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Effects of nitrate and sulfate on greenhouse gas emission potentials from microform-derived peats of a boreal peatland: A ^{13}C tracer study

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A B S T R A C T

Increasing natural and anthropogenic deposition of nitrate (NO_3^-) and sulfate (SO_4^{2-}) to peatlands may modify CH_4 oxidation, CO_2 and N_2O production, thereby affecting the balance of greenhouse gases (GHG) globally. Among environmental factors controlling these biogeochemical processes, effects of peatland microrelief are poorly understood. Fluxes of CO_2, CH_4 and N_2O were measured before and after incubation with NO_3^- and SO_4^{2-} for peat samples collected from various microrelief positions of a boreal oligotrophic mire in Eastern Finland. Soil was spiked with $^{13}CH_4$ to understand the processes of CH_4 oxidation, its microbial utilization and incorporation into soil organic matter (SOM). We hypothesized that the addition of NO_3^- and SO_4^{2-} would 1) stimulate CO_2 and N_2O production (nutritional effect), but 2) decrease CH_4 oxidation due to acceleration of other more energetically favorable processes (e.g. denitrification), and 3) these patterns should follow the naturally established aerobic zone of a microform type and decrease with depth.

Microbial biomass (MB) at 50 cm below all microforms was 9–15 folds higher than in the topsoil. MB controlled the GHG dynamics and was related to specific depth-dependent environmental conditions, rather than oxygen availability. Indeed, production of CO_2 and N_2O, and oxidation potentials of CH_4 revealed no clear linkage with the naturally established aeration zone of the peatland's microforms. Following NO_3^- and SO_4^{2-} addition, production of CO_2 decreased by 20–65% compared to the control, with the greatest reduction in CO_2 emission occurring in the topsoil of hollows. In turn, CH_4 oxidation was suppressed by 20–94% with NO_3^- addition at 50 cm in lawns and with both NO_3^- and SO_4^{2-} at 50 cm in hollows. The N_2O production was increased up to 180–240 times under NO_3^- treatment at 50 cm in hollows and lawns. In conclusion, human-induced deposition of NO_3^- and SO_4^{2-} may suppress CO_2 emissions from and CH_4 oxidation by boreal oligotrophic mires especially under the conditions of deposition increase. Finally, the deposition of inorganic compounds is strongly important to be considered in the estimation of ecosystem C and N balances.

1. Introduction

Peatlands are a subgroup of wetlands, defined as areas with naturally accumulated peat (organic soil layer) due to a decomposition rate of organic remnants that is lower than the net primary production (Saarnio et al., 1997). Even though peatlands cover only 4% of the land surface (some 4 million km^2) they contain around 20% of the global terrestrial carbon (C) stocks (Gorham, 1991; Roulet, 2000). Peatlands can be considered as CO_2 sinks due to the sequestration of atmospheric CO_2, but on the other hand, they are CH_4 sources due to the process of methanogenesis and CH_4 emissions (Gorham, 1991; Lafleur et al., 1997; Saarnio et al., 1997; Ye et al., 2012). Since CO_2 and CH_4 are important greenhouse gases (GHG) that contribute to global warming (IPCC, 2014), and the northern peatlands cover the area of ca. 3.7 million km^2 in total (Yu, 2012), understanding CO_2 production and CH_4 oxidation processes in boreal peatlands is essential for estimating the global C budget.

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Nitrous oxide (N_2O) is another important GHG, which is emitted in quantities up to three orders of magnitude smaller than CO_2 emissions, in absolute terms. Though N_2O warming influence (in W m^{-2}) was ca. 6.4% in 2015 from the total GHG (NOAA, 2015), its cumulative forcing of the global warming potential over 100-year time frame is 265 per kg pulse as compared to CO_2 (global warming potential 1) (IPCC, 2014). N_2O now has the third largest forcing of the anthropogenic gases, at 0.17 ± 0.03 W m^{-2} an increase of 6% since 2005 (Myhre et al., 2013). Moreover, N_2O is the most important gas in terms of stratospheric ozone destruction (Regina et al., 1996; Marushchak et al., 2011).

Generally, CO_2 and N_2O production and CH_4 oxidation in peatlands are controlled by a number of environmental parameters, such as water table (WT) level, temperature and plant communities (Lai, 2009). Among other factors, deposition of some anions, such as sulfate (SO_4^{2-}) and nitrate (NO_3^-), may affect GHG fluxes (Eriksson et al., 2010; Sutton-Grier et al., 2011). Supply of peatlands with SO_4^{2-} occur through air pollution, intensive volcanic activity, mineral weathering and acidic deposition from the atmosphere, whereas NO_3^- inputs originate from the anthropogenic eutrophication of inland waters and/or acidic deposition from the atmosphere (Sutton-Grier et al., 2011). SO_4^{2-} and NO_3^- anions have two main functions related to the GHG balance: (i) they serve as nutrients, stimulating plant growth and rhizodeposition (Kuzyakov and Domanski, 2000) and microbial activity (Blagodatskaya et al., 2010) and (ii) they participate in redox reactions as alternative electron acceptors (AEAs) when oxygen availability is low. The presence of AEAs can reduce CH_4 production (Bodegom and Stams, 1999; Eriksson et al., 2010; Smemo and Yavitt, 2011; Segarra et al., 2013). This is due to a combination of inhibition and competitive effects between organisms which use AEAs and methanogens for electron donors (Bodegom and Stams, 1999; Eriksson et al., 2010). SO_4^{2-} has been reported to suppress methanogenesis (Gauci et al., 2004) or to have no effects on CH_4 production (Vile et al., 2003a,b). There is a lack of evidence that SO_4^{2-} amendments affect aerobic CH_4 oxidation (Eriksson et al., 2010).

N_2O is produced in soils as a facultative byproduct of aerobic nitrification and anaerobic denitrification (Goldberg et al., 2010; Marushchak et al., 2011). Waterlogged conditions are usually associated with low N_2O production due to the low rates of nitrification and, subsequently, denitrification. In contrast, when water table is lowered, resulting in strong acceleration of OM mineralization leading to mineral N release, N_2O emission rates also increase. (Goldberg et al., 2010).

Prevailing environmental factors in peatlands (WT level, temperature, vegetation, water chemistry) are strongly interrelated, leading to formation of specific local conditions on the peatland surface and development of microrelief forms – so-called microform types. The three microform types are: elevated hummocks, depressed hollows and intermediate lawns (Dorodnikov et al., 2011, 2013 and references therein). The water table level relative to the soil surface varies between microforms, increasing in the order hummocks < lawns < hollows. This results in variable thickness of the oxidative zone and the growth of distinct vegetation communities. The existing differences between microforms promote the formation of specific microbial populations, thereby affecting GHG fluxes (Kotiaho et al., 2013; Deng et al., 2014). The patterns of GHG dynamics also change with peat depth, mostly due to the temperature decrease, low oxygen availability and limited access to fresh plant-derived inputs (Dorodnikov et al., 2013).

In the current study, we tested the effects of NO_3^- and SO_4^{2-} addition on CO_2 and N_2O production as well as potential CH_4 oxidation in a peat soil (Histosol), and their dependence on peatland microforms and peat depth. We modeled the situation of lowering of the WT, thus promoting aerobic soil organic matter (SOM) decomposition and CH_4 oxidation. We put forward the following hypotheses: (i) microbially-driven GHG production (CO_2, N_2O) and oxidation (CH_4) should follow the naturally established aerobic zone of a microform type and increase from hollows to lawns and further to hummocks; (ii) CO_2 and N_2O production and CH_4 oxidation should decrease with depth due to *in situ* decreasing availability of oxygen and fresh rhizodeposits; (iii) addition of NO_3^- and SO_4^{2-} should stimulate CO_2 and N_2O production (nutritional effect), but decrease CH_4 oxidation due to acceleration of other more energetically favorable processes (e.g. nitrification-denitrification).

2. Materials and methods

2.1. Study site and peat sampling

The experimental site was an ombrotrophic minerogenic fen Salmisuo in Eastern Finland (62°47′N, 30°56′E). The site is described in detail elsewhere (Alm et al., 1999; Becker et al., 2008; Saarnio et al., 1997). The surface of the experimental site was subdivided into three relief microform types according to the topography, water table level and vegetation communities: 1) dry and elevated hummocks with average WT around −20 cm (below peat surface) and dominant plant species *Eriophorum vaginatum, Pinus sylvestris, Andromeda polifolia, Sphagnum fuscum*; 2) intermediate lawns with average WT from −5 to −15 cm (dominant plants *Eriophorum vaginatum, Sphagnum balticum, Sphagnum papillosum*) and 3) the most wet - hollows with the average WT between 0 and 5 cm above the peat surface (dominant plants *Scheuchzeria palustris, Sphagnum balticum*) (Becker et al., 2008; Dorodnikov et al., 2013). The soil of the Salmisuo peatland could be classified as a Dystric Histosol (WRB, 2014) with an organic layer up to 2–2.3 m depth, consisting predominantly of *Sphagnum* remnants. The soil was randomly sampled from each microform type of a study site (50 × 50 m) from 3 depths (15, 50 and 200 cm) using a stainless-steel peat auger with a gouge-with-flap principle (EijkelkampAgrisearch Equipment, Giesbeek, Netherlands). Samples (81 altogether) were collected in plastic bags, trapped air was maximally removed and bags were transported in a thermobox to the laboratory, where they were kept tightly closed for 20 days at low temperature (4 °C) in darkness until the experiment. The natural moisture content of the samples comprised 90–95% of the peat fresh weight and generally decreased with depth. The pH varied between 3.9 and 4.6 in all microforms and increased with depth.

2.2. Experiment set-up

The following treatments were included in order to estimate the effect of microforms, depth, and the addition of NO_3^- and SO_4^{2-} on CO_2 and N_2O production and CH_4 oxidation under aerobic conditions. These were:

(i) Addition of NO_3^- as KNO_3 and SO_4^{2-} as Na_2SO_4 in final concentrations chosen after Smemo and Yavitt (2007): NO_3^- (10 mM) and SO_4^{2-} (1 mM) (corrected for the dilution with the natural soil moisture content). A control treatment without anions (amended with ultrapure deionized water) and soil-free blank (pure water of similar volume to soil) were included to follow the process of gas sampling and physical gas leakage. All the solutions and water were added in volume of 0.5 ml, thus increased total moisture content by ca. 3% from the natural soil moisture content (on the weight basis).

(ii) Addition of labeled $^{13}CH_4$ (5 atom% with a headspace concentration of 0.5–0.6%) to all treatments with and without NO_3^- and SO_4^{2-} amendments.

Soil samples (15–20 g of fresh weight) were put into 100-ml glass bottles with wide necks. The bottles were closed with tight-fitting butyl rubber septa and screw caps. The measurements of CO_2, N_2O and CH_4 along with ^{13}C-isotope signatures were done microform by microform. The duration of the incubation period lasted 7–10 days after addition of $^{13}CH_4$, NO_3^- and SO_4^{2-}. During the experiment, all microcosms were stored in a dark room at a temperature of 21–23 °C. Gas fluxes (CO_2, CH_4) and $\delta^{13}C$ values of CO_2 were measured on a cavity ring-down spectroscope (CRDS) Picarro G2131-*i* (Picarro, Inc. Santa Clara, CA, USA) by injection of gas headspace subsamples (1 ml + 59 ml N_2) with syringes. Its operational range for CO_2: 0.01–0.4%; for CH_4: 0–1000 ppm; precision of $\delta^{13}C$ in CO_2: 0.1–0.25‰. For N_2O analysis, microcosm headspace was sampled with a 1-ml syringe, gas samples were transferred to 12-ml prevacuated and N_2-flushed glass vials, diluted with 20 ml N_2, and measured on a gas chromatograph GC 6000 (Carlo Erba Instruments) equipped with ECD and FID detectors.

2.3. Microbial biomass C and bulk soil C, N and $\delta^{13}C$ measurements

Microbial biomass was measured based on extracted total DNA using FastDNA Spin Kit for Soil (BIO 101/Qbiogene, MP Biomedicals), according to the protocol of the manufacturer for the FastPrep-24 TM instrument (MP Biomedicals, LLC, Santa Ana, CA, USA). Briefly, soil samples (0.2 g fresh weight) were put into Lysing Matrix E tubes and 978 µl sodium phosphate buffer and 122 µl of lysis solution buffer were added. Suspended soil was homogenized in the FastPrep-24 for 40 s at a speed level 6.0. Lysing Matrix E tubes were centrifuged at 14,000×*g* (Centrifuge 5416, Eppendorf AG, Hamburg, Germany) for 10 min and the supernatant was transferred to other microcentrifuge tubes (2.0 ml). 250 µl of protein precipitation solution was added and mixed well by shaking. The 2-ml tubes were centrifuged again for 5 min and supernatant was transferred to 15-ml centrifuge tubes, where1.0 ml of binding silica matrix suspension was added. Tubes were put on a shaker for 5 min to allow the DNA binding. About 500 µl of the suspension from the top was discarded and the remainder was transferred into SPIN-TM filters and centrifuged at 14,000×*g* for 1 min. Prepared SEWS-M wash solution (500 µl) was added to the filters. They were centrifuged a second time at 14,000×*g* for 2 min to dry the matrix of the residual washing solution. SPIN-TM filters were air dried for 5 min at room temperature and 150 µl DES (DNase/Pyrogen-Free water) was added. Filters were placed in a heat block for 5 min at 55 °C. Finally, SPIN-TM filters were centrifuged for 1 min and the supernatant in catch tubes was the extracted DNA. The extracts were either stored in a freezer at −20 °C or at 55 °C when measured immediately. The quantity of DNA extractions was detected with a PicoGreen (Invitrogen TM, Life Technologies GmbH, Darmstadt, Germany) and TE buffer (Tris EDTA, MP Biomedicals) solutions after necessary dilution. Measurement was carried out in 96-well black polystyrene microplates (Brand GmbH, Wertheim, Germany) on a Victor^3 1420-050 Multilabel Counter (Perkin Elmer, Waltham, MA, USA) according to a protocol with fluorescence excitation at 485 nm and emission at 535 nm (1.0s). Based on measured standards, the amount of DNA was calculated and converted to microbial biomass C (µg g^{-1} of dry soil) according to Blagodatskaya et al. (2014).

Bulk soil C and N contents were measured in dried and ground peat samples on an ElementarVario EL Cube CN analyzer (ElementarAnalysensysteme GmbH, Hanau, Germany). Values are presented as mg C (N) per gram of dry soil (mg g^{-1} soil DW). Stable C isotope composition was measured in the same soil samples at the Competence Center for Stable Isotopes (KOSI, University of Göttingen, Germany) on an Isotope Ratio Mass Spectrometer (IRMS) Delta V Advantage with a Conflo III interface (Thermo Electron, Bremen, Germany) equipped with an elemental analyzer Flash 2000 (Thermo Fisher Scientific, Cambridge, UK).

2.4. Calculations and statistics

Gross CO_2, CH_4 and N_2O fluxes were estimated from the linear rate of change in CO_2, CH_4 and N_2O concentrations overtime. The Ideal Gas Law was used to convert the raw data from the instrument (in ppm) to mass units:

$$n = P^*V/R^*T \quad (1)$$

where n is the amount of gas (in moles), P is the atmospheric pressure (101.325 kPa), V is the volume of gas in the headspace (L), R is the Ideal Gas Constant (8.31 J $K^{-1}mol^{-1}$) and T is the temperature as absolute temperature in Kelvin (K). CO_2 efflux and CH_4 oxidation rate are presented as amount of C (ng) per gram soil (dry weight) per hour. Net flux rates were derived by subtraction of the respective values in blanks from the gross values, to correct for potential gas losses through leakage and sampling removal.

The amount of new C derived from labeled $^{13}CH_4$ that was incorporated into incubated soil was calculated using a 2-pool isotope mixing model:

$$\mathrm{NewC-CH_4} = \frac{AT\%^{13}C_{AI} - AT\%^{13}C_{BI}}{AT\%^{13}C_{CH4} - AT\%^{13}C_{BI}} \times 100\% \quad (2)$$

where $AT\%^{13}C_{AI}$is the atom percentage of ^{13}C isotope in peat soil after incubation, $AT\%^{13}C_{BI}$ is the initial atom percentage of ^{13}C in peat soil, and $AT\%^{13}C_{CH4}$ is the atom percentage of ^{13}C of the added CH_4. All values can be found in the Supplementary Information (Table 1S).

All the measured and calculated parameters were statistically analyzed with R-Studio, a free and open-source integrated development environment for R (a programming language for statistical computing and graphics). All data presented are mean values from three replications (±SE). ANOVA was used for estimating significant differences ($p < 0.05$) either between different depths within one microform of each treatment or between different microforms of each depth and treatment. All the coefficients of significance (p-values) are presented in the Supplementary Materials (Tables S2-S10). Main and interaction effects between microforms, depths and treatments were tested with the two-way ANOVA (Tables S11–S13).

3. Results

3.1. C, N content and C-to-N ratio in peat profile of studied microforms

The total organic carbon content (C) was similar in all microforms at the same depths and the content significantly increased with depth (Table 1). In contrast, total nitrogen (N) content was significantly lower for hummocks at all depths as compared to both lawns and hollows (Table 1). The C:N ratio strongly decreased with depth, being 2.5–3 times lower in deeper horizons (30–37) as compared with top 15 cm (85–98). A significantly higher C:N ratio was found in hummocks at 50 and 200 cm depths as compared to lawns and hollows (Table 1).

3.2. CO_2 production from soil with and without nitrate and sulfate amendment

Average CO_2 production rate in soil without NO_3^- and SO_4^{2-}

Table 1
Carbon (C), nitrogen (N) contents (g kg^{-1}) and the C-to-N ratio (C:N) in peat samples of three microform types (hummocks, lawns, hollows) at three depths (15, 50 and 200 cm). Values are averages of three replicates (±SE). All values were significantly different between the three depths of each microform ($p < 0.05$).

Depth (cm)	Hummocks			Lawns			Hollows		
	C	N	C:N	C	N	C:N	C	N	C:N
15	448.5 (3.1)	4.6 (0.4)*	98.8 (9.9)	451.7 (5.6)	5.3 (0.3)	85.4 (3.9)	448.9 (0.2)	5.3 (0.2)	85.4 (3.7)
50	492.7 (6.2)	13.3 (0.2)*	37.1 (0.3)*	502.7 (3.3)	15.3 (0.1)	32.8 (0.1)	508.3 (0.3)	15.1 (0.3)	33.8 (0.7)
200	562.3 (1.9)	16.9 (0.0)*	33.3 (0.0)*	566.1 (5.8)	19.1 (0.2)	29.6 (0.2)	568.3 (6.2)	19.0 (0.2)	29.9 (0.1)

*Significantly different values between microforms ($p < 0.05$).

additions revealed contrasting patterns between microforms with depth (Fig. 1, blue color). Thus, CO_2 efflux for hollows showed the expected pattern: the highest efflux was in the topsoil and significantly decreased with depth (Fig. 1c). In contrast, the

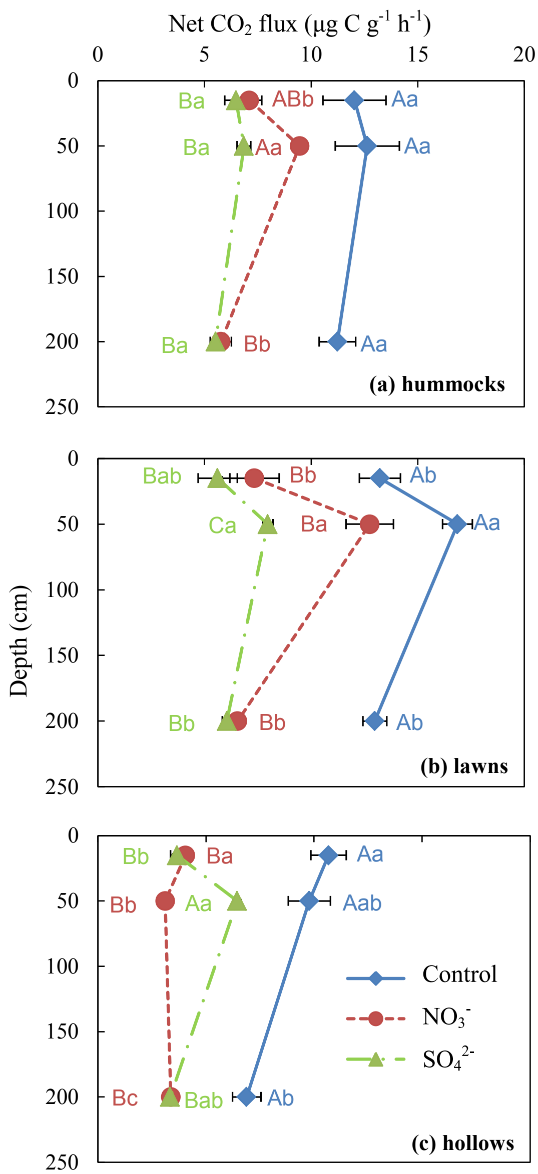

Fig. 1. Net CO_2 flux (per gram (g) of peat dry weight) for: a) hummocks, b) lawns and c) hollows with and without addition of NO^{3-} and SO_4^{2-}. Values are averages of three replicates over the incubation period (±SE). Values followed by different letters are significantly different between the three treatments of the same depth of each microform (uppercase letters) and between the three depths under each treatment within the same microform (lowercase letters) at $P \leq 0.05$.

highest CO_2 efflux (among all microforms) was measured at 50 cm in lawns, whereas the top 15 cm and 200 cm did not differ between each other (Fig. 1b). The average CO_2 flux in hummocks showed a similar pattern to lawns. However, CO_2 efflux at depth horizons between hummocks and lawns was not significantly different (Fig. 1a).

For all microforms and at all depths, amendment with NO_3^- and SO_4^{2-} decreased CO_2 efflux by a factor of 1.3–2.9 relative to soil without NO_3^- and SO_4^{2-} addition (Fig. 1). The largest suppression was achieved with the addition of SO_4^{2-} in hummocks and lawns, whereas NO_3^- decreased CO_2 flux most strongly for hollows. Except for NO_3^- addition in hollows, the highest CO_2 efflux was observed at 50 cm depth in all amended microforms (Fig. 1). In the top and bottom horizons, the difference in CO_2 effluxes between NO_3^- and SO_4^{2-} additions was negligible for all microforms. Main and interaction effects between microforms, depths and treatments as related to CO_2 production were highly significant, except the "depth-treatment" interaction effect (Table S11).

3.3. CH_4 oxidation from soil with and without nitrate and sulfate amendment

The most intensive CH_4 oxidation (1.5–1.7 µg C g^{-1} h^{-1}) was recorded for the topsoil from lawns and hollows (Fig. 2b, c, blue color, shown as negative values representing the decrease of added CH_4). Remarkably, the CH_4 oxidation in topsoil from hummocks was ca. 10 times lower, compared with the other two microforms (Fig. 2a). For all microforms, the oxidation dropped significantly with depth, approaching near-zero values at 200 cm. There was no difference in CH_4 oxidation at each of 50 and 200 cm between the three microforms (Fig. 2).

Similar to the CO_2 response, the addition of NO_3^- and SO_4^{2-} decreased CH_4 oxidation in all microforms relative to soil without addition. Though, this effect was only observed at 15 cm (lawns and hollows) and 50 cm depths (all microforms) (Fig. 2). There was no significant effect of NO_3^- and SO_4^{2-} amendments in the topsoil of hummocks and at 200 cm depth for any microforms as compared to the unamended soil. The suppressing effect of NO_3^- was more pronounced in lawns (Fig. 2b), but SO_4^{2-} caused higher suppression in hollows (Fig. 2c), whereas NO_3^- and SO_4^{2-} both caused a similar decrease in CH_4 oxidation for hummocks (Fig. 2a). The main effects of microform type, peat depth and treatment with NO_3^- and SO_4^{2-} on CH_4 oxidation, as well as the interaction effects between parameters were significant at $P < 0.05$ level (Table S12).

3.4. N_2O production from soil with and without nitrate and sulfate amendment

The N_2O production rate in peat soil without added NO_3^- and SO_4^{2-} was 4–5 orders of magnitude lower than the release of C as CO_2 (0.1–1.2 ng N g^{-1} h^{-1}). In two cases – hummocks at 15 cm and hollows at 50 cm – a negative flux (uptake) was recorded

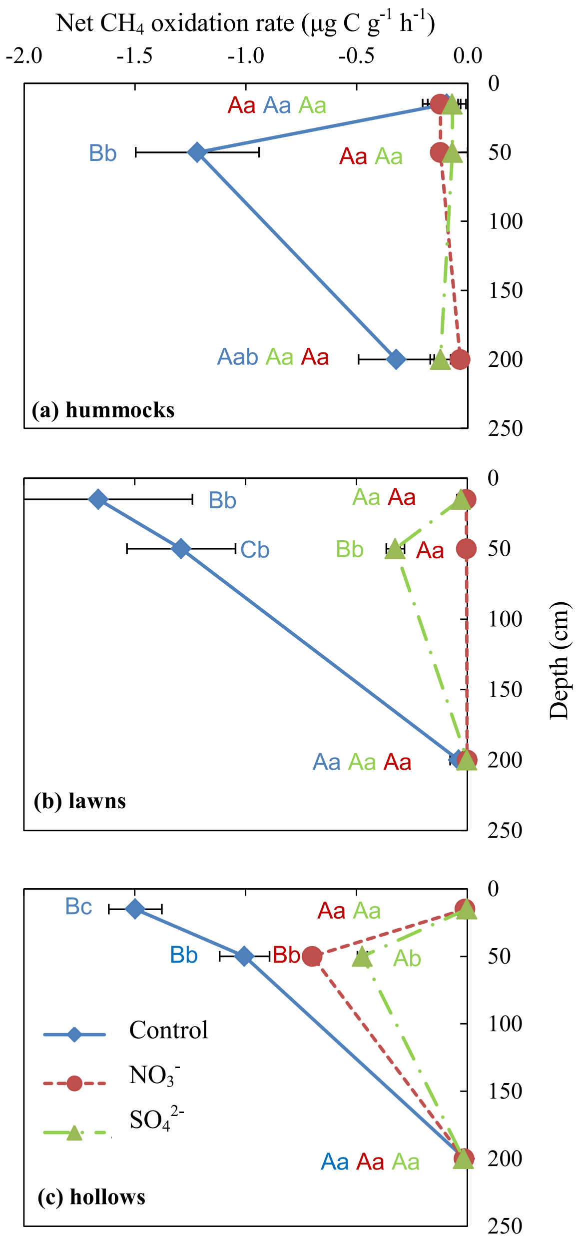

Fig. 2. Net CH_4 oxidation (per gram (g) of peat dry weight) for: a) hummocks, b) lawns and c) hollows with and without addition of NO_3^- and SO_4^{2-}. Values are averages of three replicates over the incubation period (±SE). Values followed by different letters are significantly different between the three treatments of the same depth of each microform (uppercase letters) and between the three depths under each treatment within the same microform (lowercase letters) at $P \leq 0.05$.

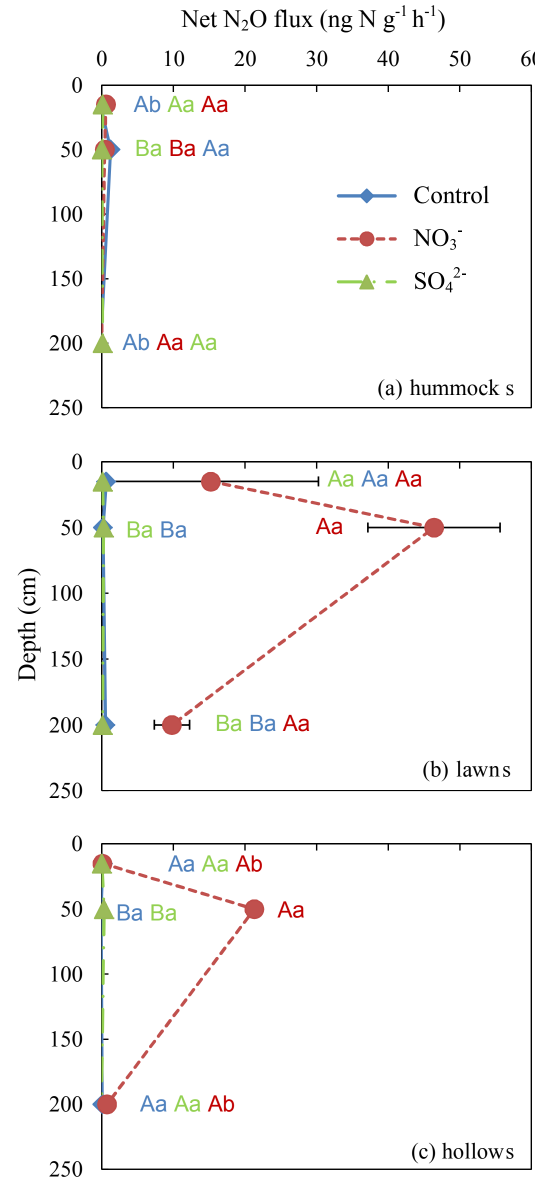

Fig. 3. Net N_2O flux (per gram (g) of peat dry weight) for: a) hummocks, b) lawns and c) hollows with and without addition of NO^{3-} and SO_4^{2-}. Values are averages of three replicates over the incubation period (±SE). Values followed by different letters are significantly different between the three treatments of the same depth of each microform (uppercase letters) and between the three depths under each treatment within the same microform (lowercase letters) at $P \leq 0.05$.

(Fig. 3). This indicated an overall low natural N_2O production potential for the studied boreal peatland. Addition of SO_4^{2-}did not change the pattern observed in the unamended soil, whereas NO_3^- amendment resulted in the N_2O release. Thus, the highest rate of 46.4 ± 9.1 ng N g^{-1} $h^{-1}$was measured for lawns at 50 cm depth (Fig. 3b), followed by a 2-fold lower rate (21.3 ± 0.7 ng N g^{-1} h^{-1}) for hollows at the same depth (Fig. 3c). The rate of N_2O production was significantly increased after NO_3^- amendment for lawns at 200 cm, whereas in the topsoil of lawns, as well as in the top and bottom horizons of hollows, the N_2O production did not significantly differ from that of the unamended soil. The addition of NO_3^- had no effect in soil of hummocks from any depth (Fig. 3a). This also reflected the insignificant interaction effect between microform type and depth (Table S13), whereas other main effects of microform type, depth and treatment with other respective interaction effects were highly significant ($p < 0.01$).

3.5. CO_2 produced from oxidation of labeled CH_4

Application of ^{13}C-labeled CH_4 allowed the tracing of released $^{13}C{-}CO_2$ (Fig. 4), and a comparison with the mass-based CH_4 oxidation (Fig. 2). In general, the intensity of CH_4 oxidation corresponded to the ^{13}C enrichment of CO_2. Thus, the highest CH_4 oxidation rate measured in topsoil of lawns under the soil without NO_3^- and SO_4^{2-} addition (Fig. 2b) corresponded to the most enriched $\delta^{13}C{-}CO_2$ (up to 170‰) detected in the same treatment, microform and depth (Fig. 4b). CH_4 oxidation in hummocks (50 cm, control),

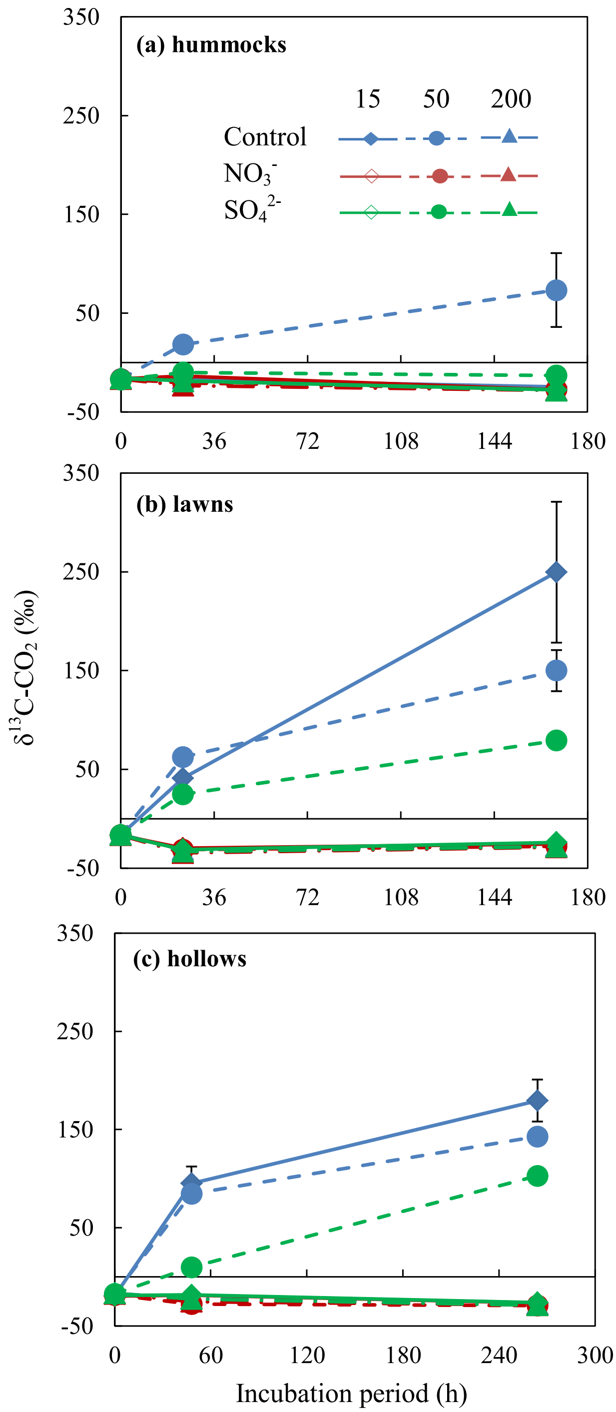

Fig. 4. Delta^{13}C of CO_2 values for: a) hummocks, b) lawns and c) hollows with and without addition of NO^{3-} and SO_4^{2-}. Diamonds, circles and triangles represent three depth horizons (15, 50 and 200 cm), respectively. Values are averages of three replicates (±SE).

lawns (50 cm, control and SO_4^{2-}) and hollows (15 cm, control; 50 cm, control and SO_4^{2-}) corresponded well with the respective dynamics of $\delta^{13}C$–CO_2 values (Fig. 4). However, for soil from 50 cm depth of hollows with NO_3^- addition (Fig. 2c) the substantial rate of CH_4 oxidation did not result in production of labeled CO_2 (i.e. CO_2 originating from CH_4 oxidation), $\delta^{13}C$–CO_2values were close to the natural abundance of CO_2 efflux (Fig. 4c). For other samples, their much less intensive or near-zero CH_4 oxidation rates revealed no clear ^{13}C–CO_2 enrichment, which was most probably diluted and masked by the background CO_2 derived from SOM decomposition. Moreover, $\delta^{13}C$ values of CO_2 decreased (became more negative) during incubation and this decrease was more pronounced with NO_3^- and SO_4^{2-} addition, indicating an increasing contribution of native SOM decomposition with time.

3.6. *Relationship between microbial biomass carbon and new $^{13}CH_4$-derived carbon in soil*

Microbial biomass C (MBC) content was highest at 50 cm depth for all microforms (Fig. 5). Between microforms, lawns contained the highest MBC (Fig. 5b). Amendment with NO_3^- and SO_4^{2-} resulted in an overall decrease of the DNA-extractable C relative to the unamended soil (Fig. 5). Thus, for hummocks, MBC was 41–62% lower with NO_3^- and 23–57% lower with SO_4^{2-}as compared with the unamended soil, depending on depth. For lawns, the decrease was 33–50% and 26–54% with NO_3^- and SO_4^{2-} amendment, respectively. Addition of NO_3^- in hollows decreased the MBC content by 12–57% and the decrease due to SO_4^{2-} amendment was 0–81% between all depths (Fig. 5).

The ^{13}C enrichment of total OM before and after the incubation experiment (Table 1S) and the portion of new^{13}C–CH_4 incorporation into OM showed new C share from the MBC (Fig. 5, X-axis). As the MBC constitutes a part of the total OM in soil, the new C was derived from microorganisms consuming CH_4 (methanotrophs). The relationship between total MBC and the amount of new C roughly demonstrates the relative contribution of methanotrophs to the total microbial biomass in various microforms (Fig. 6).

The amount of new CH_4-derived C for hummocks without addition of anions increased with depth (15 < 50<200 cm). The amendment with NO_3^- did not reveal particular trend (50 > 15>200 cm), whereas a decreasing trend was detected with depth with SO_4^{2-} addition (15 > 50>200 cm) (Fig. 5a). In soil after the addition of NO_3^- and SO_4^{2-}, the ratio of new $^{13}CH_4$-derived C to total MBC was highest in the top horizon, indicating a greater presence of methanotrophs or their higher activity as compared with deeper soil horizons (Fig. 6, hummocks). However, this was not true in soil without addition, for which no measurable differences in new C incorporation and microbial biomass (negative values) were detected between different depths (Fig. 6, hummocks).

In contrast to hummocks, the observed incorporation of new CH_4-derived C in soil from lawns without NO_3^- and SO_4^{2-} amendment decreased with depth: 15 > 50>200 cm. The same pattern was detected after NO_3^- addition. No clear depth effect was recorded after SO_4^{2-} addition: 50 > 15>200 cm (Fig. 5b). The highest ratio ofnew $^{13}CH_4$-derived C to total MBC was detected in the topsoil (Fig. 6, lawns). NO_3^- amendment promoted incorporation of new C which comprised up to 100% of MBC, whereas SO_4^{2-} addition did not affect the ratio of new C to MBC as compared to other treatments at 15 cm depth. The relatively low ratio of new C to MBC in deeper horizons in comparison to the topsoil may result from several factors: (i) "dilution" by abundant unlabelled MBC e.g. at 50 cm depth, Fig. 5b, (ii) much lower activity of methanotrophs at the very depth (200 cm) and/or (iii) low level of electron acceptors in soil microzones of the bottom horizon, where O_2 diffusion is restricted due to the overall high moisture content.

For hollows, the highest amount of new C (more than 70 µg g^{-1}) was observed for unamended soil from 50 cm depth, followed by 15 cm depth, whereas no incorporation of new C was detected for 200 cm depth under the same treatment (Fig. 5c). NO_3^- and SO_4^{2-} amendments decreased the amount of new C at 15and 50 cm as compared to the control. In contrast, at 200 cm,

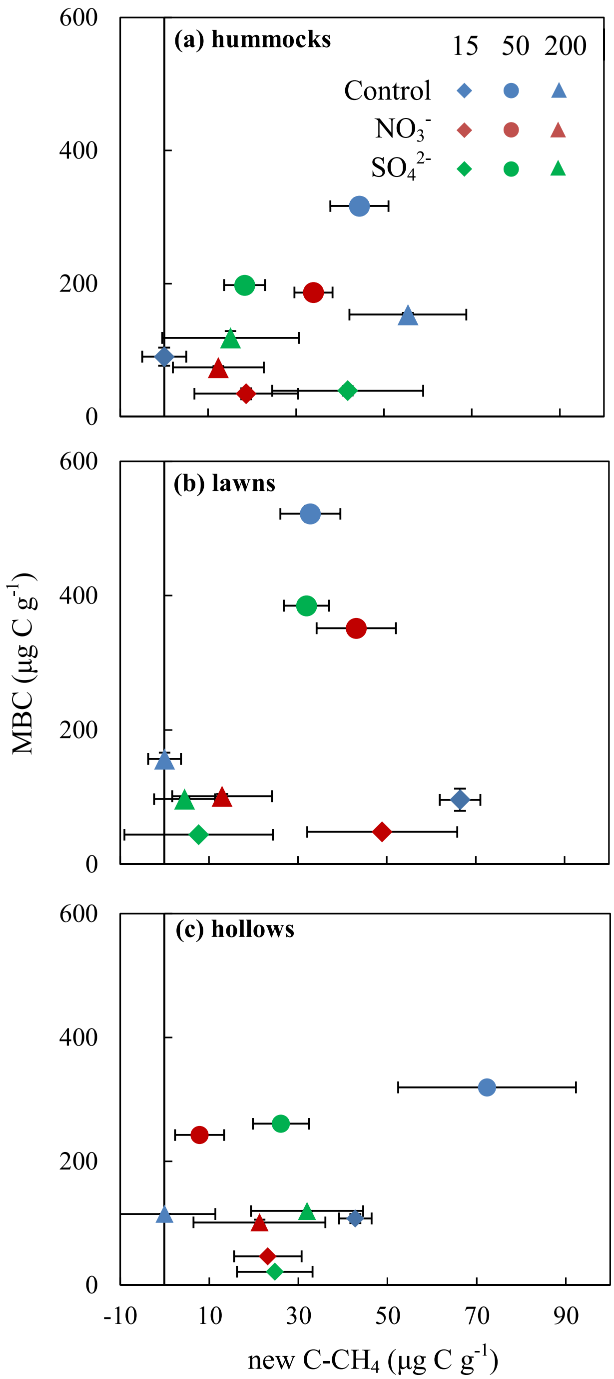

Fig. 5. Amount of microbial biomass carbon (MBC) and amount of new $^{13}CH_4$-derived carbon (per gram (g) of peat dry weight) for: a) hummocks, b) lawns and c) hollows with and without addition of NO^{3-} and SO_4^{2-}. Diamonds, circles and triangles represent three depth horizons (15, 50 and 200 cm), respectively. Values are averages of three replicates (±SE).

the new CH_4-derived C increased after the addition of NO_3^- and SO_4^{2-} (Fig. 5c). Similar to hummocks and lawns, the ratio of new C to MBC in hollows was higher in the topsoil of the control treatment as compared to 50 and 200 cm and further increased after the addition of NO_3^- and especially of SO_4^{2-} (Fig. 6, hollow). There was no difference in the ratio of new C to MBC between soils with and without NO_3^- and SO_4^{2-} addition for 50 and 200 cm-deep horizons.

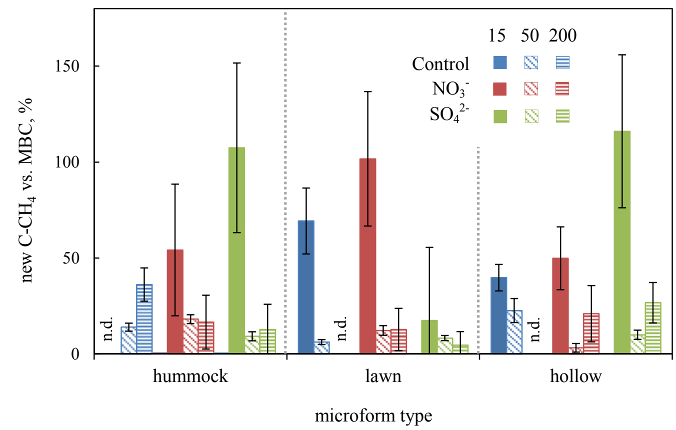

Fig. 6. Proportion between new $^{13}CH_4$-derived carbon and total MBC content for hummocks, lawns and hollows in three depth horizons. The source of the values is data from Fig. 5 (new $^{13}CH_4$–C/MBC*100%). Blue color corresponds to the control treatment (without NO^{3-} and SO_4^{2-}), red to NO^{3-} and green to SO_4^{2-} amendment. Uniformly filled bars and bars with downward diagonal and horizontal patterns represent the three depth horizons (15, 50 and 200 cm), respectively. Values are averages of three replicates (±SE). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Effect of microform types and soil depth on CO_2 efflux, CH_4 oxidation and N_2O production (hypothesis 1 and 2)

The lowest CO_2 efflux was attributed to the hollows (Fig. 1, blue color), which naturally experience stronger anaerobic conditions due to the higher water table (WT) level as compared to lawns and hummocks (Becker et al., 2008; Dorodnikov et al., 2013). However, the pattern was not clearly linked to O_2 availability: the overall CO_2 efflux of the driest microform – hummocks – did not significantly differ from the wettest hollows (data not shown). *In vitro* conditions strongly decreased limitations of fluctuating natural environmental factors, thereby revealing the differences in the constituent soil properties. Therefore, under controlled conditions, i) the type and abundance of decomposers (Basiliko et al., 2007; Strakova et al., 2012), and consequently ii) the quality and quantity of the substrate they are decomposing (Moore and Dalva, 1997; Yavitt et al., 2000; Blagodatskaya et al., 2010; Strakova et al., 2012) become the main determinants of CO_2 fluxes among the microforms. Thus, the MBC explained ca. 21% of the variation in all measured CO_2 fluxes (Fig. S1a). The highest correlation ($R^2 = 0.75$) was observed in soil of the top 15 cm horizon, with and without NO_3^- and SO_4^{2-} (Fig. S1d). Within the total microbial population, part of the CO_2 efflux was also connected with the activity of methanotrophs. However, we observed a negative relationship (Fig. S2a): samples showing higher CH_4 oxidation did not express increased CO_2 efflux. Between microforms, such a pattern was the most pronounced in hummocks (explaining 49% of the measured variation, Fig. S2b), and between depths – in the topsoil of microforms (explaining 68% of the variation, Fig. S2d). Therefore, measured soil CO_2 efflux conditionally confirmed the hypothesis of more intensive OM decomposition in soils better adapted to aerobic conditions (Hypothesis 1) and was related to MBC. However, seemingly other environmental factors as oxygen availability controlled MBC distribution and related CO_2 fluxes among the microforms (see below). Decrease in CO_2 production with the microforms' depth was hypothesized to be linked with SOM turnover through the depletion of fresh plant-derived C inputs available for decomposition and strict anaerobic conditions. Aerobic decomposition in the topsoil typically reduces the quality of litter entering the deeper horizons (Strakova et al., 2012), thereby affecting CO_2 production (Saarnio et al., 1998). Since the organic C content increased with depth (Table 1), the occurrence of the lowest CO_2 production at the bottom of the profile for all microforms (Fig. 1) can be attributed to (i) the properties of the substrate for decomposition and (ii) properties of the soil microbial biomass (e.g. strict anaerobes at the bottom soil horizons could not tolerate the increased O_2 availability in the incubation experiment). Remarkably, decomposability of the organic substrate in the studied soil could not be described by the commonly used C:N parameter, because the significant decrease of C:N with depth (Table 1) was uncoupled from the rate of CO_2 efflux (Fig. 1). In contrast to the hypothesized patterns (Hypothesis 2), in hummocks and especially in lawns, the highest CO_2 efflux corresponded to 50 cm depth and not to the topsoil. This highest CO_2 efflux was related to the largest microbial biomass content at this depth (Fig. 5, Y-axis, blue color) and the positive correlation between both parameters explained 34% of their variation (Fig. S1d).

While the natural aeration gradient is partly responsible for differences in CO_2 production from the microforms, this gradient was not associated with the expected CH_4 oxidation patterns. Namely, there was higher CH_4 oxidation where natural aeration is lower, e.g. in lawns and hollows rather than hummocks (Fig. 2, blue color). Several authors have reported positive correlation between CH_4 fluxes and CH_4 oxidation rates (Basiliko et al., 2007; Hornibrook et al., 2009). This may suggest that CH_4 oxidation is substrate (CH_4)-dependent rather than limited by the availability of O_2 (Sundh et al., 1994; Saarnio et al., 1997). Current data demonstrate that in the topsoil of hummocks, neither mass-based oxidation (Fig. 2a) nor the incorporation of new $^{13}C{-}CH_4$ to the total OM (Fig. 5a), nor its ratio to MBC (Fig. 6), suggest high oxidation potential of the aerobic zone of hummocks. Instead, low *in situ* CH_4 fluxes from these microforms are presumably related to their low methanogenic potential (Saarnio et al., 1997).

Interestingly, indirect evidence of methanotrophic activity, shown as a relationship between the amount of new C derived from CH_4 and the CO_2 flux (Fig. S3), demonstrated the highest correlation ($R^2 = 0.64$) at 50 cm depth for all microforms (Fig. S3d). The correlation between new CH_4-derived C incorporated into OM during incubation and CH_4 oxidation was surprisingly weak, explaining only 9% of the overall variation between the two variables (Fig. S4a). However, the estimated negative relationship between new C and CH_4 oxidation generally counteracted the observed production of labeled CO_2 (Fig. 4) and a positive correlation between MBC content and new C (Fig. S5a). Relatively weak correlation between new C and CH_4 oxidation, as well as between new C and MBC, was observed because the oxidized $^{13}CH_4$ was either 1) strongly diluted in the bulk of organic matter or 2) was rapidly turned over and released as $^{13}CO_2$ without substantial incorporation into SOM.

The production of N_2O in the microforms and with the depth of the unamended soil (reference, natural conditions) appeared to be not testable with the proposed hypotheses as the majority of fluxes showed close to "zero" rates (Fig. 3, blue color). Markedly low N_2O flux was most probably related to the analytical approach as the substantial dilution of the headspace gas samples with N_2 was required for the equipment. Still, the occurrence of microorganisms responsible for nitrification/denitrification processes was indirectly revealed in two of the three microforms (lawns and hollows) after the addition of NO_3^- (Fig. 3b, c).

Summarizing, the expected increase in the GHG production with the naturally established aeration zone of microforms (Hypothesis 1) was conditionally approved for CO_2 fluxes (hollows < hummocks ≤ lawns), whereas CH_4 oxidation potential was the lowest in the most aerated hummocks followed by hollows and lawns. With depth, neither CO_2 fluxes, nor CH_4 oxidation and N_2O production revealed the expected gradual decrease (Hypothesis 2 rejected). Instead, the highest values corresponded to the 50 cm peat horizon. Therefore, the *in situ* differences in oxygen availability among the studied microforms appeared to be less significant factor for GHG dynamics, whereas other constituent soil properties, such as the microbial biomass content, were responsible for GHG dynamics.

4.2. Effects of nitrate and sulfate addition on CO_2 efflux, CH_4 oxidation and N_2O production (hypothesis 3)

In *in vitro* incubation, there is no competition with plants and the soil microorganisms have access to the whole amount of NO_3^- and SO_4^{2-} added. The properties of the microbial community inherited from *in situ* conditions revealed differences between microforms and depths. In general, addition of NO_3^- and SO_4^{2-} suppressed CO_2 production, as compared to soil without addition, for all microforms (Fig. 1; significant effect of the treatment, Table S11). These results do not support the hypothesis of increased CO_2 fluxes due to the nutritional effect of NO_3^- and SO_4^{2-} (Hypothesis 3). Suppression due to NO_3^- addition was less pronounced as compared to SO_4^{2-} amendment (change in MBC under NO_3^- treatment could explain just 4% of the variation in CO_2 flux vs. 29% under SO_4^{2-} addition, Fig. S1c). This confirms that NO_3^- participated in processes related to the broader functionality of the microbial community, not just the decomposition of SOM.

CH_4 oxidation was suppressed under NO_3^- and SO_4^{2-} addition (Fig. 7; treatment main effects, Table 12S). On average 40% lower CH_4 flux was measured in soil from several northern peatlands after the addition of SO_4^{2-}, whereas around 90% reduction was measured with added NO_3^- in comparison to reference soil (Dettling et al., 2006). However, it remained unclear whether the decrease resulted from the CH_4 oxidation or suppression of methanogenesis. The latter phenomenon was explained, in the case of NO_3^- amendment, by the occurrence of denitrification intermediates such as nitrite (NO_2^-), nitrogen dioxide (NO_2), nitric oxide (NO), which are known to have suppressing effects on CH_4 production (Chen and Lin, 1993; Clarens et al., 1998; Eriksson et al., 2010). Despite decreased CH_4 oxidation in amended soil, the proportion between new C incorporation to SOM and MBC content showed the highest values (up to 100%) under both NO_3^- and SO_4^{2-}, especially in the topsoil (Fig. 6, green and red color). This finding may indicate the following processes: (i) increased substrate use efficiency by methanotrophs in the topsoil as compared with deeper soil horizons, when $^{13}C{-}CH_4$ retains in microbial cells instead of being quickly metabolized and respired (thus, no pronounced $^{13}C{-}CO_2$ enrichment was detected (Fig. 4)); (ii) relative suppression of methanotrophs due to NO_3^- and SO_4^{2-} amendment was not as intensive as of other microbial groups because total MBC decreased under the respective treatments (Fig. 5); (iii) predation of methanotrophs by other microorganisms or animals distributed the ^{13}C label within the soil but diluted $^{13}CO_2$ with $^{12}CO_2$ from other metabolic processes. These mechanisms should be tested in separate experiments with the determination of microbial community structure. Although the decreased CH_4 oxidation was assumed to be due to the more energetically favorable processes, e.g. nitrification/denitrification (Hypothesis 3 was conditionally supported), a positive correlation between CH_4 oxidation and new C in SOM was detected under NO_3^- amendment (Fig. S4c, relationship explained 57% of the observed variation). This may suggest that CH_4 oxidation was not fully outcompeted by denitrification or other processes, e.g. anaerobic oxidation of methane (AOM) may occur (see below).

Similar to soil without additions, SO_4^{2-} had no significant effect on N_2O production and the fluxes were close to zero for all microforms and depths (Fig. 3, green color) suggesting that S was not a

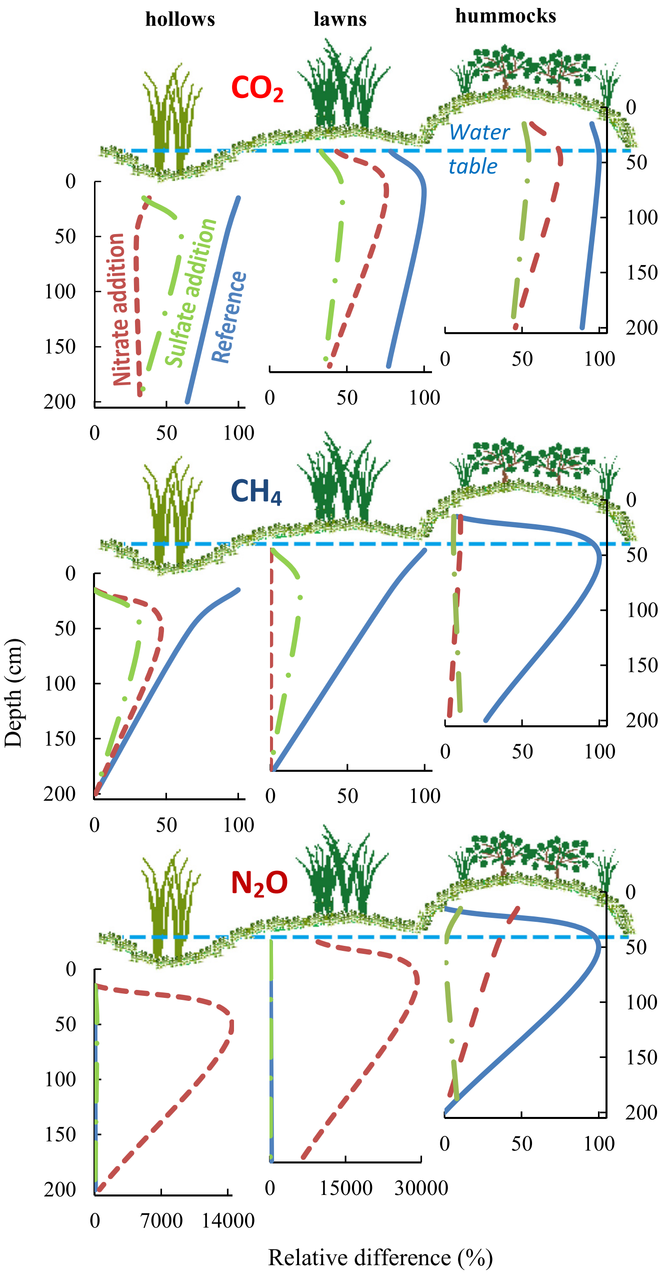

Fig. 7. Effects of sulfate (green dashed-dotted lines) and nitrate (red dashed lines) additions on fluxes of CO_2 (top), CH_4 (middle) and N_2O (bottom) for hummocks, lawns and hollows at increasing peat depth as compared to a control treatment without addition (reference, blue line). Effects are shown as relative difference between control treatment (100%) and respective sulfate or nitrate treatments. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

limiting nutrient for nitrifying/denitrifying microorganisms. As expected, NO_3^- amendment increased N_2O production in comparison to unamended soil (by 15,000-30,0000%), but the effect was observed only for lawns at 50 and 200 cm and for hollows at 50 cm (Fig. 7). Surprisingly, no effect of NO_3^- addition on N_2O was measured for hummocks at any depth (Fig. 3a). Such a contrasting pattern between microforms and depths could be related to strong variations in microbial community structure (Kotiaho et al., 2013; Deng et al., 2014) and multiple factors may affect the occurrence and/or activity of nitrifying/denitrifying microorganisms.

It is important to note, that in hollows at 50 cm both N_2O production and CH_4 oxidation were observed under NO_3^- addition (Figs. 2c and 3c). Despite the aerobic incubation, the water content of the peat soil reached 95% by weight, therefore microzones with anaerobic conditions may have persisted in the samples during the experiment. Hence, the CH_4 oxidation could also happen via AOM processes (Smemo and Yavitt, 2011). AOM based on NO_3^- as an alternative electron acceptor to oxygen was predicted to occur in peatlands, because reduction of N oxides provides sufficient free energy to fuel CH_4 oxidation (Smemo and Yavitt, 2011). The potential of added NO_3^- and SO_4^{2-} as electron acceptors for AOM in the studied soil would have to be tested under anaerobic conditions in a separate experiment.

5. Conclusions

The undertaken measurements of CO_2 and N_2O production, CH_4 oxidation, microbial biomass content and incorporation of $^{13}CH_4$-derived C into peat soil samples with and without amendment of NO_3^- and SO_4^{2-}, lead to the following conclusions:

- Effects of microforms: CO_2 efflux decreased in the order lawns ≥ hummocks > hollows (Hypothesis 1 conditionally accepted), however CH_4 oxidation did not follow the naturally established aerobic zone of a microform type and increase from hollows to lawns and to hummocks. In contrast to oxygen availability, MBC content was the key factor controlling the processes in the microforms. Patterns of N_2O production were not testable with the Hypothesis 1 due to low fluxes in peat under natural conditions.
- Effects of depth: CO_2 efflux, CH_4 oxidation and N_2O fluxes did not confirm the hypothesized descend with depth due to *in situ* decreasing availability of oxygen and fresh plant-derived deposits (Hypothesis 2). Remarkably, the highest GHG fluxes as well as MBC content were observed at 50 cm depth below all microforms (Fig. 7).
- Effects of NO_3^- and SO_4^{2-} amendments: CO_2 efflux decreased under both NO_3^- and SO_4^{2-} amendments as compared to soil without addition, for all microforms and depths, following the decrease in the microbial DNA-extractable C. This rejected the nutritional aspect in the Hypothesis 3. Contrastingly, the CH_4 oxidation was retarded by 20–94% after the amendment and did not generally coexist with the N_2O production, hereby supporting the preferential process aspect in the Hypothesis 3.

6. Outlook

In a broader ecological view, nitrate and sulfate deposition may suppress CO_2 efflux, which is positive for GHG mitigation and climate change. On the other hand, CH_4 oxidative potential could be suppressed either. This would lead to more intensive CH_4 release to the atmosphere, presumably due to the CH_4 produced from older C stored in the system, thereby compensating positive effect of reduced CO_2 production. Moreover, increased NO_3^- deposition would stimulate N_2O formation and promote contribution of this very potent GHG to the atmosphere. Taken together, human-induced deposition of NO_3^- and SO_4^{2-} may suppress CO_2 emissions from and CH_4 oxidation by boreal oligotrophic mires especially under the conditions of deposition increase. Therefore, the deposition of inorganic compounds is strongly important to be considered in the estimation of ecosystem C and N balances.

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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.2016.06.018.

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