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Factors controlling nitrous oxide emissions from managed northern peat soils with low carbon to nitrogen ratio

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ABSTRACT

Managed northern peatlands are an important source of the strong greenhouse gas nitrous oxide (N_2O). However, N_2O emissions from these managed peatlands display a high spatial variability, and processes governing N_2O production and emissions from these ecosystems are still not well understood. To constrain the factors regulating N_2O emissions from managed northern peat soils, we determined a wide set of soil physical and chemical properties of peatlands with different management histories spread across Finland, Sweden and Iceland. We included eleven peatland sites with available *in situ* N_2O flux data, and complemented our analyses with detailed measurements of soil nitrogen (N) cycling processes such as N_2O production, gross N mineralization and gross nitrification and, in addition, soil microbial biomass. This study included drained peatlands with different land-use types and management intensities, comprising forested, cultivated or only drained peatlands and afforested or abandoned agricultural peatlands. All selected peatland sites displayed a low soil carbon to nitrogen (C/N) ratio of 15–27, traditionally used to predict high N_2O emissions. Despite the narrow C/N range, the N_2O emissions at our sites varied greatly within and between land-use groups, ranging from 0.03 to 2.38 g N m^{-2} y^{-1}. Thus, our findings provide valuable insights into the regulatory factors underlying the variability in N_2O emissions and show that a low C/N ratio in managed peatlands cannot be used to predict high N_2O emissions. Instead, our results demonstrate that higher N_2O emissions are linked to higher peat phosphorus (P) and copper (Cu) content, suggesting that low P and Cu concentrations can limit N_2O production in peat even with sufficient N availability. While known factors such as soil moisture, oxygen content and the degree of peat humification partially explained the variability in N_2O emissions, this study directly links soil P and Cu availability to N_2O production processes. The availability of P and especially Cu seemed to promote nitrification activities, thereby increasing N_2O production. Our study highlights the link between N_2O emissions and soil P and Cu availability and the strong coupling of the soil N and P cycles in peatlands, which is to date severely understudied.

1. Introduction

Nitrous oxide (N_2O), carbon dioxide (CO_2) and methane (CH_4) are important greenhouse gases. The global warming potential of N_2O is 265 times greater than that of CO_2 and almost ten times greater than that of CH_4 (100-year time horizon; Myhre et al., 2013). With increasing application of nitrogen (N) fertilizers, the tropospheric N_2O concentration is rising (Canfield et al., 2010; Davidson, 2012; Vitousek et al., 1997). While N_2O is stable in the troposphere, in the stratosphere N_2O participates in reactions destroying the ozone layer (Ravishankara et al., 2009). The main natural N_2O sources are terrestrial ecosystems where N_2O is produced by soil microbial processes. From all anthropogenic N_2O sources, including biomass burning and fossil fuels, agriculture is the most important (Fowler et al., 2009). Anthropogenic N_2O emissions contribute with 30–45% to the total N_2O emissions (IPCC, 2013), and over 80% of the anthropogenic emissions are derived from agriculture (Davidson, 2012).

Peatlands cover only 3% of the Earth's surface, but they store one third of the global organic carbon pool (Köchy et al., 2015; Strack, 2008). Among managed Northern soils, drained peatlands are one of

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Table 1
The study sites and their soil characteristics: degree of peat humification (*H*), C/N ratio, N_2O flux, water table level (WT), field bulk density (BD) and soil phosphorus (P) concentration. L1 refers to the surface layer of 0–10 cm and L2 to the deeper layer of 10–20 cm. The first letter of the site code refers to land-use type: F = forest, C = cultivated, A = afforested field, D = drained but not used for agriculture or forestry, B = abandoned field. The letter in subscript defines the site. The N_2O values are annual averages and in all cases ± denotes standard deviation.

Land-use	Site	Location	Country	Soil sampling	*H**		C/N ratio		N_2O flux	WT	BD	P (mg kg^{-1})	
					L1	L2	L1	L2	(g N m^{-2} y^{-1})	(cm)	0-20 cm	L1	L2
Forests	F_S	63°54′N, 23°56′E	Finland	18/06/2012	7–8	8	23 ± 0.0	22 ± 0.4	1.43 ± 0.59[a]	−41[a]	0.20[a]	943	1260
	F_J	63°52′N, 23°44′E	Finland	18/07/2011	6–7	7–8	19 ± 0.1	18 ± 0.1	0.07 ± 0.03[a]	−36[a]	0.17[a]	861	1340
Cultivated fields	C_S	63°54′N, 23°56′E	Finland	22/09/2011	8–9	8–9	17 ± 0.0	17 ± 0.0	2.38 ± 1.49[b]	−60[b]	0.22[b]	3280	3060
	C_I	64°34′N, 21°46′W	Iceland	12/07/2011	7–8	7–8	15 ± 0.1	16 ± 0.1	0.03[c]		0.23[g]	1660	964
	C_K	60°54′N, 23°31′E	Finland	23/04/2012	9	9	23 ± 0.2	22 ± 0.1	0.73 ± 0.12[d]	−82[d]	0.48[h]	1470	1560
Afforested fields	A_L	64°06′N, 24°21′E	Finland	23/08/2011	7	7–8	17 ± 0.1	18 ± 0.2	2.14 ± 0.60[e]	−52[e]	0.25[e]	2870	1760
	A_R	64°06′N, 24°21′E	Finland	23/08/2011	8–9	8–9	24 ± 0.2	27 ± 0.1	0.07 ± 0.07[e]	−25[e]	0.25[e]	1640	1190
	A_G	58°23′N, 12°09′E	Sweden	09/05/2011	7–8	9–10	25 ± 0.2	27 ± 0.0	0.26 ± 0.08[f]	−80[f]	0.20[i]	1000	862
Drained	D_I	64°34′N, 21°46′W	Iceland	12/07/2011	5–6	6–7	15 ± 0.0	16 ± 0.1	0.04[c]		0.34[g]	956	801
Abandoned fields	B_A	63°54′N, 23°56′E	Finland	25/04/2012	8–9	8–9	20 ± 0.2	23 ± 0.0	0.41 ± 0.17[e]	−35[e]	0.30[e]	1460	1270
	B_B	63°54′N, 23°56′E	Finland	25/04/2012	9–10	9–10	25 ± 0.5	26 ± 1.3	1.42 ± 0.68[e]	−51[e]	0.42[e]	944	1010

* Degree of humification was estimated according to von Post (1922).
[a]Maljanen et al. (2014), [b]Maljanen et al. (2009), [c]Maljanen et al. (2010a,b), [d]Regina et al. (2004), [e]Maljanen et al. (2012), [f]Klemedtsson et al. (2010), [g]Hlynur Óskarsson; personal communication, [h]Lohila et al. (2003), [i]Björk et al. (2010).

the largest emitters of N_2O (Maljanen et al., 2010a) due to their high N stocks and high N mineralization rates, which are the key for the high N_2O production in these soils (Strack, 2008). In the Northern latitudes, most of the peatlands are located in Russia, Canada, USA and the Nordic countries of Europe. Agricultural use, forestry, and peat extraction require drainage of peatlands, but the extent of drainage varies. In most countries agriculture is the main use of peatlands (Strack, 2008). In Finland, however, only 1% of peatlands are currently used for agriculture (Myllys and Sinkkonen, 2004), whereas over half of the peatlands have been drained for forestry (Strack, 2008).

Nitrous oxide is produced by soil microbial processes, especially during nitrification and denitrification (Butterbach-Bahl et al., 2013). During ammonium oxidation N_2O can be produced through two pathways, either as a by-product in the first step of nitrification or during nitrifier denitrification (De Boer and Kowalchuk, 2001; Wrage et al., 2001). During denitrification, nitrate (NO_3^-) is reduced to N_2O by facultative anaerobic bacteria, which can be further reduced to N_2, depending on the environmental conditions such as pH (Šimek and Cooper, 2002) and oxygen (O_2) status (Khalil et al., 2004). Although nitrification and denitrification are the main known processes for N_2O production in soils, other less well studied processes can also produce N_2O in soils (Butterbach-Bahl et al., 2013).

Natural peatlands display negligible N_2O emissions and can even act as net sinks for N_2O. After drainage, however, when the peat is exposed to O_2, N_2O emissions can increase strongly (Martikainen et al., 1993; Regina et al., 1996). Exposure to O_2 accelerates organic matter (OM) decomposition and N mineralization, as well as nitrification. After drainage, the increase in N_2O emissions is higher in nutrient rich than in nutrient poor peatlands. Cultivated peat soils, which are generally rich in nutrients due to fertilization, show the highest N_2O emissions among drained peatlands (Kasimir-Klemedtsson et al., 1997; Maljanen et al., 2010a). Although only 10% (250 000 ha) of the total cropland area in Finland is on peat soils, N_2O emissions from cultivated peat soils account for 43% of N_2O emissions from agricultural soils (Statistics Finland, 2017). Nitrous oxide emissions from cultivated peatlands are generally 5–20 times higher than those from peatland forests (Martikainen et al., 1993; Kasimir-Klemedtsson et al., 1997). Yet, while N_2O emissions from peatland forests are often negligible (Ojanen et al., 2010), some peatland forests display N_2O emissions that are nearly as high as those from cultivated peat soils (Maljanen et al., 2010a, 2010b).

Drainage and associated lowering of the water table is a key factor enhancing N_2O emissions from peatlands (Martikainen et al., 1993). Therefore, regulating the water table level in managed peatlands is suggested to be the most efficient way to mitigate N_2O emissions (e.g. Regina et al., 2015). The soil C/N ratio is often used to predict the magnitude of N_2O emissions, which are generally highest in drained peatlands with a low (< 30) C/N ratio (Klemedtsson et al., 2005; Leppelt et al., 2014; Maljanen et al., 2010a). In drained peatland forests N_2O emissions have been shown to decrease straightforwardly with increasing C/N ratio (Klemedtsson et al., 2005). However, over the wide variety of land-use types and management practices in northern peatlands and other organic soils, N_2O emissions display a high spatial and temporal variability (Leppelt et al., 2014; Maljanen et al., 2010a; Tiemeyer et al., 2016): even within the narrow C/N range of 15–30, which is considered the optimum range for high N_2O production and emissions, N_2O fluxes vary greatly.

The aim of this study was to identify factors explaining the high variability in N_2O fluxes from managed northern peatlands within this narrow C/N range, where N_2O production is clearly not limited by N availability. We selected eleven sites with available year-round *in situ* N_2O flux data and a low (< 27) C/N ratio. The selected sites were managed peatlands under different land-use, and were spread across Finland, Sweden and Iceland. We determined a wide set of peat physical-chemical characteristics, including trace elements and macronutrients, for two soil layers, 0–10 and 10–20 cm, of each site. We complemented these soil analyses with a detailed array of process-based measurements related to N-cycling, including N_2O production (both layers), gross N mineralization (10–20 cm) and gross nitrification (10–20 cm), as well as soil microbial biomass C (10–20 cm). The aim of our study was to investigate whether these soil physical, chemical, and biological parameters provide new insights for predicting N_2O emissions from managed peatlands that cannot be fully explained by the C/N ratio.

2. Materials and methods

2.1. Study sites

The site selection was based on the data availability of annual N_2O emissions, including wintertime emissions, since a major part of the

annual N_2O emissions can occur during wintertime (Maljanen et al., 2010b). In addition, chosen sites had a peat C/N ratio of 15–30 – the optimum range for N_2O emissions (Klemedtsson et al., 2005). Soil samples were collected from eleven drained peatland sites with various land-use practices (Table 1): a) two forested (F) peat soils in Finland (F_S, F_J); b) three cultivated (C) peat soils, two in Finland (C_S, C_K) and one in Iceland (C_I); c) three afforested (A) fields, two in Finland (A_L, A_R) and one site in Sweden (A_G); d) one drained (D) site in Iceland not used for agriculture or forestry (D_I) and e) two abandoned (B) fields in Finland (B_A, B_B). The subscript in the codes identifies the study site. More detailed information on drainages, peat depths and dominant tree and understory plant species can be found in Table S1.

Soil samples from the sites (Table 1) were taken at two depths (0–10 and 10–20 cm). Except for the particle density, all physical and chemical analyses were determined for both soil layers. Process-based measurements (gross N mineralization, gross nitrification, soil microbial biomass C) were limited to the deeper soil layer.

2.2. Soil physical and chemical properties

Soils were homogenized manually and large, visible roots were removed. The degree of humification (*H*) was determined using the von Post (1922) approach. Soil gravimetric water content (GWC) was determined by drying soils at +65 °C for 24 h. Soil pH_{H2O} and electrical conductivity (EC) were measured from milli-Q-H_2O-soil slurry (1:2 v/v) with pH (WTW pH 240) and EC (Fennolab) meters, respectively. The soil organic matter content (OM) was determined by loss on ignition at 550 °C. Nitrate (NO_3^-) and nitrite (NO_2^-) concentrations were analyzed from water extracts with an ion chromatograph (DX 120, Dionex Corporation, USA), and ammonium (NH_4^+) concentrations were measured from 1 M KCl extracts with a spectrophotometer (Ultrospec 3000 Pro, Biochrom, UK). Analyses of NO_3^-, NO_2^- and NH_4^+ are described in more detail by Liimatainen et al. (2014). Dissolved organic carbon (DOC) was extracted using 0.25 M K_2SO_4 and analyzed with a TOC analyzer (Shimadzu TOC Vcph, Shimadzu Scientific, Japan). The soil C and N content as well as the soil $\delta^{15}N$ and $\delta^{13}C$ isotopic signatures were analyzed with an isotope ratio mass spectrometer (IRMS Thermo Finningan Advantage, Germany) coupled to an elemental analyzer (Flash EA 1112, Italy) in University of Jyväskylä, Finland. A certified birch leaf standard (Elemental Microanalysis, UK) was used as a reference in C, N, $\delta^{15}N$ and $\delta^{13}C$ analyses. The total concentration of trace elements and macronutrients (Al, B, Ca, Cd, Cr, Cu, Fe, K, Na, Ni, Mg, Mn, P, Pb, S, Zn) were analyzed with nitric acid/hydrogen peroxide (HNO_3/H_2O_2) extraction combined with microwave digestion. Extracts were analyzed with inductively coupled plasma atomic emission spectroscopy (ICP-AES) (Table S2).

Bulk density values listed in Table 1 were determined in the field from intact soil cores. Because we conducted laboratory experiments using homogenized soil, we determined the bulk density also for homogenized peat in the laboratory. Soil particle density (n = 5) was determined by boiling dried and ground soil in pycnometers with milli-Q-H_2O to get rid of O_2. Soil particle density (PD) was calculated using water density, soil dry weight and mass and volume of the pycnometer. From PD and BD we calculated total porosity (TP) of the soil. Further, water filled pore space (WFPS) was calculated based on the volumetric water content, PD and BD.

2.3. Soil microbial biomass

To determine the soil microbial biomass C (MBC), we applied the substrate induced respiration (SIR) method (Anderson and Domsch, 1978). For this purpose, the moisture was adjusted to 60% of the maximum water holding capacity (WHC). Soils having a water content of > 60% WHC were dried at room temperature to achieve a moisture content close to the desired 60% WHC. The amount of glucose needed to achieve the maximum respiration was determined separately for each soil. Fresh soil that equals a dry weight of 2 g was weighed into 550 ml flasks in 5 replicates. After addition of the glucose solution, the WHC of the soil was 60%. Flasks were kept open for 30 min, aerated with a fan for 1 min and then closed with a septum and a screw cap. Laboratory air was added to create an overpressure allowing gas sampling. Soils were incubated at room temperature for 165 min and gas samples were taken four times during the incubation from the headspace using a 60 ml polypropylene syringe. Gas samples were immediately injected into pre-evacuated 12 ml glass vials (Labco, Exetainer®) and the CO_2 concentration was analyzed on the same day with a gas chromatograph (GC, Agilent 6890N Network GC System, Agilent Technologies, USA). The MBC results were calculated from the respiration rates using the formula by Anderson and Domsch (1978).

2.4. Gross N mineralization and nitrification rates

Gross N mineralization rates were determined once during one growing season. A pool dilution method (Kirkham and Bartholomew, 1954, 1955) was used to study the gross N mineralization rate as described by Marushchak et al. (2011). Fresh homogenized and sieved soils (n = 6) that were pre-incubated at +15 °C for one week were weighed (2.5 g_{fw}) into 50 ml plastic tubes (Sarstedt, non-pyrogenic tube, PP, Germany). The labeled $(^{15}NH_4)_2SO_4$ (98 at-%) soil was incubated for 4 h and 24 h at +15 °C. After incubation, the samples were extracted with 2 M KCl. From these extracts, NH_4^+ was analyzed with a spectrophotometer as described above. Gross nitrification rates were studied similarly as gross N mineralization, but $K^{15}NO_3$ (60 at-%), was added as a label. From these extracts NO_3^- was analyzed with an ion chromatograph as described above. In both experiments, gross N mineralization and nitrification, on average 300 µl of ^{15}N labeled solution with a concentration of 0.25 µmol l^{-1} was added to the soil samples.

The microdiffusion method (Brooks et al., 1989) was applied to determine the isotopic ratio $^{15}N/^{14}N$ in NH_4^+ and NO_3^-. For the determination of gross N mineralization, 0.1 g of MgO was added to the flasks and at the same time one acid trap made according to Marushchak et al. (2011) was placed into each flask. The flasks were closed with a septum and screw cap and kept in a heated shaker (+35 °C, 150 rpm) for 5 days. During the shaking of these alkaline extracts, acidic filter papers trapped the released ammonia (NH_3). The filter papers from these acid traps were subsequently placed into a desiccator where they were dried in sulphuric acid (H_2SO_4) atmosphere before transferring them to tin cups for further analyses. The $^{15}N/^{14}N$ analyses were done at the University of Eastern Finland, Kuopio, using an isotope ratio mass spectrometer (IRMS, Thermo Finnigan Flash DELTA XP_{plus}, San Jose, CA, USA) coupled to an elemental analyzer (Thermo Finnigan Flash EA 1112 series) and open split interface (Thermo Finnigan Conflow III) (Marushchak et al., 2011).

The microdiffusion method was used also for gross nitrification samples. First, 8–10 ml of extracts, the corresponding volume of 4 M KCl, as well as 0.1 g of MgO were added into 150 ml flasks. The flasks were kept open during 4 h of shaking, after which an acid trap and 0.5 g of Devarda's alloy were added, and the flasks were closed. Flasks were incubated similarly as the flasks for the gross N mineralization in a heated shaker. Corrections taking into account the background and different amounts of N in the samples were made using blanks (same procedure as with samples but without soil extracts or ^{15}N labeling), and drift correction was applied using standards with known mineral N concentrations.

2.5. Nitrous oxide production in soil incubations

Nitrous oxide production was studied with incubation experiments according to Liimatainen et al. (2014) using field moist soil, with an exception of the Icelandic soils (C_I and D_I). These soils were rather dry and their moisture was adjusted to 60% of the maximum WHC before incubation experiments. Soil samples were weighed into 550 ml glass

Table 2
Mean content (± SD) of soil organic matter (OM), dissolved organic carbon (DOC), gravimetric water content (GWC), maximum water holding capacity (Max. WHC), and water-filled pore space (WFPS). The WFPS was calculated for homogenized soil samples using laboratory bulk density values and it described the WFPS when the soil samples were collected. L1 refers to the surface layer of 0–10 cm and L2 to the deeper layer of 10–20 cm. The site code refers to land-use type: F = forest, C = cultivated, A = afforested field, D = drained, B = abandoned field and the subscript defines the site (see Table 1).

Site	OM (%)		DOC (mg C gdw^{-1})		GWC (g H2O gdw^{-1})		Max. WHC (g H2O gdw^{-1})		WFPS (%)	
	L1	L2	L1	L2	L1	L2	L1	L2	L1	L2
F_S	95 ± 0.1	96 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	2.6 ± 0.1	3.5 ± 0.1	5.8 ± 0.4	5.8 ± 0.1	31	42
F_J	90 ± 0.2	93 ± 0.1	2.0 ± 0.3	0.6 ± 0.1	4.0 ± 0.1	3.8 ± 0.0	7.8 ± 0.0	8.3 ± 0.1	37	37
C_S	87 ± 0.2	86 ± 0.6	0.7 ± 0.1	0.5 ± 0.0	3.8 ± 0.0	2.7 ± 0.2	5.0 ± 0.2	4.4 ± 0.1	95	50
C_I	49 ± 0.7	64 ± 0.2	0.5 ± 0.1	0.7 ± 0.1	1.9 ± 1.0	1.9 ± 0.6	5.5 ± 0.2	5.4 ± 0.0	25	42
C_K	50 ± 1.6	49 ± 0.5	0.2 ± 0.0	0.2 ± 0.0	1.2 ± 0.0	1.1 ± 0.0	1.8 ± 0.0	1.8 ± 0.0	36	36
A_L	82 ± 0.3	89 ± 0.0	0.3 ± 0.0	0.5 ± 0.1	2.3 ± 0.0	3.0 ± 0.1	4.3 ± 0.1	5.4 ± 0.0	35	38
A_R	60 ± 1.8	41 ± 3.9	0.2 ± 0.0	0.1 ± 0.0	1.7 ± 0.0	1.3 ± 0.1	3.0 ± 0.1	2.1 ± 0.1	38	36
A_G	91 ± 0.9	92 ± 0.9	0.3 ± 0.1	0.2 ± 0.0	1.8 ± 0.0	2.2 ± 0.1	4.6 ± 0.1	5.0 ± 0.6	23	37
D_I	52 ± 0.4	57 ± 0.5	0.4 ± 0.1	0.3 ± 0.0	1.1 ± 0.8	1.6 ± 0.3	3.1 ± 0.0	3.9 ± 0.1	28	46
B_A	51 ± 0.3	48 ± 0.5	0.5 ± 0.0	0.3 ± 0.0	2.7 ± 0.1	2.0 ± 0.0	3.3 ± 0.8	2.3 ± 0.1	92	91
B_B	37 ± 1.6	57 ± 0.9	0.3 ± 0.0	0.2 ± 0.0	1.6 ± 0.0	2.4 ± 0.2	2.4 ± 0.2	3.7 ± 0.0	89	46

flasks and incubated in the dark at +15 °C for two weeks. During this two-week incubation, gas sampling was performed twice; in the beginning of the experiment, and 2 weeks after starting the experiment, at the end of the incubation. During the measurement of N_2O production, gas samples were taken 4 times (at 1, 2, 4 and 6 h time points). To measure the N_2O production, the flasks were first aerated for 1 min and then closed with rubber septa and screw cap. Room air was added into the flasks to achieve overpressure, allowing gas sampling. Nitrous oxide sampled from the headspace of the flasks was analyzed via GC (Agilent 6890N Network GC System, Agilent Technologies, USA) equipped with an electron capture detector and using an autosampler (Gilson 222XL, Gilson Company Inc., USA), as described by Maljanen et al. (2014). We use the term 'N_2O emissions' when referring to N_2O fluxes measured *in situ*, and 'N_2O production' when referring to the N_2O production rate measured from soil samples in the laboratory. At the end of the incubation, soil pH, EC and concentrations of NO_3^-, NO_2^-, NH_4^+ and DOC were determined as described above, to follow their concentration changes during the 2-week incubation experiment.

2.6. Statistics

We used bulk density (BD) values determined in the laboratory (data not shown) for all subsequent calculations and correlation analyses, since *in situ* BD data (Table 1) was not available for both soil layers. This approach was reasonable since these two values matched well.

Statistical analyses were performed with IBM Statistics software version 21. Kolmogorov-Smirnov and Shapiro-Wilk tests were used to test for normal distribution of data. For soil MBC, N_2O production rates, isotopic composition of bulk soil ($\delta^{15}N$ and $\delta^{13}C$), gross N mineralization and nitrification, the data was not normally distributed. Therefore, we applied the non-parametric Kruskal-Wallis test for independent samples. Correlations between the N_2O flux and soil characteristics were calculated using the non-parametric two-tailed Spearman rank bivariate correlation test, separately for the 0–10 cm soil layer (Table S3) and the 10–20 cm soil layer (Table S4).

Significances are shown as *** when $p < 0.001$, ** when $p < 0.01$ and * when $p < 0.05$.

In addition to correlation analyses, we applied principal component analysis (PCA) for this multidimensional data set using packages FactoMineR (Lê et al., 2008) and factoextra (Kassambara and Mundt, 2016) in R version 3.2.2 (R Core Team, 2015). The variables included in the PCA were standardized to unit variance. Variables not complying with assumptions for normal distribution due to obvious occurrence of outliers were log-normalized prior to PCA. Variables with low explanatory power (loadings, Table S5) for the first three components were excluded from the analysis, unless they were presumed to be essential in explaining the variation in N_2O fluxes. Gross nitrification, gross N mineralization, MBC and TP were included only for the PCA of the 10–20 cm dataset, as these variables were not determined for the 0–10 cm peat layer. To identify the most important variables explaining the variation in N_2O production and emissions, we applied linear regression models using stepwise forward selection of predictor variables based on the AIC (Akaike Information Criterion) (R package MASS; Venables and Ripley, 2002), and tested for multicollinearity of predictor variables in the final model by computing variance inflation factors (VIFs). Additionally, we determined measures of relative importance of predictor variables using R package relaimpo (Grömping, 2006).

3. Results

3.1. Soil physical and chemical properties

Basic soil physical and chemical properties are shown in Tables 1 and 2. The peat humification varied from 5 to 10 in the von Post scale (Table 1) and WFPS ranged from 23 to 95% (Table 2). The OM content of peat was between 41 and 96% among study sites (Table 2). DOC concentrations were rather similar between the study sites (0.1–0.7 mg C g_{dw}^{-1}) with an exception of one forested site (F_J), where DOC concentrations were more than twice as high (2.0 mg C g_{dw}^{-1}) as in other sites.

The cultivated C_K soil displayed the highest and the forest soils (F_S, F_J) the lowest nutrient contents (Table S2). The highest P content occurred at site C_S and the lowest in the Icelandic D_I soil (10–20 cm; Table S2). In the surface layer (0–10 cm) the P content was lowest in forested peat soils (F_S, F_J) as well as in the abandoned field (B_B) and Icelandic site (D_I), the latter being only drained without cultivation or forestry use (ranging from 861 to 956 mg P kg^{-1}). In both soil layers, the concentration of Cu was highest in the C_S soil, intermediate in C_I, D_I and C_K soils and low in all other soils (Table S2). The Icelandic soils (C_I, D_I) had a high sodium content compared to other soils.

Soil pH varied from 3.62 to 5.84, being similar in both soil layers. The EC varied between 21 and 106 µS cm^{-1} in the surface soil layer and between 36 and 195 µS cm^{-1} in the deeper soil layer of 10–20 cm with no clear trend relating to land-use type (Table S6). The NO_3^- content ranged from below detection limit to 49 µg NO_3-N g_{dw}^{-1} whereas the NH_4^+ concentration was between 2 and 108 µg NH_4-N g_{dw}^{-1} in both soil layers (Table S6). The site F_S had the highest NO_2^- concentration in the soil, 6.92 (± 1.98) µg NO_2-N g_{dw}^{-1} in the surface soil and 5.24 (± 0.28) µg g^{-1} in the deeper soil layer, respectively. In other sites soil NO_2^- concentrations were negligible (data not shown).

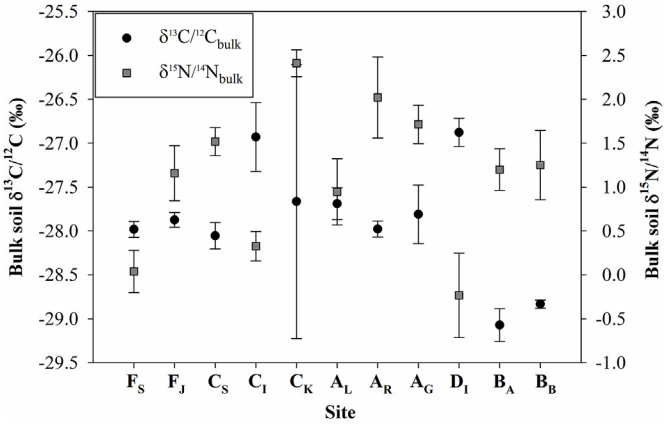

Fig. 1. Isotopic composition (± SD) of N and C for the peat layer of 0–20 cm of the sites. The left y-axis shows the bulk soil $\delta^{13}C$ (black circles) and the right y-axis the bulk soil $\delta^{15}N$ (grey squares). n = 4 except for BB where n = 3.

The $\delta^{15}N$ and $\delta^{13}C$ values in bulk peat were similar in both soil layers (0–10 cm and 10–20 cm). Therefore, the mean isotopic compositions were calculated for the two layers. The peat at the cultivated C_K site was the most enriched in ^{15}N whereas in the forest site F_S and Icelandic sites C_I and D_I the soils were the most depleted (Fig. 1). In contrast, the C_I and D_I soils were the most enriched in ^{13}C and the abandoned fields B_A and B_B soils the most depleted in ^{13}C (Fig. 1). The isotopic $\delta^{15}N$ value of the soil correlated positively with the degree of peat humification. This trend was stronger in the in the deeper ($p < 0.01$) than in the surface peat layer ($p < 0.05$).

3.2. Microbial biomass C

Microbial biomass C (MBC) was highest in the cultivated C_S soil, 1945 (± 346) μg C g_{dw}^{-1} (Fig. 2). Clearly the lowest MBC among all sites occurred in the A_R and D_I soils, 182 (± 34) and 329 (± 98) μg C gd_w^{-1}, respectively, especially compared to the C_S site ($p < 0.001$). All other sites displayed a medium MBC ranging from 454 to 754 μg C gd_w^{-1}. The MBC of the soil correlated positively with WHC of the sites ($p < 0.05$) (Table S4).

3.3. Gross N mineralization and gross nitrification rates

The A_L and C_I soils (Fig. 3) displayed the highest gross N mineralization rates, (> 7 mg N kg_{dw}^{-1} d^{-1}), and the soils B_A and A_R the lowest (< 3 mg N kg_{dw}^{-1} d^{-1}). The gross nitrification rate was highest in the A_L and F_S soils, albeit with high variation (Fig. 3), whereas the lowest gross nitrification rate occurred in the C_I soil. The gross nitrification result for site A_G was excluded from this study due to a negative gross rate. In the correlation and PCA analyses we used gross nitrification data from Holz et al. (2015) for the A_G site.

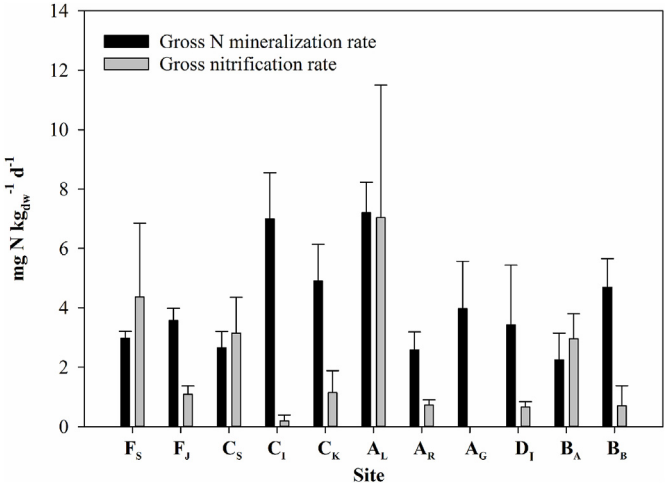

Fig. 3. Gross N mineralization and gross nitrification rates (mg N kg_{dw}^{-1} d^{-1} ± SD) determined for 10–20 cm soil layer. *Gross nitrification result is missing from the A_G soil.

3.4. Nitrous oxide emissions in situ and production in laboratory experiments

Published N_2O flux data for our sites showed the lowest N_2O fluxes from Icelandic soils (C_I, D_I), ranging between 0.03 and 0.04 g N m^{-2} y^{-1}, and the highest from C_S and A_L soils, 2.38 and 2.14 g N m^{-2} y^{-1}, respectively (Table 1, Fig. 4). The N_2O emissions correlated positively with the soil NO_3^- concentration ($p < 0.01$, Table S4) in the 10–20 cm soil layer measured after 2 weeks of incubation, as well as with gross nitrification (p < 0.01, Table S4). It has to be noted that gross nitrification was determined only for the deeper soil layer. The sites displaying the highest *in situ* N_2O emissions had also the highest P content in the 10–20 cm soil layer ($p < 0.05$) (Fig. 4, Tables 1 and S4).

In the beginning of the incubation experiments (0 wk) the N_2O production in the 0–10 cm layer was highest in the C_S soil, amounting to 46.5 (± 17.6) ng N_2O g_{dw}^{-1} h^{-1}. In all other soils, the N_2O

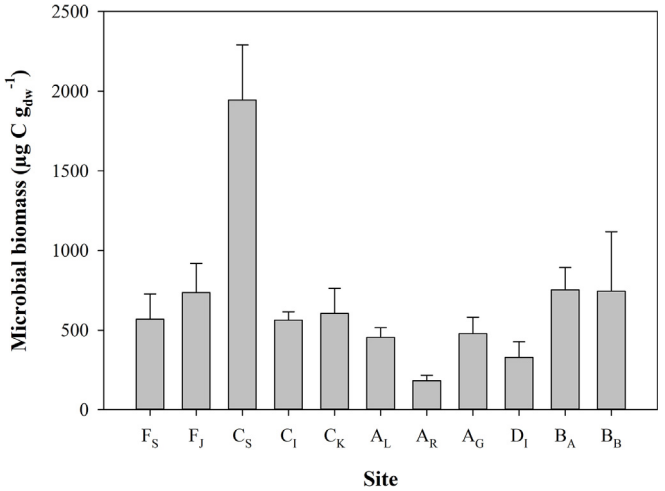

Fig. 2. Microbial biomass C for the sites (μg microbial C g_{dw}^{-1} ± SD, n = 5) determined for 10–20 cm soil layer.

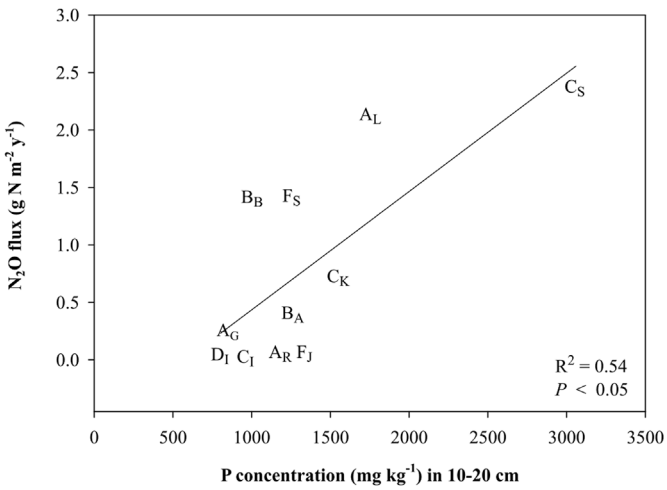

Fig. 4. Correlation between N_2O emissions (g N m^{-2} y^{-1}) *in situ* and the content of total P (mg kg^{-1}) in soil at the depth of 10–20 cm.

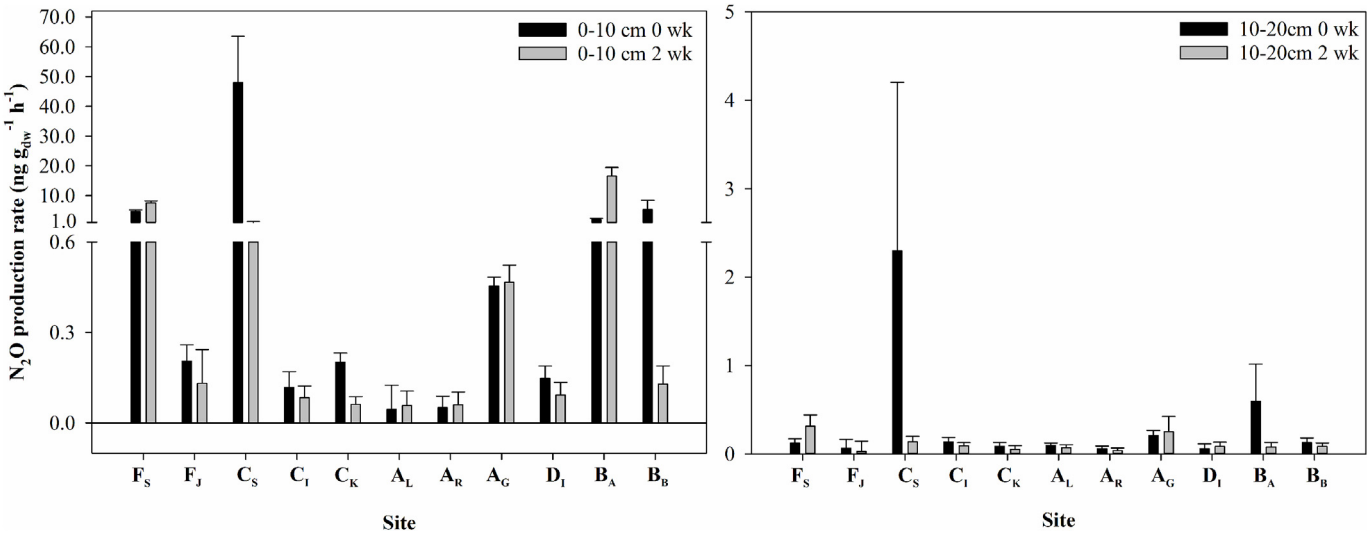

Fig. 5. The mean N_2O production rates (± SD) in aerobic incubation of samples from 0- 10 cm (left figure) and 10–20 cm (right figure) soil layers in the beginning (0 wk, black bars) and after the 2 week incubation (2 wk, grey bars) at +15 °C.

production was 10% or less of that in the C_S soil (Fig. 5), and significantly lower ($p < 0.001$) especially in the A_L and A_R soils, where N_2O production was only 0.05 ng N_2O g_{dw}^{-1} h^{-1}. After a 2-week incubation, the N_2O production in the C_S soil decreased and the highest N_2O production took place in the F_S and B_A soils. The N_2O production was higher in the 0–10 cm soil layer than in the 10–20 cm layer. At the start of the incubation the C_S soil showed higher N_2O production rates than most of the other soils also in the 10–20 cm layer (Fig. 5). Similar to the surface soil layer, the N_2O production rate in the deeper soil layer was rather similar between all sites after 2 weeks of incubation.

After determining the N_2O production rate in the aerobic incubation experiments for the two-week incubation at +15 °C, soil samples were extracted for NO_3^-, NO_2^-, NH_4^+, pH and EC analyses. The pH measured after 2 weeks of incubation (data not shown) did not significantly differ from the pH measured at the beginning of the incubation (Table S6). The F_S and A_G soils had the highest EC, amounting to > 190 μS cm^{-3}. Generally, EC increased in all soils during the incubation, except in F_J where EC showed constant values (Table S6). Nitrate concentrations also increased during the incubation, especially in F_S, C_S, A_G and A_L soils. Ammonium concentrations increased especially in the A_G, F_S and F_J soils and decreased in the B_A, C_S and C_K soils (Table S6). After incubation, the NO_2^- concentration in all soils were negligible (data not shown).

3.5. Correlation of N_2O production and emissions with soil characteristics and nitrogen turnover processes

Six components were extracted in the PCA, explaining in both layers together 91% of the total variance, with the first three components accounting for 69–70% of the variance (Table S7).

The component 1 illustrated especially the nutrient status of the sites (Table S2); forested sites (F_S, F_J) with lowest nutrient status in general were clearly separately from the cultivated site C_K with highest nutrient status (Fig. 6). In the PCA, the sites with similar land-use formed clusters: in both soil layers, (0–10 cm and 10–20 cm) the forest sites (F_S, F_J), the afforested sites (A_L, A_R, A_G) and the abandoned, formerly cultivated (B_A, B_B) sites formed an own cluster. An exception from this clustering were the cultivated sites (C_K, C_S, C_I), showing large variability. Also, forested sites (F_S, F_J) were closer to afforested fields (A_L, A_R, A_G) than actively cultivated fields (C_K, C_S, C_I) or abandoned fields (B_A, B_B). The Icelandic sites C_I (cultivated hay field) and D_I (drained) formed a separate cluster: besides having the lowest N_2O fluxes, these sites also differed from the remaining sites in their soil chemical properties caused by volcanic ash deposition.

The results of the PCA (Fig. 6) indicate that in the surface soil layer the N_2O production and fluxes interact especially with the $\delta^{15}N$ of the bulk soil, the C/N ratio, WFPS, degree of humification (*H*), bulk density (BD) and the concentration of certain metals and nutrients (P, Cd, B, K). Step-wise linear regression (Table 3) identified the P concentration as the key variable to the N_2O flux from the surface layer (model strength 46%, Table 3). Nitrous oxide production in the surface soil on the other hand was best explained by WFPS and the Cu concentration, in addition to the OM content and the C/N ratio (model strength 98%, Table 3).

For the deeper soil layer PCA showed that N_2O flux and production interrelate with $\delta^{15}N$ of bulk soil, degree of humification (*H*) and some metals and nutrients (P, Cd, Cu), but also with MBC, NH_4^+ concentration and gross nitrification (Fig. 6B). According to the step-wise linear regression (Table 3), gross nitrification and P concentration were the most important factors explaining the N_2O flux (model strength 75%), whereas N_2O production was best explained by MBC, soil Cu concentration, gross N mineralization and gross nitrification (model strength 96%).

4. Discussion

4.1. Links between nitrate availability, soil water content and nitrous oxide production and emissions

In contrast to nutrient poor peatland forests, N_2O emissions in nutrient rich boreal peatland forests can be high (Martikainen et al., 1993). In peatland forests, N_2O emissions depend on the peat C/N ratio, high emissions being expected in N rich soils with C/N < 25–30 (Klemedtsson et al., 2005). A low soil C/N ratio supports net N mineralization and associated nitrification, increasing the availability of NH_4^+, NO_3^- and NO_2^- in the peat profile, the two latter ions being the key substrates for denitrification, the most potential process for N_2O production in soils (Butterbach-Bahl et al., 2013). In agricultural soils regularly receiving N fertilizers, nitrification and denitrification are less dependent on N mineralization than in peatland forest soils that receive extra N almost exclusively through atmospheric deposition. While studies conducted in boreal peatland forests do not support this hypothesis of high N_2O emissions at optimum C/N ratio, peatland forests with a cultivation history do exhibit high N_2O emissions within this optimum C/N range (Ojanen et al., 2010). Thus, across the variety of land-use options, peatlands display a high variability in N_2O emissions within this optimum C/N ratio of 15–30 (Leppelt et al., 2014; Maljanen et al.,

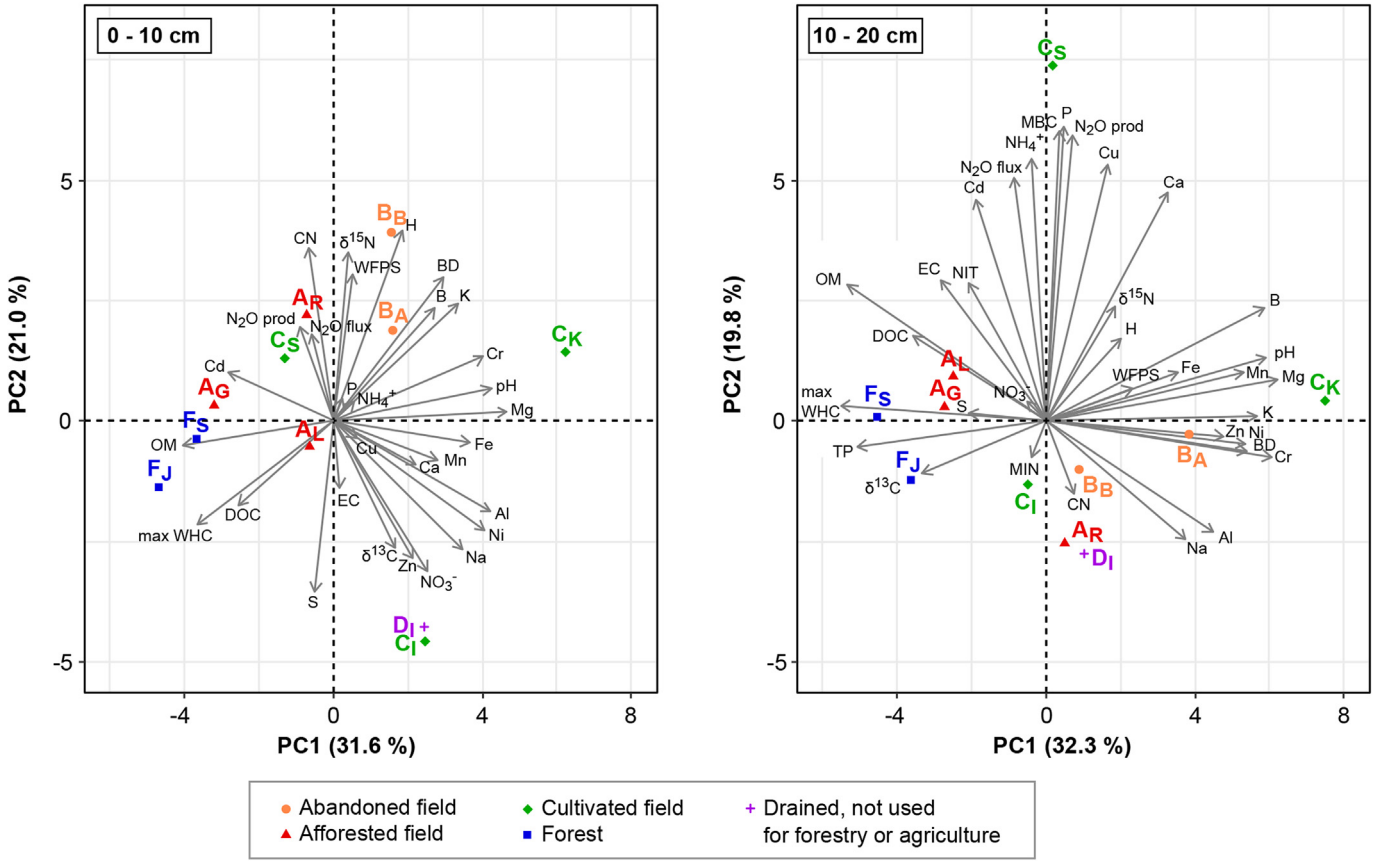

Fig. 6. Principal component analyses (PCA) for N_2O emissions/production and soil parameters, showing also the location of various land-use types. The analyses were done separately for the soil layers of 0–10 cm (A) and 10–20 cm (B). Variables in the figures are: DOC = dissolved organic carbon, H = peat humification (von Post scale), N_2O flux = flux measured in the field, MIN = gross N mineralization, NIT = gross nitrification, N_2O prod = production measured in the laboratory, MBC = microbial biomass C, WFPS = water filled pore space, max WHC = maximum water holding capacity, BD = bulk density, $\delta^{13}C$ = bulk soil $\delta^{13}C$ value, $\delta^{15}N$ = bulk soil $\delta^{15}N$ value, OM = organic matter, CN = C/N ratio, NO_3^- = nitrate concentration, NH_4^+ = ammonium concentration, EC = electrical conductivity, concentrations of Al = aluminum, P = phosphorus, Fe = iron, Cr = chromium, Na = sodium, K = potassium, Ca = calcium, Zn = zinc, Ni = nickel, Mg = magnesium, Cu = copper, Mn = manganese, B = boron, Cd = cadmium, S = sulphur. MBC, MIN, NIT and TP were determined only for the 10–20 cm layer.

Table 3
Step-wise linear regression models. N_2O flux refers to field measurements and N_2O production to laboratory experiments. Predictor variables in the table refer to: P = phosphorus concentration in bulk soil (mg kg^{-1}), Cu = copper concentration in bulk soil (mg kg^{-1}), WFPS = water filled pore space (%), OM = organic matter content (%), C/N = carbon to nitrogen ratio, NIT = gross nitrification (mg N $kgdw^{-1}$ d^{-1}), MBC = microbial biomass C (μg C g_{dw}^{-1}), MIN = gross N mineralization (mg N kg_{dw}^{-1} d^{-1}). MBC, NIT and MIN were not determined for the 0–10 cm soil layer and therefore not included in the regression analysis for the surface layer. *** Significant at the level $p < 0.001$, **$p < 0.01$, *$p < 0.05$.

Soil depth (cm)	Response variable	Predictor variables	Relative importance of the variable	P value		Proportion of variance explained by model (%)
0–10	N_2O flux	P	–	0.0211	*	46.35
	N_2O production	Cu	0.5947	0.0008	***	97.75
		WFPS	0.2483	0.0033	***	
		OM	0.0907	0.0058	**	
		C/N	0.0438	0.0912		
10–20	N_2O flux	P	0.3836	0.0285	*	74.93
		NIT	0.3657	0.0338	*	
	N_2O production	MBC	0.4673	0.0161	*	95.58
		Cu	0.3949	0.0349	*	
		MIN	0.0683	0.0763		
		NIT	0.0253	0.1925		

2010a). Consequently, other environmental parameters besides the C/N ratio have to be considered when attempting to predict N_2O emission rates from drained peatlands.

In our study, the availability of NO_3^- was a predictor for N_2O emissions which correlated positively with the soil NO_3^- concentration ($p < 0.01$, Table S4) measured after 2 weeks of incubation, showing net nitrification. Net nitrification also correlated positively with N_2O emissions from drained peat soil under *in situ* conditions (Regina et al., 1998a). As a result of NO_3^- production and consumption (including plant N uptake), the initial NO_3^- concentration poorly describes NO_3^- production. Also, net nitrification rates obtained in soil incubation experiments are not an exact measure of NO_3^- production either (Hart et al., 1994), because such experiments do not show immobilization of NH_4^+ and NO_3^-. By using a ^{15}N technique, we determined gross N mineralization and nitrification rates which were in the range reported for mineral and peatland forest soils (Stark and Hart, 1997; Verchot et al., 2001; Westbrook and Devito, 2004) and for a mineral arable soil (Luxhøi et al., 2004). In our study, the initial NO_3^- concentration did not correlate with N_2O emissions, as expected, but gross nitrification rates did correlate positively with the N_2O emissions (10–20 cm; Table 3, Table S4) further stressing the importance of nitrification and NO_3^- production in promoting N_2O emissions. While we did not determine gross nitrification rates for the surface soil layer, a similar correlation between gross nitrification rates and N_2O emissions can be expected also in the surface soil. In a study by Regina et al. (1996), focusing on both nutrient poor and nutrient rich drained boreal

peatlands, N_2O emissions correlated positively with the number of nitrifiers and the nitrification potential. Our results thus suggest that, surprisingly, a lack of NO_3^- can limit N_2O production even in peat soils where, based on their low C/N ratio, we would expect a sufficient NO_3^- availability to allow high N_2O production.

During the nitrification process, ^{15}N-depleted NO_3^- is produced and loss of this NO_3^- via leaching and denitrification causes ^{15}N-enrichment in the soil (Callesen et al., 2013; Högberg and Johansson, 1993). In our study, ^{15}N enrichment of the bulk soil increased with increasing peat humification (Tables S3 and S4, Fig. 1) that is known to increase with soil OM mineralization. A higher degree of humification thus reflects higher cumulative N mineralization and NO_3^- production with time. More humified soils have also lost higher amounts of ^{15}N depleted NO_3^- leading to ^{15}N enrichment in the residual organic matter.

The C/N ratio of the peat is linked to the degree of humification (Kasimir-Klemedtsson et al., 1997; Klemedtsson et al., 2005), and more decomposed peat was shown to emit larger rates of N_2O (Regina et al., 2004). In our study, the PCA (Fig. 6) but not the regression models indicated that there was a link between the degree of humification and the N_2O flux and production in both soil layers. The degree of peat humification alone is not sufficient in explaining the variation in N_2O emissions, as N_2O production is, besides other peat physical and chemical characteristics, regulated by the presence and activity of denitrifiers. The growth and activity of heterotrophic microbes including denitrifiers are regulated by the availability of substrates, especially organic C. The DOC pool contains easily available organic compounds for microbial use and in our study, DOC concentrations in the upper soil layer correlated positively with N_2O production ($p < 0.05$) after 2 weeks of incubation.

In addition to a sufficient supply of mineral N the soil water content needs to fall within a certain range to support N_2O production. If the soil is water-saturated, N_2O emissions from peat soils without external N input are minor because anaerobic conditions limit mineralization and nitrification (Martikainen et al., 1993). Nitrous oxide production is also limited if the soil water content is too low because microbial activities and substrate diffusion are restricted under low soil water content conditions (Stark and Firestone, 1995; Bateman and Baggs, 2005). In Finland, afforested former arable land on mineral soils is usually well drained and aerated whereas on organic soils the drainage system may not work adequately and often tree growth on organic soils is limited due to the bad aeration (Wall and Heiskanen, 2009). The optimum WFPS for N_2O production in boreal peat soils varies from 50 to 90% (Regina et al., 1998a). In our study the WFPS ranged from 23 to 95%. According to the PCA, WFPS was closely connected with N_2O flux and production, especially in the 0–10 cm layer (Fig. 6A). This suggests that in some cases the upper soil layer is too dry for optimum N_2O production, as denitrification is limited by too high O_2 content. It is logical that the initial NO_3^- content in the surface layer displayed a reverse relationship with WFPS (Table S3): the NO_3^- content increased with decreasing WFPS indicating that nitrification is on-going, while denitrification is limited, leading to an accumulation of NO_3^-. In the correlation analyses, however, none of the moisture parameters correlated with N_2O production (Tables S3 and S4), likely due to interlinkages between moisture and other variables, but regression models showed that in the surface soil layer WFPS is one of the key parameters to explain N_2O production (Table 3). Results obtained in the Mt. Kilimanjaro region, Tanzania (Gütlein et al., 2017) demonstrate the importance of both C/N ratio and soil water content on N_2O fluxes also in tropical ecosystems. There, similar to our study, regression analysis revealed that besides the C/N ratio and soil water content also the soil N content controlled N_2O emissions.

4.2. Soil chemistry and nitrous oxide emissions and production

Agreeing with results obtained by Regina et al. (1996), our study suggests that, besides mineral N availability, soil P concentration plays an important role in regulating N_2O production and emissions in managed boreal peat soils (Figs. 4 and 6, Table 3, Table S4). Soil P content was low in the forested peat soils (Tables 1 and S2) and a low P content is known to limit tree growth on boreal drained peatlands (e.g. Moilanen et al., 2015). Thus, there is a large competition between plants and microbes for P in peatland forest soils, where also microbial activities and growth could suffer from a lack of P. The PCA showed that MBC (determined in 10–20 cm) was connected with the P concentration. A study conducted on peat soils by Amador and Jones (1993) showed that microbial respiration in peat soils can be limited by the amount of total P. As a result of fertilization, agricultural soils displayed higher amounts of P (Tables 1 and S2) than forest soils, and P is less likely to limit microbial processes in agricultural soils. A higher P content could promote either nitrification, denitrification, or both of these processes, leading to increased N_2O production and emissions (Mehnaz and Dijkstra, 2016). The direct effect of soil P concentration on N_2O production remains unclear, but P input was shown to stimulate microbial activity (Wang et al., 2014) and to enhance N_2O emissions in N fertilized mineral soils (Mehnaz and Dijkstra, 2016; Ullah et al., 2016). Importantly, these three studies used mineral soils with external P input in the laboratory, whereas our study shows the direct link between N_2O production and *in situ* P variability among managed peatland sites. Our study thus highlights the need for in-depth studies on the linkage between the N and P cycle in northern peatlands, in order to improve our understanding of N_2O emission from these ecosystems.

In addition to the P concentration, the soil Cu content seemed to have an important role in N_2O production. Copper is an essential component in ammonium monooxidase (AMO) of ammonium oxidizers (Gilch et al., 2009), and in nitrous oxide reductase (NOS) of denitrifiers (Richardson et al., 2009). Therefore, a low availability of Cu in soil could limit denitrification processes (Richardson et al., 2009). The NOS is the last enzyme in the denitrification catalyzing reduction of N_2O to N_2. If there is lack of Cu, the NOS activity can be limited, thereby enhancing N_2O release from denitrification by inhibiting the last step of denitrification (reduction of N_2O to N_2). Ensuring a sufficient Cu availability is suggested to be one N_2O mitigation option in agricultural soils (Thompson et al., 2012) as well as in waste water treatments (Desloover et al., 2012). Interestingly, the effect of Cu availability on N_2O emissions in our study was vice versa, i.e. with higher Cu availability the N_2O emissions were higher. According to the PCA, the soil Cu concentration was linked to N_2O production and fluxes in both soil layers, but especially in the deeper one (Fig. 6A and B). The fact that N_2O emissions were higher with higher Cu concentration indicates that, unexpectedly, denitrification was not the main process for N_2O production at our sites. In correlation analyses the Cu content did not correlate with either N_2O production or fluxes, which is understandable since in correlation analyses only two variables are considered at a time, showing only clear and straight-forward correlations. Instead, when considering the whole data set, the regression analyses revealed that for both soil layers Cu was an important predictor for N_2O production, more significantly in the surface soil layer than in the deeper soil layer (Table 3.). Previous studies have shown that ammonium oxidation contributes to N_2O production in forested peat soil (Liimatainen et al., 2014), especially in the uppermost peat horizon (Regina et al., 1998b). The importance of ammonium oxidation for N_2O production in peat soils with low C/N ratio and water table has been shown also for subarctic peatlands (Gil Lugo, 2017). There, the relative contribution of nitrification and denitrification to the N_2O emissions depend on peat moisture conditions; the role of nitrification is higher during dry summers when the peat water content is low (Gil Lugo, 2017). The studies mentioned above (Desloover et al., 2012; Gil Lugo, 2017; Liimatainen et al., 2014; Regina et al. 1998a,b; Thompson et al., 2012) and the positive relationship between the Cu content and N_2O production observed here points to the potential role of ammonium oxidizers for N_2O production in peat soils.

Soil pH can affect the overall denitrification activity and the ratio of

N_2O to N_2 produced (Richardson et al., 2009). Moreover, nitrification processes are regulated by soil pH, but as pointed out above, the organisms involved in nitrification and the factors regulating nitrification in acidic soils are poorly known. In our study, focusing on nutrient rich sites, soil pH did not correlate with N_2O production or N_2O emissions in either PCA or correlation analyses. These findings are in contrast to the results obtained by Regina et al. (1996), studying both nutrient poor and nutrient rich peatlands, and Weslien et al. (2009) in forested organic soils, both studies showing a strong positive correlation with pH. In accordance with our results, Maljanen et al. (2010a) found no significant correlation between the pH and N_2O flux, even though their data set included a larger number of sites than in studies by Regina et al. (1996) and Weslien et al. (2009).

4.3. The effect of land-use history and soil characteristics on nitrous oxide emissions

The land-use history affects the grouping of the peatland sites in the PCA: all land-use types, except the cultivated fields, formed rather coherent groups (Fig. 6) based on their management intensity and geographical origin (others vs. Iceland, see below). However, as pointed out above, N_2O emissions largely varied within each land-use group (Table 1).

The physical, chemical and biological properties of the cultivated peatlands differ from their original state depending on the variable drainage, fertilization and management histories. Nitrous oxide emissions also varied within agricultural sites, which were all fertilized at some point in their history, but the management type and intensity vary. The highest emissions occurred from present (C_S) and past (A_L) agricultural sites (Table 1), that also displayed the highest P contents likely due to their fertilization history. The PCA analysis shows the differences in the nutrient status between study sites reflecting the results from element analyses (Table S2) in a visual form. As seen in the element analyses, also in the PCA analysis the site C_K differed from other sites, especially in terms of nutrient concentrations in the soil. This site had an exceptionally long cultivation history (100 years) with heavy fertilization (Regina et al., 2004).

The Icelandic sites C_I and D_I have to be regarded separately from the sites in other Nordic countries in terms of their N_2O emissions (Fig. 6). These soils experience frequent volcanic ash deposition which influences the general soil chemical characteristics and favors the formation of stable aluminum-humus complexes typical for Icelandic wetland soils. Compared to those from other sites, Icelandic soils differed in nutrient composition and isotopic composition, being ^{13}C enriched (as the volcanic C, see Rizzo et al., 2014) and ^{15}N depleted The Icelandic soils had low P content, gross nitrification rates and MBC, which explain their low N_2O emissions.

5. Conclusions

Besides the water table level, the soil C/N ratio is a known key regulator of N_2O emissions from drained peatlands. Our study shows, however, that the peat C/N ratio does not adequately predict either N_2O production or N_2O emissions in managed peatland soils. Although all study sites had a low C/N ratio traditionally predicting high N_2O emissions, the N_2O emissions varied greatly within and between land-use groups. Thus, our study provides valuable insights into the regulatory factors underlying the variability in N_2O emissions in drained peatlands. Most importantly, our findings show that an increased P content promotes N_2O emissions, implying that a lack of P could limit N_2O production and emissions. Interestingly, our study also indicates that increased Cu concentrations in peat may lead to enhanced N_2O production and emissions, suggesting that ammonium oxidizing nitrifiers contribute to N_2O production in managed peatlands. Our study sheds light upon the link between N_2O emissions and soil P and Cu availability in managed northern peatlands, and highlights the strong coupling of the soil N and P cycles in peatland ecosystems.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2018.04.006.

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