidation at low concentrations (0.01%–0.1%) and also the reduction of N_2O to N_2 in denitrification at the percentage level (Davidson et al. 1986). 2-Chloro-6-trichloromethyl pyridine (nitrapyrin) is a traditional inhibitor of autotrophic NH_4^+ oxidation (Goring 1962), but it loses part of its inhibition efficiency in soils due to hydrolysis and adsorption (Bremner et al. 1978). Dimethyl ether (DME) is a gaseous inhibitor that does not block N_2O reduction in denitrification (Oremland and Culbertson 1992). Because the efficiency of different inhibitors may vary from one soil to another (Sahrawat et al. 1987), we studied the mechanism of N_2O formation in peat soil using nitrapyrin, acetylene and dimethyl ether as inhibitors of autotrophic nitrification. The mechanism of NO formation was studied using an acetylene blocking technique.

Materials and methods

Site and sampling

Peat samples were taken at the end of August 1993 from a Finnish peatland (62°46′N, 30°58′E) which had been drained and forested about 50 years earlier. Before drainage the site had been a herb-rich, birch-pine fen, whereas at present it is covered by a fast-growing mixed forest. The mean groundwater level is 30 cm below the soil surface. The 0–10 cm peat profile studied here was moist but not saturated (Table 1). The total N and C contents of the peat are 2.8% and 50%, respectively. Six replicate cores (diameter 10 cm) were taken from the peat profile and divided into two layers (0–5 cm and 5–10 cm). The six samples from each layer were pooled, homogenized manually and frozen at −20 °C. Litter consisting mostly of birch leaves was collected in September 1994 and stored at +4 °C until used in the experiments in November.

Experiment with field-moist peat

Field-moist peat samples equivalent to 1 g of dry peat (~7 cm^3) were used in a 2-week study in which they were incubated at +20 °C in an aerobic atmosphere in 120-ml flasks closed with silicone septa. Three replicates received 100 mg nitrapyrin in 0.5 ml of water (100 mg g dry $soil^{-1}$), and three replicates received acetylene (final concentration 2.5% v/v) or DME (5% v/v) and 0.5 ml of water. This high concentration of acetylene was used to inhibit nitrification because lower concentrations were thought to be ineffective due to adsorption of acetylene to the peat. The gases were added through the septa using a syringe fitted with a needle. Nitrapyrin, which is not soluble in water, was injected as a water suspension after vigorous shaking. Three replicates were left as controls, receiving 0.5 ml of water, and three were used for NO_3^- extraction (50 ml of 2 M KCl) at the beginning of the experiment. A gas sample for the measurement of N_2O and CO_2 (25 ml) was taken from each flask, after the incubation period of 7 days, using a needle and a syringe closed with a three-way stopcock. N_2O and CO_2 were analysed with a gas chromatograph equipped with electron capture and thermal conductive detectors (Nykänen et al. 1995). The diffusion through the silicone stoppers (about 10%) was taken into account in the gas flux calculations. At the end of the experiment all the samples were extracted with 50 ml of 2 M KCl. The sum of NO_3^- and NO_2^- in the samples was analysed with an automatic chemical analysis system (AKEA, Instrumentarium Ltd, Helsinki), in which NO_3^- is reduced to NO_2^- by Cd and converted to a purple azo dye for colorimetric analysis.

Statistical differences in NO_3^- production and gas evolution were tested using log-transformed values of the variables in a one-way analysis of variance (SPSS statistical package).

Aerobic slurry incubation

Peat from the two layers (0–5 cm and 5–10 cm) was used in the aerobic slurry incubations. Suspensions containing amounts of peat equivalent to 2 g of dry weight in 100 ml of a mineral medium were incubated in 600-ml flasks on a rotary shaker (100 rpm) at +20 °C. The medium contained 0.5 mM $(NH_4)_2SO_4$, 0.2 mM KH_2PO_4, 0.2 mM $MgSO_4 \times 7H_2O$ and 0.2 mM $CaCl_2$. Three replicates were adjusted to pH 4 and three to pH 6 using Na_2CO_3 or H_2SO_4. As the flasks were sealed with silicone stoppers and could not be opened during the period of gas measurement, separate flasks (2 replicates) were kept for adjusting the pH. The amount of Na_2CO_3 or H_2SO_4 required to adjust the pH to 4 or 6 in these flasks was then injected into the sealed flasks through the septa. Samples for NO_3^- analysis (1.5 ml) were taken at the beginning of the experiment and after 1 week. In addition to the control samples there were three replicates at both pH 4 and pH 6 that received the nitrification inhibitors. Nitrapyrin was added as a water suspension as above (final concentration in the slurry 10 mg ml^{-1}), and acetylene (2.5% v/v) and dimethyl ether (5% v/v) were added through the septa with a syringe. Samples for the chromatographic analysis of N_2O and CO_2 (25 ml) were taken after 3 days and 7 days. Ambient air (60 ml) was added to the flasks at the beginning of the experiment to enable two gas samplings a week. The proportion of N_2O dissolved (Moraghan and Buresh 1977) and the diffusion through the silicone stoppers (about 10%) were taken into account in the gas flux calculations. NO_3^- and NO_2^- were analysed with a capillary electrophoresis system (Applied Biosystems 270A-HT) using a buffer containing 2.5 mM hexadecyltrimethyl NH_4Cl and 12.5 mM Na_2SO_4 at pH 4.

Experiments with litter

The importance of the litter layer for NO emissions was studied with an in situ experiment in which NO fluxes were measured with the litter covering the soil and in the same chamber area after the litter had been removed. Eight pairs of such measurements were made on 27 May 1993, four on 7 July 1993, and four on 21 September 1994. An Environnement s.a. AC31M chemiluminescent NO_x analyser (Environnement s.a., Poissy, France) and a dynamic measurement system with a PVC chamber of diameter 20 cm and height 20 cm were used for the NO analysis. The ambient air could be used as replacement air in the chamber because the ambient NO concentration was below the detection limit in this remote area. The concentration in the outflow (0.5 l min^{-1}) increased until it reached a steady value, which was used for calculating the production rate.

The litter for the laboratory study was collected manually and included material that had fallen in previous years and had not yet fully decayed. In a 6-day experiment 80 g of litter were incubated in 3.2-l plastic containers covered with a thin layer of polythene to allow the exchange of O_2 and CO_2 but not water vapour. For the gas measurements the containers were sealed with gas-tight lids equipped with butyl rubber septa, and 25-ml gas samples for chromatographic analysis of N_2O and CO_2 were extracted by syringe after 5 min, 15 min and 30 min. The air sample for the measurement of NO was pumped out through one septum on the lid and passed directly to the NO analyser; this was replaced by NO_x-free air which was taken in through the other septum. NO_x-free air was obtained by filtering the ambient air through activated C and a Sorboxifil filter ($SiO_2 + KMnO_4$; Kemira Ltd., Finland). As NO analysis with the chemiluminescent analyser is impossible in the presence of acetylene (Davidson 1992), we exposed the samples to acetylene for 24 h before the analysis, but acetylene was no longer present in the gas phase during sampling (Davidson 1992; Kester 1996). The gas analyses were conducted once for all the replicates before the addition of acetylene. On the

Table 1 Characteristics of the peat. *WFPS* Water-filled pore space; *n.d.* not determined

Layer	Bulk density g dry soil cm^{-3}	Moisture %	WFPS %	pH (H_2O)	NH_4^+-N	NO_3^--N	CO_2 production (at 20 °C)
					μg g dry $soil^{-1}$		μg g dry $soil^{-1}$ h^{-1}
Litter	n.d.	77	n.d.	6.0	11	0.4	370
0–5 cm	0.15	81	65	4.1	57	34	19
5–10 cm	0.16	85	90	4.3	24	48	8

2nd day of incubation five replicates received acetylene to achieve a concentration of 2.5% (v/v). After 24 h the containers were opened and flushed with compressed air and closed for the measurement of N_2O, CO_2 and NO. The third measurement was conducted using the same samples on the 6th day of incubation, after adding and then flushing out the acetylene as described above. The sum of NO_3^- and NO_2^- was analysed using the N autoanalyser as above after extracting 10 g of litter with 100 ml of 2 M KCl at the beginning and at the end of the experiment.

Results and discussion

Experiment with field-moist peat

The uppermost 0–5 cm peat layer and the 5–10 cm layer had similar net nitrification activities (Table 2). High variation between the replicate samples was typical of the peat, causing difficulties in interpreting the results. There were differences between the inhibitors in their capacity to retard autotrophic nitrification in peat. Acetylene was the most effective inhibitor of net nitrification in the field-moist peat. Nitrapyrin had no effect on net nitrification, whereas acetylene and DME inhibited more than half of the net NO_3^- production. The weak inhibition of nitrification by nitrapyrin may be partly explained by poor distribution of this solution in the soil as compared with the gaseous inhibitors, hydrolysis of nitrapyrin to 6-chloropicolinic acid, or the adsorption of nitrapyrin to the soil (Bremner et al. 1978). The inhibiting effect of nitrapyrin has been shown to diminish with increasing soil organic matter content (Sahrawat et al. 1987). The effect of gaseous inhibitors can also be weakened by degradation in soil. DME is consumed by NH_4^+-oxidizing bacteria (Hyman et al. 1994) and acetylene by heterotrophic bacteria (De Boer et al. 1993). In conclusion, the experiments with field-moist peat samples suggested that the gaseous inhibitors are superior to nitrapyrin and that autotrophic nitrifiers were the most important nitrifying organisms. The contribution of heterotrophic nitrifiers cannot be totally excluded, however, because some heterotrophic nitrifiers may also be inhibited by the inhibitors of autotrophic nitrification (Papen et al. 1991; Anderson et al. 1993).

Nitrapyrin and acetylene inhibited more than half of the N_2O production from the uppermost layer (0–5 cm) in the field-moist peat, while all the inhibitors had a weak effect on N_2O production in the lower layer (5–10 cm). The results suggest that in the uppermost peat layer nitrification produced most of the N_2O, whereas denitrification produced most in the lower layer. The importance of denitrification in N_2O production in the deeper layer was supported by the finding that more than half of the NO_3^- production was inhibited by acetylene and DME (Table 2) but they had a minor effect on N_2O production in this layer. The conditions in the homogenized peat do not represent the field situation, however, and a field study on the effects of acetylene on N_2O emissions at this site indicated that the contribution of nitrification and denitrification to N_2O production varied greatly across the site (Regina et al. 1996). Part of this variability still existed in the homogenized samples used here. The processes involved in N dynamics were probably more unevenly distributed than microbial activity in general, as CO_2 production did not vary markedly between the replicate samples (results not shown). The O_2 status of the peat, based on the water-filled pore space (WFPS; Table 1), allowed N_2O production due to both nitrification and denitrification in the surface layer. A WFPS of 60–80% is the most suitable for simultaneous nitrification and denitrification (Linn and Doran 1984), whereas the high WFPS of >80% found below the uppermost layer limits nitrification in situ and favours denitrification. The ratio of N_2O production to NO_3^- production was higher in the lower layer than in the uppermost layer (Table 2). Poorer availability of C compounds for denitrifying organisms, which is reflected in lower CO_2 production (Table 1), could explain the lower N_2O production in relation to NO_3^- accumulation in the deeper layer. Denitrification activity is known to depend on C availability (Wijler and Delwiche 1954).

Aerobic slurry incubation

Aerobic slurry incubations were conducted to study the nitrification potential of the peat, the effect of nitrifica-

Table 2 The effect of inhibitors on net nitrification (means ± SE) and N_2O production (means ± SE) in field-moist peat samples. No statistical differences were found. *DME* Dimethyl ether

Treatment[a]	N_2O-N pg g dry soil^{-1} h^{-1}	Change %	NO_3^--N ng g dry soil^{-1} h^{-1}	Change %	N_2O:NO_3^- %
Layer (0–5 cm)					
Control	630 ± 480		240 ± 280		0.26
Nitrapyrin	220 ± 21	−65	290 ± 37	+ 21	0.08
Acetylene	84 ± 14	−87	−89 ± 40	−137	−
DME	510 ± 420	−19	88 ± 95	− 63	0.58
Layer (5–10 cm)					
Control	50 ± 7.9		290 ± 52		0.02
Nitrapyrin	41 ± 2.9	−18	290 ± 0	0	0.01
Acetylene	36 ± 1.0	−28	52 ± 170	− 82	0.07
DME	34 ± 3.1	−32	100 ± 100	− 66	0.03

[a] Concentrations used were 100 μg g^{-1} for nitrapyrin, 2.5% (v/v) for acetylene and 5% (v/v) for DME

Table 3 The effect of inhibitors on nitrification potential (means ±SE) and production of N_2O (means ±SE) in peat slurries incubated in an aerobic atmosphere

Treatment[a]	N_2O-N				NO_3^--N				$N_2O:NO_3^-$	
	pg g dry soil^{-1} h^{-1}		Change (%)		ng g dry soil^{-1} g^{-1}		Change (%)		%	
	pH 4	pH 6	pH 4	pH 6	pH 4	pH 6	pH 4	pH 6	pH 4	pH 6
Layer (0–5 cm)										
Control	610±48	2490±110			3820±2670	20800±530			0.02	0.01
Nitrapyrin	140±50	560±160	−77	−78	63± 110	−220±140*	− 98	−101	0.22	–
Acetylene	310±20	760±590	−49	−69	−210± 100	460±120*	−105	− 98	–	0.17
DME	300±17	270± 19*	−51	−89	160± 450	500±270*	− 96	− 98	0.19	0.05
Layer (5–10 cm)										
Control	77± 4	130± 5			330± 170	570±330			0.02	0.02
Nitrapyrin	90± 7	120± 9	+17	− 8	190± 7.0	180±520	− 42	− 68	0.05	0.07
Acetylene	86± 8	120± 7	+12	− 8	270± 90	−530±420	− 18	−193	0.03	–
DME	100± 4	180± 17*	+30	+38	210± 20	16±700	− 36	− 97	0.05	1.13

[a] Concentrations used were 10 μg ml^{-1} for nitrapyrin, 2.5% for acetylene, and 5% for DME
* Data statistically different from the control at $P=0.05$

tion inhibitors and the pH dependence of nitrification under optimum conditions without NH_4^+ or O_2 limitation. The inhibition efficiency of the various nitrification inhibitors in the slurries varied according to pH and peat layer. Nitrification was reduced by 96–100% in the surface peat (0–5 cm) with nitrapyrin, acetylene and DME at both pH 4 and pH 6 (Table 3). The high variation between replicate samples was also found with the water-peat suspensions, indicating that microsites with different aeration and microbial activities may have been retained in the slurries. The inhibition of nitrification in the lower layer was more effective at pH 6 than at pH 4. There are some earlier results showing that the inhibition efficiency of acetylene may depend on the peat layer and the pH (Lång et al. 1994).

The chemicals caused the highest inhibition of N_2O production in the slurries of the uppermost peat layer (Table 3), where 50–90% of the N_2O production was inhibited at pH 4 and pH 6, indicating that at least a half of it was closely associated with nitrification. In the lower layer the effect of the inhibitors on N_2O production was negligible at both pH 4 and pH 6. The weaker inhibition in the deeper layer compared to the surface layer indicated that nitrification was of less significance for N_2O production in the former. The results showed that both nitrification and denitrification were responsible for N_2O production in the aerobic peat slurries, where anaerobic processes such as denitrification should be inactive but may be found due to the existence of soil crumbs (Conrad 1996). The rates of production of both N_2O (Table 3) and CO_2 in slurries (results not shown) were greater at pH 6 than at pH 4. Thus the higher heterotrophic activity at pH 6, including denitrification, could explain the greater N_2O production.

The nitrification potential was higher in the profile at pH 6 than at pH 4, indicating that the pH optimum of the nitrifiers in this soil was higher than the actual soil pH (Table 1). It is common for the pH optimum of nitrifiers to differ from the pH of the bulk soil (Paul and Clark 1989), and key factors for their survival at a low prevailing pH may be the existence of microsites with higher pH (De Boer et al. 1988) and/or aggregation (De Boer et al. 1991). Both the production of N_2O and the nitrification rates were higher at pH 6 than at pH 4 in all peat layers. These results contrast with those reported for the fermentation layer in a Dutch coniferous forest soil and the organic and mineral layers in a Finnish coniferous forest soil, where nitrification rates were similar at both pH levels but N_2O production was higher at pH 4 than at pH 6 (Martikainen and De Boer 1993; Martikainen et al. 1993).

Experiments with litter

Most of the NO emitted from this soil in situ originated from the litter layer, the decrease in NO emission after removing the litter being 57–91% (mean 75%), depending on the time of measurement (Fig. 1). These observations led us to study the mechanisms of NO production in the litter alone using acetylene as an inhibitor of nitrification.

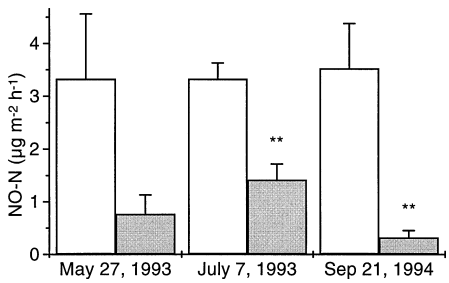

Fig. 1 NO flux in situ from intact peat soil (*white*) and from soil after removal of the litter layer (*grey*). *Bars* indicate 1 SE. ** $P=0.01$

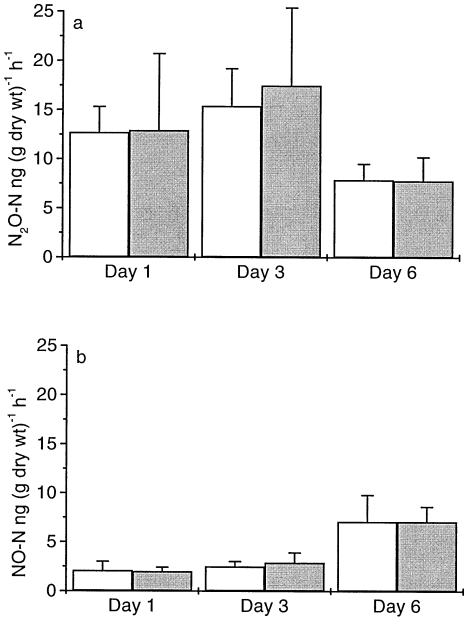

Fig. 2 Production of N_2O (**a**) and NO (**b**) in the litter. A 24-h incubation with 2.5% (v/v) acetylene (*grey*) or no acetylene (*white*) preceded the measurements on the 3rd and 6th day. *Bars* indicate 1 SE

Since acetylene did not inhibit N_2O production in the litter (Fig. 2a), denitrification was most probably responsible for it. The low net nitrification rates compared with those recorded in the field-moist peat samples probably indicate high denitrification and N immobilization rates. The litter consisted mostly of birch leaves and formed a thick layer in which O_2 may diffuse weakly, enabling denitrification. In an earlier study with boreal coniferous litter, N_2O was also mostly produced by denitrification (Martikainen et al. 1993). In our experiment, N_2O production was much higher in the litter than in the field-moist peat (Table 2, Fig. 2a). Similarly, the litter layer in an upland boreal coniferous forest exposed to high N deposition showed higher N_2O production than the deeper horizons (Martikainen et al. 1993). The higher production of CO_2 in the litter than in the peat layers (Table 1) was evidence of a higher amount of available C in the litter, which may have favoured N_2O production through denitrification (Wijler and Delwiche 1954). NO production was not inhibited by acetylene, suggesting that nitrification did not contribute greatly to the production of NO in this litter (Fig. 2b). Davidson (1992) suggested that abiotic reactions which interact with autotrophic NH_4^+ oxidation could be an important source of NO in dry soil. Acid organic soils are potential environments for chemodenitrification (Van Cleemput and Samater 1996) and the possibility that this process occurred in the soils under study cannot be excluded, either.

Since NO_3^- was produced at a net rate of 0.9 ± 0.8 ng (g dry litter)$^{-1}$ h^{-1} in the control group and -0.1 ± 0.8 ng (g dry litter)$^{-1}$ h^{-1} at a concentration of 2.5% acetylene during the 6-day experiment, it was clear that nitrification was inhibited to a great extent by the 24-h exposure to 2.5% acetylene.

The production of N_2O plus NO was about 20 ng N g^{-1} h^{-1} during the whole 6-day experiment, even after exposure to acetylene (Fig. 2). This seems a high rate considering the initial NO_3^- concentration of 400 ng g^{-1} (Table 1) and low net nitrification (see above), but the nitrification potential of the litter in an aerobic suspension with added NH_4^+ was found to be quite high, i.e. 1100 ng (g dry litter)$^{-1}$ h^{-1} (Regina et al., 1998). Thus the results strongly suggest that not all nitrification was inhibited by acetylene during the short incubation with this compound, and that a substantial part of the NO_3^- formed was denitrified.

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