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Denitrification triggered by nitrogen addition in *Sphagnum magellanicum* peat

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Abstract Ombrotrophic (rain-fed) *Sphagnum*-mires do not significantly contribute to gaseous nitrogen (N) emissions to the atmosphere. However, increasing levels of N deposition reduce *Sphagnum* growth and moss cover. As a consequence, higher amounts of mineral N reach the underlying peat beneath the moss layer. The aim of our work was to determine the effects of supplementary N inputs to peat beneath *Sphagnum magellanicum* carpets. Peat cores were incubated in controlled laboratory conditions of temperature and humidity, and the impact of increasing N inputs was evaluated on denitrification rates, basal respiration and methane emissions. Rates of denitrification were quickly stimulated by addition of 1 g N m^{-2} but rates were not significantly elevated in the short-term (9 days) by further additions of up to 10 g N m^{-2}. Over a longer term period (up to 45 days), denitrification rates followed an exponential (10 g N m^{-2} addition) or a gamma (1 g N m^{-2}) function. Findings from this study support the hypothesis that mineral-N addition in atmospheric deposition will have a negative effect on peat biogeochemistry, by modifying its N sink capacity via denitrification leading to a potential increase in N_2O emissions.

Keywords Nitrogen deposition · *Sphagnum*-mire · Peat · Denitrification · Nitrate · Ammonium · Microbial biomass · N cycling

Abbreviations

N	Nitrogen
N_2O	Nitrous oxide
NO_3^-	Nitrate
NH_4^+	Ammonium
C	Carbon
DOC	Dissolved organic carbon
MB-C	Microbial biomass carbon
CO_2	Carbon dioxide
CH_4	Methane

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Introduction

Atmospheric inputs are the major source of nutrients in ombrotrophic (rain-fed) *Sphagnum*-mires and the consequent low nutrient availability is one of the main environmental factors contributing to organic matter accumulation as peat (Clymo 1983). Most of the

mineral N in precipitation is recovered in *Sphagnum* mosses and continuous *Sphagnum* carpets act as a strong sink of atmospheric N (Francez and Loiseau 1999; Heijmans et al. 2002).

Anthropogenic activities have strongly increased the rate of N inputs to ecosystems and global N deposition is predicted to increase (Lamarque et al. 2005). In *Sphagnum*-mires, elevated N-inputs can both reduce the growth and production capacity of *Sphagnum* (Gunarsson and Rydin 2000) and enhance the losses of C and N from peat or litter (Bragazza et al. 2006; Breeuwer et al. 2008), finally reducing the mires' capacity as a sink for C and N (Gunarsson et al. 2008).

Elevated N inputs also modify the environmental conditions of microbial communities at the surface of the mire. As the *Sphagnum* mosses do not take up all of the added N, the water surrounding them becomes N-enriched (Limpens and Berendse 2003). This N-enrichment modifies the structure of microbial communities living in *Sphagnum* layers. For instance, Cyanobacteria and Diatoms increase their biomass and activity whereas the contribution of Thecamoeba, a major group of bacterial predators, strongly decreases with N-addition (Gilbert et al. 1998).

Under natural conditions, nitrification is limited by low pH in *Sphagnum*-mires resulting in low NO_3^- production and low denitrification activity (Urban et al. 1988; Hayden and Ross 2005) and pristine *Sphagnum*-mires function as N sink ecosystems rather than N source for the atmosphere. Recently, Repo et al. (2009) showed that in tundra, peat circles (bare peat surfaces created by cryoturbation) can emit large amounts of N_2O. In *Sphagnum*-mires subjected to elevated N-inputs and losses of *Sphagnum* carpets, the direct transfer of atmospheric N to peat becomes an important factor in determining whether or not N (and C) will be released to the atmosphere. The responses of microbial activities in peat to added N to the mire then need to be understood. NH_4^+ is likely to be immobilized by the microbial biomass because of the high C:N ratio of *Sphagnum* whereas NO_3^- can also be denitrified thus raising N released to the atmosphere as either N_2O or N_2, modifying the N sink capacity of *Sphagnum*-mires. Hayden and Ross (2005) suggested that an increase in N inputs to *Sphagnum* would enhance denitrification in ombrotrophic mires by increasing N availability. However, the impact of increasing N inputs on denitrification has not been evaluated. We expected that N excess from precipitation or surface run-off would reduce *Sphagnum* carpets and reach the peat where it would affect microbial activity by promoting N-enrichment and availability. This extra N input could increase denitrification activity and alter N- and C-cycling in the ecosystem.

In order to test this hypothesis, we conducted a set of laboratory experiments to address three complementary questions: (i) how rapidly can denitrification be enhanced by external N input, under aerated and anaerobic conditions? (ii) how do different loads of N affect the short term and long term rates of denitrification? and (iii) are the microbial biomass and activity affected in peat by elevated-N inputs? Specifically, we added different loads of N to *Sphagnum magellanicum* peat monoliths and incubated them in a climatic chamber under aerated and anaerobic conditions for 45 days. We measured N_2O, CO_2 and CH_4 fluxes and microbial biomass C.

Materials and methods

Sphagnum magellanicum peat

Surface peat monoliths (6 cm diameter × 12 cm height) were harvested in the dominant *Sphagnum magellanicum* community in Les Pradeaux mire using open PVC tubes. The site is located in the east of the French Massif central (3°55E; 45°32N) at an altitude of 1,250 m. The main bulk peat properties (Table 1) are typical of bog peat of this region

Table 1 Basic characteristics of peat sampled beneath living *Sphagnum magellanicum* (DOC, NH_4-N, NO_3-N, PO_4-P = extractable forms in K_2SO_4 solution; DP = dry peat)

	Surface peat (0–10 cm)
Bulk density (g l^{-1})	46 ± 11
pH–KCl	3.7 ± 0.4
C:N	33.1 ± 12.3
Total organic N (μg g DP^{-1})	15.4 ± 6.8
Dissolved organic C (μg g DP^{-1})	569 ± 26
Microbial biomass C (μg g DP^{-1})	372 ± 62
NH_4-N (μg g DP^{-1})	352 ± 58
NO_3-N (μg g DP^{-1})	9 ± 1
PO_4-P (μg g DP^{-1})	3 ± 1

(Francez 1992). Mean annual wet N deposition ranges from 0.9 to 1.0 g m^{-2} $year^{-1}$.

Experimental set-up

A set of 126 closed jars, each containing a surface peat monolith laid in a Petri dish (8 cm diameter × 1 cm height) filled with water, was incubated in the dark at 15°C temperature in an environmental chamber. Peat was incubated with different amounts of N addition, i.e. 0 (N0), 1 (N1) and 10 (N10) g m^{-2}. Two ml of an ammonium-nitrate solution containing 1 and 10 g N l^{-1} (NH_4-N:NO_3-N ratio = 1:1) were spread at the start of the experiment, on the peat surface of the monolith, using a multiple needle syringe.

At each date, three replicate jars of each treatment were randomly selected. Peat NO_3-N concentration and N_2O-N emissions were measured after 1, 2, 3, 6, 7, 9, 15, 30 and 45 days of incubation. Denitrification rates under aerated conditions (air-unclosed jars) and an anaerobic (helium-closed jars) atmosphere were compared at 1, 2, 3, 6 and 9 days of incubation. Peat NH_4-N and DOC concentrations, CO_2-C and CH_4-C emissions and microbial biomass C were monitored after 7, 15, 30 and 45 incubation days.

Denitrification, CO_2 and CH_4 measurements and gas analysis

Denitrification was assayed using the static core acetylene inhibition method (Yoshinari et al. 1977). Despite some possible problems, i.e. underestimation of denitrification (Watts and Seitzinger 2000) and/or incomplete acetylene diffusion into cores (Dowrick et al. 1999), the acetylene block method is considered a robust method for soils with moderate or high nitrate fluxes (Groffman et al. 2006), and has already been used for peat soils (Regina et al. 1996; Hayden and Ross 2005). The atmosphere concentration of acetylene in the closed jars was brought to 10 kPa (10% V/V) acetylene and 90 kPa air (aerated conditions) or He (anaerobic conditions). Aliquots (5 ml) of the jar atmosphere were sampled via a septum with a syringe and then analysed by gas chromatography. After 4 h of incubation, gas samples were analysed for N_2O using a gas chromatograph (Chrompack 9001) equipped with an electron capture detector and a stainless Porapack Q column 2 m in length with a 2 mm-i.d. CH_4 and CO_2 concentrations were estimated using a two lines micro gas chromatograph (Chrompack CP 2002P) equipped with TC detectors and two column modules i.e., a CP Molsieve 5 Å PLOT (HR) and a PoraPLOT Q. All gas fluxes were expressed as mg or µg N or C g^{-1} oven dry peat (DP) day^{-1}.

Microbial biomass C and nutrient analyses

Microbial biomass carbon (MB-C) was estimated, using a modified protocol of the fumigation-extraction method (Williams and Silcock 1997). Peat samples were fumigated during 18 h at 20°C with ethanol-free $CHCl_3$ vapour. DOC in the fumigated and un-fumigated samples was extracted by shaking 20 g fresh peat in 100 ml of a 0.5 M K_2SO_4 solution for 1 h. Suspensions were filtered and DOC concentrations in the extracts were measured using a TOC 5000 Shimadzu Analyser (Touzard & Matignon, Paris, France). Microbial biomass was calculated from the extracted flush using the recovery factor of K_{EC} of 0.45 derived for peat-soils by Sparling et al. (1990). Results were expressed as µg per gram of dry peat (µg C g DP^{-1}).

Concentrations of NO_3^- and NH_4^+ were measured colorimetrically in the K_2SO_4 extracts. NO_3^- was measured after reduction to nitrite on a cadmium-copper column (Henriksen and Selmer-Olsen 1970), using a BRAN + LUEBBE AutoAnalyzer 3 (Norderstedt, Germany). NH_4^+ was measured following the indophenol-blue method (Weatherburn 1967). After 30 min incubation at 37°C, the optical density was measured at 630 nm.

Statistical analyses and modeling procedures

Data for DOC, MB-C and C fluxes were log transformed to homogenize variance prior to running a multifactor ANOVA to examine for the main effect of time or N addition and for corresponding interactions. Due to non-homogeneity of variances following transformations, the effects of N addition or aeration on denitrification were evaluated using the non-parametric Kruskal–Wallis test. Spearman rank correlations were calculated to determine the degree of the relationship between two variables. Statistical significance was assigned for $P < 0.05$ for all analyses.

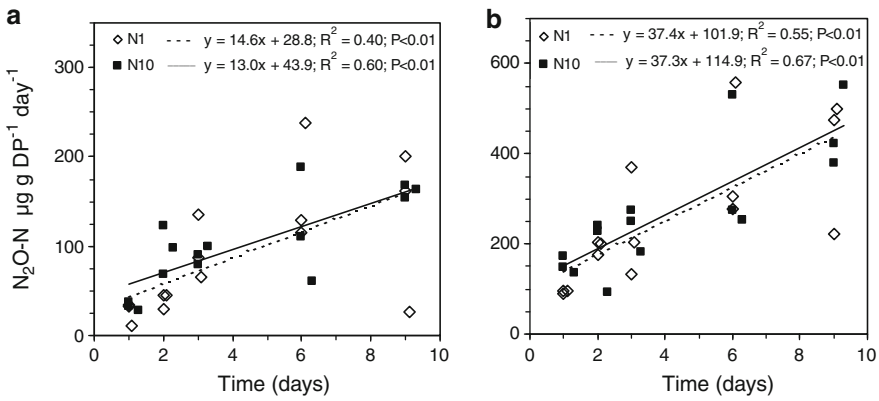

Fig. 1 Denitrification in *Sphagnum*-peat samples at 15°C under aerated (**a**) and anaerobic (**b**) conditions

Denitrification rate (y) vs. time (x) was fitted to exponential regression (Eq. 1) or gamma function (Eq. 2) expressed as:

$$y = a\left(1 - e^{-bx}\right) + c \quad (1)$$

$$y = ax^b e^{cx^d} + f \quad (2)$$

where a–f are fitted constants. Non-linear regression analysis and fitting procedures were carried out with SYSTAT 10 (SPSS Inc 2000).

Results

Denitrification over time under aerated vs. anaerobic conditions

Low denitrification rates were measured both under aerated and anaerobic conditions in peat cores with ambient N (N0) levels but were significantly higher under anaerobiosis ($H = 10.4$, $P = 0.001$). The maximum denitrification rate under aerated conditions was 4.3 ± 1.8 and 5.9 ± 2.9 N_2O-N µg g DP^{-1} day^{-1} under anaerobic conditions.

There was a significant positive effect of N addition on denitrification ($H = 55.1$, $P < 0.001$). Responses of denitrification to N addition were linear in the short-term, both under aerated and anaerobic conditions and there was no significant difference between N treatments (Fig. 1a, b). During long-term anaerobic incubation (45 days), denitrification rates increased in response to the N10 treatment and followed an exponential function reaching a plateau after 30 days of incubation. In contrast, denitrification rates in the N1 treatment peaked after 9 days and then decreased regularly until the end of the 45 days of incubation (Fig. 2).

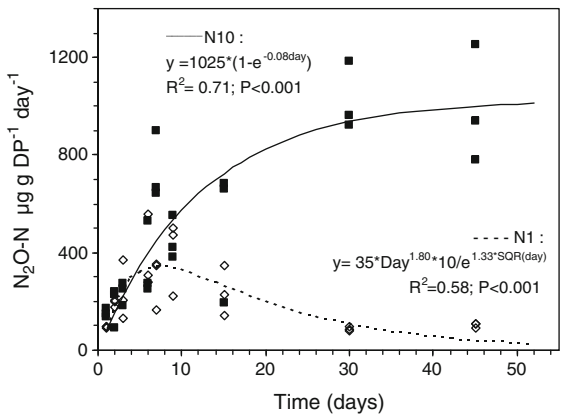

Fig. 2 Modeling of denitrification through time (anaerobiosis)

Denitrification rates vs. control factors

NO_3^- concentrations decreased significantly after 7 days of incubation in the N1 treatment while a decrease was measured only after 15 days under the N10 treatment (Day × N modality: F ratio = 4.35, $P < 0.01$; data not shown). We did not find any correlation between denitrification and DOC ($r = -0.06$; $n = 34$; $P = 0.71$).

N inputs and peat C

MB-C decreased in the N0 treatment over the course of the experiment (Fig. 3a; Table 2) while it remained fairly constant in the N amended treatments. CH_4 emission decreased significantly over the

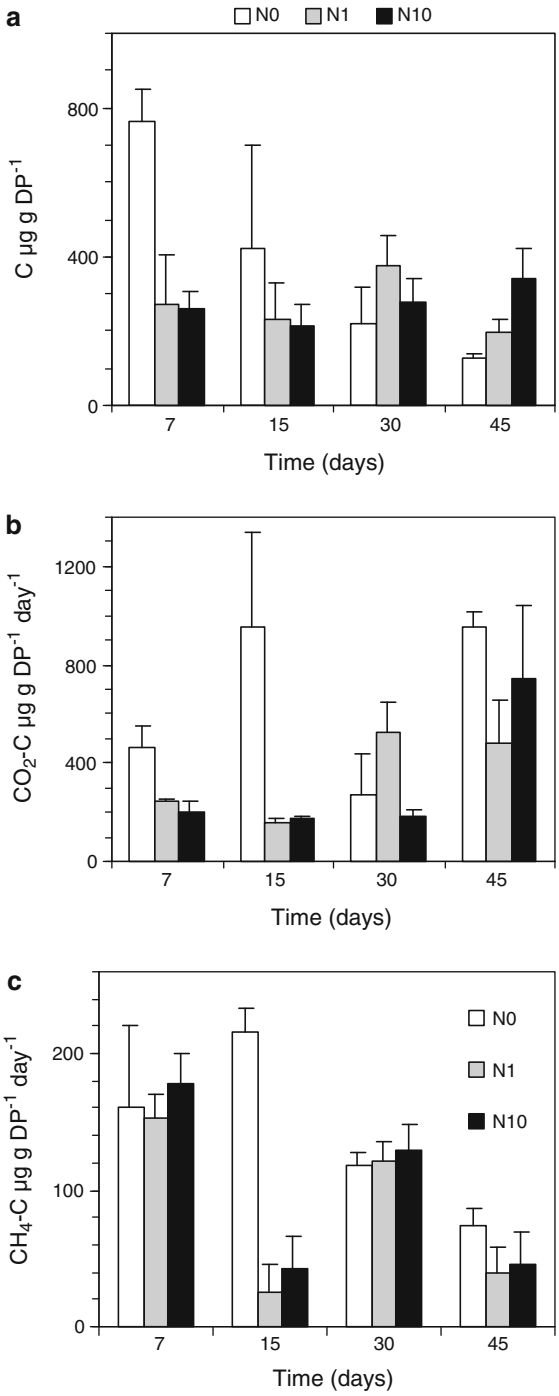

Fig. 3 Fluctuations through time of (**a**) microbial biomass carbon, (**b**) CO_2-C and (**c**) CH_4-C released from *Sphagnum*-peat samples at 15°C, incubated in anaerobic conditions under N-treatment

course of the 45 days experiment, regardless of the N addition (Table 2; Fig. 3c). No other significant temporal trend could be seen.

There were no differences in DOC concentrations (data not shown), microbial biomass C and CH_4 emission rate between N-treatments (Table 2; Fig. 3). On the contrary, basal respiration was significantly lower in N1 and N10 at 7 and 15 days of incubation (Table 2; Fig. 3b).

There was a negative correlation between NH_4^+ and basal respiration ($r = -0.453$; $n = 35$; $P < 0.005$, data not shown) while CH_4 emission was positively correlated to DOC ($r = 0.403$; $n = 33$; $P = 0.022$) but no trend was detected with denitrification ($r = -0.123$; $n = 31$; $P = 0.499$).

Discussion

Denitrification rates in the control (N0) were low compared to riparian wetlands rates, for instance (Pinay et al. 2007), but in accordance with the few published data for *Sphagnum*-dominated mires (Urban et al. 1988; Regina et al. 1996; Dowrick et al. 1999). Our results support the view that under natural conditions, ombrotrophic mires are poor denitrifying ecosystems because of the natural paucity of NO_3^- in *Sphagnum* peat (Urban et al. 1988; Regina et al. 1996).

The rapid response of the denitrifiers to NO_3^- addition is consistent with the presence of an active denitrifying bacterial community. N additions appeared to stimulate the denitrifying enzyme synthesis in the pre-existing denitrifying community, resulting in similar denitrification rates, whatever the N application (Fig. 1). The similar linear increase in denitrification rates measured (with either 1 or 10 g N m^{-2} application) for the first 9 days can be interpreted as an increase of the denitrifying community density under a non-limiting NO_3^- supply, both under aerated and anaerobic conditions (Fig. 1a, b). The maximum denitrification rate obtained after 45 days of anaerobic incubation with the N10 treatment (1.00 ± 0.17 N_2O-N mg g DP^{-1} day^{-1}) was comparable to already published data for meso- or eutrophic mires (Aerts 1997; Wray and Bayley 2007;

Table 2 Analysis of variance for dissolved organic carbon (DOC), microbial biomass C (MB-C), basal respiration and methane emission in samples of *Sphagnum* peat (log-transformed data)

Sources of variation	DOC		BM-C		CO_2-C		CH_4-C	
	F ratio	*P* value	*F* ratio	*P* value	*F* ratio	*P* value	*F* ratio	*P* value
Main effects								
A. Days	16.7	<0.001	2.18	0.116	4.73	<0.05	5.05	<0.01
B. N-treatment	3.32	0.729	0.09	0.918	7.24	<0.01	2.09	0.150
Interactions								
A × B	3.32	<0.05	3.29	<0.05	2.62	<0.05	0.96	0.473

All *F* ratios are based on the residual mean square error

Tauchnitz et al. 2008) and disturbed peat soils (Jörgensen and Richter 1992). These results support the view that NO_3^- input to *Sphagnum*-dominated mires will increase denitrification activity and potentially increase emissions of N_2O measured in such environments (Repo et al. 2009). The decrease in denitrification rate activity under N1 treatment suggests that NO_3^- supply becomes a limiting factor after 9 days of incubation. The plateau in denitrification rate observed after 30 days under N10 treatment could be due to a limitation of bioavailable organic substrate, with N additions possibly acting as a depressor of certain C-enzyme activities (Waldrop and Zak 2006). In our experiment, we did not show any significant relationship between denitrification and DOC. In peat soils, C availability and quantities are of importance for denitrification activity (Jörgensen and Richter 1992). Denitrifiers can potentially use readily hydrolysable C as well as recalcitrant compounds (Jörgensen and Richter 1992).

We used basal respiration as an indicator of global microbial activity in peat. Our results seem to confirm that N addition reduced CO_2 release from *Sphagnum magellanicum* surface peat (Williams and Silcock 1997), at least during the first 2 weeks after N application, when compared to non N amended cores (Fig. 3b). Yet, these changes in microbial activity measured by basal respiration under N addition treatment did not result in a significant decline in the total microbial biomass, in contrast to what is observed in many ecosystems, especially at high levels of N addition (Treseder 2008). We measured a decrease of CH_4 emission potential after N applications (Fig. 3c). CH_4 emissions correspond to the difference between the production and the oxidation of CH_4 (Nykänen et al. 2002), two processes that are, respectively, modified by NO_3^- and NH_4^+. In anaerobic conditions, the addition of NO_3^- can lead to a decrease of methanogenesis because some microbes, e.g. denitrifiers, use NO_3^- as electron acceptors when they oxidize organic C-substrates such as acetate (Nykänen et al. 2002). In our experiment, the decrease of CH_4 emission also measured in the control after 15 days of incubation suggests a depletion of bioavailable C through time as indicated by the concomitant decrease of DOC.

Conclusion

Our aim was to assess the short- and long-term effects of mineral N addition on denitrification rates in peat beneath *Sphagnum magellanicum* carpets. The experiment showed that the *Sphagnum* peat denitrifying community was significant and physiologically able to react rapidly to N addition, both under aerated and anaerobic conditions. The destruction of the *Sphagnum magellanicum* carpets entails an increasing risk of N_2O emission via denitrification in the peat and a decreasing N-sink functioning at the ecosystem level.

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