

## How do sand addition, soil moisture and nutrient status influence greenhouse gas fluxes from drained organic soils?



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### ABSTRACT

Drainage turns peatlands from natural carbon sinks into hotspots of greenhouse gas (GHG) emissions from soils due to alterations in hydrological and biogeochemical processes. As a consequence of drainage-induced mineralisation and anthropogenic sand addition, large areas of former peatlands under agricultural use have soil organic carbon (SOC) contents at the boundary between mineral and organic soils. Previous research has shown that the variability of GHG emissions increases with anthropogenic disturbance. However, how and whether sand addition affects GHG emissions remains a controversial issue. The aim of this long-term incubation experiment was to assess the influence of hydrological and biogeochemical soil properties on emissions of carbon dioxide (CO<sub>2</sub>), nitrous oxide (N<sub>2</sub>O) and methane (CH<sub>4</sub>). Strongly degraded peat with sand addition (peat-sand mixtures) and without sand addition (earthified peat) was systematically compared under different moisture conditions for fen and bog peat. Soil columns originating from both the topsoil and the subsoil of ten different peatlands under grassland use were investigated. Over a period of six months the almost saturated soil columns were drained stepwise *via* suction to –300 hPa. The CO<sub>2</sub> fluxes were lowest at water-saturated and dry soil moisture conditions, resulting in a parabolic dependence of CO<sub>2</sub> fluxes on the water-filled pore space (WFPS) peaking at 56–92% WFPS. The highest N<sub>2</sub>O fluxes were found at between 73 and 95% WFPS. Maximum CO<sub>2</sub> fluxes were highest from topsoils, ranging from 21 to 77 mg C m<sup>-2</sup> h<sup>-1</sup>, while the maximum CO<sub>2</sub> fluxes from subsoils ranged from 3 to 14 mg C m<sup>-2</sup> h<sup>-1</sup>. No systematic influence of peat type or sand addition on GHG emissions was found in topsoils, but CO<sub>2</sub> fluxes from subsoils below peat-sand mixtures were higher than from subsoils below earthified peat. Maximum N<sub>2</sub>O fluxes were highly variable between sites and ranged from 18.5 to 234.9 and from 0.2 to 22.9 μg N m<sup>-2</sup> h<sup>-1</sup> for topsoils and subsoils, respectively. CH<sub>4</sub> fluxes were negligible even under water-saturated conditions. The highest GHG emissions occurred at a WFPS that relates – under equilibrium conditions – to a water table of 20–60 cm below the surface in the field. High maximum CO<sub>2</sub> and N<sub>2</sub>O fluxes were linked to high densities of plant-available phosphorus and potassium. The results of this study highlight that nutrient status plays a more important role in GHG emissions than peat type or sand addition, and do not support the idea of peat-sand mixtures as a mitigation option for GHG emissions.

### 1. Introduction

Globally, peatlands hold more than one third of the soil organic carbon (SOC) store (Scharlemann et al., 2014; Yu et al., 2010), although they cover just 330 to 463 million ha (2.2–3%) of the global terrestrial surface (Leifeld and Menichetti, 2018; Tubiello et al., 2016). A total of 22.5–50.9 million ha of peatlands worldwide have been drained for agricultural use (Leifeld and Menichetti, 2018; Tubiello et al., 2016), 60% of which are located in Europe alone (Tubiello et al., 2016). Intact

peatlands are a net sink of carbon dioxide (CO<sub>2</sub>) but release methane (CH<sub>4</sub>) (Wilson et al., 2016). Drainage, however, turns peatlands into sources and hotspots for CO<sub>2</sub> and nitrous oxide (N<sub>2</sub>O) emissions from soils while, at the same time, they are either minor sources or even small sinks of CH<sub>4</sub> (Maljanen et al., 2010; Tiemeyer et al., 2016).

Besides increased mineralisation of soil organic matter (SOM) by aerobic decomposition, drainage causes soil consolidation due to the loss of buoyancy. Both processes lead to the subsidence of the soil surface and the initiation of secondary pedogenetic processes in peat.

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With this formation of aggregates, shrinkage cracks and earthification, the peat structure gradually changes (Ilnicki and Zeitz, 2003). As a consequence, soil physical properties of drained organic soils differ from undisturbed peat soils. For example, macroporosity and total porosity are lower while bulk density ( $\rho$ ) is higher in drained organic soils (Dettmann et al., 2014; Schwärzel et al., 2002; Zeitz and Velty, 2002).

As a consequence of both the preferential release of  $\text{CO}_2$  by mineralisation and fertilisation, the chemical composition of peat changes and N, phosphorus (P) and potassium (K) contents increase in topsoils of agriculturally used peatlands (Holden et al., 2004; Laiho et al., 1998). The increase in nutrient densities is even greater, partly due to the simultaneous increase in bulk density. In agricultural peatlands, nutrients are furthermore added as fertilizer. Field studies have shown that the  $\text{CO}_2$  emissions depend on N densities in the aerobic zone (Tiemeyer et al., 2016). Previous studies on N, P and K addition have demonstrated an increase in microbial respiration with increasing nutrient content (Larmola et al., 2013; Pinsonneault et al., 2016; Sundström et al., 2000). The availability of P has a positive influence on  $\text{CO}_2$  (Amador and Jones, 1993; Brake et al., 1999) and  $\text{N}_2\text{O}$  fluxes (Liimatainen et al., 2018; Regina et al., 1996).

In addition to drainage, peat soils may have been covered by mineral soil (mainly sand) (Göttlich, 1990) to enhance trafficability and increase yields. Under ideal circumstances the sand layer should only be ploughed shallowly, however at most sites the underlying peat has subsequently been mixed with the sand which creates peat-sand mixtures (Fig. S1). These topsoils are not to be confused with the “German sand-mixing culture” by which deep ploughing into the mineral subsoil has created alternating tilted bars of sand and peat (Fig. S1). Mixing peat with sand adds to and intensifies the alteration of soil physical parameters and soil structure. As a result the soil hydraulic properties are also changed which is reflected by the percentage of different pore sizes (Rovdan et al., 2002; Walczak and Rovdan, 2002). Soil hydraulic properties are crucial for the response of soil moisture to boundary conditions (groundwater level, precipitation, evapotranspiration) as the same boundary conditions will result in different water contents. Furthermore, changes in the physical structure of peat affect decomposition rates and nutrient mobilisation (Ross and Malcolm, 1988).

As a joint consequence of drainage-induced mineralisation and peat-sand mixing, peatlands under agricultural use can have SOC contents at the boundary between mineral and peat soils ( $> 300 \text{ g SOM kg}^{-1}$  according to the German classification system, Ad-hoc AG Boden, 2005). Studies on SOC dynamics of such “low C organic soils” are rare, but a synthesis study on 48 drained grasslands has shown that emissions of  $\text{CO}_2$  and  $\text{N}_2\text{O}$  from “low C organic soils” are as high as emissions from “true” peat soils (Tiemeyer et al., 2016). Tiemeyer et al. (2016) also reported that there is a large variability in GHG emissions from these soils, which cannot easily be explained due to the interaction of soil properties, hydro-meteorological conditions and management in field studies. Field studies, however, have shown that SOC content in the topsoil does not influence  $\text{CO}_2$  emissions (Leiber-Sauheitl et al., 2014) or that  $\text{CO}_2$  emissions actually increase when peat is mixed with mineral soil (Maljanen et al., 2004). Others have found that the German sand-mixing culture (Bambalov, 1999) as well as sand cover on peat (Höper, 2015; Zaidelman and Shvarov, 2000) may reduce  $\text{CO}_2$  emissions. Therefore, laboratory studies with defined boundary conditions such as temperature and moisture can help identify to factors that control GHG emissions and allow a systematic evaluation of the hydrological, biogeochemical and management-induced drivers.

There are multiple laboratory studies on GHG fluxes from peat soils. These studies have frequently used constant water content (Ausec et al., 2009; Hardie et al., 2011) or studied the influence of soil moisture on GHG emissions using disturbed samples (Hogg et al., 1992; Moore and Dalva, 1997; Moore and Knowles, 1989). Under such circumstances, the effects of soil physical parameters cannot be captured. However, there are some studies on GHG emissions that have incubated intact samples

at different water contents, but the samples only came from one or two sites (Berglund and Berglund, 2011; Brouns et al., 2016; Kechavarzi et al., 2010; Norberg et al., 2018; van Lent et al., 2018) or GHG sampling only occurred sporadically (Berglund and Berglund, 2011; Norberg et al., 2018; van Lent et al., 2018). There is a lack of a systematic evaluation of hydrological and biogeochemical factors, such as peat type and nutrient availability, influencing GHG fluxes on a broader basis using intact samples. Furthermore an investigation of “low C organic soils” in such laboratory experiments is missing. As sand addition on peatlands is a common practice e.g. in northern Germany (Schulz and Waldeck, 2015) and Norway (Sognnes et al., 2006) and is sometimes proposed as an emission mitigation measure (Bambalov, 1999; Zaidelman and Shvarov, 2000), the focus of the present study was on peat-sand mixtures.

Soil columns originating from six fen and four bog peatlands under grassland use were investigated. Half of these peatlands have anthropogenic peat-sand mixtures as topsoils. The aim of this long-term incubation experiment was to assess the influence of hydrological and biogeochemical soil properties on GHG emissions from drained organic soils with and without sand addition. Accordingly, we had four major objectives: (i) to identify the optimum soil moisture for the occurrence of maximum GHG fluxes, (ii) to assess the impact of sand addition to the peat topsoil on GHG fluxes, (iii) to analyse the sensitivity to drainage of different peat types by comparing topsoils and subsoils as well as fen and bog peat, and (iv) to determine the importance of nutrient contents for GHG fluxes.

## 2. Material and methods

### 2.1. Sampling sites

The choice of sampling sites was based on profile descriptions and soil properties acquired within the German Agricultural Soil Inventory, in which agricultural soils of Germany were sampled in an  $8 \times 8 \text{ km}$  grid (Vos et al., 2018). The selection criteria included grassland use, the presence of a well-preserved peat horizon in the soil profile and the best possible coverage of the SOC, C:N ratio and pH value ranges. Six fen peat and four bog peat sites were sampled. All the sites have a well-preserved peat subsoil horizon that is permanently below groundwater level and either a strongly degraded (“earthified”) topsoil horizon or sand added and mixed to different degrees into the topsoil (“peat-sand mixture”; Table 1; Fig. 1). Around 2200 to 2500 t sand  $\text{ha}^{-1}$  (bog peat-sand mixtures) or 600 to 800 t sand  $\text{ha}^{-1}$  (fen peat-sand mixture) were added 35–60 years before sampling. For sampling, a soil pit was opened at each site down to 1 m to take intact soil columns ( $n = 3$  each) from both the topsoil and the subsoil (upper limits between 5 to 15 and 20–140 cm, respectively, Table S1). Intermediate temporarily water-saturated horizons between strongly decomposed topsoils and well-preserved subsoils were not sampled. Prior to sampling, approximately 5 cm of topsoil including vegetation and roots were removed to avoid artefacts by living biomass and germinating plants during incubation. After digging to the intended depth, the soil was pre-cut with a knife, and plexiglas cylinders (18 cm high, 14.5 cm i.d.) were gently pushed vertically into the soil until the soil column within the cylinder reached a height of 10 cm. Afterwards, the cylinders were carefully dug out. The soil profile was classified according to the German manual of soil mapping (Ad-Hoc-AG Boden, 2005).

### 2.2. Microcosm incubation experiment

The columns were stored in darkness at  $6^\circ\text{C}$  until the commencement of the incubation experiment. Before starting the experiment, the samples were saturated from the bottom until constant weight over a period of three weeks. All 60 soil columns were installed in a microcosm system (Fig. S2; Hantschel et al., 1994) at a constant temperature of  $10^\circ\text{C}$  that approximates the mean annual temperature of Germany.

**Table 1**

Sampling sites and their main soil characteristics. The degree of decomposition in accordance with von Post (H) was determined according to Ad-Hoc-AG Boden (2005), but it is not applicable (NA) for peat-sand mixtures. All topsoils are amorphous peat (partially mixed with sand) without any recognisable plant remains. Sample identifiers: s – peat-sand mixture in the topsoil, e – earthified peat in the topsoil, B – bog, F – fen.

ID	Peatland type	Peat-sand mixture topsoil	Degree of decomposition topsoil subsoil	Peat composition subsoil
sB1	Bog	yes	NA H3	<i>Sphagnum</i> spp., <i>Eriophorum vaginatum</i> L., <i>Ericaceae</i>
sB2	Bog	yes	NA H2	<i>Sphagnum</i> spp., <i>Scheuchzeria palustris</i> L., <i>Ericaceae</i>
eB1	Bog	no	H10 H4	<i>Sphagnum</i> spp., <i>Scheuchzeria palustris</i> L., <i>Ericaceae</i>
eB2	Bog	no	H10 H2	<i>Sphagnum</i> spp., <i>Ericaceae</i> (i.a. <i>Vaccinium oxycoccos</i> L.)
sF1	Fen	yes	NA H6	<i>Carex</i> spp., <i>Alnus glutinosa</i> (L.) Gaertn.
sF2	Fen	yes	NA H6	<i>Carex</i> spp., <i>Eriophorum vaginatum</i> L., <i>Sphagnum</i> spp., <i>Ericaceae</i>
sF3	Fen	yes	NA H6	<i>Carex</i> spp., <i>Alnus glutinosa</i> (L.) Gaertn.
eF1	Fen	no	H10 H2	<i>Carex</i> spp., <i>Phragmites australis</i> (Cav.) Trin. ex. Steud.
eF2	Fen	no	H10 H3	<i>Carex</i> spp., <i>Phragmites australis</i> (Cav.) Trin. ex. Steud.
eF3	Fen	no	H10 H3	<i>Carex</i> spp.

The head space of the soil columns was permanently flushed with  $10 \text{ mL} \cdot \text{min}^{-1}$  synthetic  $\text{CO}_2$  free air (20%  $\text{O}_2$ , 80%  $\text{N}_2$ ) that was humidified using gas-washing bottles. The use of this gas mixture improves the accuracy of  $\text{CO}_2$  measurements, but precludes the determination of any  $\text{N}_2\text{O}$  or  $\text{CH}_4$  uptake. An automatic flow meter switching every 3 min measured flow rates for each column separately, resulting in one measurement per column every 3 h. The initially water-saturated soil columns were drained via suction plates at the bottom of the columns by increasing the suction step by step, starting at 0 hPa (–20, –30, –60, –150, –300 hPa). Each suction step was continued until soil hydrological equilibrium was achieved and  $\text{CO}_2$  fluxes showed quasi-constant values. The resulting suction steps took 3, 8, 12, 18, 46 and 108 days, respectively.

### 2.3. Analytical methods

Concentrations of  $\text{CO}_2$ ,  $\text{N}_2\text{O}$  and  $\text{CH}_4$  in the headspace gas of each column were measured automatically every 8 h via online gas chromatography (GC-2014, Shimadzu, Kyoto, Japan). The percolate was sampled from the suction bottles when reaching an amount of at least 5 mL and was stored in darkness at  $6^\circ\text{C}$  until further analysis. As the water had passed the membrane of the suction plate ( $0.2 \mu\text{m}$ ), no further filtration was necessary. The dissolved organic carbon (DOC) concentrations were measured using a DimaTOC 2000 (DIMATEC, Essen, Germany). Total dissolved carbon (TDC) and dissolved inorganic carbon (DIC) were measured separately by combustion (TDC  $850^\circ\text{C}$ ; DIC  $165^\circ\text{C}$ ) to calculate DOC as the difference between TDC and DIC.

After the final suction step, the soil columns were dried at  $80^\circ\text{C}$ , sieved to  $< 2 \text{ mm}$  and soil properties were determined for each individual column. The bulk density ( $\rho$ ) was determined by drying the soil

columns at  $80^\circ\text{C}$  until constant mass and subsequent weighing. The porosity was calculated from the weights of the fully saturated soil at the start and the dried soil at the end of the experiment. The texture of the peat-sand mixtures was determined by sieve-pipette analysis (Sedimat 4–12, UGT, Müncheberg, Germany) after aggregate destruction and the removal of salt and soil organic matter using  $\text{H}_2\text{O}_2$  (DIN ISO 11277, 1998).

The pH values were measured with a glass electrode after an extraction with a  $0.01 \text{ mol L}^{-1}$   $\text{CaCl}_2$  solution. Total SOC and total N contents ( $\text{N}_t$ ) were measured by dry combustion (RC 612, LECO Corporation, St. Joseph, USA). Plant-available concentrations of P and K were determined by calcium acetate lactate extraction ( $\text{P}_{\text{CAL}}$  and  $\text{K}_{\text{CAL}}$  respectively) (Schüller, 1969; VDLUFA, 2012). The  $\text{P}_{\text{CAL}}$  concentrations were measured using the molybdenum blue method (Murphy and Riley, 1962) and  $\text{K}_{\text{CAL}}$  concentrations via atomic emission spectroscopy. Calcium acetate lactate extraction is commonly used in agronomics. It mostly determines easily available P and is comparable to Olsen P values (Neyroud and Lischer, 2003). For further data analyses, SOC,  $\text{N}_t$ ,  $\text{P}_{\text{CAL}}$  and  $\text{K}_{\text{CAL}}$  concentrations were converted into densities ( $\text{mg cm}^{-3}$  or  $\mu\text{g cm}^{-3}$ ).

### 2.4. Data analyses

Data analyses were performed using the R software environment (R Core Team, 2018). To compare the results of samples with different porosities, the water-filled pore space (WFPS [-]), i.e. the ratio of volumetric water content at the end of each suction step and saturated volumetric water content, was used as a measure of soil moisture. Despite efforts to minimise loss of water due to gravitation during the installation process, the soil columns had WFPS of between 0.83 and

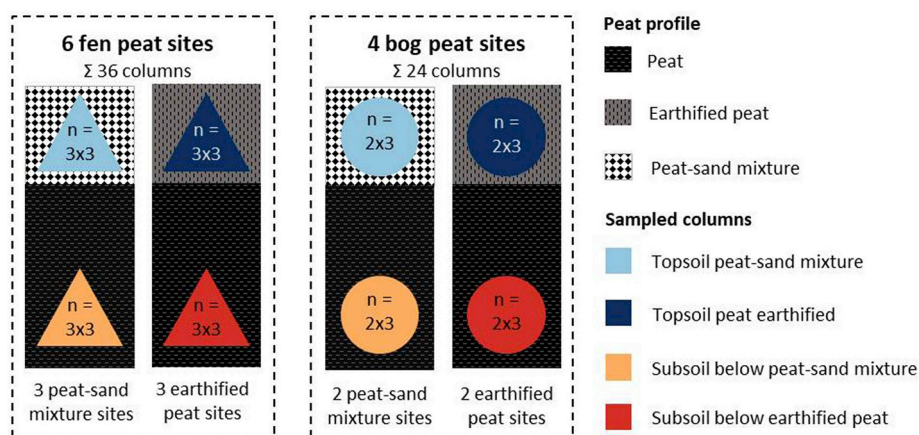


Fig. 1. Schematic overview of the sampling design: 60 soil columns collected from ten different peatland sites.

0.96 at the start of the experiment.

DOC losses for each suction step were calculated by multiplying the amount of percolate by the average DOC concentration of the respective suction step. It was assumed that DOC would largely be mineralised at some point and DOC concentrations were converted into CO<sub>2</sub> and thus named CO<sub>2DOC</sub> (IPCC, 2014).

With Equation (1) the measured gas concentrations *c* (ppm) of CO<sub>2</sub>, N<sub>2</sub>O and CH<sub>4</sub> in the headspace of each column were converted to fluxes for each time step:

$$F = \frac{M}{V_m} c \frac{273.15}{273.15 + T} v 10^{-6} 60 \frac{1}{A} \quad (1)$$

where *F* is the flux in mg C m<sup>-2</sup> h<sup>-1</sup> or μg N m<sup>-2</sup> h<sup>-1</sup> respectively, *M* is the molecular mass in g mol<sup>-1</sup>, *V<sub>m</sub>* is the ideal gas mole volume (22.4 L mol<sup>-1</sup>), *T* is the air temperature of the microcosm system (10 °C), *v* is the flow rate in mL min<sup>-1</sup> and *A* is the cross-sectional area of the soil column in m<sup>2</sup>. The mean and standard error of the last 10 values of each replicate (30 values) of each suction step were used to determine the equilibrium CO<sub>2</sub> fluxes. N<sub>2</sub>O and CH<sub>4</sub> fluxes are given as the mean and standard error of the triplicates over of each suction step due to the erratic behaviour of N<sub>2</sub>O.

The GHG balance was compiled for the -60 hPa suction step. At this point most of the peat's macropores are drained, field capacity is reached (Dettmann et al., 2014) and conditions for microbial activity are favourable. The N<sub>2</sub>O and CH<sub>4</sub> concentrations were converted into CO<sub>2</sub> equivalents by multiplying them by the 100-year time horizon global warming potential of 298 and 25 respectively (Forster et al., 2007).

Spearman's rank correlation coefficient *r* (*n* = 10 when topsoils or subsoils tested separately; *n* = 20 for the whole sample set) was calculated for the fluxes and all measured soil properties using the R package *Hmisc* (Harrell, 2016). This approach allows for nonlinear monotonic relationships. The *p* values were adjusted using the Bonferroni method. All the correlation coefficients given in this paper have *p* values < 0.001 unless stated otherwise. Differences between the CO<sub>2</sub> and N<sub>2</sub>O fluxes of the different treatments were determined using linear mixed effects models with the sampling site as random factor (R package *lme4*, Bates et al., 2015) and Tukey's honest significant difference test ( $\alpha = 0.05$ ) for linear mixed effect models implemented in the R package *emmeans* (Lenth, 2018).

### 3. Results

#### 3.1. Soil properties

Fig. 2 summarises the soil properties of the four different classes: topsoil of peat-sand mixture, earthified peat topsoils, subsoil below peat-sand mixture and subsoil below earthified peat (see Table S1 for details). It is important to bear in mind that the subsoils were neither mixed with sand nor earthified, but were well-preserved peat.

The mean SOC content covered a broad range from peat-sand mixtures to well-preserved subsoil peat. Due to having higher bulk densities than subsoils, the highest mean SOC densities were found in the topsoils. Nutrient densities were also generally much higher in topsoils than in subsoils. The densities of N<sub>t</sub> followed a similar pattern as SOC. The C:N ratios in the topsoils were much narrower than in the subsoils, while the opposite was found for pH values. The P<sub>CAL</sub> and K<sub>CAL</sub> densities of the topsoils were 6–145 times (P<sub>CAL</sub>) and 3 to 45 times (K<sub>CAL</sub>) greater than in the subsoils.

The SOC density of peat-sand mixtures was lower than that of earthified topsoils, but still as high as the subsoil values (bog peat) or even higher (fen peat). Surprisingly, subsoils below the peat-sand mixtures differed from the other subsoils. Particularly in the case of bog peat, they showed higher N<sub>t</sub> contents, lower C:N ratios, slightly higher bulk densities, and higher pH values (bog peat only). These might all be indicators of anthropogenic influence. P<sub>CAL</sub> and K<sub>CAL</sub> (fen peat only)

densities in peat-sand mixture topsoils were also higher than in earthified peat topsoils.

As expected, fen peat had higher values of N<sub>t</sub> than the equivalent bog peat class. Thus the C:N ratio was higher in bog peat than in fen peat, while pH values followed an opposite pattern with more variable pH values in fen peat than in bog peat. Surprisingly, P<sub>CAL</sub> and K<sub>CAL</sub> densities were clearly higher in bog peat topsoils than in fen peat topsoils. In contrast, mean K<sub>CAL</sub> and P<sub>CAL</sub> densities of bog and fen peat subsoils were similar.

#### 3.2. Time series of GHG fluxes

Fig. 3 shows class-wise mean CO<sub>2</sub> fluxes from fen peat (a) and bog peat (b). Average CO<sub>2</sub> fluxes from all topsoil classes showed an increase with the start of drainage, but fluxes slowly decreased over the whole experiment with decreasing soil moisture. During the first suction steps in particular, initial flux peaks occurred immediately after increasing the suction, but fluxes levelled out after several days. Significantly lower flux rates were measured for the subsoils of all sites. Flux peaks from subsoils following increased suction events were also less distinctive. In contrast to the behaviour of topsoils, fluxes from subsoils did not decrease over the course of the experiment, but actually steadily increased until the -150 hPa suction step in the case of peat-sand mixtures. CO<sub>2</sub> fluxes from earthified topsoils of bog peat were approximately 1.8 times higher than fluxes from all the other topsoil classes, which all showed similar ranges. Thus, in contrast to the bog peat, there were only minor differences between fluxes from peat-sand mixtures and earthified topsoils for the fen peat sites.

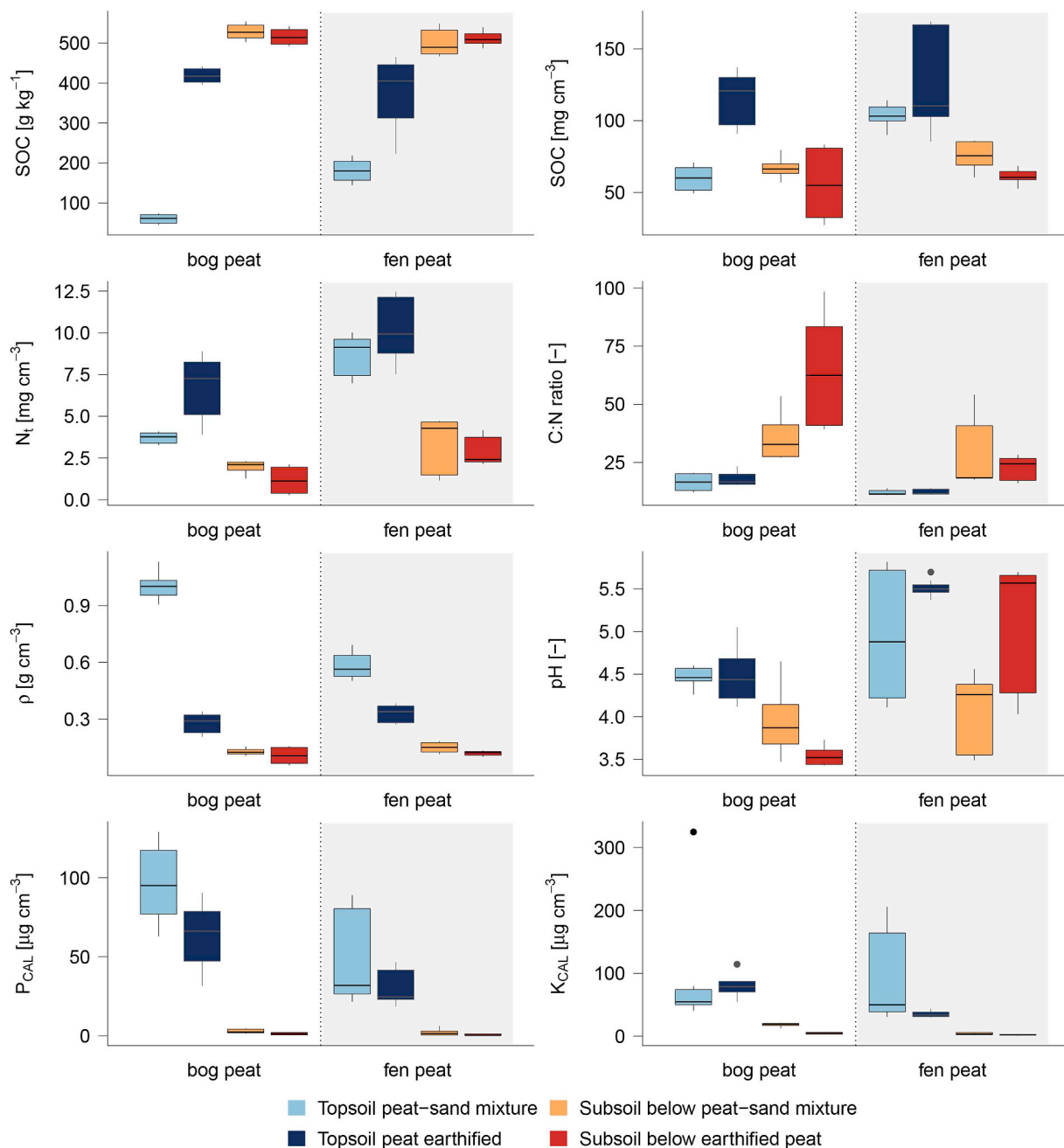
Mean N<sub>2</sub>O fluxes (Fig. S3) from topsoils peaked early during the experiment under slight drainage. Afterwards, N<sub>2</sub>O slowly decreased until the suction step of -150 hPa. With further drying, only minimal N<sub>2</sub>O fluxes occurred. N<sub>2</sub>O fluxes from the subsoils were negligible except for some slightly elevated values in the case of earthified bog peat subsoils. Fen peat-sand mixtures and earthified bog peat topsoils showed the highest N<sub>2</sub>O fluxes.

CH<sub>4</sub> fluxes were generally negligible for all samples (< 1 μg CH<sub>4</sub>-C m<sup>-2</sup> h<sup>-1</sup>) even at the start of the experiment under quasi-saturated conditions. Due to the use of CH<sub>4</sub>-free air, we could not determine any potential uptake of CH<sub>4</sub> by the soil.

#### 3.3. Influence of water-filled pore space, peat type and peat-sand mixing

A distinct parabolic dependence was detected between WFPS and CO<sub>2</sub> fluxes for all topsoils (Fig. 4a) and all subsoils (Fig. 4b), except for one fen peat and one bog peat subsoil. At the start of the experiment, soils had a mean WFPS (± standard error) of 0.93 ± 0.01. The CO<sub>2</sub> fluxes increased to their maxima at a mean WFPS of 0.84 ± 0.02 (topsoils, Fig. 4a) and 0.83 ± 0.05 (subsoils, Fig. 4b). Subsequently, they decreased until minimal mean WFPS of 0.68 ± 0.02 (topsoils, Fig. 4a) and 0.76 ± 0.04 (subsoils, Fig. 4b) at the -300 hPa suction step. Maximum CO<sub>2</sub> fluxes were up to four times higher than those under quasi-saturated conditions, but there were no significant differences between sample groups regarding the ratios of maximum CO<sub>2</sub>-C fluxes and CO<sub>2</sub>-C fluxes under water saturation (Table 2). Maximum CO<sub>2</sub> fluxes (mean ± standard error) from topsoils covered a range from 21.4 ± 0.3 to 77.3 ± 1.4 mg C m<sup>-2</sup> h<sup>-1</sup>, whereas subsoils showed a high variability (2.7 ± 0.1 to 14.0 ± 2.0 mg C m<sup>-2</sup> h<sup>-1</sup>, Table S2). An influence of peat-sand mixing on CO<sub>2</sub> fluxes was observed for bog peat only, with significantly lower CO<sub>2</sub> fluxes from peat-sand mixtures. No general influence of peat-sand mixing was detected for fen peat topsoils. For subsoils, considerably, but not significantly, higher fluxes occurred from peat-sand mixture sites compared to earthified sites. Although there was no general dependence of CO<sub>2</sub> fluxes on peat type, CO<sub>2</sub> fluxes from earthified bog peat topsoils were significantly higher than those from earthified fen peat topsoils.

N<sub>2</sub>O fluxes showed sudden peaks and distinctive differences in



**Fig. 2.** Properties of the soil columns: soil organic carbon (SOC) content, SOC density, total nitrogen (Nt) density, C:N ratio, bulk density ( $\rho$ ), pH value, calcium acetate lactate extractable phosphorus ( $P_{CAL}$ ) density, calcium acetate lactate extractable potassium ( $K_{CAL}$ ) density. Sample size: bog peat  $n = 6$ , fen peat  $n = 9$ .

maximum  $N_2O$  fluxes (Fig. 4c and d; Table 2). The highest  $N_2O$  fluxes occurred at WFPS between 0.78 and 0.95 (topsoil, Fig. 4c) and 0.73 and 0.95 (subsoils, Fig. 4d). Overall, bog peat topsoils showed lower but more variable maximum  $N_2O$  fluxes than their fen peat counterparts. The high variability was mainly caused by high fluxes from one site (eB2, Table S2). The opposite pattern was observed for subsoils, with fen peat sites having lower fluxes than bog peat sites. The impact of sand addition was also ambiguous as fen peat-sand mixtures showed higher  $N_2O$  fluxes, but bog peat-sand mixtures lower  $N_2O$  fluxes than the respective earthified peat samples. The maximum values of  $N_2O$  fluxes from peat-sand mixtures tended to occur at lower WFPS than those of earthified peat. No other patterns were identified.

For all subsequent analyses, except for GHG balance which was compiled for the  $-60$  hPa suction step, the maximum fluxes of  $CO_2$  and  $N_2O$  were used, *i.e.* the highest equilibrium flux of every sample during

the six suction steps of the experiment (maximum values of Fig. 4a–d, Table S2). Cumulative fluxes over the course of the experiment were also calculated, which strongly correlated with maximum fluxes ( $r = 0.99$  and  $0.91$  for  $CO_2$  and  $N_2O$ , respectively). Therefore, all the results are also valid for cumulative fluxes.

The normalised soil moisture expressed as WFPS and the suction steps of the present experiment could be used to approximate water retention characteristics, which describe the relationship between suction and soil moisture. As these characteristics determine the reaction of the sites to hydrological boundary conditions, the locations of the maximum fluxes within the WFPS-suction-space are shown in Fig. 5. The occurrence of maximum  $CO_2$  fluxes differed greatly between subsoils and topsoils (Fig. 5a): the corresponding suction of maximum  $CO_2$  fluxes was between  $-20$  and  $-60$  hPa for topsoils and  $-20$  and  $-300$  hPa for subsoils, while WFPS were similar. Except for one site, the peat-

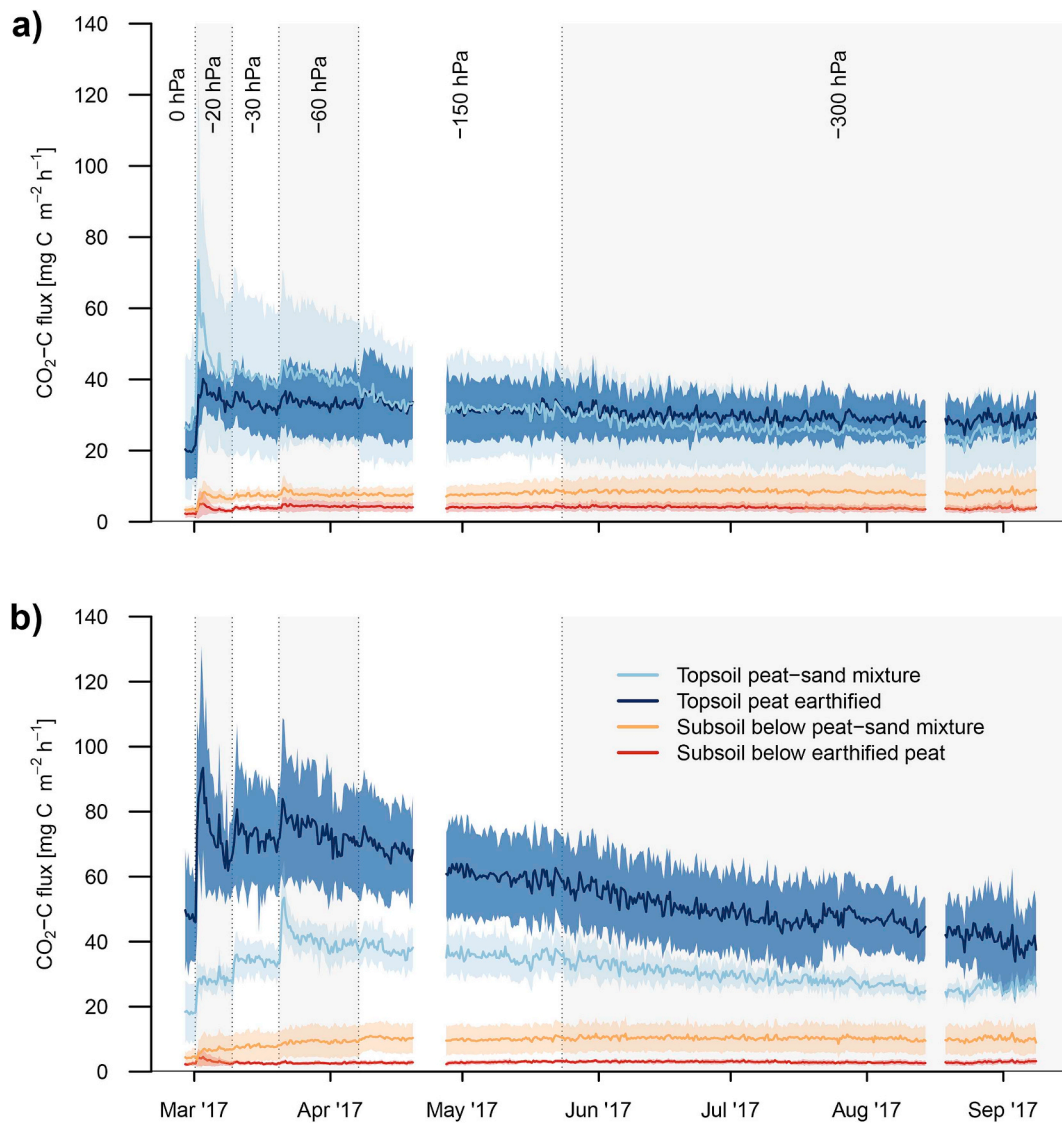


Fig. 3. CO<sub>2</sub>-C fluxes (mean values and standard deviations) over the course of the experiment and suction steps for (a) fen peat and (b) bog peat.

sand mixture topsoils tended to have a lower WFPS at the same suction than the earthified topsoils. In other words, peat-sand mixture sites drained to the same depth as earthified sites will be drier. Nonetheless, the earthified topsoils and peat-sand mixtures showed maximum CO<sub>2</sub> fluxes at the same suction, but not at the same WFPS. Similarly, earthified bog peat was slightly drier than fen peat at the same suctions (not shown).

Most of the maximum N<sub>2</sub>O emissions already occurred at low suctions between initial saturation and -30 hPa (Fig. 5b). On average, fen peat subsoils proved to be drier than bog peat when maximum N<sub>2</sub>O fluxes occurred.

### 3.4. Influence of soil properties and nutrient status on fluxes

SOC content was negatively correlated ( $r = -0.78$ ) with maximum CO<sub>2</sub> fluxes, while SOC density ( $r = 0.54$ ) showed an – although non-significant positive correlation (Fig. 6a, Table S3). However, these (and other) correlations mainly reflected the differences both in terms of fluxes and soil properties between topsoils and subsoils: when only topsoil samples were considered, there was no correlation either in SOC content or in SOC density (Table S3). A similarly strong dependence of  $r = 0.68$  was observed for N<sub>t</sub> density, but again this mainly highlighted

the general differences between topsoils and subsoils and had only some explanatory power for CO<sub>2</sub> fluxes of the topsoils. Maximum CO<sub>2</sub> fluxes showed an exponential increase with decreasing C:N ratios less than or equal to 25 ( $r = -0.63$ ), but as in the case N<sub>t</sub>, there was only a weak correlation for topsoil samples. In contrast, strong positive correlations between K<sub>CAL</sub> and P<sub>CAL</sub> and maximum CO<sub>2</sub> fluxes ( $r = 0.87$  and  $0.86$  respectively) covered both the whole data range and the individual layers, although the moderate to strong correlations for subsoils were not significant.

Fig. 6b shows the correlation between maximum N<sub>2</sub>O fluxes and soil properties. As in the case of CO<sub>2</sub> fluxes, there was a negative correlation with SOC content ( $r = -0.70$ ) and a strong positive correlation with SOC density ( $r = 0.70$ ) (Table S3). Compared to CO<sub>2</sub>, there were stronger positive correlation between maximum N<sub>2</sub>O fluxes and SOC density for both the whole data set and the individual layers, although the latter correlations were not significant. The N<sub>2</sub>O fluxes showed a positive correlation with N<sub>t</sub> ( $r = 0.74$ ), while the correlation with the C:N ratio again reflected differences between topsoils and subsoils. Despite one obvious outlier (topsoil of sample sB2), there were also strong correlations of K<sub>CAL</sub> and P<sub>CAL</sub> and maximum N<sub>2</sub>O fluxes ( $r = 0.70$  and  $0.73$ , respectively).

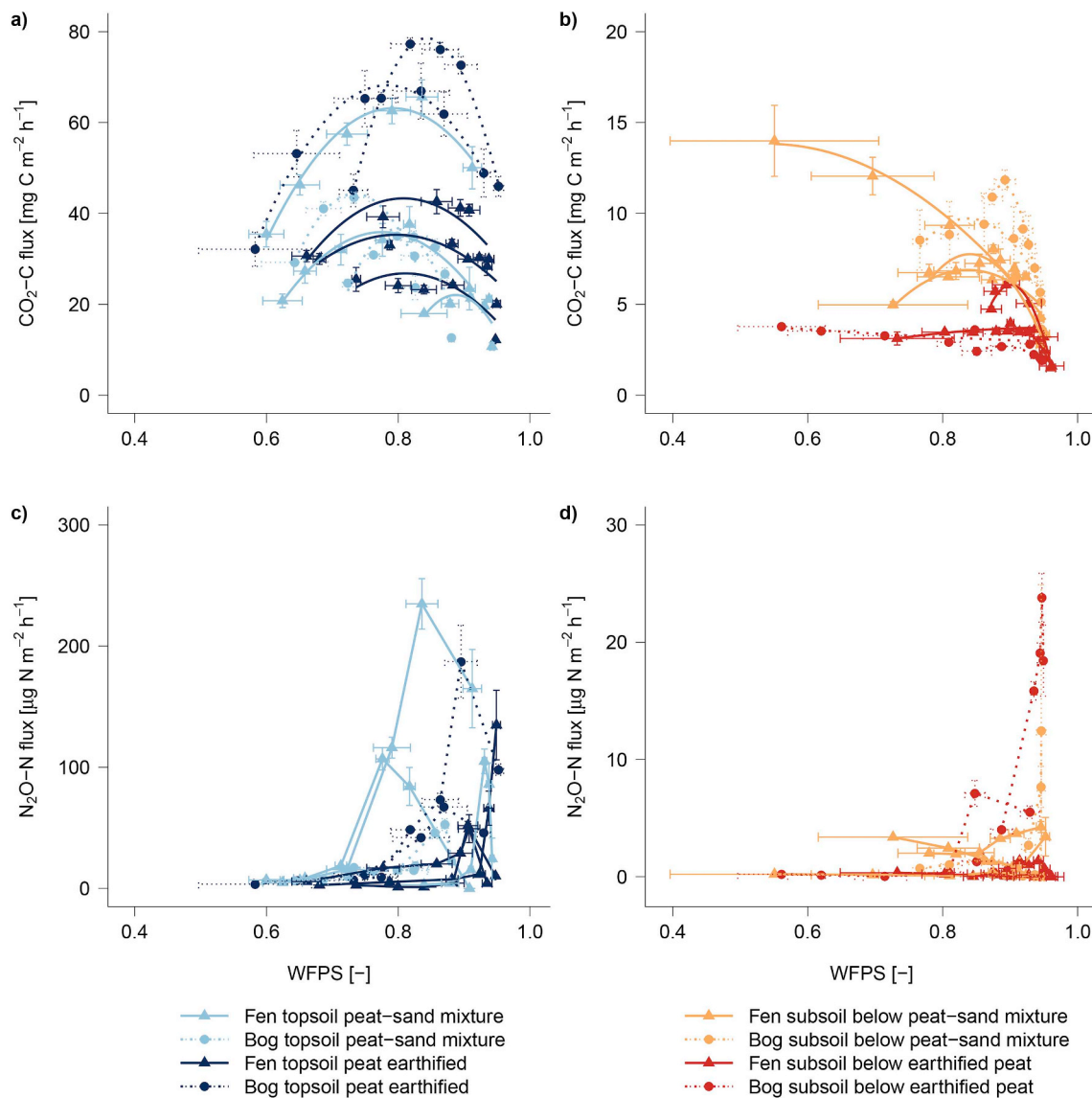


Fig. 4. Greenhouse gas fluxes and water-filled pore space (WFPS) at the end of each suction step: (a) CO<sub>2</sub>-C fluxes of topsoil samples, (b) CO<sub>2</sub>-C fluxes of subsoil samples, (c) N<sub>2</sub>O-N fluxes of topsoil samples, (d) N<sub>2</sub>O-N fluxes of subsoil samples. Means and standard errors are displayed. Lines in (a) and (b) represent fitted quadratic polynomial functions.

Table 2

Maximum CO<sub>2</sub>-C and N<sub>2</sub>O-N (mean ± standard error) fluxes per group with the respective water filled pore space (WFPS, mean ± standard error) at the occurrence of maximum fluxes and ratio of maximum CO<sub>2</sub>-C fluxes and CO<sub>2</sub>-C fluxes under water saturation (start). Different letters represent significant differences (p < 0.05). sF: fen peat-sand mixture in the topsoil, eF: fen peat site with earthified topsoil, sB: bog peat-sand mixture in the topsoil, eB: bog peat site with earthified topsoil.

		Max. CO <sub>2</sub> -C (mg C m <sup>-2</sup> h <sup>-1</sup> )	WFPS (-)	Max. N <sub>2</sub> O-N (μg N m <sup>-2</sup> h <sup>-1</sup> )	WFPS (-)	Ratio of max. CO <sub>2</sub> -C to start CO <sub>2</sub> -C (-)
top	sB	39.3 ± 4.2 <sup>a</sup>	0.77 ± 0.03	35.6 ± 17.1 <sup>abcde</sup>	0.85 ± 0.02	2.31 ± 0.47 <sup>a</sup>
	eB	72.1 ± 5.2 <sup>b</sup>	0.83 ± 0.01	127.2 ± 60.0 <sup>bde</sup>	0.88 ± 0.01	1.53 ± 0.16 <sup>a</sup>
	sF	41.5 ± 12.9 <sup>a</sup>	0.85 ± 0.03	149.0 ± 43.0 <sup>e</sup>	0.85 ± 0.05	1.64 ± 0.20 <sup>a</sup>
	eF	35.3 ± 3.8 <sup>ac</sup>	0.88 ± 0.01	78.7 ± 28.1 <sup>cde</sup>	0.92 ± 0.01	1.87 ± 0.29 <sup>a</sup>
sub	sB	10.6 ± 1.2 <sup>cd</sup>	0.88 ± 0.02	10.1 ± 2.4 <sup>abcd</sup>	0.95 ± 0.00	2.54 ± 0.71 <sup>a</sup>
	eB	3.2 ± 0.5 <sup>d</sup>	0.72 ± 0.16	15.5 ± 8.3 <sup>ac</sup>	0.90 ± 0.05	1.36 ± 0.02 <sup>a</sup>
	sF	9.3 ± 2.4 <sup>d</sup>	0.79 ± 0.12	3.7 ± 0.3 <sup>abcd</sup>	0.88 ± 0.07	2.80 ± 0.20 <sup>a</sup>
	eF	4.5 ± 0.8 <sup>d</sup>	0.90 ± 0.00	0.6 ± 0.4 <sup>ab</sup>	0.85 ± 0.06	2.41 ± 0.78 <sup>a</sup>

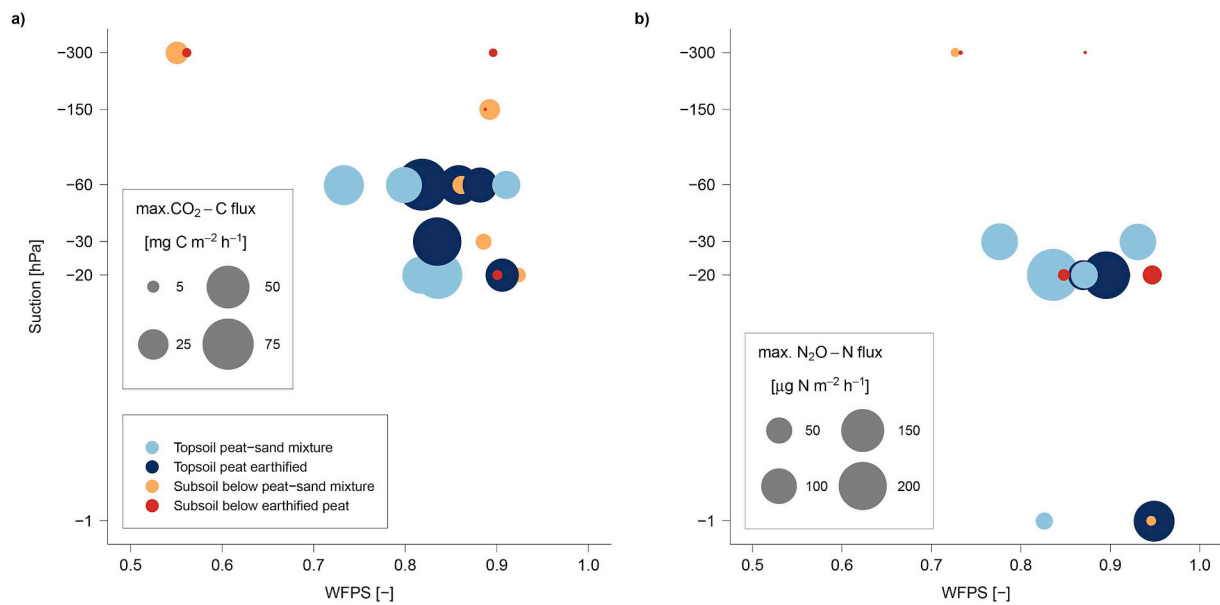


Fig. 5. Soil hydraulic conditions (water-filled pore space (WFPS) versus suction) of all topsoil and subsoil samples at the occurrence of (a) maximum CO<sub>2</sub>-C fluxes and (b) maximum N<sub>2</sub>O-N fluxes.

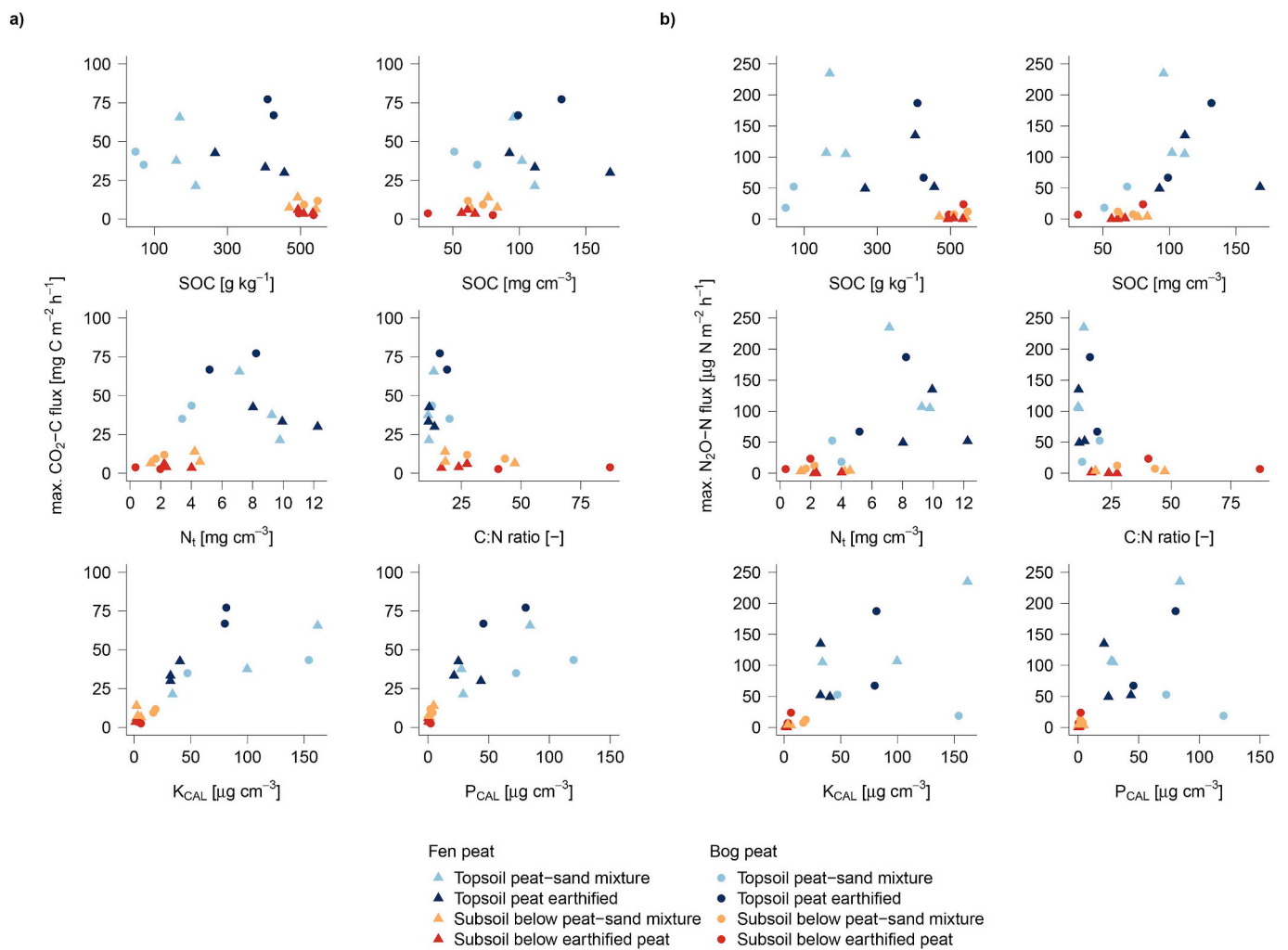


Fig. 6. Relations between (a) maximum CO<sub>2</sub>-C fluxes and (b) maximum N<sub>2</sub>O-N fluxes and soil properties: soil organic carbon (SOC) content and density, total nitrogen (N<sub>t</sub>) density, C:N ratio, calcium acetate lactate extractable phosphorus (P<sub>CAL</sub>) density, calcium acetate lactate extractable potassium (K<sub>CAL</sub>) density.



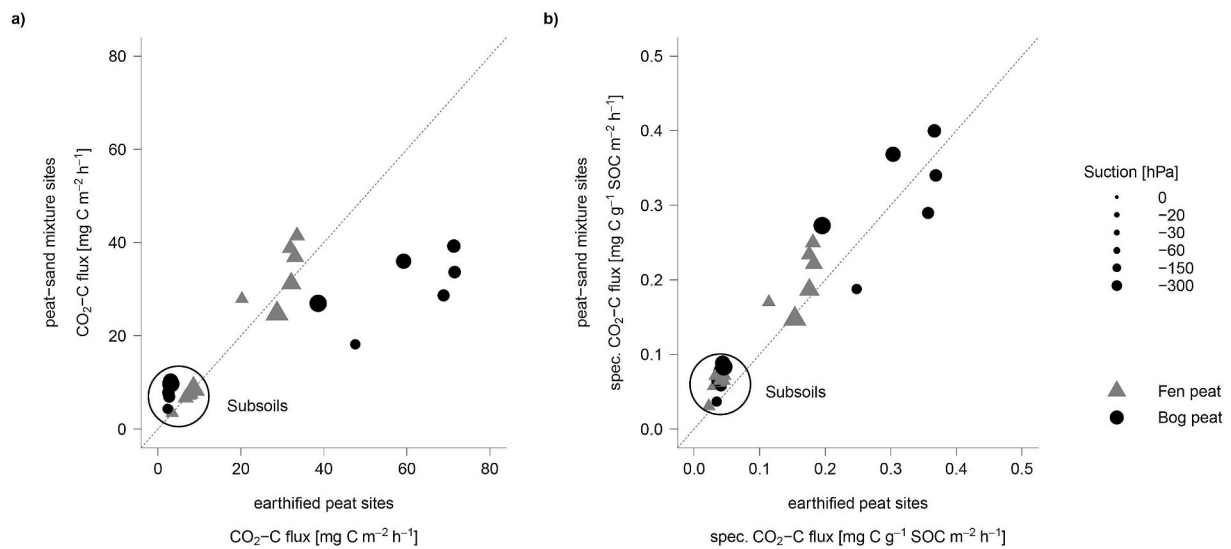


Fig. 7. Means of peat-sand mixture sites and earthified peat sites (topsoil and subsoil) for six suction steps separated into fen (n = 3) and bog (n = 2) peat (a) CO<sub>2</sub>-C fluxes and (b) specific CO<sub>2</sub>-C fluxes.

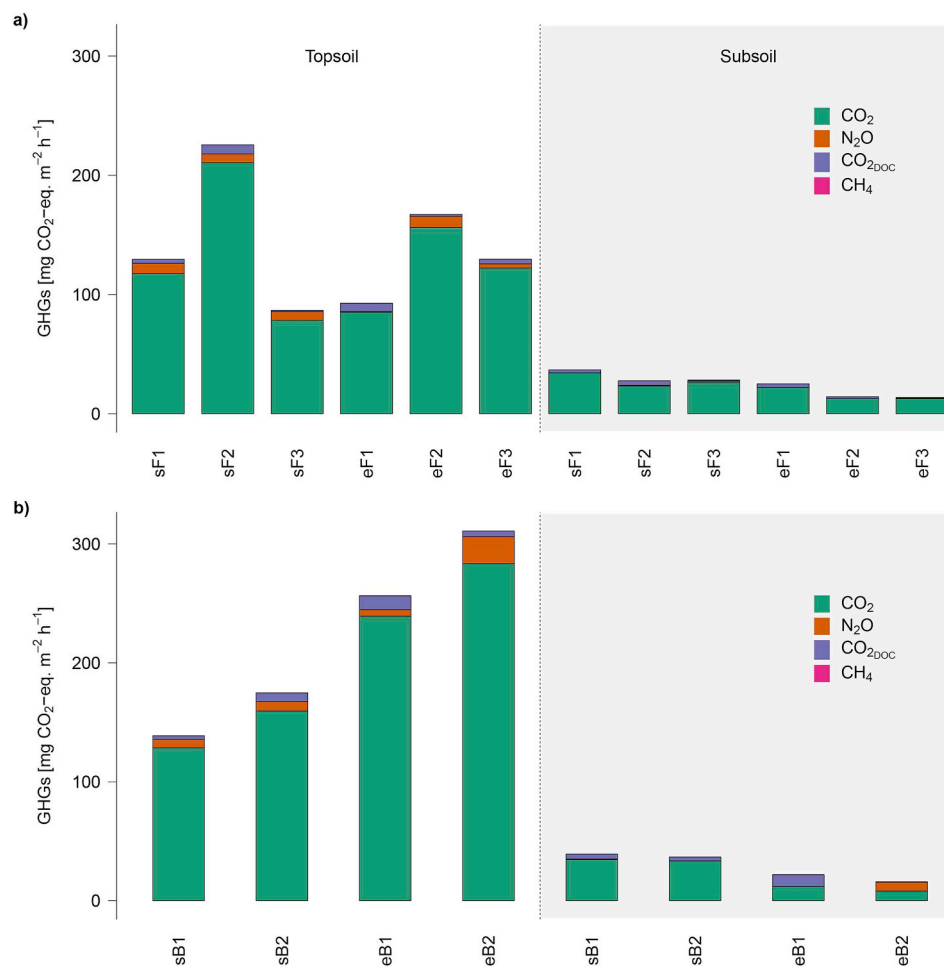


Fig. 8. Greenhouse gas (GHG) emissions and DOC export as CO<sub>2</sub> (CO<sub>2,DOC</sub>) at the suction step of –60 hPa of (a) fen peat sites and (b) bog peat sites. sF: fen peat-sand mixture in the topsoil, eF: fen peat site with earthified topsoil, sB: bog peat-sand mixture in the topsoil, eB: bog peat site with earthified topsoil.

### 3.5. Specific CO<sub>2</sub> flux and GHG balance

While absolute values of CO<sub>2</sub> fluxes (Fig. 7a) showed higher fluxes from topsoils of earthified bog peat sites compared to peat-sand mixture sites, specific CO<sub>2</sub> fluxes (Fig. 7b), i.e. fluxes normalised by the samples' SOC stock, hardly showed any differences between the peat-sand mixture and earthified sites. For both peat types' topsoil and subsoil samples, the ratio of CO<sub>2</sub> fluxes of peat-sand mixture sites to CO<sub>2</sub> fluxes of earthified peat sites was higher for specific than for normalized values.

The GHG balance of topsoils (78–311 mg CO<sub>2</sub> eq. m<sup>-2</sup> h<sup>-1</sup>) showed much higher values than that of subsoils (14–39 mg CO<sub>2</sub> eq. m<sup>-2</sup> h<sup>-1</sup>, Fig. 8). The highest emissions were observed for topsoils of the earthified bog sites and peat-sand mixture site sF2. The main component of the GHG balance at the -60 hPa suction step were CO<sub>2</sub> emissions comprising 51–94% of total GHG emissions, followed by similar shares of N<sub>2</sub>O and CO<sub>2DOC</sub> fluxes. CH<sub>4</sub> emissions were negligible for all sites, contributing on average 0.01% to total GHG fluxes. Contributions for N<sub>2</sub>O and CO<sub>2DOC</sub> in topsoils were both 1–8%. In subsoils the proportion of CO<sub>2</sub> was slightly lower than in topsoils and mainly CO<sub>2DOC</sub> showed an increase in relative importance. While in eight out of ten subsoils CO<sub>2DOC</sub> and N<sub>2</sub>O fluxes contributed 2–14% and 0.1–4% respectively to overall GHG emissions, two bog peat subsoils displayed an immense share of CO<sub>2DOC</sub> (45%, eB1) and N<sub>2</sub>O (46%, eB2). With the exception of these two subsoils, the differences between bog and fen peat were minor regarding each component's individual contribution to the GHG balance. However, higher emissions were observed from earthified topsoil bog peat than from any other group.

## 4. Discussion

The discussion follows our main objectives, i.e. the identification of the effects of soil moisture, sand addition, peat types as well as nutrient contents on the fluxes of CO<sub>2</sub> and N<sub>2</sub>O. Interaction of the different drivers necessitate that some topics overlap as, for example, the reaction of CO<sub>2</sub> fluxes on water-filled pore space depended on peat type.

### 4.1. Influence of water-filled pore space on GHG fluxes

Drainage of the different peat soils increased CO<sub>2</sub> fluxes drastically up to four-fold compared to nearly water-saturated conditions (Table S2). Overall, maximum CO<sub>2</sub> fluxes were measured at WFPS that, under equilibrium conditions (Fig. 5), corresponded to groundwater levels of 20–60 cm below the soil surface, which are typical values for grassland on peat soils (Bechtold et al., 2014).

The stepwise reduction of WFPS in the soil columns resulted in a parabolic response curve of CO<sub>2</sub> fluxes with an “optimum” WFPS at the suction step with maximal CO<sub>2</sub> fluxes (Fig. 4). This general shape is in accordance with results reported for both mineral soils (Linn and Doran, 1984; Moyano et al., 2012) and peat soils (Kechavarzi et al., 2010; Norberg et al., 2018; van Lent et al., 2018). Under water-saturated conditions, available oxygen limits microbial activity and CO<sub>2</sub> fluxes. After the WFPS falls below the optimum for CO<sub>2</sub> fluxes (Table 2), limitation is caused by the lack of water availability as also observed in field studies where some sites have become very dry in summer (Tiemeyer et al., 2016). Nonetheless, dry conditions in the topsoil under field conditions still expose thicker peat layers than incubated here to drainage and therefore to mineralisation. For the soils in the present study, maximum CO<sub>2</sub> fluxes were observed at 84 ± 2% WFPS. Maximum CO<sub>2</sub> fluxes in mineral soils were reached at 50–60% WFPS, while other incubation studies with intact soil samples of managed peatlands also showed optimum WFPS at around 80% (Kechavarzi et al., 2010; Norberg et al., 2018). The latter study reports, possibly due to errors in units, unrealistically high average CO<sub>2</sub> fluxes (36–167 mg g<sup>-1</sup> min<sup>-1</sup>), but the relationship between CO<sub>2</sub> fluxes and WFPS is plausible. While at maximum CO<sub>2</sub> fluxes, topsoils of peat-sand mixtures tended to be drier than earthified peat topsoils (Fig. 4, Table 2), the influence of WFPS on

CO<sub>2</sub> fluxes in peat-sand mixture topsoils was still more similar to organic soils than to mineral soils. Overall, the results of the present study emphasize that peat soils need to be very wet to reduce emissions, while moist conditions might even increase emissions compared to very dry conditions.

The reaction of microbial activity towards soil moisture might depend on the peat type. In contrast to our results, Kechavarzi et al. (2010) found more pronounced parabolic response curves for fibrous peat subsoil than for amorphous peat topsoil, concluding that deeper, fibrous peat has greater oxidation potential, while Norberg et al. (2018) found hardly any differences between topsoil and subsoil samples. The hydrological reaction of our subsoils to drainage was surprising given that other studies have reported that less decomposed peat already gives a large percentage of water at low suctions (Boelter, 1968; Rovdan et al., 2002; Schwärzel et al., 2002; Zeitz and Velty, 2002). However, the slightly higher capability of subsoil peat to retain water can only explain their slower reaction compared to the topsoils, but not the lower CO<sub>2</sub> fluxes, as optimum values of WFPS were still reached in all but one case (Fig. 4).

Nitrification and denitrification are the major pathways producing N<sub>2</sub>O in soil. Among other factors, depending on soil moisture and concomitantly the amount of oxygen in the soil, N<sub>2</sub>O is either produced by ammonium oxidation or nitrate reduction (Butterbach-Bahl et al., 2013). As denitrification is limited by water availability whereas nitrification is limited by aeration, early studies on mineral soil suggest that the highest N<sub>2</sub>O fluxes should occur at approximately 60% WFPS when both processes occur simultaneously (Davidson et al., 2000; Linn and Doran, 1984). The influence of WFPS on N<sub>2</sub>O fluxes in the present study varied considerably between samples, however the majority of increased N<sub>2</sub>O fluxes were observed at WFPS over 80% (Fig. 4). This optimum for N<sub>2</sub>O fluxes diverges from the theory of Davidson et al. (2000) as do the results of other studies (Berglund and Berglund, 2011; Liimatainen et al., 2018; van Lent et al., 2018) and the meta-analysis of Butterbach-Bahl et al. (2013), which also found an optimum of 80–90% WFPS. The fact that N<sub>2</sub>O fluxes predominantly occurred at WFPS > 80% indicates that the N<sub>2</sub>O primarily originated from denitrification.

### 4.2. Influence of sand addition on GHG fluxes

In contrast to other studies (Bambalov, 1999; Zaidelman and Shvarov, 2000), mixing sand into the topsoil and thus reducing the SOC content did not systematically reduce either CO<sub>2</sub> or N<sub>2</sub>O fluxes. In fen peat topsoils, there was no difference in absolute and specific CO<sub>2</sub> fluxes from peat-sand mixtures and earthified peat (Fig. 7). In contrast, absolute CO<sub>2</sub> fluxes from earthified peat bog topsoils were significantly higher than from bog peat-sand mixtures, but the specific CO<sub>2</sub> fluxes of both classes did not differ (Fig. 7, Table 2). This indicates that soil organic matter of the peat-sand mixtures in the present study was not stable.

To interpret the effects of anthropogenically changed peat properties, it is crucial to distinguish between SOC content and SOC density. While the peat-sand mixtures showed much lower SOC content, the SOC density was only slightly lower than in the respective earthified topsoils due to their higher bulk densities (Fig. 2). Furthermore, all topsoils showed lower SOC contents, but mostly higher densities than the subsoils. Ross and Malcolm (1988) measured the respiration rates of artificial peat-sand mixtures for different sizes of peat cubes and detected increasing CO<sub>2</sub> fluxes with a decreasing peat cube size. The effects of physical disturbance might compensate for the lower SOC densities since mixing destroys the intrinsic peat structure and increases the available surface area of the organic matter.

Mixing sand into the topsoil peat was accompanied by higher CO<sub>2</sub> fluxes from well-preserved and unmixed subsoils (Fig. 4b). As in Zaidelman and Shvarov (2000), the 23% higher dry bulk densities of subsoil peat below peat-sand mixtures could have been caused by the extra load from the relatively heavy sandy topsoil and are the reason for

the higher SOC densities (Fig. 2). This and higher specific CO<sub>2</sub> fluxes than from subsoil below earthified sites (Fig. 7b) might indicate more favourable microbial conditions. Given the higher hydraulic conductivity of peat-sand mixture topsoils compared to earthified peat more of the topsoils' nutrients might have leached into deeper layers and increased amounts of N, P and K there, which in turn increased microbial activity (Fig. 3, see section 4.4).

In theory, ploughing the underlying peat layer into the topsoil sand layer should be avoided to minimise peat mineralization (Göttlich, 1990). However, in practice, the SOC contents of covered peat soils are highly variable, and ideal sand covers are much rarer than peat-sand mixtures (Wittnebel, pers. comm.). This was also the case here: the peat-sand mixtures had lower SOC contents than the earthified peat sites (Fig. 2), however only the two bog peat topsoils with the lowest SOC content (49 and 71 g kg<sup>-1</sup>) come close to an ideal sand cover (Fig. S1). Although these two topsoils did show lower CO<sub>2</sub> fluxes compared to their earthified peat counterparts, the values are still four-fold higher than those of the subsoils and in the same range as all the fen topsoils. Furthermore, the comparable specific fluxes of earthified peat and peat-sand mixtures indicated ongoing soil organic matter transformation in the latter soils (Fig. 7). These results corroborate field studies which have observed similar or even increased CO<sub>2</sub> or GHG emissions from peat-sand mixtures (Leiber-Sauheitl et al., 2014; Maljanen et al., 2004), from a bog peat site covered with sand (88 g SOC kg<sup>-1</sup>) and a neighbouring peat soil (Beyer, 2014) or from “low C organic soils” compared to peat soils (Tiemeyer et al., 2016).

The influence of sand addition on N<sub>2</sub>O fluxes was ambiguous as fens and bogs showed opposite reactions, i.e. fluxes from earthified bog peat tended to be higher than from bog peat-sand mixtures, while the opposite was true for the fen peat sites. The reasons for this are not entirely clear, but this pattern might be explained by the higher bulk density and lower pH values of fen peat-sand mixtures compared to earthified topsoils, while N<sub>t</sub> density was higher for earthified bog peat than for bog peat-sand mixtures. Leiber-Sauheitl et al. (2014) and Maljanen et al. (2004) observed no clear differences between N<sub>2</sub>O emissions from true peat and peat-sand mixtures under grassland use.

#### 4.3. Influence of sampling depth and peat type on GHG fluxes

Fluxes of CO<sub>2</sub> and N<sub>2</sub>O displayed immense differences between topsoil and subsoil peat (Figs. 4 and 7). All sites have been under agricultural use and drained for many decades. It could be assumed that, as a result, the peat topsoils would be of poor organic matter quality (Leifeld et al., 2012), with lower decomposability (Urbanová and Bárta, 2015) and are therefore less suitable for microbial use than “freshly drained” subsoils. However, physically disturbed peat-sand mixture topsoils that are under intensive management could have more accessible organic matter surfaces that enhance microbial activity and concurrently increase nutrient mobilisation (Ross and Malcolm, 1988). Furthermore, nutrient availability was much higher in the topsoils (see section 4.4).

Lower CO<sub>2</sub> fluxes from samples from deeper peat layers have also been found in other studies on both managed and unmanaged peatlands (Bader et al., 2018; Brake et al., 1999; Glatzel et al., 2004; Hardie et al., 2011; Hogg et al., 1992). These lower CO<sub>2</sub> fluxes have been explained by lower nutrient levels, a smaller abundance of fresh plant biomass and poorer substrate quality of subsoil horizons. Therefore, topsoil horizons have been shown to generally have higher microbial activity than subsoil horizons (Brake et al., 1999; Fisk et al., 2003; Preston et al., 2012). Although the uppermost centimetres of the soil were intentionally removed before sampling, remaining roots in the peat topsoils cannot be excluded as a possible source of CO<sub>2</sub>. For managed grassland topsoils, Bader et al. (2017) showed that crop residues were accountable for 40% of the CO<sub>2</sub> emissions. The sites in the present study showed a few fine roots even down to 50 cm. However, even if it were assumed that 50% of the CO<sub>2</sub> emissions came from roots, this would not

explain the on average nine-fold greater values of the topsoils.

As in the present study, lower N<sub>2</sub>O fluxes from subsoil samples were observed in Berglund and Berglund (2011). Well et al. (2005) also showed that denitrification capacity decreases with depth. The reasons for higher maximum N<sub>2</sub>O fluxes from topsoils were probably a combination of higher nutrient availability, higher pH values, narrower C:N ratios and higher bulk densities (see section 4.4).

Surprisingly, no consistent differences could be found between fen and bog peat, i.e. peat composition in terms of peat genesis and peat-forming plants had a marginal influence on GHG fluxes. Under natural conditions faster decomposition processes occur in fens under minerotrophic conditions (Blodau, 2002). Natural bogs however are characterised by low pH values, ombrotrophic conditions and recalcitrant peat substrates (Urbanová and Bárta, 2014; Verhoeven and Liefveld, 1997). Consistent with expectations, the fen peat subsoils in the present study did contain more nitrogen and showed narrower C:N ratios and higher pH values than bog peat subsoils (Fig. 2). Due to drainage, the biogeochemical characterisation and microbial composition of bogs and fens become more similar (Urbanová and Bárta, 2015). However, for the sites in the present study that were all drained, differences between the topsoils of bog and fen peat were still visible in terms of wider C:N ratios and lower pH values in bog peat topsoils compared to fen peat topsoils (Fig. 3). Nevertheless, higher CO<sub>2</sub> fluxes were found from bog peat than from fen peat, which contrasts with a large number of field studies that have been summarised by IPCC (2014). A reason might be the high sensitivity of bog peat to anthropogenic effects: Urbanová and Bárta (2015) found that after drainage the microbial community decreases in fen peat but increases in richness and diversity in bog peat. Furthermore, the bog peat sites of our study were more intensively used than many sites in IPCC (2014), which is probably the reason for the high nutrient contents (section 4.4.).

#### 4.4. Influence of soil properties and nutrient status on GHG fluxes

The increase in oxygen following drainage increases the mineralisation of organically bound nutrients such as N, P and K, which are then enriched in the topsoils (Holden et al., 2004; Laiho et al., 1998) resulting for example in lower C:N ratios. The C:N ratio is commonly used to characterise the quality of soil organic matter as well as microbial availability and turnover (e.g. Reiche et al., 2010; Vos et al., 2018). In the present sample set, the C:N ratio clearly differentiated topsoils and subsoils (Fig. 2). When examining topsoils separately, the C:N ratio had no explanatory power for CO<sub>2</sub> fluxes as all samples showed very similar C:N ratios and as earthified bog samples showed surprisingly high CO<sub>2</sub> fluxes (Fig. 6a). Although N<sub>t</sub> densities had no decisive explanatory power for CO<sub>2</sub> fluxes, the availability of N plays an important role in organic matter stoichiometry and for microbial activity. The non-significant, but slightly positive correlation between CO<sub>2</sub> fluxes from subsoils and N<sub>t</sub> densities (r = 0.27) might indicate that mineralisation processes increase the N supply. This might suggest a shift from N to P limitation. Densities of available P and K correlated strongly with maximum CO<sub>2</sub> fluxes (r = 0.85 and 0.86 respectively; Fig. 6a). Total P is important for microbial turnover of soil organic matter (Brake et al., 1999). Amador and Jones (1993) found that high P amendment increases respiration rates in the long term: after P application the C:P ratio of organic matter decreases and soil microorganisms intensify their catabolism. K is a limiting element in agriculturally used organic soils and is known for its importance for plant growth (Zörb et al., 2014). However, the influence of K on microbial turnover of organic matter is rarely studied. Studies on nutrient addition concentrated on N, P and K amendment simultaneously and reported an increase in microbial respiration, however without specifically separating between the influence of P and K (Larmola et al., 2013; Pinsonneault et al., 2016; Sundström et al., 2000).

The availability of SOC and N<sub>t</sub> had a strong positive influence on N<sub>2</sub>O fluxes (Fig. 6b), probably as N<sub>t</sub> is correlated with denitrification

capacity in peat soils (Well et al., 2005). The exponential relationship between C:N ratio and N<sub>2</sub>O fluxes is a frequently used estimator for field N<sub>2</sub>O emissions (Klemedtsson et al., 2005; Leifeld, 2018). This relationship was generally confirmed in the whole sample set in the present study (Fig. 6b). Both in our dataset and Klemedtsson et al. (2005), there were very low N<sub>2</sub>O fluxes at C:N ratios > 25, while topsoils displayed large differences in N<sub>2</sub>O fluxes despite a narrow range in C:N ratios. This highlights the limitations of the predictive power of the C:N ratio and shows that a C:N ratio of 25 is more of a threshold than a predictor. At low C:N ratios, factors other than N limitation seem to be regulating the high variability in N<sub>2</sub>O fluxes (Liimatainen et al., 2018). In contrast to other studies (e.g. Regina et al., 1996; Weslien et al., 2009), there was no correlation between N<sub>2</sub>O fluxes and pH values in the present study (data not shown). Densities of plant-available P and K showed very strong influences on N<sub>2</sub>O fluxes. Although the exact reasons are unknown, P is known for its important positive role on N<sub>2</sub>O fluxes from peat soils (Liimatainen et al., 2018; Regina et al., 1996). P possibly favours nitrification and/or denitrification processes (Mehnaz and Dijkstra, 2016), e.g. the denitrification enzyme activity in wetland soils (White and Reddy, 1999). N and P addition experiments emphasized the importance of the interaction of both nutrients with P possibly becoming the limiting factor (Wang et al., 2014; White and Reddy, 1999). This could be due to the fact that P availability increases the microbial biomass, which in turn increases the potential for N mineralisation (White and Reddy, 2000).

#### 4.5. GHG balance

The GHG emissions primarily consisted of CO<sub>2</sub> emissions (Fig. 8), which is in accordance with field data from grassland on organic soils (Tiemeyer et al., 2016). Fluxes of CH<sub>4</sub> were negligible at –60 hPa suction as WFPS was beyond the anoxic conditions that favour methanogenesis. Although CH<sub>4</sub> consumption could not be determined with the present experimental setup, there might be uptake of CH<sub>4</sub> by drained organic soils under field conditions (Maljanen et al., 2002). However, this uptake generally plays only a minor role for the GHG balance of drained organic soils. For example, of the 48 drained grassland sites synthesized by Tiemeyer et al. (2016), 17 sites were slight sinks of CH<sub>4</sub>, but, in terms of CO<sub>2</sub>-equivalents, this amounted to only 0.1–0.8% of the CO<sub>2</sub> emissions.

Only two horizons of each site's profile were incubated in the present study. Even though the earthified peat horizon and the peat-sand mixture horizon displayed most of the anthropogenic disturbance, the contribution of GHG emissions from underlying peat horizons needs to be taken into consideration. These horizons are also drained and soil organic matter continues to mineralise. CO<sub>2DOC</sub>, as a measure of C that is lost from the soil in the liquid phase, showed similar shares to N<sub>2</sub>O. The loss of CO<sub>2DOC</sub> tends to decrease for subsoils compared to topsoils. This is in agreement with a field study on bog peat under grassland use, which found much higher DOC concentrations in the topsoil than in the subsoil (Frank et al., 2017). Although concentration levels can be compared between the samples within this experiment, it is not advisable to relate actual numbers of CO<sub>2DOC</sub> losses to values measured in field studies as there had been no input of (rain or irrigation) water for around six months in the present laboratory study.

#### 5. Conclusions

The aim of this long-term incubation experiment was to assess the influence of hydrological and biogeochemical soil properties on GHG emissions from drained organic soils with and without sand addition. Although the experiment was conducted under controlled laboratory conditions, there was still an enmeshed interplay of the effects of soil moisture, soil physical and chemical properties, and soil microbial activity.

First and as expected, soil moisture was closely connected to CO<sub>2</sub>

and N<sub>2</sub>O fluxes. However, this dependence was clearer for CO<sub>2</sub> where parabolic dependencies could be found for most samples. Optimum values of WFPS indicate that, under equilibrium conditions, a water level of 20–60 cm below soil surface in the field provides conditions for the occurrence of maximal CO<sub>2</sub> emissions.

Second, mixing sand into the topsoil peat layer decreased CO<sub>2</sub> emissions from bog peat sites compared to earthified topsoils, but not from fen peat sites. However, the specific CO<sub>2</sub> fluxes of peat-sand mixture sites and earthified sites were similar regardless of peat type, which indicates that the SOM of peat-sand mixtures still is prone to decomposition. Furthermore, mixing sand into the topsoil peat seems to have a negative impact on the well-preserved subsoils, which is apparent both in the soil properties (e.g. bulk density) and in the increased CO<sub>2</sub> fluxes. There was no systematic impact of peat-sand mixtures on N<sub>2</sub>O fluxes. The results of the present study do not support peat-sand mixtures to be advanced as a way of mitigating GHG emissions from drained peatlands.

Third, even after decades of drainage and agricultural use, all topsoils were still emitting considerable amounts of CO<sub>2</sub>, which was in all cases the major component of the GHG balance. Subsoil fluxes were clearly lower. Surprisingly, sites with bog peat showed higher CO<sub>2</sub> fluxes than their fen counterparts, probably due to higher contents of P and K.

This shows that, fourth and finally, the influence of soil characteristics and nutrients on GHG fluxes was more important than the impact of sand addition or peat type. Increased P and K availability in particular showed a strong positive influence on CO<sub>2</sub> as well as on N<sub>2</sub>O fluxes.

#### Declarations of interest

None.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2019.04.013>.

#### References

- Ad Hoc Arbeitsgruppe Boden, 2005. *Bodenkundliche Kartieranleitung KA5 (Manual of Soil Mapping)*, fifth ed. E. Schweizerbart'sche Verlagsbuchhandlung, Hanover, Germany.
- Amador, J., Jones, R.D., 1993. Nutrient limitations on microbial respiration in peat soils with different total phosphorus content. *Soil Biology and Biochemistry* 25, 793–801. [https://doi.org/10.1016/0038-0717\(93\)90125-U](https://doi.org/10.1016/0038-0717(93)90125-U).
- Ausec, L., Kraigher, B., Mandic-Mulec, I., 2009. Differences in the activity and bacterial community structure of drained grassland and forest peat soils. *Soil Biology and Biochemistry* 41, 1874–1881. <https://doi.org/10.1016/j.soilbio.2009.06.010>.
- Bader, C., Müller, M., Schulin, R., Leifeld, J., 2018. Peat decomposability in managed organic soils in relation to land-use, organic matter composition and temperature. *Biogeosciences* 15, 703–719. <https://doi.org/10.5194/bg-15-703-2018>.
- Bader, C., Müller, M., Schulin, R., Leifeld, J., 2017. Amount and stability of recent and aged plant residues in degrading peatland soils. *Soil Biology and Biochemistry* 109, 167–175. <https://doi.org/10.1016/j.soilbio.2017.01.029>.
- Bambalov, N., 1999. Dynamics of organic matter in peat soil under the conditions of sand-mix culture during 15 years (a short communication). *International Agrophysics* 13, 269–272.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models

- using lme4. *Journal of Statistical Software* 67 (1), 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Bechtold, M., Tiemeyer, B., Laggner, A., Leppelt, T., Frahm, E., Belting, S., 2014. Large-scale regionalization of water table depth in peatlands optimized for greenhouse gas emission upscaling. *Hydrology and Earth System Sciences* 18, 3319–3339. <https://doi.org/10.5194/hess-18-3319-2014>.
- Berglund, Ö., Berglund, K., 2011. Influence of water table level and soil properties on emissions of greenhouse gases from cultivated peat soil. *Soil Biology and Biochemistry* 43, 923–931. <https://doi.org/10.1016/j.soilbio.2011.01.002>.
- Beyer, J.C., 2014. Greenhouse Gas Exchange of Organic Soils in Northwest Germany. PhD Thesis. University of Bremen, Germany.
- Blodau, C., 2002. Carbon cycling in peatlands - a review of processes and controls. *Environmental Reviews* 10, 111–134. <https://doi.org/10.1139/a02-004>.
- Boelter, D.H., 1968. Important physical properties of peat materials. In: *Proceedings of the Third International Peat Congress*. National Research Council of Canada, Quebec City 10.1.1.628.9973.
- Brake, M., Höper, H., Joergensen, R.G., 1999. Land use-induced changes in activity and biomass of microorganisms in raised bog peats at different depths. *Soil Biology and Biochemistry* 31, 1489–1497. [https://doi.org/10.1016/S0038-0717\(99\)00053-X](https://doi.org/10.1016/S0038-0717(99)00053-X).
- Brouns, K., Keuskamp, J.A., Potkamp, G., Verhoeven, J.T.A., Hefting, M.M., 2016. Peat origin and land use effects on microbial activity, respiration dynamics and exo-enzyme activities in drained peat soils in The Netherlands. *Soil Biology and Biochemistry* 95, 144–155. <https://doi.org/10.1016/j.soilbio.2015.11.018>.
- Butterbach-Bahl, K., Baggs, E.M., Dannenmann, M., Kiese, R., Zechmeister-Boltenstern, S., 2013. Nitrous oxide emissions from soils: how well do we understand the processes and their controls? *Phil. Trans. Roy. Soc. B* 368, 20130. <https://doi.org/10.1098/rstb.2013.0122>.
- Davidson, E., Keller, M., Erickson, H.E., Verchot, L.V., Veldkamp, E., 2000. Testing a conceptual model of soil emissions of nitrous and nitric oxides. *BioScience* 50, 667–680. [https://doi.org/10.1641/0006-3568\(2000\)050\[0667:TACMOS\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2000)050[0667:TACMOS]2.0.CO;2).
- Dettmann, U., Bechtold, M., Frahm, E., Tiemeyer, B., 2014. On the applicability of unimodal and bimodal van Genuchten-Mualem based models to peat and other organic soils under evaporation conditions. *Journal of Hydrology* 515, 103–115. <https://doi.org/10.1016/j.jhydrol.2014.04.047>.
- DIN ISO 11277, 1998. *Soil Quality - Determination of Particle Size Distribution in Mineral Soil Material - Method by Sieving and Sedimentation*. Beuth Verlag GmbH, Germany.
- Fisk, M.C., Ruether, K.F., Yavitt, J.B., 2003. Microbial activity and functional composition among northern peatland ecosystems. *Soil Biology and Biochemistry* 35, 591–602. [https://doi.org/10.1016/S0038-0717\(03\)00053-1](https://doi.org/10.1016/S0038-0717(03)00053-1).
- Forster, P., Ramaswamy, V., Artaxo, P., Bernsten, T., Betts, R., Fahey, D.W., Haywood, J., Lean, J., Lowe, D.C., Myhre, G., Nganga, J., Prinn, R., Raga, G., Schulz, M., Van Dorland, R., 2007. Changes in atmospheric constituents and in radiative forcing. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), *Climate Change 2007: The Physical Science Basis*. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Frank, S., Tiemeyer, B., Bechtold, M., Lücke, A., Bol, R., 2017. Effect of past peat cultivation practices on present dynamics of dissolved organic carbon. *Science of the Total Environment* 574, 1243–1253. <https://doi.org/10.1016/j.scitotenv.2016.07.121>.
- Glatzel, S., Basiliko, N., Moore, T., Unit, L.E., 2004. Carbon dioxide and methane production potentials of peats from natural, harvested and restored sites, eastern Québec, Canada. *Wetlands* 24, 261–267. [https://doi.org/10.1672/0277-5212\(2004\)024\[0261:CDAMPP\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2004)024[0261:CDAMPP]2.0.CO;2).
- Göttlich, K., 1990. *Moor- und Torfkunde*. E. Schweizerbart'sche Verlagsbuchhandlung (Nägele u. Obermiller), Stuttgart, Germany.
- Hantschel, R.E., Flessa, H., Beese, F., 1994. An automated microcosm system for studying soil ecological processes. *Soil Science Society of America Journal* 58, 401–404.
- Hardie, S.M.L., Garnett, M.H., Fallick, A.E., Rowland, A.P., Ostle, N.J., Flowers, T.H., 2011. Abiotic drivers and their interactive effect on the flux and carbon isotope ( $^{14}\text{C}$  and  $^{13}\text{C}$ ) composition of peat-respired  $\text{CO}_2$ . *Soil Biology and Biochemistry* 43, 2432–2440. <https://doi.org/10.1016/j.soilbio.2011.08.010>.
- Harrell, F., 2016. Hmisc: Harrell Miscellaneous. R Package Version 3.17-4. available at: <http://CRAN.R-project.org/package=Hmisc>.
- Hogg, E.H., Lieffers, V.C., Wein, R.W., 1992. Potential carbon losses from peat profiles - effects of temperature, drought cycles, and fire. *Ecological Applications* 2, 298–306. <https://doi.org/10.2307/1941863>.
- Holden, J., Chapman, P.J., Labadz, J.C., 2004. Artificial drainage of peatlands: hydrological and hydrochemical process and wetland restoration. *Progress in Physical Geography* 28, 95–123. <https://doi.org/10.1191/0309133304pp403ra>.
- Höper, H., 2015. *Treibhausgasemissionen aus Mooren und Möglichkeiten der Verringerung*. Telma Beih. 5, 133–158.
- Ilnicki, P., Zeitz, J., 2003. Irreversible loss of organic soil functions after reclamation. In: Parent, L.E., Ilnicki, P. (Eds.), *Organic Soils and Peat Materials for Sustainable Agriculture*. CRC Press LLC, Boca Raton, USA.
- IPCC (Intergovernmental Panel on Climate Change), 2014. In: Hiraishi, T., Krug, T., Tanabe, K., Srivastava, N., Baasansuren, J., Fukuda, M., Troxler, T.G. (Eds.), 2013 Supplement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories: Wetlands. IPCC, Switzerland.
- Kechavarzi, C., Dawson, Q., Bartlett, M., Leeds-Harrison, P.B., 2010. The role of soil moisture, temperature and nutrient amendment on  $\text{CO}_2$  efflux from agricultural peat soil microcosms. *Geoderma* 154, 203–210. <https://doi.org/10.1016/j.geoderma.2009.02.018>.
- Klemetsson, L., Von Arnold, K., Weslien, P., Gundersen, P., 2005. Soil C/N ratio as a scalar parameter to predict nitrous oxide emissions. *Global Change Biology* 11, 1142–1147. <https://doi.org/10.1111/j.1365-2486.2005.00973.x>.
- Laiho, R., Sallantausta, T., Laine, J., 1998. The effect of forestry drainage on vertical distributions of major plant nutrients in peat soils. *Plant and Soil* 207, 169–181. <https://doi.org/10.1023/A:1026470212735>.
- Larmola, T., Bubier, J.L., Kobyljanec, C., Basiliko, N., Juutinen, S., Humphreys, E., Preston, M., Moore, T.R., 2013. Vegetation feedbacks of nutrient addition lead to a weaker carbon sink in an ombrotrophic bog. *Global Change Biology* 19, 3729–3739. <https://doi.org/10.1111/gcb.12328>.
- Leiber-Sauheitl, K., Fuß, R., Voigt, C., Freibauer, A., 2014. High  $\text{CO}_2$  fluxes from grassland on historic Gleysol along soil carbon and drainage gradients. *Biogeosciences* 11, 749–761. <https://doi.org/10.5194/bg-11-749-2014>.
- Leifeld, J., 2018. Distribution of nitrous oxide emissions from managed organic soils under different land uses estimated by the peat C/N ratio to improve national GHG inventories. *Science of the Total Environment* 631–632, 23–26. <https://doi.org/10.1016/j.scitotenv.2018.02.328>.
- Leifeld, J., Menichetti, L., 2018. The underappreciated potential of peatlands in global climate change mitigation strategies. *Nature Communications* 9, 1–7. <https://doi.org/10.1038/s41467-018-03406-6>.
- Leifeld, J., Steffens, M., Galego-Sala, A., 2012. Sensitivity of peatland carbon loss to organic matter quality. *Geophysical Research Letters* 39, 1–6. <https://doi.org/10.1029/2012GL051856>.
- Lenth, R., 2018. Emmeans: Estimated Marginal Means, Aka Least-Squares Means. R Package Version 1.3.0. <https://CRAN.R-project.org/package=emmeans>.
- Liimatainen, M., Voigt, C., Martikainen, P.J., Hytönen, J., Regina, K., Oskarsson, H., Maljanen, M., 2018. Factors controlling nitrous oxide emissions from managed northern peat soils with low carbon to nitrogen ratio. *Soil Biology and Biochemistry* 122, 186–195. <https://doi.org/10.1016/j.soilbio.2018.04.006>.
- Linn, D.M., Doran, J.W., 1984. Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and nontilled soils. *Soil Science Society of America Journal* 48, 1267–1272. <https://doi.org/10.2136/sssaj1984.03615995004800060013x>.
- Maljanen, M., Martikainen, P.J., Aaltonen, H., Silvola, J., 2002. Short-term variation in fluxes of carbon dioxide, nitrous oxide and methane in cultivated and forested organic boreal soils. *Soil Biology and Biochemistry* 34, 577–584. [https://doi.org/10.1016/S0038-0717\(01\)00213-9](https://doi.org/10.1016/S0038-0717(01)00213-9).
- Maljanen, M., Komulainen, V.M., Hytönen, J., Martikainen, P.J., Laine, J., 2004. Carbon dioxide, nitrous oxide and methane dynamics in boreal organic agricultural soils with different soil characteristics. *Soil Biology and Biochemistry* 36, 1801–1808. <https://doi.org/10.1016/j.soilbio.2004.05.003>.
- Maljanen, M., Sigurdsson, B.D., Guðmundsson, J., Oskarsson, H., Huttunen, J.T., Martikainen, P.J., 2010. Greenhouse gas balances of managed peatlands in the Nordic countries present knowledge and gaps. *Biogeosciences* 7, 2711–2738. <https://doi.org/10.5194/bg-7-2711-2010>.
- Mehnaz, K.R., Dijkstra, F.A., 2016. Denitrification and associated  $\text{N}_2\text{O}$  emissions are limited by phosphorus availability in a grassland soil. *Geoderma* 284, 34–41. <https://doi.org/10.1016/j.geoderma.2016.08.011>.
- Moore, T.R., Dalva, M., 1997. Methane and carbon dioxide exchange potentials of peat soils in aerobic and anaerobic laboratory incubations. *Soil Biology and Biochemistry* 29, 1157–1164. [https://doi.org/10.1016/S0038-0717\(97\)00037-0](https://doi.org/10.1016/S0038-0717(97)00037-0).
- Moore, T.R., Knowles, R., 1989. The influence of water table levels on methane and carbon dioxide emissions from peatland soils. *Canadian Journal of Soil Science* 69, 33–38.
- Moyano, F.E., Vasilyeva, N., Bouckaert, L., Cook, F., Craine, J., Curiel Yuste, J., Don, A., Epron, D., Formanek, P., Franzluebbers, A., Ilstedt, U., Kätterer, T., Orchard, V., Reichstein, M., Rey, A., Ruamps, L., Subke, J.-A., Thomsen, I.K., Chenu, C., 2012. The moisture response of soil heterotrophic respiration: interaction with soil properties. *Biogeosciences* 9, 1173–1182. <https://doi.org/10.5194/bg-9-1173-2012>.
- Murphy, J., Riley, J.P., 1962. A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta* 27, 31–36. [https://doi.org/10.1016/S0003-2670\(00\)88444-5](https://doi.org/10.1016/S0003-2670(00)88444-5).
- Neyroud, J.A., Lischer, P., 2003. Do different methods used to estimate soil phosphorus availability across Europe give comparable results? *Journal of Plant Nutrition and Soil Science* 166, 422–431. <https://doi.org/10.1002/jpln.200321152>.
- Norberg, L., Berglund, Ö., Berglund, K., 2018. Impact of drainage and soil properties on carbon dioxide emissions from intact cores of cultivated peat soils. *Mires and Peat* 21, 1–14. <https://doi.org/10.19189/Map.2017.OMB.284>.
- Pinsonneault, A.J., Moore, T.R., Roulet, N.T., 2016. Effects of long-term fertilization on peat stoichiometry and associated microbial enzyme activity in an ombrotrophic bog. *Biogeochemistry* 129, 149–164. <https://doi.org/10.1007/s10533-016-0224-6>.
- Preston, M.D., Smemo, K.A., McLaughlin, J.W., Basiliko, N., 2012. Peatland microbial communities and decomposition processes in the James Bay Lowlands, Canada. *Frontiers in Microbiology* 3, 1–15. <https://doi.org/10.3389/fmicb.2012.00070>.
- R Core Team, 2018. *A Language and Environment for Statistical Computing*. R-3.5.0. R Foundation for Statistical Computing, Vienna, Austria available at: <http://www.R-project.org/>.
- Regina, K., Nykanen, H., Silvola, J., Martikainen, P.J., 1996. Fluxes of nitrous-oxide from boreal peatlands as affected by peatland type, water-table level and nitrification capacity. *Biogeochemistry* 35, 401–418.
- Reiche, M., Gleixner, G., Küsel, K., 2010. Effect of peat quality on microbial greenhouse gas formation in an acidic fen. *Biogeosciences* 7, 187–198. <https://doi.org/10.5194/bg-7-187-2010>.
- Ross, S.M., Malcolm, D.C., 1988. Modelling nutrient mobilisation in intensively mixed peaty heathland soil. *Plant and Soil* 107, 113–121. <https://doi.org/10.1007/BF02371552>.
- Rovdan, E., Witkowska-Walczak, B., Walczak, R., Sawiński, C., 2002. Changes in the hydrophysical properties of peat soils under anthropogenic evolution. *International Agrophysics* 16, 219–226.

- Scharlemann, J.P.W., Tanner, E.V.J., Hiederer, R., Kapos, V., 2014. Global soil carbon: understanding and managing the largest terrestrial carbon pool. *Carbon Management* 5, 81–91. <https://doi.org/10.4155/cmt.13.77>.
- Schüller, H., 1969. Die CAL-Methode, eine neue Methode zur Bestimmung des pflanzenverfügbaren Phosphates in Böden. *Journal of Plant Nutrition and Soil Science* 123, 48–63. <https://doi.org/10.1002/jpln.19691230106>.
- Schulz, S., Waldeck, A., 2015. Kohlenstoffreiche Böden auf Basis hochauflösender Bodendaten in Niedersachsen, *GeoBerichte* 33. State Authority for Mining, Energy and Geology, Hanover, Germany.
- Schwarzl, K., Renger, M., Sauerbrey, R., Wessolek, G., 2002. Soil physical characteristics of peat soils. *Journal of Plant Nutrition and Soil Science* 165, 479–486. [https://doi.org/10.1002/1522-2624\(200208\)165:4<479::aid-jpln479>3.0.co;2-8](https://doi.org/10.1002/1522-2624(200208)165:4<479::aid-jpln479>3.0.co;2-8).
- Sognnes, L.S., Fystro, G., Øpstad, S.L., Arstein, A., Børresen, T., 2006. Effects of adding moraine soil or shell sand into peat soil on physical properties and grass yield in western Norway. *Acta Agriculturae Scandinavica Section B Soil and Plant Science* 56, 161–170. <https://doi.org/10.1080/09064710500218845>.
- Sundström, E., Magnusson, T., Hånell, B., 2000. Nutrient conditions in drained peatlands along a north-south climatic gradient in Sweden. *Forest Ecology and Management* 126, 149–161. [https://doi.org/10.1016/S0378-1127\(99\)00098-5](https://doi.org/10.1016/S0378-1127(99)00098-5).
- Tiemeyer, B., Albiac Borrás, E., Augustin, J., Bechtold, M., Beetz, S., Beyer, C., Drösler, M., Ebli, M., Eickenscheidt, T., Fiedler, S., Förster, C., Freibauer, A., Giebels, M., Glatzel, S., Heinichen, J., Hoffmann, M., Höper, H., Jurasinski, G., Leiber-Sauheitl, K., Peichl-Brak, M., Rofskopf, N., Sommer, M., Zeitz, J., 2016. High emissions of greenhouse gases from grasslands on peat and other organic soils. *Global Change Biology* 22, 4134–4149. <https://doi.org/10.1111/gcb.13303>.
- Tubiello, F.N., Biancalani, R., Salvatore, M., Rossi, S., Conchedda, G., 2016. A worldwide assessment of greenhouse gas emissions from drained organic soils. *Sustainability* 8, 1–13. <https://doi.org/10.3390/su8040371>.
- Urbanová, Z., Bárta, J., 2015. Effects of long-term drainage on microbial community composition vary between peatland types. *Soil Biology and Biochemistry* 92, 16–26. <https://doi.org/10.1016/j.soilbio.2015.09.017>.
- Urbanová, Z., Bárta, J., 2014. Microbial community composition and *in silico* predicted metabolic potential reflect biogeochemical gradients between distinct peatland types. *FEMS Microbiology Ecology* 90, 633–646. <https://doi.org/10.1111/1574-6941.12422>.
- van Lent, J., Hergoualc'h, K., Verchot, L., Oenema, O., van Groenigen, J.W., 2018. Greenhouse gas emissions along a peat swamp forest degradation gradient in the Peruvian Amazon: soil moisture and palm roots effects. *Mitigation and Adaptation Strategies for Global Change* 1–19. <https://doi.org/10.1007/s11027-018-9796-x>.
- VDLUFA, 2012. Bestimmung von Phosphor und Kalium im Calcium-Acetat-Auszug. In: *Methodenbuch I 6. Teillieferung*. VDLUFA-Verlag, Darmstadt, Germany.
- Verhoeven, J.T.A., Liefveld, W.M., 1997. The ecological significance of organochemical compounds in Sphagnum. *Acta Botanica Neerlandica* 46, 117–130. <https://doi.org/10.1111/plb.1997.46.2.117>.
- Vos, C., Jaconi, A., Jacobs, A., Don, A., 2018. Hot regions of labile and stable soil organic carbon in Germany - spatial variability and driving factors. *Soil* 4, 153–167. <https://doi.org/10.5194/soil-4-153-2018>.
- Walczak, R., Rovdan, E., 2002. Water retention characteristics of peat and sand mixtures. *International Agrophysics* 16, 161–165.
- Wang, M., Moore, T.R., Talbot, J., Richard, P.J.H., 2014. The cascade of C:N:P stoichiometry in an ombrotrophic peatland: from plants to peat. *Environmental Research Letters* 9, 024003. <https://doi.org/10.1088/1748-9326/9/2/024003>.
- Well, R., Höper, H., Mehranfar, O., Meyer, K., 2005. Denitrification in the saturated zone of hydromorphic soils - laboratory measurement, regulating factors and stochastic modeling. *Soil Biology and Biochemistry* 37, 1822–1836. <https://doi.org/10.1016/j.soilbio.2005.02.014>.
- Weslien, P., Kasimir Klemedtsson, Å., Börjesson, G., Klemedtsson, L., 2009. Strong pH influence on N<sub>2</sub>O and CH<sub>4</sub> fluxes from forested organic soils. *European Journal of Soil Science* 60, 311–320. <https://doi.org/10.1111/j.1365-2389.2009.01123.x>.
- White, J.R., Reddy, K.R., 2000. Influence of phosphorus loading on organic nitrogen mineralization of everglades soils. *Soil Science Society of America Journal* 64, 1525–1534. <https://doi.org/10.2136/sssaj2000.6441525x>.
- White, J.R., Reddy, K.R., 1999. Influence of nitrate and phosphorus loading on denitrifying enzyme activity in Everglades wetland soils. *Soil Science Society of America Journal* 63, 1945–1954. <https://doi.org/10.2136/sssaj1999.6361945x>.
- Wilson, D., Blain, D., Couwenberg, J., Evans, C.D., Murdiyarso, D., Page, S.E., Renou-Wilson, F., Riele, J.O., Sirin, A., Strack, M., Tuittila, E.-S., 2016. Greenhouse gas emission factors associated with rewetting of organic soils. *Mires and Peat* 17, 1–28. <https://doi.org/10.19189/Map.2016.OMB.222>.
- Yu, Z., Loisel, J., Brosseau, D.P., Beilman, D.W., Hunt, S.J., 2010. Global peatland dynamics since the last glacial maximum. *Geophysical Research Letters* 37, 1–5. <https://doi.org/10.1029/2010GL043584>.
- Zaidelman, F.R., Shvarov, A.P., 2000. Hydrothermic regime, dynamics of organic matter and nitrogen in drained peaty soils at different sanding modes. *Archives of Agronomy and Soil Science* 45, 123–142. <https://doi.org/10.1080/03650340009366117>.
- Zeitz, J., Velt, S., 2002. Soil properties of drained and rewetted fen soils. *Journal of Plant Nutrition and Soil Science* 165, 618–626. [https://doi.org/10.1002/1522-2624\(200210\)165:5<618::AID-JPLN618>3.0.CO;2-W](https://doi.org/10.1002/1522-2624(200210)165:5<618::AID-JPLN618>3.0.CO;2-W).
- Zörb, C., Senbayram, M., Peiter, E., 2014. Potassium in agriculture - status and perspectives. *Journal of Plant Physiology* 171, 656–669. <https://doi.org/10.1016/j.jplph.2013.08.008>.