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Rewetting former agricultural peatlands: Topsoil removal as a prerequisite to avoid strong nutrient and greenhouse gas emissions

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ABSTRACT

Globally 15%, and in Europe over 50%, of all peatlands have been drained for agricultural use leading to high carbon (C) losses, severe land subsidence and increased flooding risks. For the restoration of C sequestration and peat formation, abandoned peatlands are being rewetted at a large scale, but this transforms them into strong methane (CH_4) sources. Furthermore, due to the high topsoil nutrient contents and/or high buffering capacities of water used for rewetting, this will inevitably result in eutrophication of restored peatlands and downstream areas, which may compromise the regrowth of peat forming vegetation including *Sphagnum* spp.

To experimentally determine the extent of these negative side effects in relation to water quality, and to test topsoil removal as an abatement strategy, we used a controlled laboratory approach in which topsoil and subsoil monoliths of a former agricultural peatland were rewetted with water of different qualities (+P, $+HCO_3^-$, $+P/+HCO_3^-$ and Control), mimicking rainwater vs. surface water storage. In addition, two different *Sphagnum* moss species (*S. squarrosum* and *S. palustre*) were compared.

Without topsoil removal, rewetting led to high P and N mobilisation, algal blooms, and high CH_4, carbon dioxide (CO_2) and dissolved organic carbon (DOC) emissions. P-rich water resulted in further eutrophication. Bicarbonate (HCO_3^-) enrichment by surface water not only stimulated P release and CO_2 emission, but also strongly reduced *Sphagnum* vitality.

We conclude that topsoil removal will, at least in initial stages of rewetting, strongly reduce eutrophication problems (by 80–90%), CH_4 emission (99%), DOC loss (60%) and global warming potential (50–70%) of rewetted former agricultural peatlands. Furthermore, to reduce mineralisation rates and enable *Sphagnum* growth, storage of rainwater rather than surface water is preferred. Finally, removed topsoils can be reused in adjacent subsiding agricultural areas, and thereby optimise the overall C balance and allow higher water levels in rewetted peatlands.

1. Introduction

Land use change, hydrological operations and other forms of anthropogenic forcing have severely compromised the functioning of global wetlands and their services including flood protection, water purification, biodiversity and C sequestration (Foley et al., 2005; Zedler and Kercher, 2005). Approximately 15% of peatlands worldwide have been drained to accommodate agriculture, peat extraction, forestry or urbanisation (Joosten, 2009), although considerable differences exist between countries, with 10% to 85% of peatlands drained within a single country (e.g. Brock et al., 1999; Hooijer et al., 2012; Zanello et al., 2011; Meckel et al., 2006; Hoeksema, 2007). While the accumulation of thick peat layers has generally taken thousands of years ($-1.1\ mm\ yr^{-1}$; Ovenden et al., 1998), drainage of these systems has resulted in strong degradation by oxygen intrusion, enhancing aerobic decomposition of organic matter and carbon (C) emission. Together with compaction and consolidation (Hooijer et al., 2012), this has caused fast land subsidence ($2–150\ mm\ yr^{-1}$; Syvitski et al., 2009). Given the projected sea-level rise, this continuing subsidence of peatlands – often located in heavily populated coastal areas, river deltas and

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floodplains – poses a serious risk to public safety due to higher flooding risks (Syvitski et al., 2009; Temmerman et al., 2013).

Pristine, growing peatlands (mires) generally form net C sinks, in which the fixation of carbon dioxide (CO_2) into layers of organic matter exceeds the emission of methane (CH_4) and CO_2, leading to net ecosystem exchange (NEE) rates ranging from −5 to −40 g C m^{-2} yr^{-1} (Belyea and Malmer, 2004; Gorham, 1991; Lamers et al., 2015; Saarnio et al., 2007). Drained and degraded peatlands, on the other hand, are almost always net C sources (Alm et al., 1999; Waddington et al., 2001), with NEE rates ranging from +80 to +880 g C m^{-2} yr^{-1} (Lamers et al., 2015) and a yearly global emission of 30 to 370 Mt C yr^{-1} (Armentano, 1980). These high C emission rates from drained peatlands are the result of strongly increased aerobic ecosystem respiration rates and therefore mainly consist of CO_2 (Nykänen et al., 1995; Silvola et al., 1996; Waddington and Day, 2007). Emissions of CH_4, on the other hand, are much lower for drained peatlands than for pristine or rewetted peatlands (Moore and Knowles, 1989; Salm et al., 2009), as a result of the inhibition of CH_4 production and stimulation of CH_4 oxidation under aerobic conditions (Lai, 2009; Maljanen et al., 2010). Since CH_4 is a much more potent greenhouse gas than CO_2, its enhanced emission after rewetting strongly increases the global warming potential (GWP) of these restored systems. Due to the high availability of easily degradable organic matter (and therefore of acetate, CO_2 and H_2), and nutrients for methanogens (Aerts and Toet, 1997; Fiedler and Sommer, 2000), CH_4 emissions from rewetted, former agricultural peatlands may be considerable (Lamers et al., 2015). So far, however, only few studies have been published on CH_4 fluxes in these systems (e.g. Hendriks et al., 2007; van de Riet et al., 2013).

Since over 85% of drained peatlands have been used for agriculture (Joosten, 2009), they have been heavily fertilised and often also limed, resulting in an extremely nutrient-rich, buffered top layer of the soil. Especially phosphate (PO_4^{3-}) has accumulated in these soils, since it is strongly bound in iron (Fe) complexes and to organic matter under aerobic conditions (Lamers et al., 2015; Smolders et al., 2006, 2008). Upon rewetting, however, there is a considerable risk of PO_4^{3-} mobilisation and eutrophication of the peatland and downstream areas (Patrick and Khalid, 1974; Rupp et al., 2004; van Dijk et al., 2007). Furthermore, heavily fertilised soils often also turn into sources of N after rewetting (van de Riet et al., 2013; Van Dijk et al., 2004; Zak and Gelbrecht, 2007). Thus, although rewetting of drained peatlands may counteract land subsidence and CO_2 losses by restoring the anaerobic soil conditions and inhibiting complete organic matter oxidation, it may have several negative side effects in former agricultural systems. Therefore, despite seeming counterintuitive, removal of the easily degradable eutrophic topsoil may be a useful abatement strategy to prevent strong greenhouse gas (GHG) emission and nutrient mobilisation after rewetting and thus restore peat formation (Emsens et al., 2015).

The actual effect of rewetting a drained peatland will also strongly depend on the quality of the water used. Instead of conserving rainwater by building dams to counteract desiccation in peatlands, many areas have been rewetted by flooding them with surface water (Grootjans et al., 2002; Lamers et al., 2002; Roelofs, 1991). Especially in agricultural areas, the quality of this surface water may be compromised, with high nutrient concentrations and/or high buffering capacity (alkalinity). Both factors can be expected to have a strong influence on the peatlands' biogeochemistry and other services, including C sequestration (Lamers et al., 2015).

To fully restore the C sequestering function of a system and promote regrowth of peat, restoration of the original peat-forming vegetation is essential. Limitations in seed or spore dispersal, absence of viable seeds or spores in the soil or unfavourable habitat conditions may hamper natural return of peat-forming vegetation, such as *Phragmites*, *Carex* or *Sphagnum* species (Aggenbach et al., 2013; Campeau and Rochefort, 1996). Of these species, *Sphagnum* mosses produce more recalcitrant organic matter than other peat-forming species due to the unique characteristics of these ecosystem engineers (Van Breemen, 1995), including habitat acidification (Clymo, 1963; Hajek and Adamec, 2009; Van Breemen, 1995), production of organic matter with high phenolic contents (Yavitt et al., 2000), and high water retention, keeping the environment moist and anaerobic (Clymo, 1973). While *Sphagnum* can be reintroduced successfully on oligotrophic, acidic cut-over peatlands (Campeau and Rochefort, 1996; Robroek et al., 2009; Smolders et al., 2003), revegetation of eutrophic or alkaline soils may pose a serious problem to these mosses, since they may easily be out-competed by vascular plants (Aggenbach et al., 2013; Berendse et al., 2001; Smolders et al., 2008) or suffer from high pH (Andrus, 1986; Clymo, 1973; Hajek et al., 2006; Lamers et al., 1999).

Increased CH_4 production and nutrient mobilisation after rewetting of former agricultural peatlands have already been shown in the field (e.g. Hendriks et al., 2007; Zak and Gelbrecht, 2007). In field studies, however, determining the extent and impact of these two processes is difficult due to multiple biogeochemical interactions, complex hydrology and large variations in climatic parameters. Therefore, we chose a controlled, experimental approach to determine the extent of the GHG emission and eutrophication after rewetting of a former agricultural peatland using water of different qualities, mimicking rainwater, or surface water with high P and/or HCO_3^- availability. This controlled mesocosm approach also allowed us to quantify the effect of topsoil removal on the restoration of ecosystem services, by using both topsoils (5–20 cm) and subsoils (25–45 cm). Furthermore, to test whether the original fen vegetation, characterised by *Phragmites australis* and *Sphagnum* spp., could be restored after rewetting and topsoil removal, we introduced two species of *Sphagnum* (*S. palustre* and *S. squarrosum*) that are typical of this vegetation, and studied their growth potential under the different water and soil conditions and their contribution to C sequestration.

2. Material and methods

2.1. Experimental set-up

In autumn 2013, 32 peat monoliths (25 × 12 × 20 cm; length × width × height) were randomly collected from a drained and fertilised, agricultural peatland managed as a pasture in the north-western part of The Netherlands (Ilperveld; 52°44′075″N; 4°94′960″E). Cores were taken from two depths, 5–25 cm (topsoil; n = 16) and 25–45 cm (subsoil; n = 16), immediately transferred into glass aquaria (25 × 12 × 30 cm; $l \times w \times h$) and transported to the lab. Both layers consisted of *Sphagnum*/*Carex* peat, but as a result of drainage, the top layer was decomposed further, as illustrated by a higher bulk density (0.41 ± 0.03 vs. 0.19 ± 0.01 kg DW L^{-1} FW), lower organic matter content (47.9 ± 9.3 vs. 78.4 ± 1.8) and lower content of porewater phenolic compounds (2.75 ± 0.64 vs. 4.14 ± 0.85 mg L^{-1}). The two chosen depths were based on measurements of the Olsen-P (Olsen et al., 1954) profile showing much higher P availability (951 ± 71 vs. 153 ± 22 mg P kg DW^{-1}) in the top layer due to fertilisation and decomposition.

In the lab, demineralised water was added to 2 cm above soil level (0.6 L per aquarium), after which the aquaria were left for 2 weeks to acclimatise in a water bath at 15 °C (NESLAB cryostat, Thermoflex 1400, Breda, The Netherlands) with a light regime of 16 h light (400 W, Philips, Master Son-T PiaPlus, Belgium, 150 μmol m^{-2} s^{-1} PAR), mimicking Dutch summer conditions. All soils received artificial rainwater at a rate of 750 mm yr^{-1} corresponding to Dutch annual rainfall (250 mL; three times a week), and with a composition equal to Dutch rainwater (5 mg L^{-1} sea salt (Tropic Marine, aQua united LTD, Wartenberg), 19 μmol L^{-1} KCl, 10 μmol L^{-1} $CaCl_2$, 10 μmol L^{-1} Fe-EDTA, 1 μmol L^{-1} KH_2PO_4, 0.7 μmol L^{-1} $ZnSO_4$, 0.8 μmol L^{-1} $MnCl_2$, 0.2 μmol L^{-1} $CuSO_4$, 0.8 μmol L^{-1} H_3BO_3, 8 nmol L^{-1} $(NH_4)_6Mo_7O_{24}$ and 91 μmol L^{-1} NH_4NO_3).

After two weeks, the demineralised water was replaced with treatment solutions containing 5 mg L^{-1} of sea salt (see above) and either 0 or 5 μmol L^{-1} $Na_4P_2O_7\cdot10H_2O$ and 0 or 3 mmol L^{-1} $NaHCO_3$ creating four treatments: Control, +P, +HCO_3^- and +P/+HCO_3^- (randomly applied; n = 4 for each treatment). The addition of HCO_3^- and PO_4^{3-} simulates the use of alkaline or nutrient-rich surface water for the rewetting of peatlands. Treatment solutions were flowing through the aquaria at a rate of 5.44 L $week^{-1}$ using peristaltic pumps (Masterflex L/S tubing pump; Cole-Palmer, Chicago, IL, USA), which, together with a fixed outflow, ensured a stable water layer of 2 cm above soil surface. After the first period of 2.5 months, patches of *Sphagnum palustre* (2.37 ± 0.11 g DW; 67 ± 1.3 capitula; mean ± SEM) and *S. squarrosum* (1.84 ± 0.07 g DW; 84 ± 1.4 capitula; mean ± SEM) were applied to each half of the aquaria. These two species are still abundant in natural, undisturbed parts of the peatland area where the soils were collected, and are typical fen species in The Netherlands. They differ, however, in their habitat preference, with *S. squarrosum* being more tolerant to nutrient-rich and alkaline conditions than *S. palustre* (Clymo, 1973). The upper parts of the mosses were cut at equal lengths (4 cm) and placed upright to avoid submergence of the capitula (top 8–10 mm of the photosynthetically active tissue of the mosses).

2.2. Chemical analyses

Two soil moisture samplers of 10 cm length (Rhizon SMS-10; Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands) were inserted into the sediments to allow collection of pore water using vacuum bottles. While peat was bare, both samples were pooled, whereas samples were analysed separately after application of the *Sphagnum* mosses. Surface water was sampled simultaneously with pore water.

pH was measured with a standard Ag/AgCl electrode (Orion Research, Beverly, CA, USA) combined with a pH meter (Tim840 titration manager; Radiometer analytical, Lyon, France), after which alkalinity was determined by titrating down to pH 4.2 using 0.1 M HCl using an Auto burette (ABU901, Radiometer, Copenhagen, Denmark). Total inorganic carbon (TIC) was measured by injecting 0.2 mL of sample into an N_2-flushed compartment with 1 mL phosphoric acid (0.4 M) in an Infra-red Gas Analyser (IRGA; ABB Analytical, Frankfurt, Germany), after which concentrations of HCO_3^- and CO_2 were calculated based on the pH equilibrium. Total organic carbon (TOC), dissolved organic carbon (DOC) and total nitrogen (TN) were measured in unfiltered water layer samples and filtered (Ø 0.45 μm) pore water samples, using a TOC-L CPH/CPN analyser (Shimadzu, Kyoto, Japan). Net mobilisation rates of nutrients (P, N and Fe) and TOC were calculated based on their concentrations in the water layer and the flow rate of treatment water.

At the end of the experiment, homogenised soil samples were taken, volume weighed and dried (48 h 60 °C) to determine bulk density. Organic matter content was determined through loss on ignition (3 h, 550 °C). Dried soils were digested with 4 mL HNO_3 (65%) and 1 mL H_2O_2 (30%) using a microwave oven (1200 Mega, Milestone Inc., Sorisole, Italy). Plant available P was extracted according to Olsen et al. (1954), whereas a salt extraction was performed by incubating 17.5 g of homogenised fresh soil overnight with 50 mL of 0.2 M NaCl. Furthermore, total phenol concentrations of soil pore water were determined colourimetrically on a spectrophotometer (750 nm; Lambda 25, UV/vis Spectrometer, PerkinElmer Instruments), according to Box (1983) and Carter and Gregorich (2007).

Soil extracts and water samples were analysed colourimetrically for PO_4^{3-}, NH_4^+ and NO_3^-, on an Auto Analyser 3 system (Bran & Lubbe, Norderstedt, Germany) using ammonium molybdate (Henriksen, 1965), hydrazine sulphate (Kamphake et al., 1967) and salicylate (Grasshof and Johannse, 1972), respectively. Concentrations of Ca, Fe, K, Mg and total-P in water samples and digestates were analysed by inductively coupled plasma spectrometry (ICP–OES iCAP 6000; Thermo Fischer Scientific, Waltham, MA, U.S.A.).

2.3. Greenhouse gas flux measurements

CO_2 and CH_4-fluxes were measured on bare peat (4 weeks after start of the treatments) and on *Sphagnum*-covered peat (15 weeks; i.e. 6 weeks after placing *Sphagnum*) under light and dark conditions using transparent and dark closed chambers (10 × 10 × 12 cm), respectively, connected to a Greenhouse Gas Analyser (GGA-24EP, Los Gatos Research, Mountain View, CA, USA). Dark measurements were carried out after the night-period to ensure dark-adaptation of plants. Measured fluxes were used to estimate GWPs, expressed (on a mass basis) in CO_2-eq m^{-2} d^{-1}, with CH_4 corresponding to 34 CO_2-eq over a 100 year period including climate-carbon feedbacks (IPCC, 2013). Estimates of year-round fluxes of GWP are based on an 8-month growing season to prevent overestimation during winter months.

Methane Production Potential (MPP) was determined by incubating 3 g of homogenised soil samples (2–6 cm depth) in 60 mL serum bottles with 3 mL of demineralised H_2O. An anaerobic headspace was ensured by 5 cycles of evacuation and gassing with N_2. For controls and acetate (5 mmol L^{-1} final concentration) treatments the headspace consisted of N_2, whereas the headspace of the hydrogen treatment consisted of 80% H_2/20% CO_2. Bottles were incubated on a horizontal shaker (100 rpm) at room temperature. CH_4 concentrations in the headspace were measured 7 times during one week on a HP 5890 gas chromatograph (Hewlett Packard, Wilmington, DE, USA) according to e.g. Ettwig et al. (2008). The linear part of the graph was used to calculate MPP.

2.4. Plant parameters

At the beginning and at the end of the experiment, the fresh weight (FW) and number of capitula of the mosses were determined. At the end, DW was determined (48 h, 60 °C), while initial moss DW was calculated using the DW/FW ratio determined by weighing and drying extra mosses (n = 5 per species) at the start of the experiment. At the end of the experiment, photosynthetic rates were determined by measuring CO_2 consumption of capitula (0–3 cm) from both species and all aquaria in a closed glass chamber (100 mL) connected to a greenhouse gas analyser (GGA-24EP, Los Gatos Research, Mountain View, CA, USA) at a light intensity of 200 μmol m^{-2} s^{-1}. Furthermore, health of photosystem II (F_V/F_M) was determined using pulse-amplified modulation (JUNIOR-PAM, Waltz, Effeltrich, Germany). During the experiment, the concentrations of unicellular algae in the water layer were determined three times using a PhytoPAM (Phytoplankton Analyser System, Waltz, Effeltrich, Germany).

2.5. Statistical analyses

Normality of residuals and homogeneity of variance were checked using Shapiro-Wilk's Test of Normality and Levene's Test of Equality of Error Variances, respectively. Non-normal and heteroscedastic data were log transformed before analyses to authorise use of parametric tests. All data were subsequently analysed by two-way ANOVAs at the 0.05 confidence limit followed by a Tukey post hoc test. For all analyses, *P* and F values are presented. All statistical tests were carried out using SPSS v21 (IBM Statistics, 2012).

3. Results

3.1. Soil characteristics

Topsoils were characterised by a much higher P availability than subsoils, with significantly higher Olsen-P ($P<0.001$; $F=127.870$) and total P (TP; $P<0.001$; $F=118.299$) concentrations in soil and pore water extracts, respectively (Table 1). Furthermore, topsoils had much higher salt-extractable NH_4^+ ($P<0.001$; $F=19.533$) and NO_3^- ($P<0.001$; $F=20.288$) concentrations and contained more total N (TN; $P<0.001$; $F=46.309$) than subsoils (Table 1). Topsoils were also characterised by higher concentrations of Ca ($P<0.001$; $F=20.612$, data not shown), Mg ($P=0.004$; $F=9.914$, data not shown) and HCO_3^- ($P<0.001$; $F=105.565$; Table 1). While Fe concentrations did not differ between topsoils and subsoils, the much higher total-P content of topsoils resulted in much lower Fe:P ratios (4.5 ± 0.4 mol mol^{-1}) compared with subsoils (11.8 ± 0.9 mol mol^{-1}; data not shown; $P<0.001$; $F=49.124$). Furthermore, subsoils had a 30% lower bulk density ($P<0.001$; $F=39.340$), 20% higher OM content ($P=0.007$; $F=8.860$) and 50% higher concentration of phenolic compounds ($P=0.020$; $F=6.249$) than topsoils (Table 1).

3.2. Water and pore water quality

The water layer above topsoils was characterised by a higher pH ($P=0.008$; $F=8.496$; Table 2) and alkalinity ($P<0.001$; $F=29.608$; Table 2) than the water layer of subsoils. Similar differences were observed in the soil pore water (data not shown). Rewetting with HCO_3^--rich water increased both pH ($P<0.001$; $F=231.050$) and alkalinity ($P<0.001$; $F=1956.640$) in the water layer (Table 2) and pore water (data not shown), while use of P-rich water resulted in a higher PO_4^{3-} availability in the water layer ($P<0.001$; $F=11.234$; Table 2). Furthermore, a combination of P and HCO_3^- in the inlet water resulted in an even higher pH than sole addition of HCO_3^- ($P<0.001$; $F=231.050$; Table 2).

The higher nutrient content of topsoils also resulted in a higher availability of P and N in the overlying water layers (Table 2). P and N were mobilised from topsoils to the water layer at rates of 413 ± 81 and 152 ± 21 µmol m^{-2} d^{-1}, respectively, whereas mobilisation from subsoils was limited to 27 ± 7 µmol P and 34 ± 5 µmol N m^{-2} d^{-1} ($P<0.001$ for both; data not shown). The mobilisation of P concurred with the mobilisation of Fe, at rates of 915 ± 202 and 141 ± 39 µmol m^{-2} d^{-1} from topsoils and subsoils, respectively ($P=0.003$; data not shown). The water layer above topsoils contained significantly higher concentrations of algae during the experiment ($P<0.001$; $F=45.842$; Fig. 1), whereas there was a trend ($P=0.089$; $F=2.441$; Fig. 1) indicating a stimulating effect of P, HCO_3^- or a combination of P and HCO_3^- on algal growth in the water layer.

Table 1
Sediment characteristics of topsoil and subsoil of a former agricultural peatland, after 15 weeks of rewetting. Olsen P, NH_4^+ and NO_3^- were derived from Olsen and salt extractions, respectively, and are presented as µmol L FW^{-1}. Other nutrient concentrations and concentrations of phenolic compounds and bicarbonate (HCO_3^-) were present in collected pore waters and presented per L pore water. Significant differences between topsoils and subsoils are indicated with asterisks, with * representing $P\leq0.05$ and *** $P\leq0.001$.

	Unit	Topsoil	Subsoil
Bulk density***	kg DW L FW^{-1}	0.38 ± 0.02	0.27 ± 0.01
Moisture content***	%	66.5 ± 1.1	76.3 ± 0.8
Organic matter***	%	46.8 ± 1.3	57.3 ± 2.9
Total phenolic compounds*	mg L^{-1}	3.26 ± 0.36	4.91 ± 0.51
C:N***	g g^{-1}	11.44 ± 0.11	16.29 ± 0.47
Olsen P***	µmol L FW^{-1}	434.1 ± 70.0	144.5 ± 7.4
NH_4^+***	µmol L FW^{-1}	1651 ± 398	720 ± 81
NO_3^-***	µmol L FW^{-1}	841.1 ± 475.0	5.6 ± 1.9
TP***	µmol L^{-1}	268.4 ± 39.8	7.0 ± 0.9
TN***	mmol L^{-1}	4.43 ± 0.31	1.95 ± 0.15
DOC***	mmol L^{-1}	76.6 ± 7.9	38.0 ± 3.2
HCO_3^-***	µmol L^{-1}	381.6 ± 123.2	17.5 ± 1.0

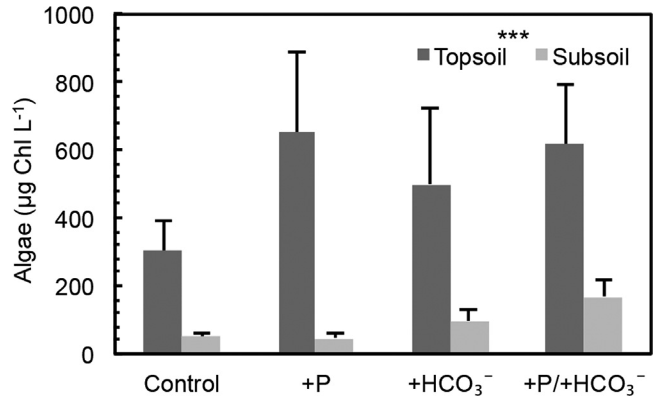

Fig. 1. Average (unicellular) algal concentrations (±SEM), expressed as µg Chl L^{-1} for topsoils and subsoils treated with a water layer with or without addition of P and/or HCO_3^-. The significant difference between topsoil and subsoils is indicated using an asterisk, with *** representing $P\leq0.001$.

3.3. *Sphagnum* growth

Both *Sphagnum* species were similarly affected by soil type and water quality, although *S. squarrosum* generally showed a higher relative growth rate (RGR) ($P<0.001$; $F=21.810$; Fig. 2) and a higher photosynthetic rate ($P=0.001$; $F=13.787$; Table A1) than *S. palustre*. Both moss species had higher growth rates ($P=0.007$; $F=8.041$; Fig. 2) on topsoils than on subsoils and a similar trend was observed for the photosynthetic rates of both species ($P=0.073$; $F=3.368$). Due to the higher availability of both N and P on topsoils, mosses grown on these soils also had higher N ($P=0.027$; $F=5.179$) and P ($P<0.001$; $F=17.279$) contents than mosses grown on subsoils (Table A1).

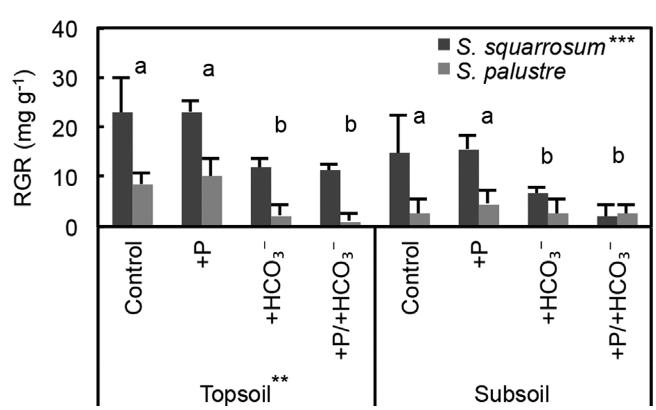

Fig. 2. Relative Growth Rate (RGR; mean ± SEM) of *S. squarrosum* and *S. palustre* growing on topsoils or subsoils treated with a water layer with or without addition of P and/or HCO_3^-. Significant differences between topsoil and subsoils, and between Sphagnum species are indicated using asterisks, with ** representing $P\leq0.01$ and *** $P\leq0.001$. Significant differences between water treatments are indicated using different letters (a, b).

Table 2
Chemical composition of the water layer overlying topsoils or subsoils, with or without addition of P and/or HCO_3^-. Significant differences between topsoil and subsoil are indicated with asterisks, with ** $P \leq 0.01$ and *** $P \leq 0.001$. Significant differences between water treatments are indicated with different letters (a, b, c).

Water layer	Soil	Control	+P	$+HCO_3^-$	$+P/+HCO_3^-$
pH	Topsoil**	5.3 ± 0.2^a	5.4 ± 0.1^a	7.6 ± 0.2^b	8.0 ± 0.2^c
	Subsoil	4.6 ± 0.1^a	4.6 ± 0.0^a	7.6 ± 0.1^b	8.2 ± 0.2^c
Alkalinity (meq L^{-1})	Topsoil***	0.25 ± 0.04^a	0.26 ± 0.07^a	2.92 ± 0.03^b	2.97 ± 0.06^b
	Subsoil	0.10 ± 0.02^a	0.09 ± 0.01^a	2.69 ± 0.06^b	2.77 ± 0.06^b
PO_4^{3-} (μmol L^{-1})	Topsoil***	6.86 ± 0.95^a	14.57 ± 4.77^b	10.23 ± 2.70^b	11.72 ± 1.20^b
	Subsoil	1.08 ± 0.07^a	3.01 ± 0.41^b	2.66 ± 0.65^b	5.31 ± 0.21^b
Total P (μmol L^{-1})	Topsoil***	15.93 ± 2.71^a	27.62 ± 6.94^b	17.78 ± 9.08^a	15.68 ± 3.80^b
	Subsoil	1.03 ± 0.26^a	7.47 ± 0.56^b	2.80 ± 0.19^a	8.05 ± 0.94^b
NH_4^+ (μmol L^{-1})	Topsoil**	5.87 ± 0.81	7.39 ± 1.84	10.96 ± 2.59	8.57 ± 2.13
	Subsoil	1.32 ± 0.19	1.34 ± 0.54	4.99 ± 2.36	7.49 ± 2.27
Ca (μmol L^{-1})	Topsoil	64 ± 9	128 ± 64	66 ± 12	54 ± 8
	Subsoil	71 ± 11	64 ± 6	79 ± 14	57 ± 10
TOC (mmol L^{-1})	Topsoil***	3.7 ± 1.1	3.9 ± 1.0	2.5 ± 1.2	3.0 ± 1.1
	Subsoil	0.7 ± 0.1	1.4 ± 0.4	1.9 ± 0.2	1.3 ± 0.1
TN (mmol L^{-1})	Topsoil***	0.29 ± 0.09	0.29 ± 0.07	0.17 ± 0.09	0.22 ± 0.08
	Subsoil	0.05 ± 0.01	0.09 ± 0.03	0.11 ± 0.01	0.07 ± 0.01

Both *S. palustre* and *S. squarrosum* species were negatively affected by addition of HCO_3^-. RGR ($P = 0.001$; $F = 6.732$; Fig. 2), number of capitula ($P < 0.001$; $F = 42.084$), moss length ($P < 0.001$; $F = 174.041$), photosynthesis ($P < 0.001$; $F = 8.266$) and PAM ($P < 0.001$; $F = 16.560$) were lower in mosses from $+HCO_3^-$ or $+P/+HCO_3^-$ treatments than in mosses from control or +P treatments (Table A1). For *Sphagnum* grown without HCO_3^-, the number of capitula increased by approximately 15–20% during the experiment, while mosses that grew under HCO_3^--rich conditions had a 50–67% lower number of capitula at the end of the experiment than at the beginning (data not shown). Addition of HCO_3^- resulted in a higher N-content ($P < 0.001$; $F = 13.805$) and a lower K-content ($P < 0.001$; $F = 116.846$) in the mosses, whereas addition of HCO_3^- together with P resulted in a higher P- ($P = 0.001$; $F = 6.402$) and N-content ($P < 0.001$; $F = 22.872$) in the moss tissue (Table A1).

3.4. C-dynamics

After four weeks of rewetting, all bare sediments showed a net emission of both CH_4 (Fig. 3a) and CO_2 (Fig. 3b). While CO_2 emissions were similar for topsoils and subsoils, emission of CH_4 was more than 100 times higher for topsoils ($P < 0.001$; $F = 32.191$). This difference was still observed after 15 weeks of rewetting (6 of which with *Sphagnum* cover; $P < 0.001$; $F = 38.848$; Fig. 3c),

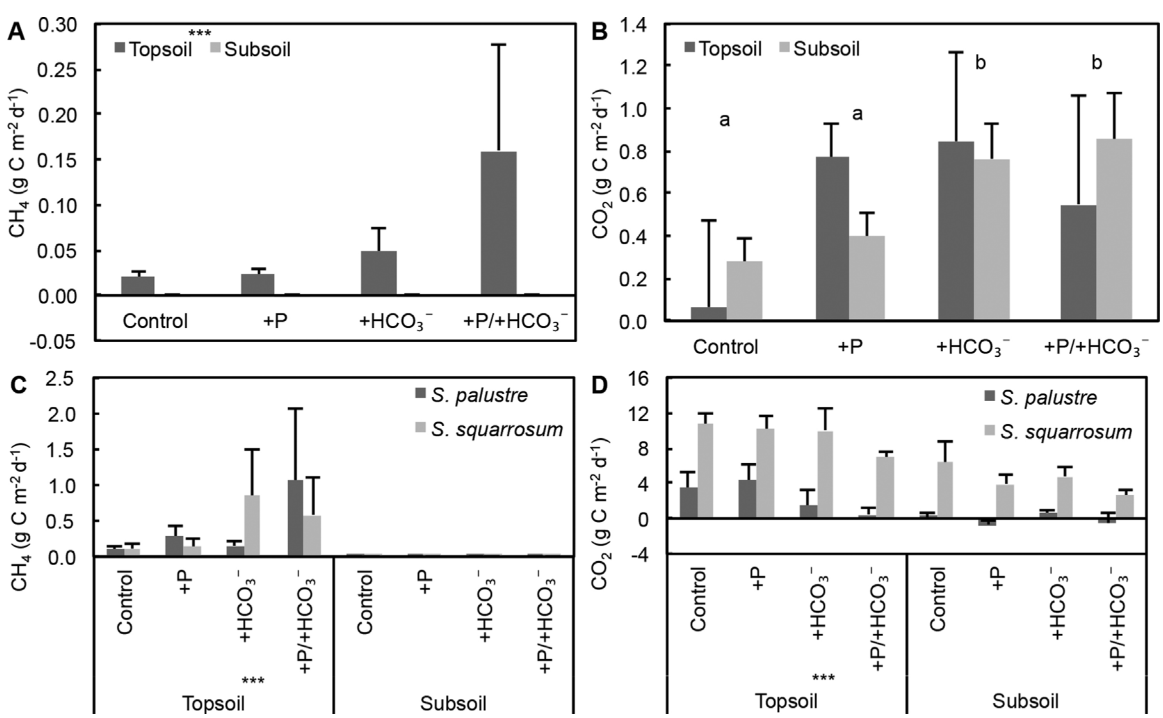

Fig. 3. Fluxes (±SEM) of CH_4 (left) and CO_2 (right) from bare soils (A and B) and soils covered by *Sphagnum* mosses (C and D). Soils are either topsoils or subsoils, treated with a water layer with or without addition of P and/or HCO_3^-. Note different scales for the *y*-axes. Some treatments show high variation in CH_4 diffusion, resulting in large SEMs. Significant differences between topsoil and subsoils are indicated using asterisks, with *** representing $P \leq 0.001$. Significant differences between water treatments are indicated using different letters (a, b).

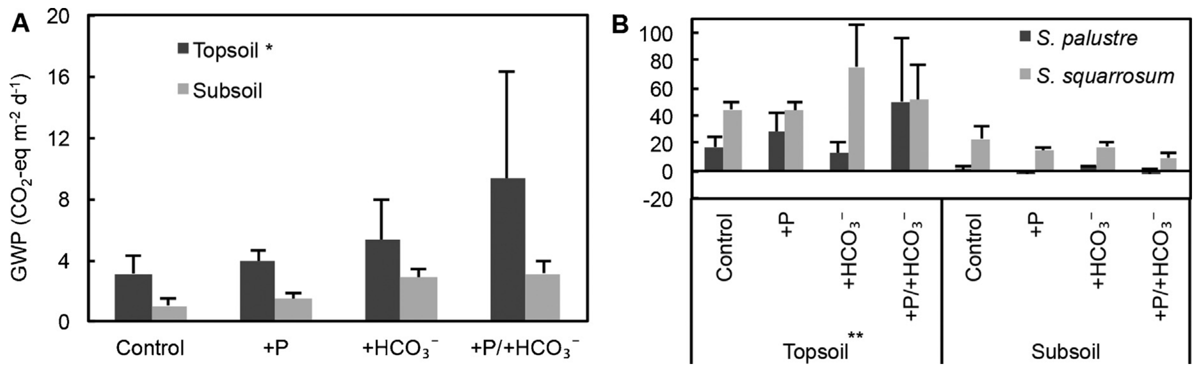

Fig. 4. Global warming potential (GWP; mean ± SEM) of bare peat soils (A) and soils covered by *S. palustre* or *S. squarrosum* (B). Values for bare peat were measured after 6 weeks of experimental treatments, whereas rates for *Sphagnum* covered soils were measured after 15 weeks of experimental treatments (6 weeks after introduction of *Sphagnum*). Soils were either topsoils (5–25 cm depth) or subsoils (25–45 cm depth), treated with a water layer with or without addition of P and/or HCO_3^-. GWP is expressed in CO_2-equivalents on a mass basis, with CH_4 representing 34 CO_2-equivalents over a 100-year period (IPCC, 2013). Significant differences between topsoil and subsoil are indicated with asterisks, with * representing $P \leq 0.05$ and ** $P \leq 0.01$.

with CH_4 emissions for topsoils reaching average emissions of 0.2 to 1.1 g C m^{-2} d^{-1}, whereas subsoils showed much lower emissions, with rates of $1.5 \cdot 10^{-4}$ to $2.5 \cdot 10^{-3}$ g C m^{-2} d^{-1}. After 15 weeks of rewetting (6 of which with *Sphagnum* cover), CO_2 emissions increased more for topsoils than for subsoils ($P < 0.001$; $F = 31.499$; Fig. 3d). While a few subsoils covered with *S. palustre* showed net CO_2-fixation, most subsoils and all topsoils showed a net release of CO_2, even when *Sphagnum* species grew on top.

GWPs of bare soils did not differ significantly, but a trend ($P = 0.097$; $F = 3.020$) was observed indicating higher GWPs (5.73 ± 1.91 CO_2-eq m^{-2} d^{-1}) for topsoils than subsoils (2.18 ± 0.34 CO_2-eq m^{-2} d^{-1}; Fig. 4a). After 15 weeks of treatment and introduction of *Sphagnum*, topsoils had a much higher GWP than subsoils, with average values of 26.94 ± 11.62 and 53.76 ± 9.40 CO_2-eq m^{-2} d^{-1} for topsoils covered with *S. palustre* ($P = 0.034$; $F = 4.884$) and *S. squarrosum* ($P = 0.001$; $F = 13.578$), respectively, compared to only -0.40 ± 1.35 and 16.30 ± 2.66 CO_2-eq m^{-2} d^{-1} for subsoils covered by the same species (Fig. 4b).

Topsoils contained higher amounts of organic carbon, with significantly higher concentrations of TOC in the water layer above topsoils ($P < 0.001$; $F = 17.619$; Table 2) and of DOC in the pore water of topsoils ($P < 0.001$; $F = 28.263$; Table 1). Based on TOC measurements from the water layer, we could calculate that organic carbon fluxes from the sediments were around 1.01 ± 0.16 and 0.41 ± 0.05 g C m^{-2} d^{-1} for topsoils and subsoils, respectively ($P = 0.002$; $F = 12.033$; data not shown).

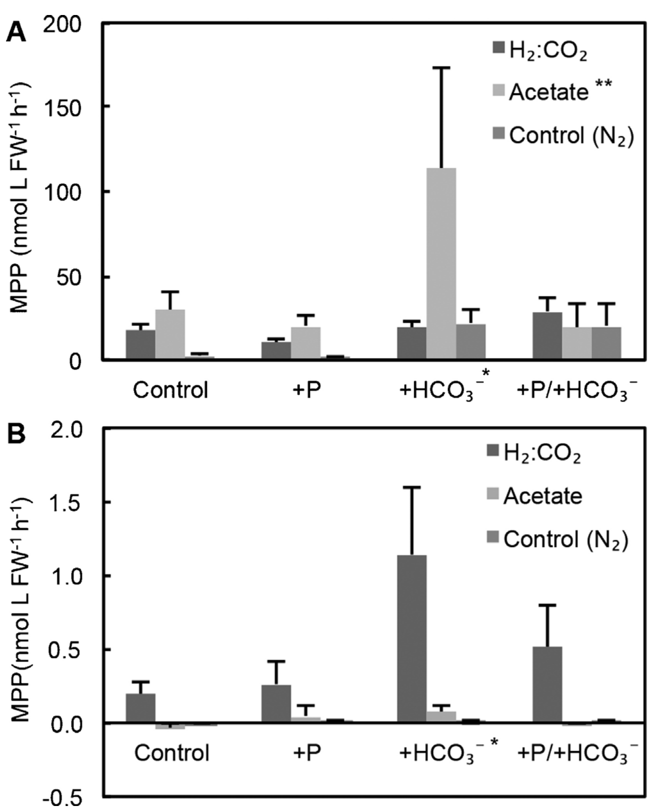

Fig. 5. Soil CH_4 production rates of topsoils (A) and subsoils (B) treated with different water layer compositions (with or without added P and/or HCO_3^-), after addition of different substrates: H_2/CO_2 (potential CH_4 production), Acetate (potential acetoclastic/fermentative CH_4 production) or N_2 (headspace control). Note different scales of the *y*-axis. Significant differences between MPP substrates or different water treatments are indicated with asterisks, with * representing $P \leq 0.05$ and ** $P \leq 0.01$.

3.5. Methane production potential (MPP)

In line with the overall higher C-fluxes from intact sediments, MPP rates were up to 99% higher in topsoils than subsoils ($P < 0.001$; $F = 31.646$; Fig. 5a and b). Incubations of homogenised soils without substrate addition (Control headspace) showed a 10-fold increase in CH_4 production rates when soils were treated with HCO_3^- ($P = 0.033$). While addition of acetate increased MPP ($P = 0.014$; $F = 4.559$) in all topsoil treatments, it had no stimulating effect on the MPP of subsoils. Furthermore, combined addition of H_2 and CO_2 did not stimulate the potential CH_4 production for either soil depth.

4. Discussion

4.1. Challenges of rewetting former agricultural peatlands

Peatlands used as arable lands or pastures for a long time have severely been altered through long-term drainage and fertilisation (Meyer and Turner, 1992). In order to halt the high C and nutrient losses associated with these changes, rewetting programmes are being carried out or planned for a growing number of drained peatlands. Projects include both the restoration of natural wetlands (Tanneberger and Wichtmann, 2011; Zak and Gelbrecht, 2007) and the change to alternative, wet agricultural use of peatlands e.g. by *Sphagnum* farming (Gaudig et al., 2013; Joosten and Clarke, 2002; Verhoeven and Setter, 2010). The rewetting of these areas causes a fast shift from aerobic to anaerobic soil processes in which alternative terminal electron acceptors are used (Knorr and Blodau, 2009). Although CO_2 and N_2O emissions are generally lowered (Salm et al., 2009), CH_4 production is strongly increased. While drained peatlands show CH_4 emission rates of -0.014 to 0.012 g C m^{-2} d^{-1}

(Hatala et al., 2012; Maljanen et al., 2010; Mander et al., 2012; Salm et al., 2009), pristine peatlands produce 0.0 to 0.2 g C m^{-2} d^{-1}, with some 'hotspots' even emitting up to 1.5 g C m^{-2} d^{-1} (Bartlett and Harriss, 1993; Drewer et al., 2010; Saarnio et al., 2007). So far, however, most studies have focused on oligotrophic bogs and pristine fens, reporting CH_4 fluxes up to 0.07 g C m^{-2} d^{-1} (Beetz et al., 2013; Green et al., 2014; Mander et al., 2010; Moore and Knowles, 1989; Wilson et al., 2013), while few have studied the effects of rewetting for eutrophic peatlands. The CH_4 fluxes we showed for rewetted, former agricultural soils, ranging from 0.05 to 4.03 (median 0.16) g C m^{-2} d^{-1}, are comparable to rates of 0.05 to 0.30 g C m^{-2} d^{-1} found in other fertilised peatlands (Hendriks et al., 2007; Schrier-Uijl et al., 2010; van de Riet et al., 2013).

Since CH_4 is a much more potent GHG than CO_2, it will strongly influence the global warming potential (GWP) of rewetted areas. GWPs of drained and degraded peatlands range from 188 to 3230 CO_2-eq m^{-2} yr^{-1} (Beetz et al., 2013; Lamers et al., 2015; Salm et al., 2009; Teh et al., 2011), whereas pristine systems generally show lower GWPs of −196 to 685 CO_2-eq m^{-2} yr^{-1} (Byrne et al., 2004; Long et al., 2010; Olson et al., 2013). We here show high GWP rates of 760 to 2253 CO_2-eq m^{-2} yr^{-1} (based on an 8-month growing season) after rewetting of a former agricultural peatland, due to high CH_4 emission. In addition, C losses through DOC production and mobilisation accounted for 35–55% of the total C loss in our system and showed high average rates of around 1 g C m^{-2} d^{-1}. These rates are on par with the daily CO_2 fluxes from these soils, indicating a substantial, but often overlooked role of DOC loss in the total C emissions in these systems (Fenner et al., 2007; Freeman et al., 2001; Kalbitz et al., 2000).

In addition to high C losses and a high GWP, we showed a strong increase in plant-available N and P after rewetting as a result of mobilisation from the nutrient loaded soils, which is in accordance with observations in similar rewetted soils (van de Riet et al., 2013; Zak and Gelbrecht, 2007). While N can easily be mobilised under aerobic conditions during agricultural use, P is usually immobilised in Fe—P complexes. In the absence of O_2 after rewetting, however, Fe^{3+} is reduced and previously Fe-bound P is mobilised to the water layer (Smolders et al., 2006), especially when Fe:P ratios of the sediment are below 10 mol mol^{-1} (Geurts et al., 2008), as was indeed the case for the topsoils in our experiment. This mobilisation of P and N resulted in a higher occurrence of algae and may, in a field situation, also favour the growth of fast-growing vascular plants, such as *Juncus* spp. (Aggenbach et al., 2013; Berendse et al., 2001; Smolders et al., 2008). As expected, eutrophication-related problems were further stimulated when P-rich water was used for rewetting, whereas an alkalinity characteristic of minerotrophic surface water stimulated additional P release and simultaneously doubled CO_2 emission rates. The latter effect may be caused by competition for anion binding sites (Roelofs, 1991; Smolders et al., 2006) and enhanced decomposition rates (Lamers et al., 2015).

4.2. Topsoil removal strongly reduces C and nutrient emissions after rewetting

Topsoil removal resulted in 99% reduction in net CH_4 emission rates. While topsoils showed very high potential CH_4 production rates, with values up to 325 μmol CH_4 m^{-3} s^{-1} for fermentative CH_4 production, these rates decreased to 0.03 and 4.10 μmol CH_4 m^{-3} s^{-1} after topsoil removal and thus fall within the range of 0.01 to 10 μmol CH_4 m^{-3} s^{-1} reported in literature (Segers, 1998). This strong reduction results from limited organic substrate (acetate) and P availability for methanogen communities due to the lower availability of easily degradable organic matter and nutrients in the subsoil (Tomassen et al., 2003; Updegraff et al., 1995; Yavitt et al., 1997).

In addition to the strong reduction in CH_4 emission, GWPs and DOC fluxes were also reduced by 50–70% and 60%, respectively. Furthermore, topsoil removal was shown to reduce the mobilisation of dissolved N and P by 80% and 93%, respectively. This will prevent algal blooms and dominance of highly competitive vascular vegetation, which makes the environment more suitable for growth of peat-forming *Sphagnum* spp. (Emsens et al., 2015).

4.3. Water quality and Sphagnum *growth: Bicarbonate toxicity*

Although we show net effluxes of both CH_4 and CO_2 from soils with dense *Sphagnum* cover, these mosses are potentially strong peat-forming species that can sequester large amounts of C as recalcitrant organic matter. Based on the biomass increase in our experiment, the net primary production (NPP) of both *Sphagnum* species was around 90–500 g DW m^{-2} yr^{-1}. Although the NPP of other peat-forming species, such as *P. australis*, may be higher, with rates around 300–1300 g DW m^{-2} yr^{-1} (Brix et al., 2001; Christensen et al., 2009), litter of these species also decomposes much faster and more completely, with an average mass loss of around 60% yr^{-1} (Christensen et al., 2009; Kirschner et al., 2001). *Sphagnum* mosses, on the other hand, have mass loss rates that only range from 5 to 20% yr^{-1} (Clymo, 1965; Coulson and Butterfield, 1978; Limpens and Berendse, 2003; Verhoeven and Toth, 1995). Furthermore, they actively slow down decomposition processes by the production of acids. Under these circumstances, average C sequestration rates for *Sphagnum* range from 28 to 240 g C m^{-2} yr^{-1} (Gerdol, 1995; Graf and Rochefort, 2009; Hajek, 2009; Samaritani et al., 2011), whereas those for *P. australis* range from 30 to 160 g C m^{-2} yr^{-1} (assuming an average C-content of 40% for both species; Kirschner et al., 2001; Longhi et al., 2008). In our study, C fixation rates of 386–663 and 121–349 g C m^{-2} yr^{-1} were reached by *S. squarrosum* and *S. palustre*, respectively, based on the increase in DW biomass and assuming a growing season of 8 months. Despite these high C fixation rates, the acidification by *Sphagnum* spp. has been shown to initially result in a net C-efflux, due to the transformation of HCO_3^- into CO_2 (Harpenslager et al., 2015).

Both moss species grew better on topsoils than subsoils, but only when rewetted with water without HCO_3^-. This was most likely due to the higher availability of nutrients on topsoils. *S. squarrosum* grew 2–5 times faster and fixed 2–3 times more C than *S. palustre*, especially on topsoils. The high nutrient availability may have favoured the growth of *S. squarrosum* (Clymo, 1973; Kooijman and Bakker, 1995), but this may also have been related to higher C availability (20 times higher HCO_3^- concentrations) in topsoils. *S. squarrosum* is more resistant to higher pH than *S. palustre* (Clymo, 1973), and its high acidification potential (Giller and Wheeler, 1988; Kooijman and Bakker, 1995) may counteract negative effects of HCO_3^- by its conversion into CO_2 (Harpenslager et al., 2015). This may also explain the higher CO_2 fluxes observed for soils covered with *S. squarrosum*. After 3–4 weeks, however, both *S. squarrosum* and *S. palustre* showed reduced growth and vitality upon increasing HCO_3^- levels, resulting in dying, algae covered mosses In a field situation, the huge nutrient stocks will also stimulate development of dense stands of fast growing vascular vegetation, which will eventually out-compete *Sphagnum* mosses (Aggenbach et al., 2013; Berendse et al., 2001; Smolders et al., 2008) and thereby hamper C sequestration. This implies that *Sphagnum* growth will also benefit from topsoil removal.

5. Conclusion

Rewetting former agricultural peatlands halts land subsidence, but simultaneously results in strongly enhanced emissions of GHG and nutrients. Removal of the nutrient-rich topsoil before rewetting strongly improves the prospects of restoring the C balance in these soils by strongly reducing eutrophication (by 80–95%), DOC mobilisation (60%), CH_4 emission (99%) and GWP (50–70%). This not only results in lower C losses, but also prevents algal blooms and monocultures of fast-growing plants, improving the regrowth of peat forming *Sphagnum* vegetation and subsequent restoration of C sequestration. Although removal of the topsoil of an already subsiding system may appear undesirable, we here show that the remaining subsoil will provide more suitable conditions for peat regrowth than the nutrient rich topsoils. The removed topsoils should subsequently be used in drained, subsiding peatlands that are still being used for agriculture, since this may help to maintain traditional agriculture on these fields by increasing the surface level. This will also allow the establishment of higher water levels in restored peatlands without increasing flooding risks of the surrounding agricultural area.

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Appendix A.

Table A1.

Table A1
Growth characteristics and mineral contents (mean ± SEM) of *S. palustre* (PAL) and *S. squarrosum* (SQU) grown on topsoils or subsoils, with a water layer with and without added P and/or HCO_3^-. Significant differences between topsoil and subsoil are indicated with asterisks, ** $P \leq 0.01$ and *** $P \leq 0.001$. Significant differences between water treatments are indicated with different letters (a, b, c). Differences between *Sphagnum* species are indicated in the first column by asterisks, similarly to soil effects.

Characteristic	Unit	Soil	Control		+P		$+HCO_3^-$		$+P/+HCO_3^-$	
			PAL	*SQU*	*PAL*	*SQU*	*PAL*	*SQU*	*PAL*	*SQU*
Photosynthetic rate (SQU > PAL**)	$\mu mol\ O_2\ gDW^{-1}\ h^{-1}$	Topsoil	$86.9^{b} \pm 12.8$	$91.7^{b} \pm 27.0$	$52.3^{b} \pm 5.6$	$99.6^{b} \pm 22.9$	$39.8^{a} \pm 9.6$	$83.4^{a} \pm 23.1$	$33.8^{a} \pm 3.9$	$48.6^{a} \pm 13.2$
		Subsoil	$40.6^{b} \pm 12.4$	$69.8^{b} \pm 7.0$	$54.3^{b} \pm 8.4$	$82.2^{b} \pm 16.6$	$42.3^{a} \pm 15.3$	$31.6^{a} \pm 9.1$	$26.5^{a} \pm 20.7$	$53.7^{a} \pm 21.8$
Final no. of capitula (SQU > PAL***)		Topsoil***	$81^{b} \pm 20$	$104^{b} \pm 9$	$77^{b} \pm 13$	$108^{b} \pm 14$	$22^{a} \pm 2$	$35^{a} \pm 4$	$20^{a} \pm 4$	$45^{a} \pm 22$
		Subsoil	$71^{b} \pm 9$	$89^{b} \pm 6$	$76^{b} \pm 10$	$94^{b} \pm 9$	$22^{a} \pm 4$	$50^{a} \pm 13$	$27^{a} \pm 8$	$39^{a} \pm 13$
Moss length	mm	Topsoil***	$74.8^{b} \pm 5.7$	$77.2^{b} \pm 4.4$	$74.0^{b} \pm 3.4$	$72.8^{b} \pm 3.5$	$39.7^{a} \pm 2.9$	$33.7^{a} \pm 1.1$	$36.6^{a} \pm 1.2$	$34.9^{a} \pm 3.9$
		Subsoil	$70.4^{b} \pm 3.0$	$68.9^{b} \pm 4.0$	$71.2^{b} \pm 3.6$	$69.5^{b} \pm 3.1$	$35.7^{a} \pm 1.2$	$36.0^{a} \pm 3.6$	$31.1^{a} \pm 1.7$	$32.6^{a} \pm 7.7$
pH vegetation		Topsoil	$5.7^{a} \pm 0.6$	$5.3^{a} \pm 0.1$	$5.1^{a} \pm 0.1$	$5.2^{a} \pm 0.1$	$6.2^{b} \pm 0.2$	$6.2^{b} \pm 0.3$	$6.9^{b} \pm 0.5$	$6.6^{b} \pm 0.2$
		Subsoil	$4.6^{a} \pm 0.1$	$5.0^{a} \pm 0.3$	$4.8^{a} \pm 0.2$	$4.7^{a} \pm 0.2$	$6.3^{b} \pm 0.6$	$6.8^{b} \pm 0.6$	$7.1^{b} \pm 0.9$	$7.2^{b} \pm 1.1$
N:P	$g\ g^{-1}$	Topsoil	$4.55^{a} \pm 1.81$	$1.68^{a} \pm 0.18$	$1.19^{a} \pm 0.11$	$1.34^{a} \pm 0.17$	$4.24^{b} \pm 1.63$	$6.23^{b} \pm 0.83$	$8.47^{b} \pm 1.10$	$8.12^{b} \pm 0.84$
		Subsoil	$4.78^{a} \pm 1.31$	$1.38^{a} \pm 0.11$	$1.65^{a} \pm 0.26$	$1.32^{a} \pm 0.26$	$4.58^{b} \pm 2.04$	$5.61^{b} \pm 1.03$	$6.72^{b} \pm 1.18$	$7.65^{b} \pm 0.34$
N:K	$g\ g^{-1}$	Topsoil	6.55 ± 1.27	5.95 ± 0.78	5.10 ± 1.31	5.27 ± 0.89	5.39 ± 0.44	4.48 ± 0.36	7.64 ± 1.86	5.56 ± 0.46
		Subsoil**	10.00 ± 2.99	7.91 ± 1.12	8.30 ± 0.96	5.77 ± 1.28	6.93 ± 0.58	7.09 ± 2.04	7.50 ± 1.18	5.75 ± 0.34
K:P										
		Subsoil**	$3.25^{c} \pm 1.51$	$5.92^{c} \pm 1.08$	$5.20^{c} \pm 0.61$	$4.32^{c} \pm 0.40$	$2.62^{b} \pm 1.10$	$1.52^{b} \pm 0.49$	$1.24^{a} \pm 0.40$	$0.76^{a} \pm 0.07$
N	$\mu mol\ gDW^{-1}$	Topsoil**	$1020^{a} \pm 112$	$845^{a} \pm 26$	$962^{a,b} \pm 49$	$969^{a,b} \pm 57$	$1099^{b} \pm 77$	$1177^{b} \pm 47$	$1230^{c} \pm 89$	$1340^{c} \pm 115$
		Subsoil	$1157^{a} \pm 149$	$777^{a} \pm 54$	$942^{a,b} \pm 77$	$780^{a,b} \pm 48$	$1098^{b} \pm 123$	$922^{b} \pm 132$	$998^{c} \pm 188$	$1109^{c} \pm 85$
P	$\mu mol\ gDW^{-1}$	Topsoil***	$78.0^{a} \pm 13.9$	$68.5^{a} \pm 11.4$	$100.7^{a,b} \pm 21.5$	$90.8^{a,b} \pm 15.7$	$94.3^{a,b} \pm 9.3$	$120.2^{a,b} \pm 9.8$	$83.6^{b} \pm 15.2$	$109.6^{b} \pm 7.6$
		Subsoil	$79.5^{a} \pm 30.4$	$49.8^{a} \pm 13.0$	$55.0^{a,b} \pm 11.5$	$73.4^{a,b} \pm 20.0$	$80.0^{a,b} \pm 13.5$	$61.1^{a,b} \pm 11.9$	$77.9^{b} \pm 26.7$	$86.9^{b} \pm 2.62$
K	$\mu mol\ gDW^{-1}$	Topsoil	$144.0^{b} \pm 61.0$	$188.5^{b} \pm 25.9$	$294.3^{b} \pm 18.3$	$273.4^{b} \pm 35.8$	$166.0^{a} \pm 63.4$	$71.4^{a} \pm 9.4$	$54.3^{a} \pm 6.2$	$60.7^{a} \pm 6.7$
		Subsoil	$99.0^{b} \pm 15.6$	$204.7^{b} \pm 15.3$	$220.7^{b} \pm 35.6$	$237.3^{b} \pm 44.8$	$172.0^{a} \pm 70.0$	$63.2^{a} \pm 9.0$	$53.9^{a} \pm 3.9$	$52.5^{a} \pm 5.3$
PAM		Topsoil	$0.542^{b} \pm 0.039$	$0.627^{b} \pm 0.008$	$0.565^{b} \pm 0.015$	$0.648^{b} \pm 0.019$	$0.626^{a} \pm 0.046$	$0.503^{a} \pm 0.062$	$0.493^{a} \pm 0.069$	$0.467^{a} \pm 0.058$
		Subsoil	$0.606^{b} \pm 0.034$	$0.634^{b} \pm 0.025$	$0.609^{b} \pm 0.027$	$0.644^{b} \pm 0.016$	$0.554^{a} \pm 0.050$	$0.414^{a} \pm 0.082$	0.529 ± 0.031	$0.397^{a} \pm 0.109$

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