



Response of C and N cycles to N fertilization in Sphagnum and Molinia-dominated peat mesocosms

Fabien Leroy, Sébastien Gogo, Christophe Guimbaud, Andre-Jean Francez, Renata Zocatelli, Christian Défarge, Léonard Bernard-Jannin, Zhen Hu, Fatima Laggoun-Défarge

► To cite this version:

Fabien Leroy, Sébastien Gogo, Christophe Guimbaud, Andre-Jean Francez, Renata Zocatelli, et al.. Response of C and N cycles to N fertilization in Sphagnum and Molinia-dominated peat mesocosms. *Journal of Environmental Sciences*, 2019, 77, pp.264-272. <10.1016/j.jes.2018.08.003>. <insu-01864513v2>

HAL Id: insu-01864513

<https://insu.hal.science/insu-01864513v2>

Submitted on 14 Sep 2018

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons CC BY 4.0 - Attribution - International License

Available online at www.sciencedirect.com

ScienceDirect

www.elsevier.com/locate/jes

SciVerse S

Q1 Response of C and N cycles to N fertilization in 2 Sphagnum and Molinia-dominated peat 3 mesocosms

Q3 Q2 Fabien Leroy^{1,2,3,*}, Sébastien Gogo^{1,2,3}, Christophe Guimbaud^{4,5}, André-Jean Francez⁶,
5 Renata Zocatelli⁷, Christian Défarge^{1,2,3,7}, Léonard Bernard-Jannin^{1,2,3}, Zhen Hu⁸,
6 Fatima Laggoun-Défarge^{1,2,3}

7 1. Université d'Orléans, ISTO, UMR 7327, 45071 Orléans, France

8 2. CNRS, ISTO, UMR 7327, 45071 Orléans, France

9 3. BRGM, ISTO, UMR 7327, BP 36009, 45060 Orléans, France

10 4. Université d'Orléans, LPC2E, UMR 7328, 45071 Orléans, France

11 5. CNRS, LPC2E, UMR 7328, 45071 Orléans, France

12 6. UMR CNRS 6553 ECOBIO, Université de Rennes 1, Rennes, France

13 7. Université d'Orléans, Cellule R&D CETRAHE, 45072 Orléans, cedex 2, France

14 8. School of Environmental Science and Engineering, Shandong University, Jinan, China

1 8 A R T I C L E I N F O

29 Article history:

20 Received 3 August 2017

26 Revised 31 July 2018

22 Accepted 16 August 2018

28 Available online xxxx

30 Keywords:

34 CO₂ and CH₄

32 N₂O

36 Peatland

34 Plant community composition

38 Sphagnum moss

36 Graminoid

A B S T R A C T

Plant communities play an important role in the C-sink function of peatlands. However, global change and local perturbations are expected to modify peatland plant communities, leading to a shift from *Sphagnum* mosses to vascular plants. Most studies have focused on the direct effects of modification in plant communities or of global change (such as climate warming, N fertilization) in peatlands without considering interactions between these disturbances that may alter peatlands' C function. We set up a mesocosm experiment to investigate how Greenhouse Gas (CO₂, CH₄, N₂O) fluxes, and dissolved organic carbon (DOC) and total dissolved N (TN) contents are affected by a shift from *Sphagnum* mosses to *Molinia caerulea* dominated peatlands combined with N fertilization. Increasing N deposition did not alter the C fluxes (CO₂ exchanges, CH₄ emissions) or DOC content. The lack of N effect on the C cycle seems due to the capacity of *Sphagnum* to efficiently immobilize N. Nevertheless, N supply increased the N₂O emissions, which were also controlled by the plant communities with the presence of *Molinia caerulea* reducing N₂O emissions in the *Sphagnum* mesocosms. Our study highlights the role of the vegetation composition on the C and N fluxes in peatlands and their responses to the N deposition. Future research should now consider the climate change in interaction to plants community modifications due to their controls of peatland sensitivity to environmental conditions.

© 2018 The Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences.

Published by Elsevier B.V.

* Corresponding author at: Université d'Orléans, ISTO, UMR 7327, 45071 Orléans, France.

E-mail address: lerfabien@gmail.com. (F. Leroy).

1. Introduction

Peatlands currently act as a major long-term carbon (C) sink ecosystem. Although these wetlands cover only 3% of the land area, they have stored a third of the global soil C since the early Holocene (Turunen et al. 2002). Most *Sphagnum* peatlands (up to 80%) are located at high latitudes of the northern hemisphere in the cool temperate zone in association with waterlogged, nutrient poor conditions and the presence of *Sphagnum* mosses (e.g. Gorham 1991). To cope with low nutrient concentrations, *Sphagnum* mosses have developed mechanisms to efficiently use nutrients thanks to their high cation exchange capacity, nutrient translocation and atmospheric interception, reducing the nutrient availability to vascular plants (e.g. Turetsky et al. 2012). However, northern temperate ecosystems receive four times more airborne nitrogen (N) today than 150 years ago (Holland et al. 1999; Lamarque et al. 2005). Increased N deposition leads to a progressive N saturation of *Sphagnum* mosses, thus favoring the invasion of vascular plants and reducing *Sphagnum* moss growth (Limpens et al. 2011). Such changes seem to reduce the C sequestration rates in peatlands (Bragazza et al. 2006; Gunnarsson et al. 2008), even if they increase the vascular plants' productivity (Wu et al. 2015). However, the effect of the increase in N loads on stocks and exchanges of N and C are still understudied in peatlands, although they are known to generally increase N₂O emissions to the atmosphere (e.g. Nykänen et al. 2002; Francez et al. 2011). Peatland C-storage capacity is often considered alone to assess the effects of climate change on peatlands without considering the N stored in the ecosystems that could account for a significant N₂O source and therefore act as a positive feedback to climate change (Repo et al. 2009).

The increase in vascular plant cover due to human activities such as nutrient supply, e.g., atmospheric N deposition, or drainage, increases organic matter decomposition (Gogo et al. 2016) and modulates CO₂ and CH₄ emissions in peatlands (Ward et al. 2013; Leroy et al. 2017). The combined effects of vascular plant invasion with N deposition on both C and N cycles and stocks still remain to be elucidated. N fertilization generally stimulates the vascular plant biomass, thereby contributing to higher primary production. However, it also leads to a higher decomposition rate due to a reduction in the C/N ratio and more root exudates that generate additional respiration (Wu et al. 2015). Our aim was therefore to assess the effect of N supply on both C and N dynamics in peat mesocosms collected in a *Sphagnum*-dominated peatland invaded by a vascular plant, *Molinia caerulea*. All the peat mesocosms contained *Sphagnum rubellum*, and half of them also contained *M. caerulea*. Half of each plant community mesocosm was subjected to an increase in N deposition by a weekly amendment to reach an addition of 3.2 g N/(m²·year). Thus, the hypotheses investigated are that N deposition will lead to the following processes under the two plant communities:

- (i) Processes involving the C cycle: (a) an increase in C fluxes by promoting ecosystem respiration (ER) due to a faster decomposition of plant tissues containing more

N (Bragazza et al. 2006); (b) stimulation of the gross primary production (GPP) by an enhancement of both *Sphagnum* mosses and graminoid biomass (e.g. Tomassen et al. 2003; Granath et al. 2009); (c) a rise in CH₄ emissions through a higher OM decomposition and increase in root exudates.

- (ii) Processes involving the N cycle: (a) higher concentrations of the dissolved NH₄⁺ and NO₃⁻ and of the N stored by *Sphagnum* mosses; (b) an increase in N₂O emissions under both plant communities (Roobroeck et al. 2010).
- (iii) Processes involving *M. caerulea* occurrence: an increase in the C fluxes in peatlands (CO₂, CH₄) and DOC content and a decrease in the ecosystem C sink function compared to *Sphagnum*-dominated peatland due to the promotion of peat decomposition (Leroy et al. 2017).

2. Materials and methods

2.1. Experimental design

Twelve peat mesocosms (depth and diameter: 30 cm) were collected in March 2015 at La Guette peatland, an acidic fen invaded by *M. caerulea* (pH about 4, 47°19'44"N, 2°17'04"E, France). The mean annual precipitation and temperature of La Guette peatland are 883 mm and 11 °C, respectively (Gogo et al. 2011). The mesocosms were buried outdoors (N 47°50'01", E 1°56'34", ISTO, Orléans) and surrounded with a tarpaulin containing water from the peatland. Air and soil temperature at 5 and 20 cm depth were monitored in each mesocosm at 15 minute intervals. The water table level (WTL) was measured by using piezometers in all the mesocosms. For each gas measurement, peat water was collected from the piezometer and filtered at 0.45 μm to analyze DOC and TN concentrations ([DOC] and [TN]) with a Shimadzu TOC-5000 analyzer and NH₄⁺ and NO₃⁻ concentrations by Dionex ICS 900 and 1100 ion chromatography. The mesocosms were first separated into two different plant communities: six containing only *S. rubellum* (called '*Sphagnum*' mesocosms) and six containing both *S. rubellum* and *M. caerulea* (called '*Sphagnum* + *Molinia*' mesocosms). *Molinia caerulea* growth started in May. The plant covered up to 60% of mesocosms until its senescence in November. Mesocosms of both plant communities were separated into two treatments with (called 'Fertilized' mesocosms) and without (called 'Control' mesocosms) additions of NH₄NO₃, commonly used as an agricultural fertilizer. A powder of NH₄NO₃ was dissolved in peat water and added every week to reach 3.2 gN/(m²·year), which represents 3.7 gN/(m²·year) during the 14 months of the experiment. This enrichment is higher than that currently observed in peatlands (Bragazza et al. 2004), but could reflect the N deposition expected for 2100 (Lamarque et al. 2005).

At the end of the mesocosm experiment (June 2016), C and N content (%) in *Molinia* leaves and litter, *Sphagnum* capitula (0–0.5 cm), living *Sphagnum* (0.5–2.5 cm) and in peat cubes (5 × 5 × 5 cm) at 2.5–7.5, 7.5–12.5, 12.5–17.5 and 17.5–22.5 cm depth were measured for each mesocosm with an elementary analyzer (Thermo-126 FLASH 2000 CHNS/O Analyzer). For each mesocosm at the previously mentioned depths, cubes 168

measuring 5 cm per side were prepared and oven dried at 50°C to calculate peat bulk density (g/cm³, Table S1) in order to evaluate the C and N stock in each layer (Eq. (1)):

$$C \text{ or } N \text{ stocks (g/m}^3\text{)} = C \text{ or } N \text{ content (\%)} \times \text{Peat bulk density (1)}$$

172

2.2. Greenhouse gas (GHG) measurements

GHG measurements were performed with the closed chamber method between once to twice per week during the growing season (April–October 2015 and April–June 2016) and every 2 weeks during winter (November 2015–March 2016). CO₂ fluxes were measured during 5 minute using a GMP343 Vaisala probe inserted in a transparent PVC chamber (D'Angelo et al. 2016). A clear chamber was used to measure the net ecosystem exchange (NEE), the balance between GPP (absorption of CO₂ by photosynthesis) and ER (release of CO₂ into the atmosphere). ER was measured by placing an opaque cover on the chamber to block photosynthesis (D'Angelo et al. 2016). CH₄ and N₂O emissions were measured during 15 minute by using SPIRIT, a portable infrared laser spectrometer (Guimbaud et al. 2011).

2.3. Data analysis and modeling

C fluxes (in g C/(m²·year)), including the GPP, ER and CH₄ emissions, were derived for the entire year at a 15 minute time step following Leroy et al. (in prep) by using CO₂ and CH₄ measurements to calibrate and validate equations based on Bortoluzzi et al. (2006) and Kandel et al. (2013) with:

$$ER = \left[\left(a^* \frac{WTL}{WTL_{ref}} \right) + (b^* MC_{leaves}) \right] * \left(\frac{(T_a - T_{min})}{(T_{ref} - T_{min})} \right)^c \quad (2)$$

ER is the ecosystem respiration flux (μmol CO₂/(m²·s)). T_{ref} is the reference air temperature and T_{min} the minimum air temperature. These two parameters were set as in Bortoluzzi et al. (2006) at 15 and –5 °C, respectively. T_a refers to the measured air temperature (°C). The reference for the WTL (WTL_{ref}) was set at –15 cm corresponding to the deepest WTL recorded in the mesocosms. The coefficients *a*, *b* and *c* (temperature sensitivity parameters) are empirical parameters.

An equation similar to Eq. (1) was used to model the emissions (Eq. (2)):

$$CH_4 = \left[d^* \frac{WTL}{WTL_{ref}} + e \right] * \left(\frac{(T_s - T_{min})}{(T_{ref} - T_{min})} \right)^f \quad (3)$$

where, WTL_{ref}, T_{min}, T_{ref} and T_{min} were set as for the ER equation. T_s refers to the measured soil temperature (°C).

The GPP was modeled by using a rectangular hyperbola saturation curve with the photosynthetic photon flux density (PPFD) and by taking into account the effect of temperature and vegetation with the Eq. (3):

$$GPP = \frac{GPP_{max} * PPFD}{k + PPFD} * RVI * \frac{(T - T_{min})(T - T_{max})}{(T - T_{min})(T - T_{max}) - (T - T_{opt})^2} \quad (4)$$

where GPP_{max} (μmol/(m²·s)) represents the GPP at light saturation, the parameter *k* (μmol/(m²·s)) is the half saturation value and RVI a vegetation index to include the effect of *Molinia* leaves number on photosynthesis. T_{min}, T_{opt} and

T_{max} represent the minimum, optimum and maximum air temperature for photosynthesis and were set at 0, 20 and 40 °C, respectively (Kandel et al. 2013).

N fluxes (concerning only N₂O emissions, g N/(m²·year)) were extrapolated for the entire year from the mean values of 12 months of measurements (in μmol N₂O/(m²·s)). Three-way repeated-measure ANOVAs were used to compare C and N fluxes and differences in environmental parameters due to the main effect of 'Vegetation' between *Sphagnum* and *Sphagnum* + *Molinia* mesocosms, and 'Nitrogen' between the Fertilized and Control mesocosms over the measurement period (Table 1). Two-way ANOVAs were used to compared C and N content, peat bulk density and C and N stocks per depth for the main effect of 'Vegetation' between *Sphagnum* and *Sphagnum* + *Molinia* mesocosms, and 'Nitrogen' between the Fertilized and Control ones (Tables 2, S1, S2).

3. Results

3.1. C and N fluxes

No significant differences in ER, GPP, CH₄ emissions or [DOC] were observed between the Control and Fertilized mesocosms for the two plant communities (Table 1). Hypothesis (i), which assumed a promotion of ER, GPP and CH₄ emissions, must therefore be rejected. Differences were driven only by the plant communities: the presence of *M. caerulea* increased the gaseous C fluxes (ER, GPP, CH₄ emissions) compared to *Sphagnum* mesocosms (Table 1). Furthermore, the number and height of *M. caerulea* leaves were similar between the Control and Fertilized mesocosms and no stimulation of *Molinia* growth with addition of N was observed (Table 1). Neither NH₄⁺ nor NO₃[–] concentrations were significantly influenced by the increase in N deposition, refuting hypothesis (ii, a), i.e. higher NH₄⁺ and NO₃[–] concentrations in peat water due to NH₄NO₃ additions (Table 1). Water in both plant communities contained low NO₃[–] concentrations, and NH₄⁺ concentrations varied with the vegetation cover (Table 1, Fig. 2), the presence of *M. caerulea* significantly reducing the NH₄⁺ concentrations (and also the TN content) compared to *Sphagnum* mesocosms (Table 1).

The only significant differences due to the NH₄NO₃ additions concerned N₂O emissions that increased in Fertilized mesocosms compared to Control ones for both plant communities. This confirms our hypothesis (ii, b), i.e. that a higher N would increase N₂O emissions under both plant communities (Table 1, Figs. 1, 2 and S1). Furthermore, N₂O emissions were also affected by the vegetation composition with a decrease in N₂O emissions in the *Sphagnum*+*Molinia* mesocosms compared to the *Sphagnum* mesocosms (Table 1, Fig. 1).

3.2. C and N stocks

Increasing N deposition triggered a short-term response with an increase in N concentrations in *Sphagnum* capitula (0–0.5 cm depth) and in its living tissues (0.5–2.5 cm depth) and in N₂O emissions (Tables 1, 2 and Fig. 1). These effects modified the N cycles and stocks in the peat mesocosms (Table S2, Fig. 2). Extrapolation of N₂O fluxes (in g N/(m²·year)) showed that

Table 1 – Mean values of 12 months measurements of Net Ecosystem Exchange (NEE), Gross Primary Production (GPP), Ecosystem Respiration (ER), CH₄ emissions (CH₄), DOC, N₂O emissions, TN, NH₄⁺ and NO₃ contents, air temperature (Ta), Water Table Level (WTL), number and height of *Molinia* leaves in *Sphagnum* and *Sphagnum* + *Molinia* mesocosms with (Fertilized) or without (Control) NH₄NO₃ addition

		<i>Sphagnum</i>		<i>Sphagnum</i> + <i>Molinia</i>		Significance	
		Control	Fertilized	Control	Fertilized	Nitrogen	Vegetation
	Interaction	C cycle					
	NEE (μmol/(m ² ·s))	1.55 ± 0.26	1.29 ± 0.22	6.50 ± 1.26	7.11 ± 1.32		***
	GPP (μmol/(m ² ·s))	2.61 ± 0.37	2.28 ± 0.33	10.24 ± 1.92	10.56 ± 1.93		***
	ER (μmol/(m ² ·s))	1.06 ± 0.26	0.99 ± 0.22	3.75 ± 0.81	3.50 ± 0.75		***
	CH ₄ (μmol/(m ² ·s))	0.018 ± 0.007	0.019 ± 0.008	0.130 ± 0.032	0.133 ± 0.03		***
	DOC (mg/L)	58.38 ± 8.29	41.71 ± 7.24	35.95 ± 7.34	24.14 ± 5.37		*
	N cycle						
	N ₂ O (μmol/(m ² ·s))	5.26–5 ± 1.48–5	19.41–5 ± 5.38–5	–0.89–5 ± 1.21–5	2.86–5 ± 5.94–6	*	*
	TN (mg/L)	5.27 ± 0.56	4.01 ± 0.36	1.70 ± 0.31	1.14 ± 0.22		**
	NH ₄ ⁺ (mg/L)	5.15 ± 0.67	4.11 ± 0.35	0.27 ± 0.13	0.16 ± 0.059		**
	NO ₃ (mg/L)	0.51 ± 0.13	0.46 ± 0.11	0.26 ± 0.09	0.55 ± 0.175		
	Environmental parameters						
	Ta (°C)	12.06 ± 1.50	12.14 ± 1.525	14.54 ± 1.57	14.66 ± 1.52		
	WTL (cm)	–6.32 ± 0.51	–3.28 ± 0.40	–7.06 ± 0.49	–7.25 ± 0.54		
	<i>Molinia</i> leaves number	n. a.	n. a.	233.54 ± 46.0	269.94 ± 48.7		n. a. n. a.
	<i>Molinia</i> leaves height	n. a.	n. a.	13.04 ± 2.29	12.02 ± 2.14		n. a. n. a.

n. a.: not applicable. Data are presented as mean ± SE, n = 12. Significant differences of repeated-measure ANOVAs are expressed as *p < 0.05, **p < 0.01, ***p < 0.001.

increasing N deposition produced an increase in N₂O emissions of 0.125 gN/(m²·year) in *Sphagnum* mesocosms and of 0.033 gN/(m²·year) in *Sphagnum* + *Molinia* mesocosms (Fig. 2). However, the increase in N₂O emissions represents only 4 and 1% of the total N additions, respectively, in *Sphagnum* mesocosms and in *Sphagnum* + *Molinia* mesocosms. Most of the NH₄NO₃ load was stored in *Sphagnum* mosses with an estimated increase of 2.9 g N/m² in the stocks of *Sphagnum* + *Molinia* mesocosms and of 4.0 g N/m² in *Sphagnum* ones in the two first layers of the Fertilized mesocosms compared to the Control ones.

The NH₄NO₃ load did not significantly impact C cycles and stocks (Table 1, Fig. 3). C compartments were only affected by

the vegetation cover which modified C absorption and mineralization (Fig. 3). The shift from *Sphagnum* to *Molinia* dominated peatland increased C emissions and absorption and led to an increase in the C balance (Table 1, Fig. 3, Leroy et al., in prep). This refutes our hypothesis (iii) which assumed a decrease in the ecosystem C balance with *M. caerulea* occurrence. Only the *M. caerulea* effect was modeled on the C flux since it was the only significant effect observed on the CO₂ and CH₄ fluxes (Fig. 2, Leroy et al., in prep). C contents were similar between vegetation treatments (Table 2), but the density was higher in *Sphagnum* plots than in *Sphagnum* + *Molinia* mesocosms (Table S1). Consequently, the C stock was

Table 2 – C and N content (%) of *Molinia* and *Sphagnum* mesocosms with (Fertilized) or without (Control) NH₄NO₃ addition per depth (in cm),

		<i>Sphagnum</i>		<i>Sphagnum</i> + <i>Molinia</i>		Significance		
		Control	Fertilized	Control	Fertilized	Nitrogen	Vegetation	Interaction
	C cycle							
	0–0.5	40.80 ± 0.39	40.41 ± 0.28	40.13 ± 0.20	39.37 ± 0.72		–	
	0.5–2.5	37.60 ± 1.02	34.69 ± 3.83	39.63 ± 2.59	38.40 ± 2.32		–	
	2.5–7.5	32.54 ± 3.07	31.67 ± 2.43	34.77 ± 1.70	31.42 ± 2.41			
	7.5–12.5	37.91 ± 1.05	32.21 ± 2.61	38.05 ± 0.37	37.22 ± 1.95	–		
	12.5–17.5	34.87 ± 1.37	34.14 ± 2.76	37.80 ± 0.26	36.38 ± 1.05			
	17.5–22.5	37.29 ± 0.38	33.45 ± 4.37	34.58 ± 2.43	36.65 ± 0.98			
	N cycle							
	0–0.5	1.10 ± 0.11	2.01 ± 0.13	1.34 ± 0.05	1.73 ± 0.10	***		*
	0.5–2.5	0.68 ± 0.09	0.90 ± 0.11	0.74 ± 0.06	1.14 ± 0.12	*		
	2.5–7.5	0.86 ± 0.19	0.98 ± 0.07	0.67 ± 0.12	0.77 ± 0.10			
	7.5–12.5	0.99 ± 0.05	1.18 ± 0.28	1.12 ± 0.07	1.51 ± 0.36			
	12.5–17.5	1.53 ± 0.08	1.31 ± 0.19	1.49 ± 0.10	1.72 ± 0.18			
	17.5–22.5	1.60 ± 0.14	1.37 ± 0.06	1.49 ± 0.05	1.64 ± 0.07			–

Data are presented as mean ± SE, n = 3. Significant differences are expressed as – for 0.05 < p < 0.1, *p < 0.05, **p < 0.01, ***p < 0.001.

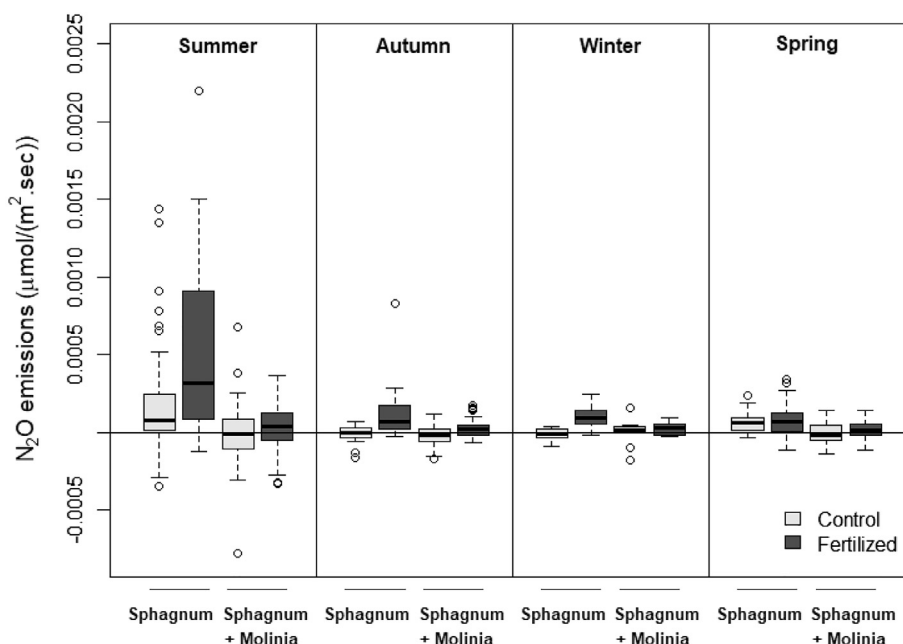


Fig. 1 – N₂O emissions measured in summer (n=19), autumn (n=8), winter (n=5) and spring (n=8) in *Sphagnum* and *Sphagnum* + *Molinia* mesocosms with (Fertilized) or without (Control) NH₄NO₃ addition (n=3).

higher in *Sphagnum* mesocosms than in *Sphagnum* + *Molinia* mesocosms (Table S2 and Fig. 3). The variability of peat density between vegetation did not affect the stoichiometry of the peat. The C/N ratio was only affected by the N treatment in the top two layers (0–0.5 and 0.5–2.5 cm) with a lower ratio in the Fertilized plots than in the Control ones (Fig. 4).

4. Discussion

4.1. N retention by *Sphagnum*

The number and height of *M. caerulea* leaves were similar between the Control and the Fertilized mesocosms and no stimulation of *Molinia* growth was observed. This is in agreement with the results of Tomassen et al. (2003) who found an effect of N addition on *M. caerulea* biomass only after 3 years of N input. In addition, the different forms of N dissolved in peat water were not affected by the N addition treatment (Table 1). However, N addition induced an increase in the concentration and stock of N in the living parts of *Sphagnum* (the first two layers of the peat mesocosms: 0–0.5 cm and 0.5–2.5 cm; Table 2, Fig. 2). Thus, the lack of a short-term effect of N fertilization on *M. caerulea* growth can be explained by the high capacity of *Sphagnum* mosses to retain N deposition (van Breemen, 1995). Indeed, *Sphagnum* species can capture the atmospheric N supply, limiting its availability for the surrounding vascular plants (van Breemen, 1995; Tomassen et al. 2003). Such a mechanism can have a long-term effect on OM decomposition. The N enrichment of living *Sphagnum* by increased N atmospheric deposition leads to a lower C:N ratio (Fig. 4). Such a change in peat stoichiometry could increase the decomposition rate of *Sphagnum* litters and in the long term, could negatively affect the C balance of *Sphagnum*-dominated peatlands (Aerts et al. 1992).

Despite the N retention by *Sphagnum* mosses, increasing NH₄NO₃ inputs enhances N₂O emissions under both plant communities (Fig. 1). When error terms are considered, the amount of N added in *Sphagnum* mesocosms (3.7 g N/m²) is recovered in the amount of N found in the combined N₂O emissions and N stocks in *Sphagnum* layers (4.0 g N/m² on average; Fig. 2). No other N output or stock is required to close the N balance. These results suggest that increased N₂O emissions may be generated by a stimulation of denitrification triggered by an increase in N availability (Hayden and Ross 2005; Francez et al. 2011). This stimulation is modulated by the vegetation.

4.2. Effect of *Molinia caerulea* on the N cycle

Vegetation composition was also found to impact N₂O emissions (Table 1) with lower N₂O emissions in the presence of *M. caerulea* (Fig. 1). The dissolved NO₃ concentration (Table 1) and the N content of living *Sphagnum* (Table S1) did not differ between *Sphagnum* and *Sphagnum* + *Molinia* mesocosms. Furthermore, the above-ground biomass production of *M. caerulea* was not stimulated by N addition (Table 1; Fig. 2). The combined increase in N₂O emissions and N stocks (2.9 gN/m²) in Fertilized mesocosms compared to the Control ones represents 80% of the N additions. The fraction of N lacking may have been either denitrified to N₂ (not possible to observe with our technique) or incorporated into the root biomass.

The competition between *M. caerulea*, a nitrophilous grass (Tomassen et al. 2004), and denitrifiers for mineral N could limit the substrate's availability for denitrification, leading to a reduction in N₂O emissions (Repo et al. 2009; Roobroeck et al. 2010). The utilization of N for biomass building by *M. caerulea* is supported by the reduction in dissolved NH₄⁺ concentration in presence of *M. caerulea*, as this plant can use NH₄⁺ as an N source (Troelstra et al. 1995). In any case, these results clearly

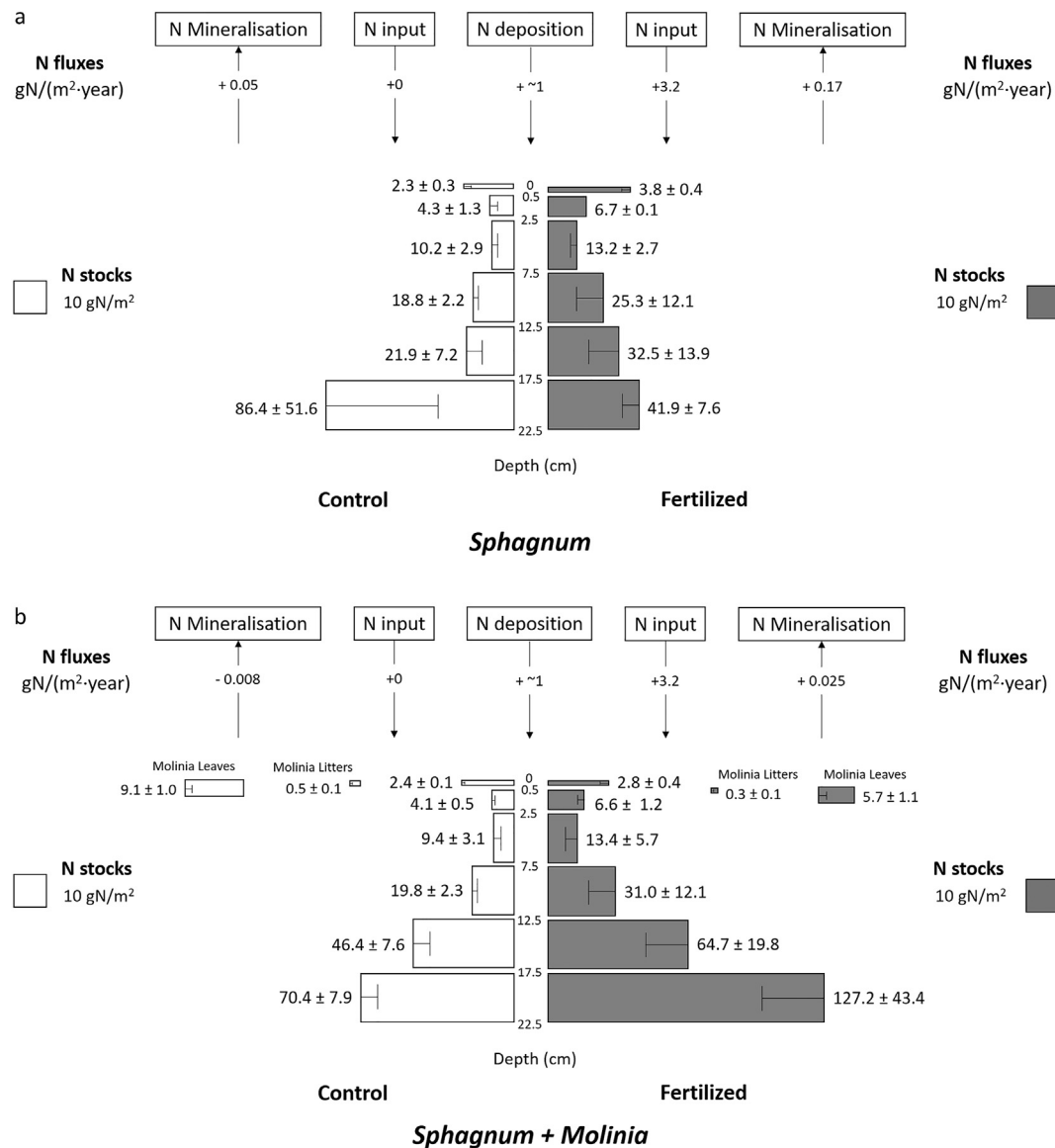


Fig. 2 – N stocks (g N/m²) and fluxes (black arrow, g N/(m²·year) in *Sphagnum* (a) and *Sphagnum* + *Molinia* mesocosms (b) with (Fertilized) or without (Control) NH₄NO₃ addition (±SE, n = 3) from July 2015 to June 2016. N deposition represents the rain N deposition, N input are the amount of NH₄NO₃ added and N Mineralization represents the quantity of N-N₂O emissions.

showed that the occurrence of *M. caerulea* modifies the C cycle either by increasing root biomass (with further modification of the C cycle) or by modulating the denitrifier microbial communities (from N₂O to N₂ emission), or both. Further studies should thus focus on the OM dynamics associated with the *M. caerulea* rhizosphere.

5. Conclusions

Increasing N deposition did not impact the C fluxes (CO₂, CH₄), [DOC], stocks or above-ground biomass of *M. caerulea* in this short-term experiment. This was due to the high capacity of *Sphagnum* mosses to intercept atmospheric N, limiting the N input effect. Despite the low N availability, NH₄NO₃ addition promoted N₂O emissions, which were also influenced by the

vegetation composition with the lowest emissions with *M. caerulea* occurrence. This modification in N₂O emissions probably results from an alteration of the denitrification activity linked to the availability of mineral N. Our results indicate that N deposition alters the N cycling in peatlands with also an important regulatory role of plant communities on C and also on N dynamics. Nonetheless, peatland ecosystem reactions to N deposition should be considered in the longer term, especially in peatlands with a *Sphagnum* layer N-saturated.

Acknowledgments

This paper is a contribution to the research conducted in the Labex VOLTAIRE (ANR-10-LABX-100-01). The authors gratefully acknowledge the financial support provided to the

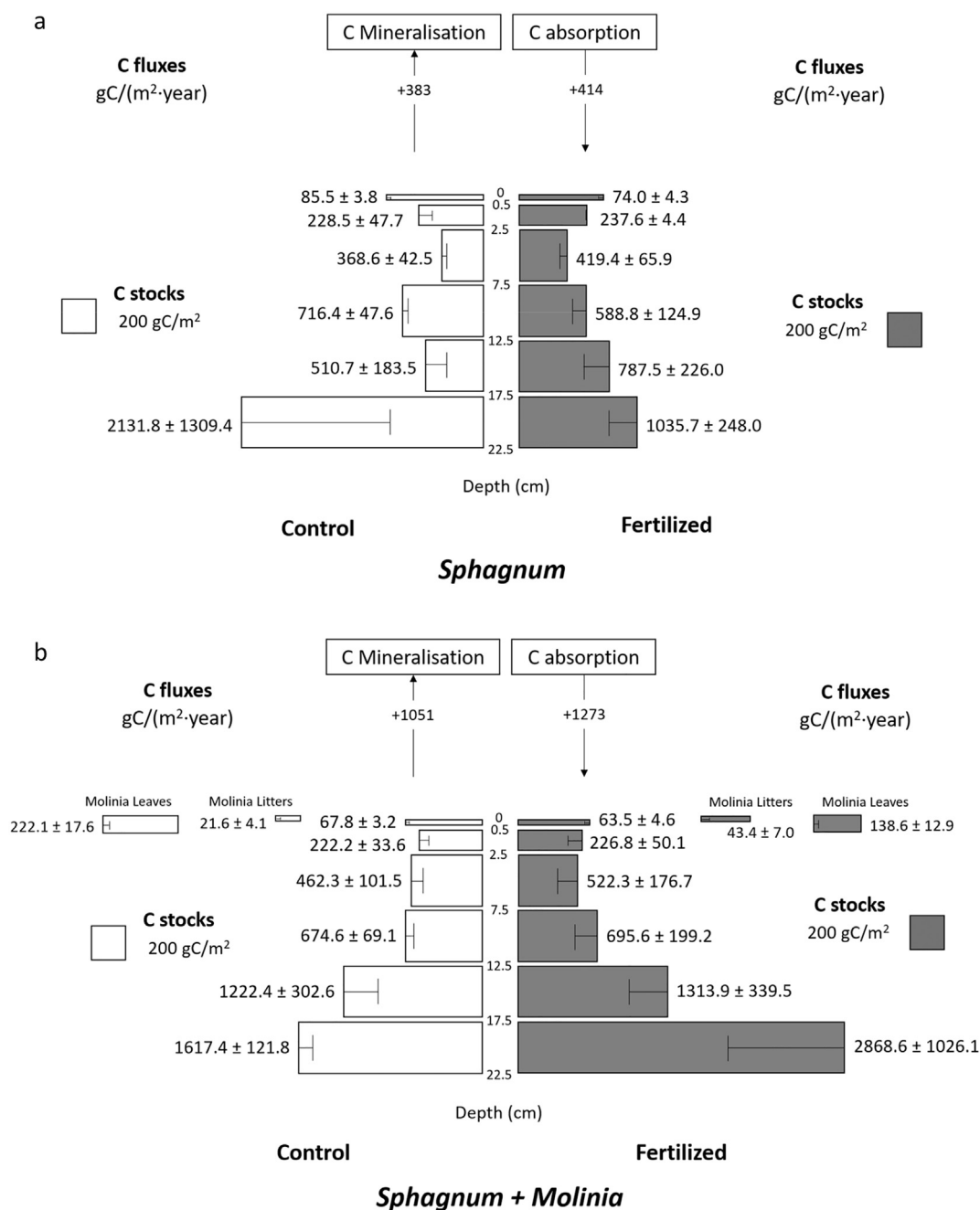


Fig. 3 – C stocks (per depth in g C/m²) and fluxes (black arrow, g C/(m²·year)) in *Sphagnum* (a) and *Sphagnum* + *Molinia* mesocosms (b) with (Fertilized) or without (Control) NH₄NO₃ addition (±SE, n = 3) from July 2015 to June 2016.

PIVOTS project by the Région Centre – Val de Loire: ARD 2020 program, CPER 2015 -2020 and the European Union who invests in Centre-Val de Loire with the European Regional Development Fund. This work is also supported by the AMIS (Fate and IMpact of Atmospheric PollutantS) project funded by the European Union, under the Marie Curie Actions IRSES (International Research Staff Exchange Scheme), within the Seventh Framework Programme FP7-PEOPLE-2011-IRSES. The authors would like to thank X. Yin, G. Belot, A. Mennequerre for their contribution to gas measurements, P. Jacquet and C.

Robert for providing assistance in SPIRIT maintenance, N. Lothier for DOC and TN analysis and A. Guirimand-Dufour for contribution to NO₃⁻ and NH₄⁺ analyses. We also thank E. Rowley-Jolivet for revision of the English version.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jes.2018.08.003>.

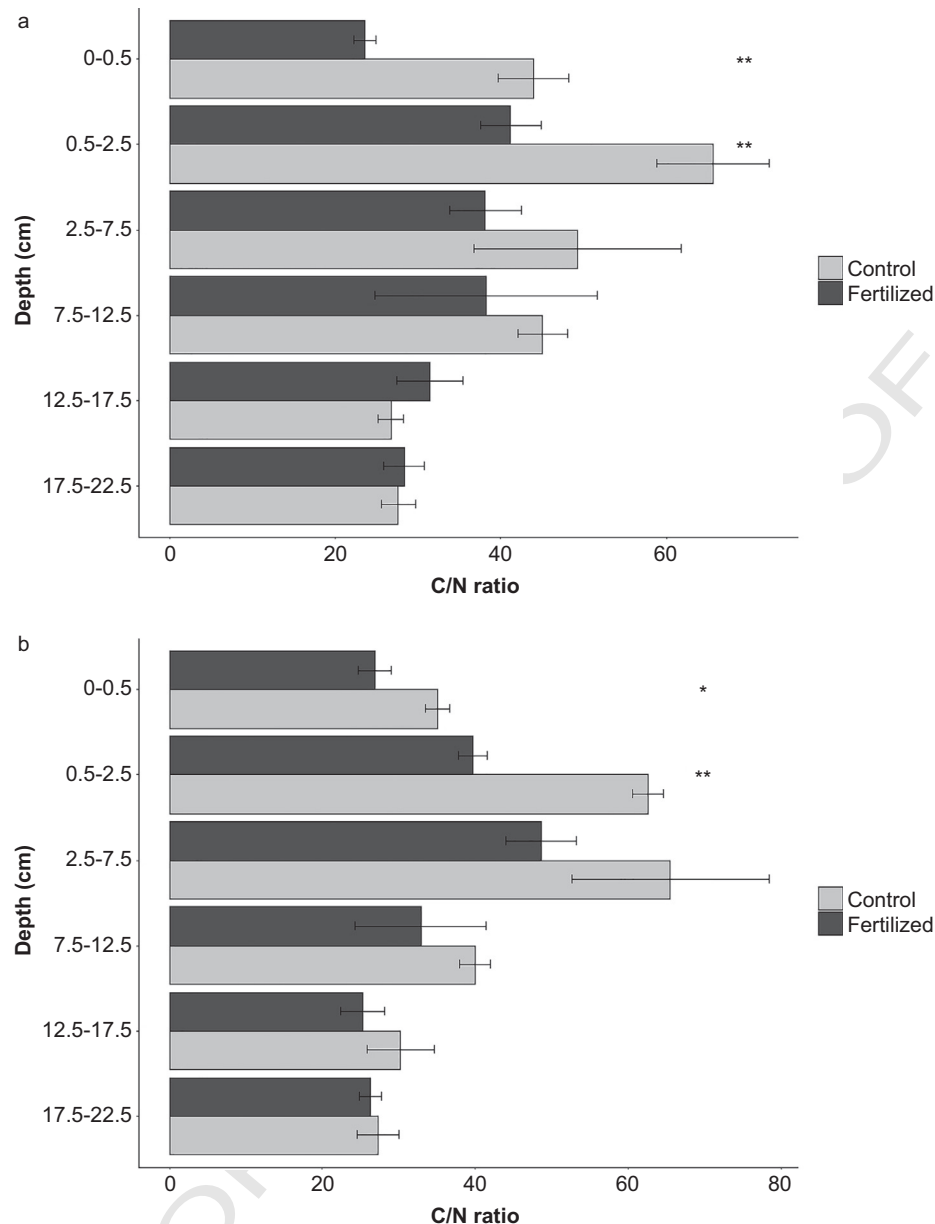


Fig. 4 – C/N ratio per layer in *Sphagnum* (a) and *Sphagnum* + *Molinia* mesocosms (b) with (Fertilized) or without (Control) NH_4NO_3 addition (\pm SE, $n = 3$). Significant differences per layer are expressed as – for $0.05 < p < 0.1$, * $p < 0.05$, ** $p < 0.01$, * $p < 0.001$.**

REFERENCES

- Aerts, R., Wallen, B., Malmer, N., 1992. Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. *J. Ecol.* 131–140.
- Bortoluzzi, E., Epron, D., Siegenthaler, A., Gilbert, D., Buttler, A., 2006. Carbon balance of a European mountain bog at contrasting stages of regeneration. *New Phytol.* 172 (4):708–718. <https://doi.org/10.1111/j.1469-8137.2006.01859.x>.
- Bragazza, L., Tahvanainen, T., Kutnar, L., Rydin, H., Limpens, J., Hájek, M., et al., 2004. Nutritional constraints in ombrotrophic *Sphagnum* plants under increasing atmospheric nitrogen deposition in Europe. *New Phytol.* 163 (3), 609–616.
- Bragazza, L., Freeman, C., Jones, T., Rydin, H., Limpens, J., Fenner, N., et al., 2006. Atmospheric nitrogen deposition promotes carbon loss from peat bogs. *Proc. Natl. Acad. Sci. U. S. A.* 103 (51), 19386–19389.
- D'Angelo, B., Gogo, S., Laggoun-Défarge, F., Le Moing, F., Jégou, F., Guimbaud, C., 2016. Soil temperature synchronisation improves representation of diel variability of ecosystem respiration in *Sphagnum* peatlands. *Agric. For. Meteorol.* 223, 95–102.
- Francez, A.J., Pinay, G., Josselin, N., Williams, B.L., 2011. Denitrification triggered by nitrogen addition in *Sphagnum magellanicum* peat. *Biogeochemistry* 106 (3), 435–441.
- Gogo, S., Laggoun-Défarge, F., Delarue, F., Lottier, N., 2011. Invasion of a *Sphagnum*-peatland by *Betula* spp and *Molinia caerulea* impacts organic matter biochemistry. Implications for carbon and nutrient cycling. *Biogeochemistry* 106 (1), 53–69.
- Gogo, S., Laggoun-Défarge, F., Merzouki, F., Mounier, S., Guirimand-Dufour, A., Jozja, N., et al., 2016. In situ and laboratory non-additive litter mixture effect on C dynamics of

- 442 *Sphagnum rubellum* and *Molinia caerulea* litters. J. Soils Sedi- 484
 443 ments 16 (1), 13–27. 485
- 444 Gorham, E., 1991. Northern peatlands: role in the carbon cycle and 486
 445 probable responses to climatic warming. Ecol. Appl. 1 (2), 487
 446 182–195. 488
- 447 Granath, G., Wiedermann, M.M., Strengbom, J., 2009. Physiological 489
 448 responses to nitrogen and sulphur addition and raised 490
 449 temperature in *Sphagnum balticum*. Oecol 161 (3), 481–490. 491
- 450 Guimbaud, C., Catoire, V., Gogo, S., Robert, C., Chartier, M., Laggoun- 492
 451 Défarge, F., et al., 2011. A portable infrared laser spectrometer for 493
 452 flux measurements of trace gases at the geosphere–atmosphere 494
 453 interface. Meas. Sci. Technol. 22 (7), 075601. 495
- 454 Gunnarsson, U., Boresjö Bronge, L., Rydin, H., Ohlson, M., 2008. 496
 455 Near-zero recent carbon accumulation in a bog with high 497
 456 nitrogen deposition in SW Sweden. Glob. Chang. Biol. 14 (9), 498
 457 2152–2165. 499
- 458 Hayden, M.J., Ross, D.S., 2005. Denitrification as a nitrogen 500
 459 removal mechanism in a Vermont peatland. J. Environ. Qual. 501
 460 34 (6), 2052–2061. 502
- 461 Holland, E.A., Dentener, F.J., Braswell, B.H., Sulzman, J.M., 1999. 503
 462 Contemporary and pre-industrial global reactive nitrogen 504
 463 budgets. Biogeochemistry 46 (1), 7–43. 505
- 464 Kandel, T.P., Elsgaard, L., Lærke, P.E., 2013. Measurement and 506
 465 modelling of CO₂ flux from a drained fen peatland cultivated 507
 466 with reed canary grass and spring barley. GCB Bioenergy 5 (5): 508
 467 548–561. <https://doi.org/10.1111/gcbb.12020>. 509
- 468 Lamarque, J.F., Kiehl, J.T., Brasseur, G.P., Butler, T., Cameron- 510
 469 Smith, P., Collins, W.D., et al., 2005. Assessing future nitrogen 511
 470 deposition and carbon cycle feedback using a multimodel 512
 471 approach: analysis of nitrogen deposition. J. Geophys. Res: 513
 472 Atmos. 110 (D19). 514
- 473 Leroy, F., Gogo, S., Guimbaud, C., Bernard-Jannin, L., Hu, Z., 515
 474 Laggoun-Défarge, F., 2017. Vegetation composition controls 516
 475 temperature sensitivity of CO₂ and CH₄ emissions and DOC 517
 476 concentration in peatlands. Soil Biol. Biochem. 107, 164–167. 518
- 477 Leroy, F., Gogo, S., Guimbaud, C., Bernard-Jannin, L., Yin, X., Belot, 519
 478 G., Shuguang, W., Laggoun-Défarge, F., In prep Carbon balance 520
 479 and global warming potential modifications in *Sphagnum*- 521
 480 dominated peat mesocosms invaded by *Molinia caerulea*. 522
 481 Submitted to Biogeosciences. 523
- 482 Limpens, J., Granath, G., Gunnarsson, U., Aerts, R., Bayley, S., 524
 483 Bragazza, L., et al., 2011. Climatic modifiers of the response to 525
 nitrogen deposition in peat-forming *Sphagnum* mosses: a 526
 meta-analysis. New Phytol. 191 (2), 496–507.
- Nykänen, H., Vasander, H., Huttunen, J.T., Martikainen, P.J., 2002. 486
 Effect of experimental nitrogen load on methane and nitrous 487
 oxide fluxes on ombrotrophic boreal peatland. Plant Soil 242 488
 (1), 147–155. 489
- Repo, M.E., Susiluoto, S., Lind, S.E., Jokinen, S., Elsakov, V., Biasi, C., 490
 et al., 2009. Large N₂O emissions from cryoturbated peat soil in 491
 tundra. Nat. Geosci. 2 (3), 189–192. 492
- Roobroeck, D., Butterbach-Bahl, K., Brüeggemann, N., Boeckx, P., 493
 2010. Dinitrogen and nitrous oxide exchanges from an 494
 undrained monolith fen: short-term responses following 495
 nitrate addition. Eur. J. Soil Sci. 61 (5), 662–670. 496
- Tomassen, H., Smolders, A.J., Lamers, L.P., Roelofs, J.G., 2003. 497
 Stimulated growth of *Betula pubescens* and *Molinia caerulea* on 498
 ombrotrophic bogs: role of high levels of atmospheric nitrogen 499
 deposition. J. Ecol. 91 (3), 357–370. 500
- Tomassen, H., Smolders, A.J., Limpens, J., Lamers, L.P., Roelofs, J. 501
 G., 2004. Expansion of invasive species on ombrotrophic bogs: 502
 desiccation or high N deposition? J. Appl. Ecol. 41 (1), 139–150. 503
- Troelstra, S.R., Wagenaar, R., Smant, W., 1995. Nitrogen utilization 504
 by plant species from acid heathland soils: I. Comparison 505
 between nitrate and ammonium nutrition at constant low pH 506
 1. J. Exp. Bot. 1103–1112. 507
- Turetsky, M.R., Bond-Lamberty, B., Euskirchen, E., Talbot, J., 508
 Frolking, S., McGuire, A.D., et al., 2012. The resilience and 509
 functional role of moss in boreal and arctic ecosystems. New 510
 Phytol. 196 (1), 49–67. 511
- Turunen, J., Tomppo, E., Tolonen, K., Reinikainen, A., 2002. 512
 Estimating carbon accumulation rates of undrained mires in 513
 Finland—application to boreal and subarctic regions. The 514
 Holocene 12 (1), 69–80. 515
- Van Breemen, N., 1995. How *Sphagnum* bogs down other plants. 516
 Trends Ecol. Evol. 10 (7), 270–275. 517
- Ward, S.E., Ostle, N.J., Oakley, S., Quirk, H., Henrys, P.A., Bardgett, 518
 R.D., 2013. Warming effects on greenhouse gas fluxes in 519
 peatlands are modulated by vegetation composition. Ecol. Lett. 520
 16 (10), 1285–1293. 521
- Wu, Y., Blodau, C., Moore, T.R., Bubier, J., Juutinen, S., Larmola, T., 522
 2015. Effects of experimental nitrogen deposition on peatland 523
 carbon pools and fluxes: a modelling analysis. Biogeosciences 524
 12 (1), 79–101. 525