



Experimental warming increased greenhouse gas emissions of a near-natural peatland and *Sphagnum* farming sites

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Abstract

Aims Drained peatlands are a major source of greenhouse gases (GHG). Paludiculture is the production of biomass under wet and peat preserving conditions. Despite the growing recognition as GHG mitigation measure, the potential influence of climate warming on paludiculture is still unknown.

Methods For two years, we quantified the exchange of carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O) using manual chambers and surveyed the vegetation composition of warmed and control sites at a near-natural bog and two *Sphagnum* farming areas in North-Western Germany. Passive warming was achieved using Open Top Chambers (OTC).

Results OTCs significantly increased air and soil temperatures, while soil moisture, humidity and light availability differed only marginally. The latter was considered when calculating gross primary

production. Warming tended to increase vascular plant cover, but differences to the control plots were still small after two years. Emissions of CO₂ and CH₄ increased with warming, dominated by CH₄ at the near-natural bog and by CO₂ at the paludiculture areas, where vegetation was in a successional stage and topsoils temporarily dried out during summer. N₂O emissions were negligible at the near-natural bog and ceased with increasing biomass at the paludiculture sites. Interannual variability was high due to a heatwave in the second measurement year.

Conclusions Climate warming could increase GHG emissions from near-natural bogs and *Sphagnum* farming. In the latter case, this puts even more emphasis on water management systems ensuring high water table depths during dry periods. Further, control of vascular plants might both reduce CH₄ emissions and improve biomass quality.

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Introduction

Climate change is one of the key challenges of our time (Grassl 2011). Salient implications will be increasing temperatures and a changing distribution of precipitation (IPCC 2021), besides warmer winter seasons also increasing the probability of prolonged

hot and dry summer periods in central and northern Europe (Beniston et al. 2007). Peatlands store more than 600 Gt carbon (C), which has a potentially significant effect on the global C budget (Yu et al. 2010). This function of organic soils as terrestrial C sinks is threatened by climate change conditions (Loisel et al. 2021) and a release of greenhouse gases (GHG) into the atmosphere could subsequently further accelerate climate change (Jones et al. 2005). A more profound understanding of the response of these key ecosystems to warming is crucial.

Peatlands have been intensively drained and exploited (Joosten and Clarke 2002; Page and Baird 2016). However, their importance in the context of climate protection goals has received more and more attention only in the past years. Paludiculture, i.e. the production of biomass under wet and peat preserving conditions (Wichtmann et al. 2016), is a new land use option considered to have large potential in mitigating GHG emissions from agriculturally used organic soils (Karki et al. 2016; Ziegler et al. 2021). On ombrotrophic bog peat with its nutrient-poor and acidic conditions, the cultivation of peat mosses (*Sphagnum* farming) is the most promising option for former peat extraction or drained agricultural areas (Günther et al. 2017; Gaudig et al. 2018). Moss fragments are spread on levelled rewetted peat and growing mosses form a new acrotelm which is later (partially) harvested. Possible application fields of harvested mosses are restoration measures (Quinty and Rochefort 2003) or renewable substrates in horticulture (Emmel 2008). In contrast to general peatland research (Gong et al. 2020), the sensitivity of this emerging land use option towards climate change and in particular the effect of warming on the GHG mitigation potential and production are still inadequately understood.

Warming and drying will weaken the mechanism of a retarded decomposition by waterlogged conditions and will therefore greatly affect microbial activity at natural peatlands (Dorrepaal et al. 2009; Robroek et al. 2015) and possibly also at paludiculture sites. Decomposition and ecosystem respiration (R_{eco}) could therefore be expected to increase in a warmer future (Lloyd and Taylor 1994; Updegraff et al. 2001; Samson et al. 2018; Gong et al. 2020). On the other hand, gross primary production (GPP) might also increase with warming (Weltzin et al. 2000; Johnson et al. 2013; Munir et al. 2015) depending on water supply and plant community structure.

While a shift from fen to bog in high latitude peatlands might promote C sequestration (Magnan et al. 2021), warming induced changes in the abundances of bryophytes, shrubs and graminoids could increase C turnover at bog peatlands (Ward et al. 2009). Several studies found no significant impact on net ecosystem exchange (NEE) at all (Sullivan et al. 2008; Pearson et al. 2015). Consequently, consensus is still lacking on the direction of a warming effect on NEE, i.e. whether the amount of increased C loss to the atmosphere or the amount of increased plant-derived C input will prevail (Davidson and Janssens 2006). In addition, the effect might differ at natural bogs and *Sphagnum* farming sites, which are characterised by the possibility to adjust water tables on the one hand but by a missing functioning acrotelm and a still developing vegetation community on the other hand.

Methane (CH_4) is produced by archaea under waterlogged conditions (Lai 2009). Besides diffusive transport through the peat matrix, aerenchymous plants play an important role for the release of CH_4 to the atmosphere (Greenup et al. 2000). Methanotrophs might use CH_4 in their metabolism, reducing it to CO_2 . They are not only found in the unsaturated zone, but are furthermore specifically associated to *Sphagnum* mosses (Raghoebarsing et al. 2005). In contrast to CO_2 , CH_4 emissions of organic soils can be expected to increase with increasing temperatures (Turetsky et al. 2014), although both, producers and consumers, are sensitive to temperature (van Winden et al. 2012) and the effect of climate warming on water availability and plant community composition needs to be considered. Here it is of interest to investigate how the different hydrological regimes of near-natural and cultivated peatlands affect the response of CH_4 exchange to warming.

Nitrous oxide (N_2O) emissions are of greater importance at degraded peatlands (Marushchak et al. 2011) or at cultivated sites with poor vegetation cover (Oestmann et al. 2022). N_2O can be produced by a number of processes, the most important in moist to wet surroundings being denitrification (Butterbach-Bahl et al. 2013). While N_2O peaks tend to occur during frost-thaw cycle, N_2O emissions might also respond positively to warming even at abundantly vegetated peat surfaces (Voigt et al. 2016), but might be more dependent on the availability of nitrogen and carbon and on vegetation dynamics (Gong and Wu 2021).

Open top chambers (OTC) are used to passively simulate and investigate climate warming conditions in remote areas (Marion et al. 1997) due to their inexpensive and easy handling. The transparent enclosures are designed to minimise convective heat flow, thereby increasing temperatures. In situ warming methods provide a more realistic insight compared to laboratory studies, but on the other hand affect a range of interrelated environmental parameters such as relative humidity, soil moisture and plant community (Dabros et al. 2010; Carlyle et al. 2011), as well as light intensity (Biasi et al. 2008) and, depending on chamber dimensions, precipitation. Due to different water uptake mechanism, mosses and vascular plants might be affected differently. In temperate regions, OTCs have been less employed and it could be possible that the warming effect is less pronounced compared to studies from high latitude areas (Johnson et al. 2013) or limited to air temperatures (Górecki et al. 2021).

The objective of this study was to investigate the response of the GHG exchange of a near-natural bog area and two *Sphagnum* farming areas differing in their irrigation management to simulated climate warming conditions. In order to evaluate drawn conclusions and to separate the warming effect from concomitant effects on other environmental parameters, a whole set of accompanying parameters was measured. The GHG balances of the non-warmed control sites are already published and discussed in more detail in Oestmann et al. (2022). In this paper, we described the annual balances of CO₂, CH₄ and N₂O of a near-natural bog and *Sphagnum* farming sites, including the contribution of irrigation management, extractable *Sphagnum* biomass and harvesting peat moss donor material at the near-natural site. The three control sites of the present study are only part of the data set (8 sites) discussed in Oestmann et al. (2022).

Instead of estimating GHG balances for the whole production system, we focus in detail on the warming effect in the present paper. The 2018 European heat wave fell in the measurement period, allowing us to report the impact of experimental passive warming and the impact of a natural climate extreme event.

Material and methods

Study sites

We measured greenhouse gas (GHG) exchange from March 2017 to March 2019 at a near-natural bog ('Meerkolk', 52°38' N, 07°08' E) and two *Sphagnum* cultivation areas ('Provinzialmoor', 52°40' N, 07°06' E and 'Drenth', 52°41' N, 07°05' E), all located in Northwest Germany (Table 1). The climate of the area is oceanic with an average annual precipitation of 791 mm and an average annual temperature of 9.8 °C (1971–2000, German Weather Service, Station Lingen, 20 km away).

The peat soil at Meerkolk can be classified as Ombric Fibric Histosol (IUSS Working Group WRB 2015). It is a silting bog pool characterised by partially floating peat moss (mainly *Sphagnum papillosum*) and *Eriophorum angustifolium* mats with a peat thickness of about 3.5 m.

The cultivation areas Provinzialmoor and Drenth are Ombric Hemic Histosols with peat thicknesses of about 0.8 m and 0.4 m, respectively. The shallow peat layer left after industrial peat extraction is highly decomposed and characterised by low hydrologic conductivities. The cultivation area Provinzialmoor was established in October 2016 and had previously been re-wetted as a shallow polder since the termination of peat extraction in 2008, while Drenth was established in October 2015 directly after the

Table 1 Study sites and areas

Area	Site	Treatment	Peat depth (m)	Irrigation
Meerkolk	M-NAT	Near-natural control	3.5	–
	M-NAT-W	Near-natural warming	3.5	–
Provinzialmoor	P-MIX	Cultivation control	0.8	Ditch irrigation + previous re-wetting
	P-MIX-W	Cultivation warming	0.8	Ditch irrigation + previous re-wetting
Drenth	D-DRIP	Cultivation control	0.4	Drip irrigation
	D-DRIP-W	Cultivation warming	0.4	Drip irrigation

termination of peat extraction. The establishment of the cultivation areas was based on the moss layer transfer technique (Quinty and Rochefort 2003). In brief, *Sphagnum* fragments from nearby areas were manually spread on the bare peat and covered with straw mulch for protection. Afterwards, Provinzialmoor was irrigated via shallow ditches connected to a polder saving rainwater. At Drenth, drip irrigation was installed and ground water was additionally pumped into the irrigation pond in dry summer periods (details in Grobe et al. 2021). The cultivation areas were occasionally mown to reduce the growth of vascular plants. Dominant moss species were *S. papillosum* at Provinzialmoor and both *S. papillosum* and *Sphagnum palustre* at Drenth. Vascular plants, e.g. *Molinia caerulea*, *E. angustifolium* and *Erica tetralix* (complete list of plant species in Table S1), grew in different quantities in both areas. In each study area, both a warming ('-W') and a control treatment were set up, each consisting of three replicate plots. The establishment of cultivation sites, their soil characteristics, the GHG balances of the non-warmed control sites and the vegetation are described in more detail in Oestmann et al. (2022) and Grobe et al. (2021).

Warming treatment

Passive warming of air and soil temperatures was achieved using permanent Open Top Chambers (OTC, Molau and Mølgaard 1996), hexagonal enclosures constructed out of trapezoid panels with a top side length of 0.87 m and a bottom side length of 1.20 m (Fig. S1). Warmed and control plots alternated randomly along boardwalks in distances of about two to three meters. The transparent polycarbonate (Makrolon 3 mm, Bayer AG, Darmstadt, Germany) offered an optimal stability and a minimal reduction of light transmittance (87.5%, details in the supplementary information) while absorbing most UV radiation. The large size of the OTCs was chosen to minimise possible effects on other environmental parameters (e.g. shading and reduced precipitation) at the measurement plots (0.75 m side length) in the centre. Overall, mean light intensities inside the OTCs were reduced by about 5% (details in the in the supplementary information), but we could not quantify the effect on precipitation.

Hydrological-meteorological parameters and vegetation

At all measurement plots, soil temperatures (2 cm, in the middle of the plot) were recorded. At the warmed plots, additional sensors were installed in the northern and south-eastern corner of the plot (Fig. S1) and the mean of the three probes was used for further analyses. Near surface volumetric water contents θ ($\text{cm}^3 \text{cm}^{-3}$) were calculated from dielectric permittivities (GS3 capacitance sensors, Decagon Devices Inc., Pullmann, WA, USA) using the standard calibration of the device for potting and peat soils. Measurements of θ were transformed to water filled pore space (WFPS) by dividing θ with the maximum θ of the time series. From March 2018 onwards, air temperature and relative humidity (RH) above soil surface (0.2 m) were recorded (IST AG, Ebnat-Kappel, Switzerland) next to each plot (distance of about 0.2 m). The thermal growing season was calculated as the number of days with mean air temperatures higher than 5 °C. Frost days were defined as days with minimum air temperatures below 0 °C.

At each site, water table depths (WTD) were measured using Mini-Divers in perforated dip wells close to the measurement plots and Baro-Divers for atmospheric pressure correction (Eijkelkamp, Giesbeek, The Netherlands). Biweekly, soil pore water was sampled from additional dip wells not used for the continuous water level measurements. Electric conductivity (EC) and pH values were measured in situ (WTW, Weilheim, Germany), while concentrations of dissolved organic carbon (DOC, DimaTOC 2000, Dimatec, Essen, Germany) and ammonium (NH_4^+ , 850 Professional Ion Chromatograph, Metrohm, Filderstadt, Germany) were determined in the laboratory after filtration to 0.45 μm (PES, Merck Millipore, Tullagreen, Ireland). A meteorological station at Provinzialmoor recorded half-hourly averages of photosynthetically active radiation (PAR, 2 m), air (2 m) and soil (2 cm) temperatures and relative humidity (2 m). Every spring and autumn, the species composition and the cover of mosses and vascular plants in all measurement plots was estimated according to the Londo scale (Londo 1976). At the cultivation areas, *Sphagnum* biomass was estimated using the correlation ($R^2=0.43$) between moss height and biomass sampled outside the measurement plots (Grobe et al.

2021) and measured moss heights in the measurement plots.

Measurement of greenhouse gases and calculation of annual balances

We manually measured GHG exchange using static chambers ($0.78 \times 0.78 \times 0.50$ m, transparent polycarbonate and opaque PVC) placed on permanently installed PVC collars. During measurement, the chamber headspace air was mixed using fans and sampled via tubes connected to an infrared gas analyser (CO_2) or a semi-automatic sampling device (CH_4 and N_2O). The period from 16th March 2017 to 15th March 2018 will hereafter be referred to as “2017” and the period from 16th March 2018 to 15th March 2019 as “2018”.

Net ecosystem exchange (NEE, transparent chambers) and ecosystem respiration (R_{eco} , opaque chambers) were measured in monthly intensive campaigns covering the daily range of soil temperatures and PAR from one hour before sunrise until the maximum light intensity and the maximum soil temperature were reached around midday and in the afternoon, respectively. The CO_2 concentration of the chamber air was measured with an infrared gas analyser (LI-820, LICOR, Lincoln, Nebraska, USA) during chamber closure times of 120 (NEE) and 180 (R_{eco}) seconds. In addition, chamber air temperature and outside PAR were continuously recorded. Per plot and campaign, at least four fluxes were measured with both transparent and opaque chambers. Fluxes were calculated by selecting the linear regression of a moving window of 40 s in summer and 50 s in winter with maximum R^2 (Oestmann et al. 2022). Fluxes with $R^2 < 0.75$ were excluded unless the change in CO_2 concentration did not exceed 3%. Chamber temperatures and PAR values were not allowed to change more than 1.5 °C and 10% from the initial value, respectively.

Next, response functions for R_{eco} and gross primary production (GPP) were fitted to the CO_2 fluxes of each campaign, pooling data from all three plots. The temperature response function of Lloyd and Taylor (1994) was used to parameterise R_{eco} , and GPP was calculated as the difference between the measured NEE flux and the nearest modelled R_{eco} value. For GPP, a Michaelis-Menten type function (Johnson and Goody 2011) depending on PAR was used (Falge et al. 2001). Details on the parametrization of

R_{eco} and GPP and on the correction for reduced light levels inside transparent chambers and inside the OTCs (Schneider et al. 2011) can be found in the in the supplementary material. To calculate annual balances, two sets of R_{eco} and GPP fluxes were interpolated for each period between two campaigns using the parameters of the response functions of these two campaigns and half-hourly PAR and temperature data. At each time step, the final flux value was calculated as a weighted average of the two fluxes. Standard errors of the annual balances were calculated by fitting R_{eco} and GPP again using random resamples of the campaign fluxes with replacement (number of bootstraps = 1000). Finally, NEE was calculated as the sum of R_{eco} and GPP.

Methane and N_2O were sampled fortnightly using opaque chambers (five samples within a closure time of 80 minutes) and a semi-automatic measurement device (details in Oestmann et al. 2022). Chamber temperature was noted for each sampling occasion. Vials were flushed with headspace air for 85 seconds before filling with slight overpressure. Concentrations were determined using a gas chromatograph (Shimadzu, Kyoto, Japan) equipped with an electron capture detector (ECD) for analysing CO_2 and N_2O and a flame ionization detector (FID) for analysing CH_4 . Fluxes were determined using robust linear or nonlinear Hutchinson-Mosier (HMR, Pedersen et al. 2010) regressions (R Core Team 2021; Fuß 2020), using the flux selection scheme described by Hüppi et al. (2018). Data points with a decrease in CO_2 concentration of more than 10 ppm compared to the preceding value, possibly indicating leakages or other shortcomings, were excluded. No flux was calculated in the case of less than four valid measurements. In addition, fluxes ($n = 27$) with a CO_2 flux smaller than 30% of the maximum flux of the other two replicates were excluded (Oestmann et al. 2022). Means and standard errors of the CH_4 and N_2O balances were calculated following a combined bootstrap and jackknife procedure (Günther et al. 2015; Oestmann et al. 2022).

Methane and N_2O were included in the GHG balances according to their global warming potentials of 28 and 265 CO_2 equivalents over a timeframe of 100 years (Myhre et al. 2013). Following the atmospheric sign convention, fluxes towards the atmosphere are specified as positive values. As the cultivation areas were not harvested during the experiment

and the mowed biomass was negligible ($< 50 \text{ kg C ha}^{-1} \text{ yr}^{-1}$), no further C-inputs and C-exports entered the GHG balance.

Data analyses

All data analyses were conducted using R software (R core team 2021).

Gaps in environmental data

Soil temperatures and moistures were measured from June 2017 onwards. In addition, insufficient power supply lead to occasional night-time gaps at Provinzialmoor and Drenth in the second winter season. This resulted in soil temperature data gaps of 19%, 31% and 32% at Meerkolk, Provinzialmoor and Drenth, respectively. For the comparison of warmed and control sites, i.e. for the determination of the OTC effect, only original data without gap filling and only time points with valid observations of all sensors of the warmed and respective control plots were used. For the calculation of CO_2 balances, soil temperature and PAR data gaps were filled via correlation with values measured at the meteorological station at Provinzialmoor and with data of the German Weather Service (DWD, Lingen, 20 km away). Air temperatures and relative humidity were measured from March 2018 onwards and gaps (29%, 11% and 51%) were filled accordingly.

Effect of OTCs on temperatures, gas fluxes and water chemistry

The difference between the mean air and soil temperature values of the three replicate warmed and control plots was analysed on the basis of hourly data. We used linear mixed effects models from the package nlme (Pinheiro et al. 2021) to investigate these differences. A full model with treatment (warmed, control) as fixed factor and measurement plot as random factor was compared to a “zero” model, where treatment was replaced by the overall mean. The autocorrelation of the time series was accounted for by applying an autocorrelation structure of order 1. A power variance function structure was added if it improved the model, as indicated by a lower AIC value (Zuur et al. 2009). The treatment effect was considered significant if the

AIC value of the full model was lower than the AIC value of the zero model at a significance level of the likelihood ratio test of 0.05. Equivalent models were set up to explore the effect of OTCs on fluxes of CH_4 and on daily mean fluxes of GPP and R_{eco} , as well as on the concentrations of DOC and NH_4^+ .

Correlation between environmental variables and methane fluxes

Spearman’s rank correlation coefficient r from the R package Hmisc (Harrell and Dupont 2020) was used to describe the relation of instantaneous CH_4 fluxes of Meerkolk and Provinzialmoor with gap-filled soil temperature sums of the preceding ten days, WTD and GPP (as a proxy for active plant biomass). The p -values were adjusted using the Bonferroni correction method. In order to consider the random variation of the replicate plots and the temporal dynamic of the measurements, linear mixed effect models were additionally used to determine the environmental variables which significantly contributed to the development of CH_4 fluxes. For this step, CH_4 fluxes were log-transformed. Following the procedure described by Zuur et al. (2009), first a beyond optimal model containing all eligible environmental parameters as fixed factors was set up. Then, potential explanatory variables were dropped one by one, if they did not significantly improve the model based on the AIC value ($p < 0.05$).

Results

The two measurement years strongly differed in their meteorological conditions. In Lingen (German Weather Service), annual precipitation amounts of 841 mm and 561 mm were measured. With $10.9 \text{ }^\circ\text{C}$ and $11.7 \text{ }^\circ\text{C}$, both years were clearly warmer than the long-term average ($9.8 \text{ }^\circ\text{C}$), 2018 being the second warmest year since records began in 1951. In comparison to 2017, where extensive rainfalls in the second half of the year led to an annual precipitation higher than the long-term average (791 mm), 2018 was an exceptionally hot and dry year, especially during summer (see Fig. S2 for time series of daily air temperature and precipitation).

Increases in air and soil temperatures

Air and soil temperatures of warmed plots were significantly ($p < 0.0001$) higher than those of the control plots. At the near-natural area, the mean (\pm standard deviation) difference in the original (gaps not filled) hourly air temperature values was 0.5 ± 0.7 °C. At Provinzialmoor and Drenth, mean differences of 0.5 ± 0.9 °C and 0.5 ± 0.6 °C were measured. Mean

differences in soil temperatures were 0.5 ± 0.7 °C, 0.3 ± 0.4 °C and 0.5 ± 0.9 °C at Meerkolk, Provinzialmoor and Drenth, respectively. Mean gap-filled soil temperatures for each site and measurement year are given in Table 3. The gap-filling preserved the higher temperatures at the warmed sites.

Temperature differences were highest around noon and afternoon. Occasional negative differences occurred mainly at night (Fig. 1). In addition,

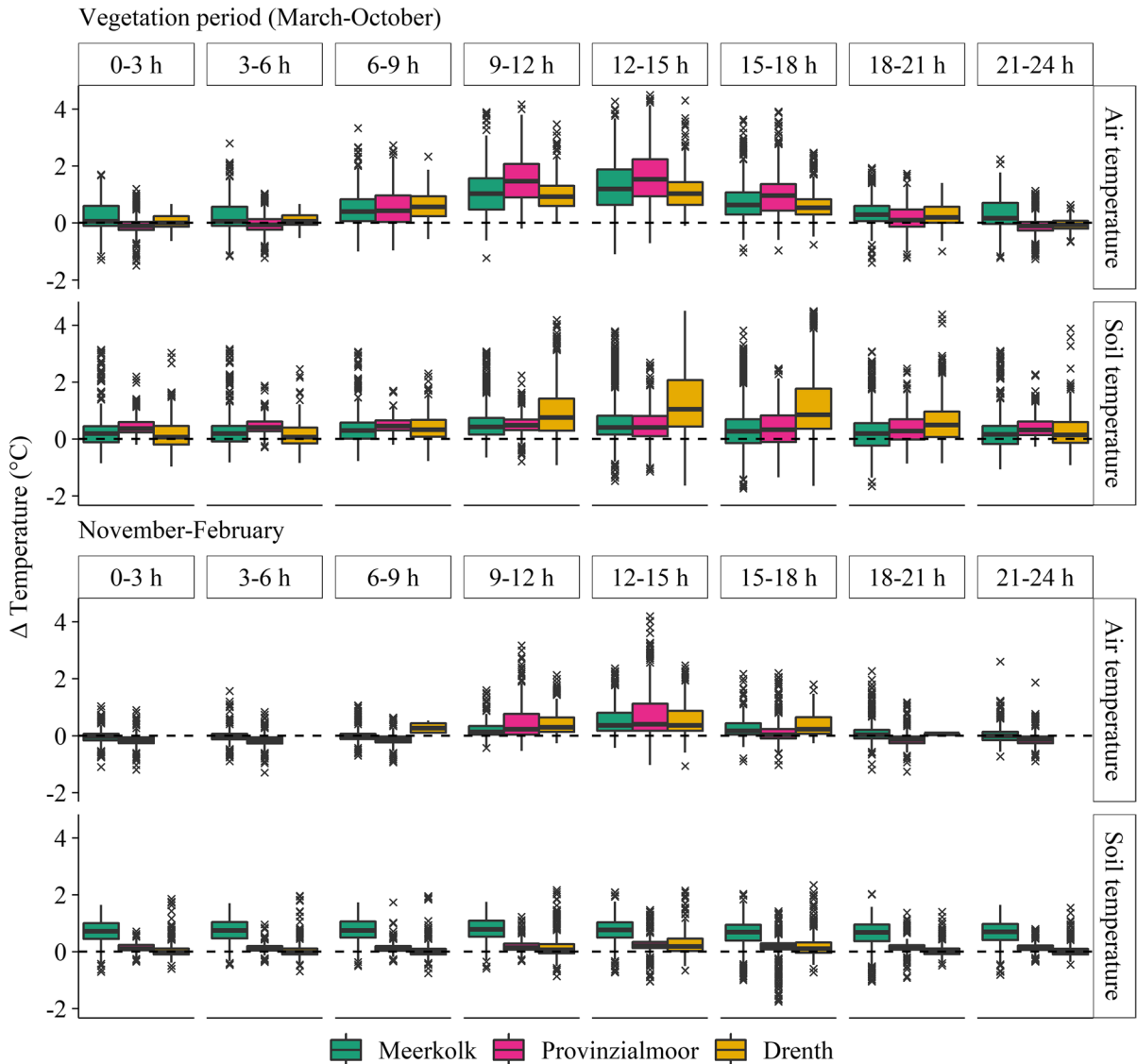


Fig. 1 Differences (warmed – control) of hourly air and soil temperatures (°C) at the near-natural area Meerkolk and the cultivation areas Provinzialmoor and Drenth; to improve the readability of the figure, high positive (> 4.5 °C,

$n=62$, $\max=6.0$ °C) and high negative (< -2 °C, $n=8$, $\min=-3.4$ °C) differences are not plotted; a direct comparison of the different areas is not possible due to differences in data gaps

temperature differences were higher during the vegetation period. Differences larger than 2 °C accounted only for a small part (about 4%) of all data points. In 2018, warming increased the thermal growing season by two, two and four days at Meerkolk, Provinzialmoor and Drenth. Further, it reduced the number of frost days by six, five and three days.

Water table depths, water-filled pore spaces and relative humidity

The water table depth (WTD) of the near-natural area was close to the surface throughout the experiment, while it dropped below −0.4 m at the cultivation areas during dry periods in summer, especially at Provinzialmoor. Mean WTDs were lower in 2018 compared to 2017 at all sites and this difference was largest at Provinzialmoor (Table 3). Accordingly, the topsoil of the cultivation areas dried out during summer (June–September) and water filled pore spaces (WFPS ± SD) of $59 \pm 10\%$ and $84 \pm 12\%$ were measured at sites P-MIX and D-DRIP, respectively.

The influence of OTCs on WTD, WFPS and relative humidity (RH) was small. Annual mean WTDs of warmed plots were similar to those of the control plots and differed only a few centimetres (Table 3). Data on WFPS was only available for the cultivation sites. No clear differences between warmed and control plots could be determined. At Provinzialmoor, mean WFPSs of $88 \pm 10\%$ and $87 \pm 12\%$ were measured at the warmed and control plots. Similar values were recorded at Drenth, $87 \pm 13\%$ and $89 \pm 12\%$, respectively. Differences between mean RH values of warmed and control plots were similarly small. At Meerkolk, $85.5 \pm 21.0\%$ and $86.1 \pm 21.1\%$ were measured, at Provinzialmoor $83.1 \pm 21.4\%$ and $82.9 \pm 20.8\%$ and at Drenth $81.3 \pm 20.6\%$ and $79.7 \pm 20.7\%$. However, RH was occasionally lower

(up to 10%) at the warmed plots when air temperatures were higher and higher at negative air temperature differences. This effect was especially apparent at Provinzialmoor.

Pore water chemistry

The pH-values at the near-natural area and the cultivation areas were similar, while the cultivation areas showed higher values of electric conductivity (EC), dissolved organic carbon (DOC) and ammonium (NH_4^+) (Table 2). Neither pH-values at any site nor EC values at the near-natural site were affected by OTCs, while significantly higher values of EC were measured at the cultivation areas. While a small but significant decrease in the mean DOC concentrations was measured at Meerkolk, mean DOC concentration increased by about a third at Provinzialmoor. Concentrations of NH_4^+ were higher at the warmed plots of the near-natural and cultivation areas.

Vegetation development

Vegetation cover strongly differed between areas. While Meerkolk was characterised by a thick *Sphagnum* carpet, Provinzialmoor and Drenth were still in the establishment phase during our study and spots of bare peat were (nearly) closed by growing vegetation over the course of the experiment. Covers of bryophyte and vascular plant species differed slightly between warmed and control plots (Fig. 2). At Meerkolk, vascular plant cover increased during the hot and dry summer 2018. This increase was more pronounced at the warmed plots and could be largely attributed to the graminoid species *Rhynchospora alba* and to a lesser extent to ericaceous dwarf shrubs. In contrast, vascular plant cover at the cultivation areas was highest in autumn 2017.

Table 2 Means and standard errors of biweekly measurements of pH and electronic conductivity (EC, $\mu\text{S m}^{-1}$), as well as concentrations (mg l^{-1}) of dissolved organic carbon (DOC)

	M-NAT	M-NAT-W	P-MIX	P-MIX-W	D-DRIP	D-DRIP-W
pH	4.6 ± 0.1	4.6 ± 0.1	4.3 ± 0.1	4.2 ± 0.0	4.4 ± 0.1	4.3 ± 0.1
EC	56.5 ± 2.8	54.2 ± 2.5	130.8 ± 4.7	$143.0 \pm 5.2^+$	111.8 ± 3.8	$124.9 \pm 7.2^{**}$
DOC	33.0 ± 2.2	$30.3 \pm 1.7^*$	68.5 ± 4.0	$93.3 \pm 5.3^*$	61.3 ± 3.3	63.2 ± 2.9
NH_4^+	0.48 ± 0.04	$0.72 \pm 0.06^{**}$	2.06 ± 0.25	2.26 ± 0.29	1.23 ± 0.23	$1.56 \pm 0.23^{***}$

and ammonium (NH_4^+) of warmed and control sites. Asterisks indicate significance levels of treatment effect at each site (+: $p=0.06$, *: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$)

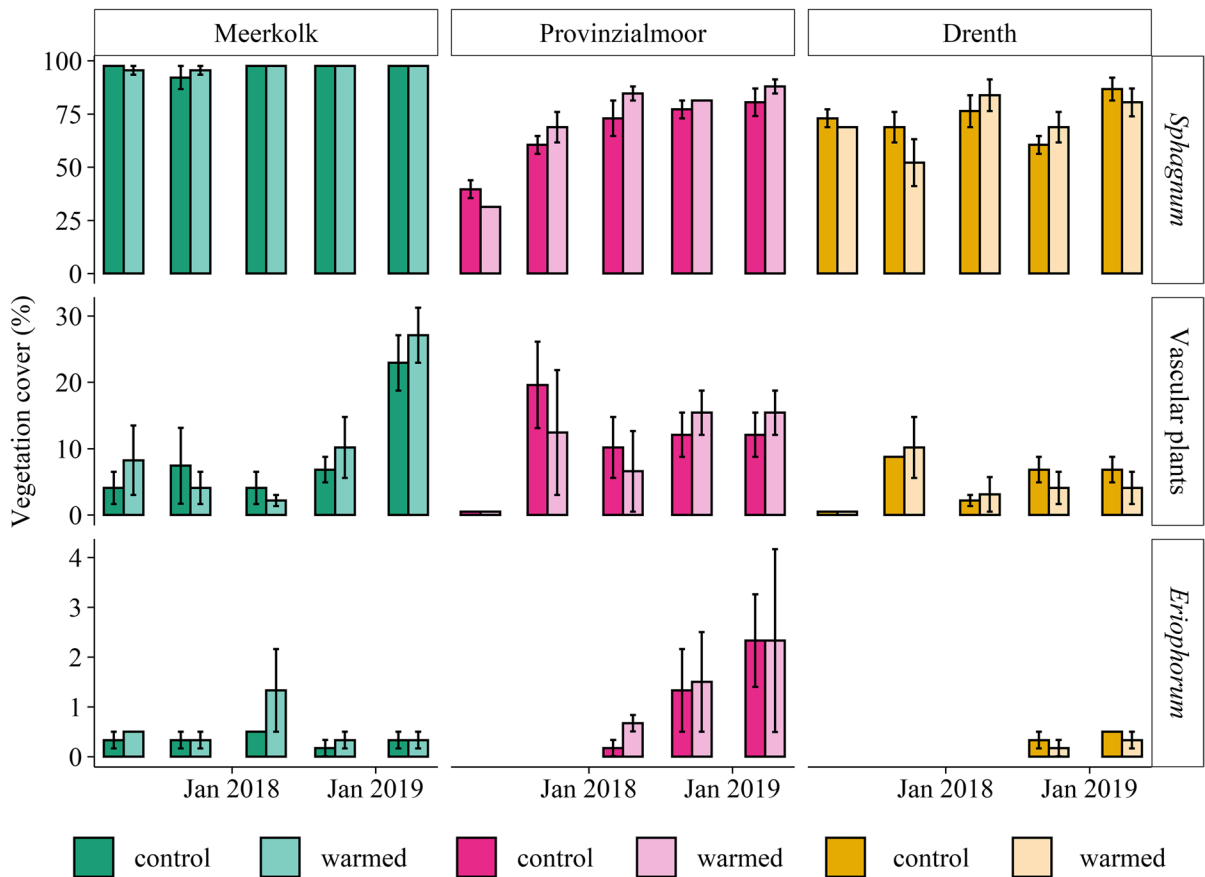


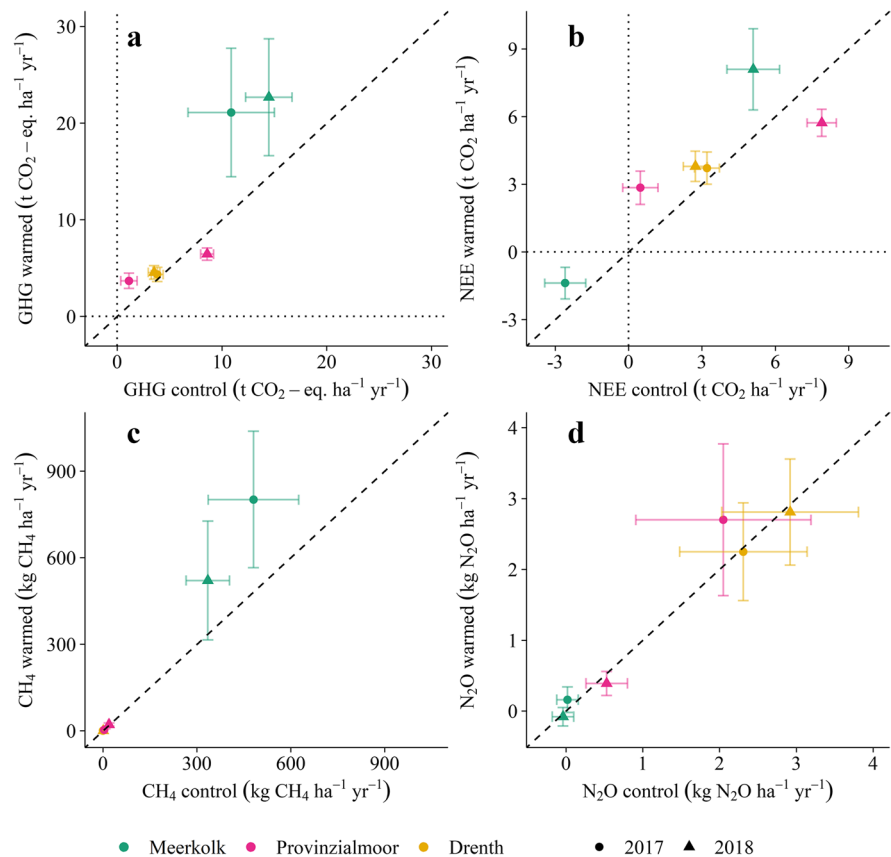
Fig. 2 Half-yearly survey of vegetation covers (means and standard errors of the 3 replicate plots) of the near-natural area Meerkolk and the two cultivation areas Provinzialmoor and Drenth; “*Eriophorum*” indicates the sum of *E. angustifolia* and *E. vaginatum*

At Povernzialmoor, covers of *M. caerulea* decreased from 2017 to 2018, while covers of *Eriophorum* sp. and, especially in the warmed plots, ericaceous dwarf shrubs increased. Here, vascular plants were less abundant in the warmed plots compared to the control plots in 2017 and more abundant in 2018, while *Sphagnum* cover was higher in the warmed plots throughout the experiment. At Drenth, the overall vegetation development was low and variable and the 2018 drought resulted in a distinct decline in *Sphagnum* development in autumn 2018. At the end of the experiment, *Sphagnum* biomass was estimated as 2.9 and 2.5 tons of dry mass per hectare at the warmed and control plots in Provinzialmoor (29 months since inoculation) and as 2.5 and 2.1 tons at Drenth (41 months since inoculation).

Greenhouse gas balances

Open Top Chambers increased total GHG emissions (t CO₂-eq ha⁻¹ yr⁻¹), i.e. the sum of CO₂, CH₄ and N₂O each multiplied with their respective global warming potential, at the near-natural site and at both cultivation sites with the exception of Provinzialmoor in 2018 (Fig. 3a). At the near-natural site, this pattern was dominated by differences in the CH₄ exchange of warmed and control plots, while differences in NEE were dominant at the cultivation sites (Fig. 3b, c). Altogether, the influence of simulated climate warming conditions on GHG exchange was higher at the near-natural site compared to the cultivation sites. Further, the extraordinary hot and dry year 2018 majorly affected GHG exchange. The interannual

Fig. 3 Annual balances of total greenhouse gas exchange (GHG, t CO₂-eq ha⁻¹ yr⁻¹) (a), net ecosystem exchange (NEE, t CO₂ ha⁻¹ yr⁻¹) (b), methane (CH₄) emissions (kg CH₄ ha⁻¹ yr⁻¹) (c) and nitrous oxide (N₂O) emissions (kg N₂O ha⁻¹ yr⁻¹) (d) of warmed and control sites; the dashed lines denote the 1:1 ratio



difference was higher at Provinzialmoor than at Meerkolk, while Drenth remained largely unaffected.

Net ecosystem exchange

NEE of warmed plots was higher compared to the control plots with the exception of Provinzialmoor in 2018 (Fig. 3b). At the near-natural area, R_{eco} of warmed plots was in the same range as the control plots in 2017 and clearly higher in 2018, while GPP was slightly lower in 2017 and not affected in 2018 (Table 3). At the cultivation areas, R_{eco} was unaffected by warming or slightly reduced and GPP was reduced except for a clear increase at Provinzialmoor in 2018.

In addition to the warming induced by the OTCs, NEE was also majorly affected by the extraordinary hot and dry summer 2018. At all sites, fluxes of GPP and R_{eco} were larger in 2018 compared to 2017. Differences in R_{eco} were clearly higher at Meerkolk and Provinzialmoor, which turned both Meerkolk sites from sinks of atmospheric CO₂ to sources and

strongly increased CO₂ emissions at the Provinzialmoor sites. At Drenth, increases in R_{eco} and GPP were similar in their size and NEE did not change between years.

Daily mean fluxes of GPP and R_{eco} of the single campaign days did not differ significantly between warmed and control sites. Differences in the annual balances seem to rather originate from the overall temperature differences than from parametrization (Fig. 4). Minor deviations in the response of R_{eco} and GPP of warmed and control plots to soil temperature and PAR, respectively, were only obtained in the case of R_{eco} at the cultivation areas and GPP at Drenth.

Methane and nitrous oxide exchanges

Annual CH₄ emissions of warmed plots were distinctively higher at Meerkolk in both measurement years and at Provinzialmoor in 2018, while fluxes were low and variable at Drenth. The annual N₂O exchange remained largely unaffected by warming, though OTCs slightly increased N₂O emissions

Table 3 Greenhouse gas (GHG) balances, net ecosystem exchange (NEE), gross primary production (GPP) and ecosystem respiration (R_{eco}) (all three are means and standard errors of bootstrap fits), methane (CH_4) and nitrous oxide (N_2O)(means and standard errors) and gap-filled annual mean soil temperature (T_{soil}) and water table depths (WTD) (means and standard deviations of daily means) of warmed and control sites of the near-natural area and cultivation areas

	WTD m	T_{soil} °C	CH_4 kg CH_4 $\text{ha}^{-1} \text{yr}^{-1}$	N_2O kg N_2O $\text{ha}^{-1} \text{yr}^{-1}$	NEE t CO_2 $\text{ha}^{-1} \text{yr}^{-1}$	GPP t CO_2 $\text{ha}^{-1} \text{yr}^{-1}$	R_{eco} t CO_2 $\text{ha}^{-1} \text{yr}^{-1}$	GHG balance t $\text{CO}_2\text{-eq ha}^{-1} \text{yr}^{-1}$
2017								
M-NAT	-0.05 ± 0.03	10.7 ± 6.5	481.1 ± 144.4	0.0 ± 0.1	-2.6 ± 0.8	-24.4 ± 0.9	21.8 ± 1.2	10.9 ± 4.1
M-NAT- W	-0.08 ± 0.03	11.2 ± 6.5	801.1 ± 236.0	0.2 ± 0.2	-1.4 ± 0.7	-23.6 ± 0.5	22.2 ± 0.6	21.1 ± 6.6
P-MIX	-0.13 ± 0.10	10.6 ± 6.9	3.9 ± 1.3	2.1 ± 1.1	0.5 ± 0.7	-17.1 ± 0.7	17.6 ± 0.5	1.1 ± 0.8
P-MIX- W	-0.09 ± 0.10	10.9 ± 7.1	3.6 ± 1.3	2.7 ± 1.1	2.8 ± 0.7	-13.3 ± 0.7	16.2 ± 0.5	3.7 ± 0.8
D-DRIP	-0.09 ± 0.12	10.6 ± 6.9	0.3 ± 0.7	2.3 ± 0.8	3.2 ± 0.5	-11.7 ± 0.3	15.0 ± 0.5	3.8 ± 0.6
D-DRIP- W	-0.09 ± 0.13	11.0 ± 7.2	0.3 ± 0.4	2.2 ± 0.7	3.7 ± 0.7	-11.4 ± 0.4	15.1 ± 0.7	4.3 ± 0.7
2018								
M-NAT	-0.07 ± 0.06	11.4 ± 6.6	335.3 ± 69.3	-0.0 ± 0.1	5.1 ± 1.1	-26.3 ± 0.9	31.4 ± 1.4	14.5 ± 2.2
M-NAT- W	-0.10 ± 0.07	11.7 ± 6.2	520.9 ± 205.7	-0.1 ± 0.1	8.1 ± 1.8	-26.7 ± 0.9	34.6 ± 1.8	22.7 ± 6.0
P-MIX	-0.25 ± 0.21	11.4 ± 7.2	19.5 ± 2.7	0.5 ± 0.3	7.9 ± 0.6	-20.4 ± 0.6	28.4 ± 0.4	8.6 ± 0.6
P-MIX- W	-0.28 ± 0.24	11.8 ± 7.3	21.7 ± 5.5	0.4 ± 0.2	5.7 ± 0.6	-22.5 ± 0.6	28.2 ± 0.5	6.4 ± 0.6
D-DRIP	-0.12 ± 0.12	11.3 ± 7.2	1.0 ± 0.7	2.9 ± 0.9	2.7 ± 0.5	-15.3 ± 0.3	18.0 ± 0.4	3.5 ± 0.6
D-DRIP- W	-0.14 ± 0.14	11.8 ± 7.7	0.1 ± 0.2	2.8 ± 0.8	3.8 ± 0.7	-13.5 ± 0.6	17.3 ± 0.4	4.5 ± 0.7

at Provinzialmoor in 2017 (Fig. 3d). At Meerkolk, CH_4 emissions were lower in 2018 compared to 2017, while they clearly increased at Provinzialmoor (Fig. 3c, Table 3). Emissions of N_2O were lower in 2018 at Provinzialmoor and slightly higher at Drenth.

At Meerkolk, the majority of instantaneous CH_4 fluxes was higher at the warmed plots than at the control plots (Fig. 5). In contrast, most differences were close to zero at Provinzialmoor and only a small number of fluxes from the warmed plots were increased. All of them were measured in the hot and dry summer 2018 when the cover of graminoid plants had increased (Fig. 2). Still, differences in CH_4 fluxes of warmed and control plots were significant ($p < 0.0001$) for both Meerkolk and Provinzialmoor.

Correlation coefficients after Spearman revealed that single CH_4 fluxes at Meerkolk were correlated ($p < 0.0001$) with soil temperature sums of the preceding ten days ($r = 0.82$), daily GPP fluxes ($r = -0.77$), air temperature ($r = 0.69$) and WTD ($r = -0.63$). At Provinzialmoor, fluxes were weakly correlated

($p < 0.01$) with soil temperature sums ($r = 0.30$), GPP fluxes ($r = -0.30$), air temperature ($r = 0.25$) and WTD ($r = -0.39$). At both areas, differences in CH_4 fluxes of warmed and control sites did not correlate well with the differences in soil temperature sums (Meerkolk: $r < 0.1$, Provinzialmoor: $r < 0.3$), and thus large temperature differences between warmed and control plots did not necessarily lead to large differences in instantaneous CH_4 fluxes. Linear mixed effects models confirmed temperature sums, daily GPP fluxes and WTD to be the significant fixed factors in explaining the CH_4 fluxes at Meerkolk, while at Provinzialmoor it was GPP and WTD.

Discussion

Observed differences in GHG balances might not only be caused by the temperature increases alone but also by an interaction of altered temperatures, moistures, radiation and vegetation covers (Kennedy

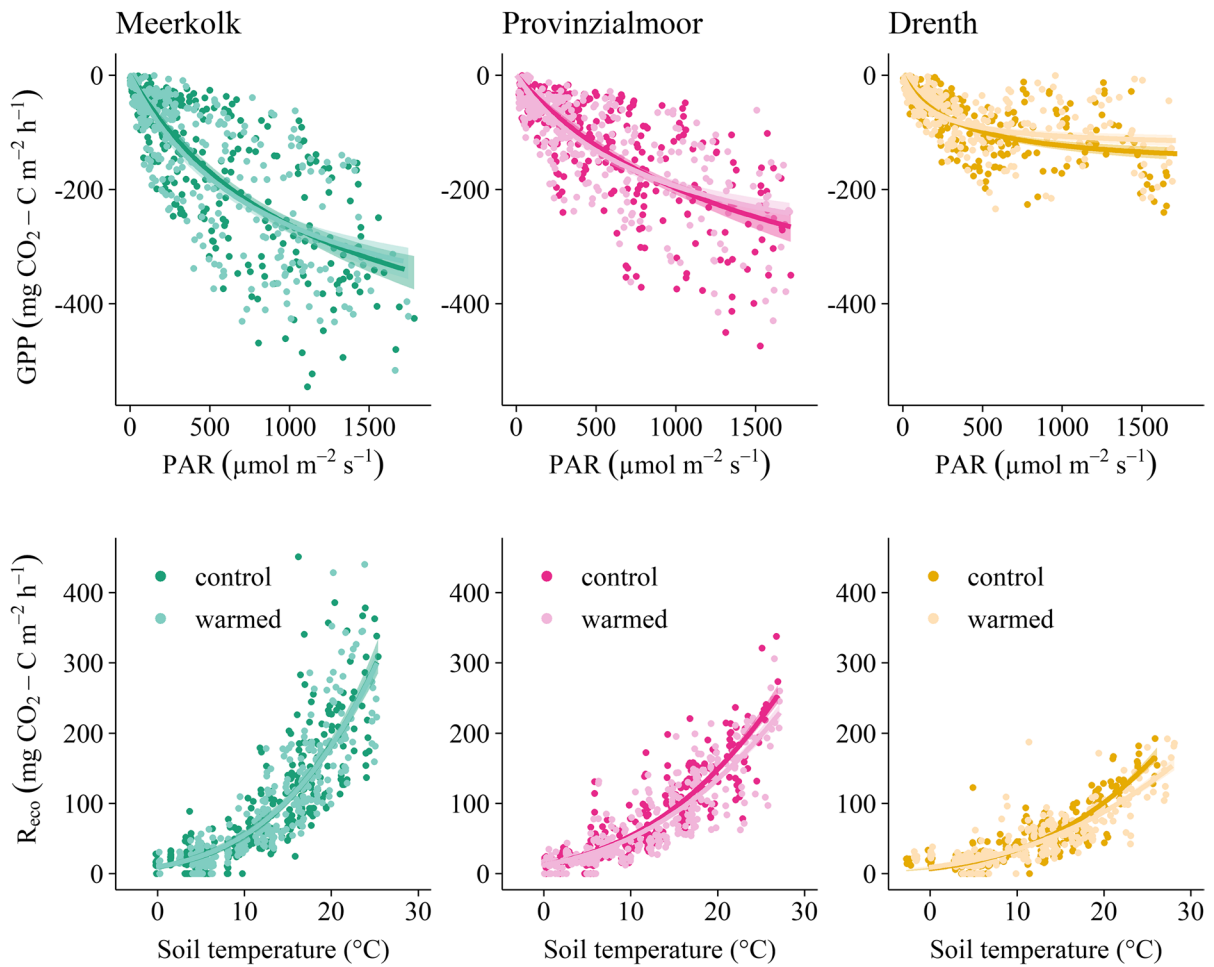
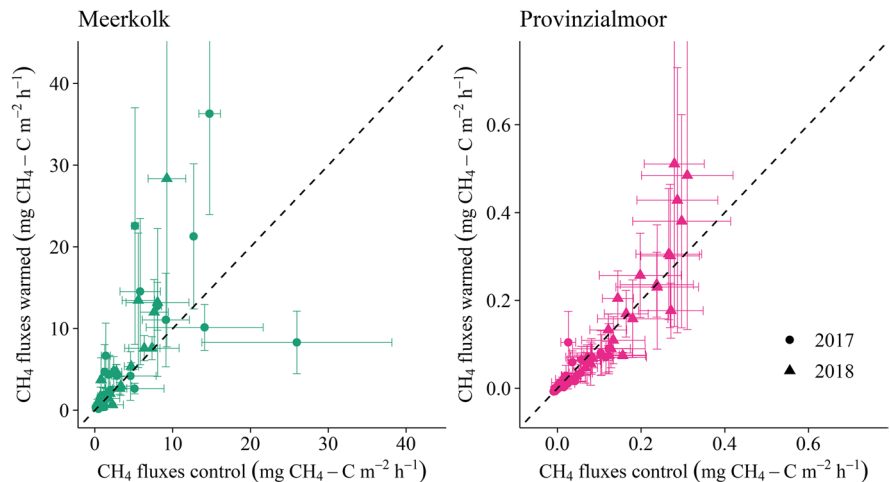


Fig. 4 Response functions relating gross primary production (GPP) to photosynthetically active radiation (PAR) and ecosystem respiration (R_{eco}) to soil temperature of warmed and control plots, pooling data of all campaigns; ribbons indicate 2.5th

and 97.5th percentiles of 1000 bootstrap runs; note that final balances were calculated using a campaign-based approach; at Meerkolk, one R_{eco} flux of the control site ($639\text{ mg CO}_2\text{-C}$) is not plotted to improve the readability of the figure

Fig. 5 Methane (CH_4) fluxes of warmed and control plots of single campaigns (means and standard errors of the three replicate plots) at the near-natural area Meerkolk and at the cultivation area Provinzialmoor; fluxes at Drenth were small and are not shown in this figure



1995; Godfree et al. 2011). In the present study, we tried to disentangle the effect of warming from additional unwanted effects in several steps. First, the large size of the OTCs minimised alterations in light and precipitation intensities (Fig. S1). Second, GPP was calculated using corrected PAR values (see supplementary material). Further, WTD, WFPS and RH of warmed and control sites did not clearly differ (section 3.2). Finally, the response of R_{eco} and GPP to soil temperature and PAR, respectively, was almost identical at the warmed and control sites (Fig. 4), excluding e.g. the possibility of differences in soil moisture causing effects on temperature sensitivity of R_{eco} . These points can be interpreted in a way that the observed changes in GHG emissions, vegetation composition and pore water quality are rather a result of warming than an artefact generated by the chambers.

Open top chambers successfully increased air and soil temperatures

Open Top Chambers significantly increased mean air and soil temperatures in comparison to the control plots by 0.5 °C and 0.3 to 0.5 °C, respectively. Temperature increases of the near-natural and cultivation areas were similar despite quite contrasting peat properties, water table depths and vegetation cover. The achieved warming was well inside the range of predicted global air temperature increase (0.1–0.3 °C) in the upcoming decades (IPCC 2018). Thus, OTCs successfully approximated future climate warming conditions. Still, the 2018 European heat wave resulted in higher differences in soil temperature between the two measurement years than the increase induced by the warming treatment (Table 3).

As in other studies (Bokhorst et al. 2013), warming induced by OTCs had both a diurnal and an annual cycle. It is dependent on solar radiation and reaches its maximum in the afternoon, while at night, colder air temperatures inside than outside the chambers due to reduced air exchange (Dabros et al. 2010) lead to a reduced overall daily mean effect. While occasional maximum temperature increases of 4 °C or more and cooling during the night do not precisely reflect future climate scenarios (Godfree et al. 2011), the trends observed in OTC studies might still hint towards effects of future climate change. Predictions would be improved by longer time series, as the interannual variability is high and long-term changes such as

changes in plant community are not adequately captured in biennial experiments (Turetsky et al. 2008; Elmendorf et al. 2012; Lamentowicz et al. 2016).

Effects of open top chambers on water availability and quality

Several studies found changes in soil moisture strongly influencing the effect of warming on GHG exchange (Turetsky et al. 2008; Mäkiranta et al. 2018). However, OTCs hardly changed WTD and WFPS in the present study. This also holds true when regarding only the vegetation period (data not shown) and demonstrates that the design of a central measurement plot lying well inside the inner edge of a large OTC (Godfree et al. 2011) successfully minimised unwanted impacts on precipitation (Voigt et al. 2016) and thus water availability.

Reduced RH could be expected as a result of increased air temperatures (Marion et al. 1997; Godfree et al. 2011). At the present study, differences in mean RH values of warmed and control plots were small. However, reduced hourly RH values were occasionally measured at higher air temperature differences between warmed and control plots. This temporal pattern might be important for the vegetation development in warmed and control plots, as especially the productivity of peat mosses seems to be dependent on a high humidity (Strack and Price 2009; Krebs et al. 2016), but no such effect could be found here (section 4.3).

Both DOC production and consumption can increase with temperature (Clark et al. 2009), but frequently warming resulted in increased DOC concentrations (Moore et al. 2008; Kane et al. 2014; Voigt et al. 2016). In our study, the effect of warming on water quality differed between the near-natural area and the cultivation areas. At the near-natural area, EC and DOC concentrations at the warmed plots were slightly lower than at the control plots. As the upper peat horizon consists of weakly decomposed peat, these similar water quality characteristics could be a result of the high hydraulic conductivity enabling an exchange of water and solutes with the plot surrounding. However, significantly higher NH_4^+ concentrations at the warmed plots point to an imperfect exchange even at this site.

At the cultivation areas, the peat was highly decomposed and periodically aerated. As at our sites,

this generally causes higher DOC concentrations than at less disturbed peatlands (Frank et al. 2014; Liu et al. 2019). Further, hydraulic conductivity of the highly decomposed peat is low (around 0.05 m d^{-1} in the upper peat layer, Oestmann et al. 2022), enabling slower exchange between the OTC plots and their surrounding than at the near-natural area. Vascular plants were frequently found to be associated with higher DOC concentrations than *Sphagnum* mosses (Armstrong et al. 2012; Vestgarden et al. 2010). However, higher concentrations of DOC at the warmed plots at Provinzialmoor despite lower vascular plant cover in 2018 rather hint towards a higher microbial activity due to warming (Kane et al. 2014). At Drenth, drip irrigation might have diluted a stronger increase in DOC. It is important to note that increased DOC concentrations induced by warming could result in increased ‘off site’ emissions of CO_2 (Evans et al. 2016) and CH_4 (Luan and Wu 2015) in runoff water from peat soils.

As at the near-natural area, NH_4^+ concentrations were higher at the warmed plots. This could also support the interpretation of more active microbial nutrient cycling. However, increases in NH_4^+ and DOC concentrations were not consistently linked with R_{eco} fluxes.

Effect of open top chambers on vegetation development

The established plant community of the near-natural area contrasts the developing community with closing vegetation gaps at the cultivation areas. The vascular plant abundance slightly differed between warmed and control plots already after two years, while the *Sphagnum* cover was only affected at the cultivation areas.

Vegetation development could be affected by increased air and soil temperatures, but also by water availability and reduced light and wind intensities. While we observed only minor effects of OTCs on WTD and WFPS, the occasionally lower RH at the warmed plots seemed not to have any negative impact on the vegetation so far. Reduced light intensities could not fully be prevented even with large OTCs encompassing small measurement plots, especially during winter and in the morning and afternoon (see supplementary material). However, the overall decrease in PAR during the two measurement years

was only about 5%. In accordance with Biasi et al. (2008), who reported a reduction of 10% and did not expect PAR differences of this size to be biologically significant for an arctic dwarf shrub community, we observed the same or even higher *Sphagnum* cover in the warmed plots and conclude that the slightly reduced light intensities did not impact the overall vegetation development. Nevertheless, it has to be mentioned that conditions were not perfectly homogeneous at the first vegetation survey. Changes induced by OTCs can only be carefully described as general trends in this study and might also be the result of natural variability.

While *Sphagnum* biomass was slightly higher at the warmed plots at the cultivation areas, mosses became pale and inactive at both warmed and control plots during the 2018 heat wave. Especially during the dry summer months, optimum WTDs near peat surface (Gaudig et al. 2018) could not be maintained. Contrasting results in literature on the response of *Sphagnum* productivity to increased temperatures might be explained by different *Sphagnum* species (Robroek et al. 2007; Jassey and Signarbieux 2019), different investigated temperature ranges (Breeuwer et al. 2009) or concomitant negative effects of drainage (Munir et al. 2015) and desiccation (Norby et al. 2019). Still, under laboratory conditions, *S. palustre* and *S. papillosum*, two promising candidates for cultivation and, in the case of *S. papillosum*, the dominant species in this study, showed maximum photosynthetic rates at temperatures of up to $35 \text{ }^\circ\text{C}$ (Haraguchi and Yamada 2011). This raises optimism for *Sphagnum* cultivation in a warmer climate given a sufficient water supply and a functioning acrotelm.

Greenhouse gas balances of warmed and control plots

Open Top Chambers increased total GHG emissions at the near-natural and cultivation sites. The near-natural area was characterised by high and stable WTD and a dense *Sphagnum* lawn. The GHG balance was dominated by CH_4 , but warming increased both CH_4 and CO_2 emissions. In contrast, WTD was lower than desired at the cultivation areas, and the GHG balances were consequently dominated by CO_2 . The two cultivation areas Provinzialmoor and Drenth strongly differed in GHG emissions and success of *Sphagnum* cultivation. Despite similar soil characteristics and even slightly higher WTDs in Drenth, the vegetation

developed better at Provinzialmoor, possibly caused by disturbances (low WTD, shearing by ice) in the initial phase at Drenth or by the previous multi-annual inundation of Provinzialmoor (Grobe et al. 2021). This hampers a comparison of the responses of differently irrigated cultivation sites to warming.

Net ecosystem exchange

When interpreting the results of our study, one main challenge lies within disentangling the effects of warming by OTC, an extraordinary warm summer 2018 and ongoing vegetation succession at a *Sphagnum* farming site in its early stage. Warming did neither consistently increase R_{eco} nor GPP across areas, contrasting previous studies (Ise et al. 2008; Samson et al. 2018; Gong et al. 2020; Biasi et al. 2008). Differences in NEE were generally rather caused by a reduced GPP, while changes in R_{eco} were smaller (Table 3).

Differences in GPP of warmed and control plots seem to depend more on the development of vascular plant cover than on temperature increase, explaining the converse interannual development of GPP in Provinzialmoor and, to a lesser extent, in Meerkolk and Drenth. Vascular plants show higher rates of C fixation and turnover than peat mosses (Ward et al. 2009), especially during dry periods. This also explains the apparent contradiction of slightly higher *Sphagnum* biomass and lower mean GPP at the warmed plots of the cultivation areas. Despite the high contribution of vascular plants to overall GPP, *Sphagnum* is nevertheless still crucial for accumulating peat due to the recalcitrance of its litter (Bragazza et al. 2016; Laiho 2006).

Open Top Chambers only increased R_{eco} fluxes at the near-natural area. Here, the overall response of R_{eco} to temperature did not differ between the warmed and the control site (Fig. 4) and the increase in R_{eco} in 2018 did not go along with increased GPP, pointing to a higher relevance of microbial processes than of differences in vegetation composition.

At the cultivation areas, patterns are more complex, as temperature effects are clearly overlain by changes in vegetation composition, i.e. a shift from the control treatment to the warmed plots regarding higher vascular plant cover. Ward et al. (2013) found that vegetation composition strongly controls the effect of warming on C loss. This complicated pattern

might be the reason for the response functions of R_{eco} and soil temperature being slightly steeper at the control plots compared to the warmed plots (Fig. 4). Minor changes in R_{eco} of warmed plots despite significant temperature increases seem counterintuitive, as temperature influences the metabolic rates of organisms. It is possible that, in contrast to the near-natural area, the cultivation areas became too dry during summer to support an increased microbial activity.

Differences in GPP and R_{eco} were higher between years than between warmed and control plots. Especially R_{eco} was clearly higher in 2018 compared to 2017 at all sites. While increasing vegetation cover at the cultivation areas and the distinct increase in vascular plant abundance at the near-natural area might explain most of the GPP development, R_{eco} at all areas was affected by increased vegetation cover and lower WTDs.

Methane and nitrous oxide

The increase in CH_4 emission induced by OTCs was most pronounced at the near-natural site. Probably due to the high water table and the presence of vascular plants, the CH_4 emissions of the near-natural site were generally rather high compared to other studies on temperate peatlands (Wilson et al. 2016), but not unprecedented in similar sites in Germany (Tiemeyer et al. 2020). A high correlation between temperature and CH_4 fluxes is not surprising. Turetsky et al. (2008) found higher methanogen abundance one year after warming and van Winden et al. (2012) found in a laboratory experiment that the response of methane producers to increased temperatures is stronger than the response of methane consumers. Possibly, the high and stable water level made temperature the limiting factor of CH_4 exchange at the near-natural area. This is also supported by the high correlation coefficients between CH_4 fluxes and temperature and the fact that soil temperature sums of the preceding ten days were a significant fixed factor in linear mixed effect modelling.

In contrast, CH_4 fluxes at the cultivation areas were not only lower by at least one order of magnitude, but also less affected by OTCs. A distinct increase at the warmed plots was only observed at Provinzialmoor in 2018 and is limited to the dry period from July to September. The increase in Provinzialmoor could therefore be caused by a leaching of plant exudates

(Voigt et al. 2016), supported by the higher DOC concentrations at the warmed plots, or by slightly higher cover of vascular plant species known to influence the CH₄ exchange at the soil-atmosphere boundary, e.g. *Eriophorum* sp. (Samaritani et al. 2011; Greenup et al. 2000).

In 2018, CH₄ emissions decreased at the near-natural sites despite higher temperatures, likewise at the warmed and control plots. The most evident reason for this and the difference to the effect induced by OTCs is the drop down in WTDs. While at Meerkolk the OTC effect was dominant, the differences in CH₄ exchange in Provinzialmoor were clearly higher between years than between treatments and could be attributed predominantly to the development of graminoid plant abundance.

At the near-natural area, high WTD (Mäkelä et al. 2022) and vegetation cover (Marushchak et al. 2011) prevented N₂O emissions. In contrast, the cultivation areas with their developing vegetation and highly decomposed peat (Liu et al. 2019) emitted N₂O, although the contribution to the total GHG balances was small. The reduced emission at Provinzialmoor in 2018 and the ongoing emission at Drenth fit to the previous identification of unvegetated peat surfaces as sources of N₂O (Marushchak et al. 2011; Oestmann et al. 2022).

Conclusions

Open Top Chambers are known to be only an approximation of climate-change induced warming and the warming effect is interwoven with water availability and plant species composition and therefore varies among sites and years. Nevertheless, the OTC approach delivers valuable insights into challenges in peatland management arising with climate warming.

Overall, the presented data on CO₂ and CH₄ fluxes highlight the risk of increased emissions from or decreased sink strength of near-natural temperate bogs and *Sphagnum* farming sites in a warmer future. We observed that increasing vascular plant abundance might be a consequence of climate warming and could enhance CH₄ emissions, making the control of vascular plants, which is current management practice for improving biomass quality, a measure for CH₄ reduction at paludiculture sites on ombrotrophic peat soil. Interestingly, increased emissions of CO₂ were only caused by higher R_{eco} at the near-natural site, where WTD was near the peat surface throughout the experiment, and rather by

reduced GPP at the *Sphagnum* farming sites, where irrigation deficiencies resulted in prolonged dry summer periods. We conclude that successful biomass production and maximum GHG mitigation in *Sphagnum* farming systems will – at least in early years – depend on a water management system ensuring near-surface WTDs even in extreme years and the control of vascular plants.

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Author contributions Bärbel Tiemeyer, Jan Oestmann and Ullrich Dettmann contributed to the study conception and design. Data collection and analysis were performed by Jan Oestmann, Dominik Düvel, Ullrich Dettmann and Bärbel Tiemeyer. The first draft of the manuscript was written by Jan Oestmann and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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