GREENHOUSE GAS BALANCE OF *SPHAGNUM* FARMING ON FORMER PEAT EXTRACTION SITES

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EIDESSTATTLICHE VERSICHERUNG

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

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SUMMARY

Peatlands drained for agriculture, forestry and peat extraction release large amounts of greenhouse gases (GHG). Here, the idea of paludiculture, which is the production of biomass under wet and peat preserving conditions, potentially combines economic and ecological goals by providing regional income from specialized wetland plants and by mitigating GHG emissions in comparison to conventional drainage-based agriculture. Under the nutrient-poor and acidic conditions at bog peatlands, the cultivation of peat mosses (*Sphagnum* farming) is most promising. Harvested *Sphagnum* biomass could be, for example, processed to renewable horticultural substrates or applied at peatland restoration areas to accelerate vegetation succession. However, despite increasing efforts in the research on the GHG balance of *Sphagnum* farming, there are still gaps in our knowledge, especially at areas of highly decomposed peat and under future climate warming conditions.

The overall objective of my thesis therefore was to determine GHG balances at a near-natural bog and two *Sphagnum* farming sites on shallow and highly decomposed peat remaining after industrial peat extraction in Northwestern Germany, including the exchanges of carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O). The high degree of peat decomposition exacerbates a successful cultivation of *Sphagnum* due to reduced porosity and hydraulic conductivity. I put particular emphasis on calculating areal balances for the whole production system, including the contribution of dams, extractable biomass and different irrigation techniques, as well as on the impact of extracting *Sphagnum* biomass on the GHG exchange of the near-natural bog area. In addition, I investigated the impact of simulated climate warming conditions on vegetation development and GHG exchange at all three study areas. Air and soil temperatures at selected measurement plots were passively increased using permanently installed open top chambers (OTC), hexagonal enclosures made from transparent polycarbonate. In order to be able to disentangle the warming effect from changes in other environmental parameters, I closely monitored and evaluated the availability of water and light inside the OTCs. Finally, I conducted a pulse labelling experiment using carbon (C) stable isotopes at the warmed and control plots at one of the *Sphagnum* farming areas to investigate in more detail the path of sequestered CO_2 from above-ground biomasses of *Sphagnum* and of the dominant vascular plant species purple moor grass (*Molinia caerulea*) to subsequent short-term and medium-term C pools.

I found that *Sphagnum* farming is possible on highly decomposed peat, although adverse hydrological conditions reduced *Sphagnum* productivity and GHG mitigation in comparison to results on less decomposed sites. In addition, temporary insufficient irrigation amounts negatively affected *Sphagnum* growth at the cultivation sites and the extraordinary hot and dry conditions during the European heatwave 2018 resulted in a clear increase in GHG emission. While drip irrigation provided more favorable conditions compared to ditch irrigation, a previous multi-annual inundation seemed to enhance *Sphagnum* growth and GHG mitigation. As open water surfaces of the irrigation system turned out to be hot spots of GHG emission, total areal GHG balances were still lowest at the drip irrigation site with its small share of irrigation surfaces. My results further highlight the risk of increased N_2O emissions even at nutrient-poor bog sites due to fluctuating water levels and poor vegetation development and the risk of increased CH_4 emissions even during drought due to plant-mediated gas transport. The near-natural area was a surprisingly high source of GHG, dominated by high CH_4 emissions. However, the impact of harvesting *Sphagnum* donor material was minor given a sufficient distance of the new vegetation surface to the water level.

OTCs significantly raised air and soil temperatures by about 0.5 °C and 0.3–0.5 °C, respectively, while water availability and light intensities were only marginally affected. The emission of CO_2 and CH_4 was generally higher at the warmed plots compared to the control plots, while no effect was found for N_2O. The cultivation areas seemed to be more resilient towards warming than the near-natural area, not as a

result of adjustable water levels but more likely because of prolonged periods of very low water levels at the former. In fact, the exchange of CO_2 was more affected by the hot and dry conditions during the European heatwave in the second measurement year than by the warming treatment itself.

The pulse labelling study revealed that vascular plants played a more dominant role in C turnover during drought compared to *Sphagnum*. However, most C was lost as respiration during the first days of the experiment and C retention at the end of the experiment (day 140) was much higher in *Sphagnum*. This underlines the high importance of *Sphagnum* in C retention even under extreme drought conditions. Interestingly, all subsequent C pools, including dissolved and emitted CO_2 and CH_4, were clearly enriched following label addition with the exception of dissolved organic carbon (DOC), which was presumably originating largely from peat mineralization at the study area. The effect of simulated warming on C allocation was small presumably due to the already extraordinary hot conditions during the experiment.

In general, my results highlight the large potential of *Sphagnum* farming as GHG mitigation measure even on highly decomposed peat. For maximizing *Sphagnum* productivity and GHG mitigation, water levels need to be kept close to the peat surface also during dry summer periods and the development of vascular plants needs to be monitored closely. This will be even more important in a warmer future.

ZUSAMMENFASSUNG

Für die landwirtschaftliche sowie forstwirtschaftliche Nutzung oder für den Torfabbau entwässerte Moore emittieren große Mengen an Treibhausgasen (THG). Hier könnte das Konzept der Paludikultur, der Biomasseproduktion unter nassen und damit torferhaltenden Bedingungen, wirtschaftliche und ökologische Zielsetzungen vereinbaren, indem der Anbau spezieller angepasster Pflanzen eine regionale Wertschöpfung ermöglicht und im Vergleich zur konventionellen entwässerungsbasierten Nutzung THG-Emissionen eingespart werden. Unter den nährstoffarmen, sauren Bedingungen an Hochmoorstandorten ist der Anbau von Torfmoosen (engl. „*Sphagnum* farming“) vielversprechend. Geerntete Torfmoosbiomasse kann unter anderem als Ausgangsstoff für nachhaltige Substrate im Gartenbau oder als Spendermaterial für renaturierte Hochmoorflächen verwendet werden. Trotz vermehrter Anstrengungen in der Forschung zur THG-Bilanz der Torfmooskultivierung bestehen jedoch noch immer offene Fragen, insbesondere im Hinblick auf Standorte mit stark zersetztem Torf und auf die Bedingungen zukünftiger Klimaerwärmung.

Das übergeordnete Ziel meiner Dissertation war daher die Bestimmung der THG-Bilanzen einer naturnahen Hochmoorfläche und zweier Torfmooskultivierungsflächen auf flachem und stark zersetztem Torf nach industriellem Torfabbau in Nordwestdeutschland, unter Berücksichtigung der Flüsse von Kohlendioxid (CO_2), Methan (CH_4) und Lachgas (N_2O). Der hohe Zersetzungsgrad erschwert eine erfolgreiche Torfmooskultivierung aufgrund der niedrigen Porosität und Wasserleitfähigkeit. Besonderes Augenmerk legte ich dabei auf die Berechnung der Bilanzen des gesamten Produktionssystems einschließlich des Anteils von Dämmen, einer geschätzten Ernte und verschiedener Bewässerungssysteme, sowie auf den Einfluss der Entnahme von Torfmoosen auf die THG-Bilanz der naturnahen Hochmoorfläche. Außerdem untersuchte ich den Einfluss simulierter Klimaerwärmung auf Vegetationsentwicklung und THG-Austausch der drei Versuchsflächen. Luft- und Bodentemperaturen ausgewählter Messplots wurden dabei passiv erwärmt mit Hilfe fest installierter, sechseckiger und nach oben hin geöffneter Kammern (engl. „open top chamber“, OTC) aus lichtdurchlässigem Kunststoff. Um den Effekt der Erwärmung von Auswirkungen anderer Umweltparameter trennen zu können, kontrollierte und bewertete ich sorgfältig die Verfügbarkeit von Licht und Wasser innerhalb der OTCs. Schließlich führte ich auf den erwärmten Messplots und Kontrollplots einer der Kultivierungsflächen ein Markierungsexperiment (engl. „pulse labelling“) mit stabilen Kohlenstoffisotopen durch, um den kurzfristigen und mittelfristigen Verbleib des aufgenommenen CO_2 in der Pflanzenbiomasse der Torfmoose und der dominierenden Gefäßpflanze Blaues Pfeifengras (*Molinia caerulea*) sowie in nachfolgenden Kohlenstoffpools genauer beschreiben zu können.

Meine Ergebnisse bestätigen, dass Torfmooskultivierung auch auf stark zersetztem Torf möglich ist, obwohl die ungünstigen hydrologischen Bedingungen die Produktivität der Torfmoose und die THG-Minderung im Vergleich zu Studien auf weniger stark zersetztem Torf reduzieren. Zusätzlich verringerte eine zeitweise unzureichende Bewässerung das Wachstum der kultivierten Torfmoose und die außergewöhnlich heißen und trockenen Bedingungen während der Europäischen Hitzewelle 2018 resultierten in einer deutlichen Zunahme der THG-Emissionen. Während die Tröpfchenbewässerung im Gegensatz zur Grüppenbewässerung günstigere Bedingungen schuf, schien eine vorhergehende mehrjährige Überflutung das Torfmooswachstum und die THG-Minderung zu fördern. Die Wasseroberflächen des Bewässerungssystems erwiesen sich jedoch als Hotspots der THG-Emission und die flächig gewichtete THG-Bilanz der Tröpfchenbewässerung war aufgrund des geringen Anteils der Bewässerungsfläche am niedrigsten. Darüber hinaus zeigten meine Messungen das Risiko erhöhter N_2O-Emissionen sogar an nährstoffarmen Hochmoorstandorten durch schwankende Wasserstände und spärliches Pflanzenwachstum, sowie das Risiko erhöhter CH_4-Emissionen sogar während

Dürreperioden durch den Gastransport innerhalb spezialisierter Gefäßpflanzen. Die naturnahe Fläche war aufgrund hoher CH_4-Emissionen eine überraschend hohe THG-Quelle. Der Einfluss der Entnahme von Torfmoosbiomasse war jedoch gering, ein ausreichend großer Abstand der neuen Vegetationsoberfläche zur Wasseroberfläche vorausgesetzt.

Die OTCs erhöhten Luft- und Bodentemperaturen signifikant um etwa 0.5 °C beziehungsweise 0.3–0.5 °C, während Wasserverfügbarkeit und Lichtintensität kaum beeinflusst wurden. Die CO_2- und CH_4-Emissionen waren höher in den erwärmten Messplots im Vergleich zur Kontrolle, während kein Einfluss auf den N_2O-Austausch festgestellt werden konnte. Die Kultivierungsflächen schienen resilienter gegenüber der Erwärmung im Vergleich zur naturnahen Fläche, allerdings nicht aufgrund einstellbarer Wasserstände, sondern eher wegen der zeitweise sehr niedrigen Wasserstände. Tatsächlich war der Einfluss der heißen und trockenen Bedingungen der Europäischen Hitzewelle im zweiten Jahr auf den CO_2-Austausch größer als die experimentelle Erwärmung selbst.

Das Markierungsexperiment zeigte, dass Gefäßpflanzen während Dürreperioden eine gewichtigere Rolle im Kohlenstoffkreislauf spielten als Torfmoose. Der meiste Kohlenstoff ging aber bereits in den ersten Tagen des Experiments wieder durch Respiration verloren und die Kohlenstoffspeicherung am Ende des Experiments (Tag 140) war deutlich größer in der Torfmoosbiomasse. Das unterstreicht die große Bedeutung der Torfmoose im Kohlenstoffrückhalt sogar während extremer Dürre. Interessanterweise waren alle Kohlenstoffpools einschließlich des gelösten und emittierten CO_2 und CH_4 nach der Markierung angereichert, mit Ausnahme des gelösten organischen Kohlenstoffs (engl. „dissolved organic carbon“, DOC), der auf der Versuchsfläche vermutlich zum größten Teil aus der Torfzersetzung entsteht. Der Einfluss der experimentellen Erwärmung auf die Kohlenstoffallokation war gering, vermutlich wegen der ohnehin außergewöhnlich heißen Bedingungen während des Experiments.

Meine Ergebnisse betonen generell das große Potential der Torfmooskultivierung als Maßnahme zur THG-Minderung auch auf stark zersetztem Torf. Um Torfmoosproduktivität und THG-Minderung zu maximieren, müssen jedoch die Wasserstände auch während trockener Sommermonate nah an der Torfoberfläche gehalten und die Entwicklung der Gefäßpflanzen regelmäßig kontrolliert werden. Diese Maßnahmen werden im Hinblick auf die voranschreitende Klimaerwärmung noch wichtiger.

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PUBLICATIONS RELATED TO THIS DISSERTATION

Chapter 3:

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Chapter 4:

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1 INTRODUCTION

1.1 Bog ecosystems: a special type of peatland

Peatlands are characterized and distinguished from other wetlands by the accumulation of organic matter (Vitt, 1994). They form where water is congregating. Dead plant material is buried beneath the water table by the weight of growing vegetation and due to a rapid depletion of oxygen (Philben et al., 2015) this biomass is only incompletely decomposed, compacted and stored as peat (Moore, 2002). More specifically, peat is the sediment of partially decomposed wetland plants with more or less visible plant structures, i.e., with different degrees of decomposition. The resulting imbalance of a primary production exceeding decomposition has made pristine peatlands important long-term carbon (C) sinks (Gorham, 1991; Moore, 2002). Since the last glacial maximum, northern peatlands have accumulated about 500 Gt C, a pool large enough to significantly impact global C budgets and atmospheric carbon dioxide (CO_2) concentrations (Yu et al., 2010).

Peatlands can be broadly distinguished into fens and bogs (Vitt, 1994; Moore, 2002). In contrast to the former, bog ecosystems largely lost their connection to the minerogenous groundwater due to ongoing peat accumulation and are finally dependent on direct precipitation as only source of water, which is called ombrotrophy. This creates a unique habitat, characterized by low nutrient concentrations and high acidity (Wheeler and Proctor, 2000) and dominated by peat mosses (*Sphagnum*). Within these broad groups, peatlands can be further differentiated according to hydrological and ecological aspects (Wheeler and Proctor, 2000; Joosten and Clarke, 2002; Lindsay, 2016). However, the focus of this research lies on temperate ombrotrophic bog ecosystems.

Sphagnum mosses (Fig. 1.1) are the ecosystem engineers of bogs. More than only being well adapted to wet and nutrient poor conditions, they actively modify their surrounding environment (van Breemen, 1995). The bottom part of the mosses dies and forms a growing peat layer due to its burial under the water table and due to its high recalcitrance against microbial decomposition (Dorrepaal et al., 2005; Hajek et al., 2011), while the upper living part continues growing. The capitulum, the uppermost apical branches (1–2 cm) of the moss, is the photosynthetically most active section (Fenner et al., 2004). As *Sphagnum* possesses neither roots nor internal water conducting tissues, it depends on the capillary rise of water from deeper saturated layers to the peat surface (Clymo and Hayward, 1982). In addition, they actively increase the water content in the peat by storing large amounts of water in specialized hyaline cells bathing the photosynthetic cells (Glime, 2017). Using this reservoir, they are able to survive harsh periods and revive at more advantageous conditions (Moore et al., 2021). Further, in addition to be able to thrive at the low nutrient levels typical for bog sites, *Sphagnum* actively keeps its environment oligotroph by efficient nutrient sequestration (Temmink et al., 2017) and acidic by absorbing cations while releasing self-produced hydrogen (Joosten and Clarke, 2002). In this environment, most other plants can hardly compete, and only a few specialized vascular plant species occur in bogs depending on site conditions such as water level (Couwenberg et al., 2011).

Fig. 1.1: ***Sphagnum*** **mosses (*****Sphagnum*** **sp.) with sundew (*****Drosera rotundifolia*****).**

Vertically, pristine bog profiles can be further divided into an acrotelm, the not permanently saturated upper layer of living plants and less decomposed plant material and a catotelm, the water-saturated peat layer (Ingram, 1978). Dead plant material is decaying relatively fast in the acrotelm due to aeration. In contrast, rapidly water-logged or more recalcitrant remains that reach the catotelm are saved from further aerobic decomposition (Clymo, 1984). Thus, the upper peat layer largely consists of weakly decomposed biomass. Depending on the oxygen exposure time before water-logging and on climatic conditions during peat formation (Philben et al., 2015), deeper layers are characterized by a higher grade of decomposition, ranging from hardly decomposed matter to peat with no or only marginally visible plant structures. In contrast to the acrotelm, where hydraulic conductivity is high, compaction and a lower porosity reduce hydraulic conductivity in the catotelm (Clymo, 1984).

In Germany, peat soils are generally defined as soils with layers of organic material thicker than 0.3 m and consisting of at least 30% of its mass of soil organic matter (Ad-hoc-AG Boden, 2005). Peat soils according to the German definition are one type of ‘organic’ soils as defined by e.g., the IPCC (2014). Definitions and classification systems differ between countries and mapping purposes (Wittnebel et al., 2021). Within the context of this thesis, peat soils are defined according to the German classification system, i.e., having on organic layer containing the remains of *Sphagnum* mosses.

1.2 Exploitation of peatlands and restoration measures

Only a few generations ago, peatlands were largely areas of impenetrable wilderness. Then, reclamation of these lands started and drainage ditches were dug to channel out the water. The main drivers of drainage were agriculture, forestry, infrastructure and peat extraction (Chapman et al., 2003). Drainage and peat extraction occurred already in the late Middle Ages but were dramatically intensified in the 19th and 20th century (Chapman et al., 2003; Gerding et al., 2015). At first, the extraction of peat turfs for combustion was the major sector of industry. In the past decades, bog peat has been increasingly craved by the horticultural industry as potting substrate (Hirschler and Osterburg, 2022).

In certain countries with large peatland areas, such as Denmark, the Netherlands and Germany, almost all peat-accumulating areas have been lost or severely affected by human activity. In Germany for example, more than 95% of the initial area has been drained to date, of which about 2% have been designated to peat extraction (Joosten et al., 2017). Undrained or protected areas in Germany cannot even be described as natural anymore, as they are largely surrounded by agriculture and settlements, which, despite strict nature conservation status, majorly affects nutrient concentrations and hydrology. With these severe changes, important ecosystem services of pristine peatlands are reduced or lost (Kimmel and Mander, 2010). Certainly, the most important ecosystem service provided by undisturbed peatlands (among water retention, nutrient retention, biodiversity conservation and many more) is the regulation of global climate by storing C in the long term (Frolking et al., 2006). Carbon which has been accumulated in millennia is now lost in decades as degraded peatlands turn from sinks to sources and even hotspots of greenhouse gas (GHG) emission (Dunn and Freeman, 2011; Tubiello et al., 2016; Loisel et al., 2021).

Fig. 1.2: Ongoing drainage and peat extraction close to the study area Provinzialmoor.

Finally, drained peatlands (Fig. 1.2) continue to release CO_2 until rewetting or loss of all peat (Bonn et al., 2014). This makes them targets for recent climate protection efforts (Leifeld and Menichetti, 2018) and the restoration of drained peatlands is now fostered in conservation programs and research projects (Höper et al., 2008; Andersen et al., 2017; Chimner et al., 2017). In order to protect and restore peatlands for climate protection and nature conservation, the German Federal Government recently summarized measures for peatland protection in a national strategy paper (‘Nationale Moorschutzstrategie’, BMU, 2022).

Peatland rewetting is a cost-effective restoration measure (Andersen et al., 2017), reducing C loss to the atmosphere by re-establishing water-logged conditions (Wilson et al., 2016b). The most common practice (and the typical measure at former peat extraction areas in Northwestern Germany designated for restoration) is to block drainage ditches, creating polders where water levels rise again and typical vegetation might establish (Rochefort and Lode, 2006).

However, reduced CO_2 emissions (Beetz et al., 2013; Regina et al., 2015; Boonman et al., 2022) and reduced nitrous oxide (N_2O) emissions (Regina et al., 2015; Liu et al., 2020) at restored areas might possibly come at the cost of increased methane (CH_4) emissions (Hemes et al., 2018).

In addition, the hydrology of degraded peat soils often remains disturbed even after rewetting and pristine conditions are hard to restore (Moore, 2002). This is especially the case at areas of former industrial peat extraction, where only a thin layer of highly decomposed catotelmic peat is left behind (Quinty and Rochefort, 2003; Schmatzler and Caspers, 2006). In this residual peat, reduced pore spaces and increased bulk density negatively affect hydraulic conductivity (Price et al., 2003; Liu and Lennartz, 2019). Consequently, the key goal of peatland restoration, the establishment of a typical hydrology and plant community crucial to re-install the sink function for atmospheric CO_2 (Dixon et al., 2014), can take years (Price et al., 2003; Waddington et al., 2010) at minorly affected sites, depending on the thickness and decomposition of the residual peat layer and on climatic conditions, or decades (Price et al., 2003; Taylor and Price, 2015) at heavily disturbed areas (Fig. 1.3).

Finally, large-scale rewetting measures in densely populated areas with intensive agricultural land use will be only applicable if regional income can be generated at parts of the rewetted area. As conventional drainage-based agriculture is impeded or reduced due to a lower trafficability of the wet peat for heavy machinery, new land use strategies are urgently needed, ultimately leading to a wise use of peatlands addressing all stake holders (Joosten and Clarke, 2002).

Fig. 1.3: Slow succession towards typical bog vegetation after rewetting of a former peat extraction site close to the study area Provinzialmoor (left) and accelerated development of a continuous vegetation cover (right).

1.3 Paludiculture: Why *Sphagnum* farming?

Paludiculture (from Latin ‘palus’ = ‘mire’, ‘swamp’) is the production of biomass under wet and peat-preserving conditions (Wichtmann et al., 2016) and could considerably contribute to large-scale peatland rewetting by combining ecological and economic goals. Paludiculture as a new land use option at degraded peatlands reduces further C loss while active water management potentially minimizes CH_4 emissions (Tanneberger et al., 2022). On the other hand, landowners and farmers can generate regional added value by the cultivation of specialized crops and eventually by the pricing of mitigated GHG (Bonn et al., 2014). Last but not least, paludiculture sites could develop into important habitats and steppingstones promoting the survival of endangered peatland flora and fauna (Muster et al., 2015; Martens et al., 2023).

While higher nutrient concentrations at fen sites support many different suitable crops for bioenergy, fodder or insulation materials, the cultivation of peat mosses (*Sphagnum* farming) is the most promising option at degraded bog sites following peat extraction (Gaudig et al., 2014; Pouliot et al., 2015) or agriculture (Gaudig et al., 2014; Huth et al., 2022). *Sphagnum* farming builds upon the moss layer transfer technique developed for bog restoration (Quinty and Rochefort, 2003). In brief, the peat surface is levelled, drainage ditches are blocked and fragments of living *Sphagnum* collected at a donor area are spread evenly and covered with straw mulch for protection against excess wind and sunlight. *Sphagnum* farming sites could then be harvested on a cyclic basis every three to five years (Gaudig et al., 2018) and a new *Sphagnum* lawn develops spontaneously if enough biomass remains at the site.

Although there are numerous possible uses for harvested *Sphagnum* biomass (Pouliot et al., 2015), the most important application lies in the horticultural industry, where non-decomposed *Sphagnum* fibers could be used as a sustainable raw material for growing substrates (Emmel, 2008; Jobin et al., 2014), this way replacing mined peat and relieving ongoing pressure on pristine bogs (Schmatzler, 2012; Hirschler and Osterburg, 2022). Desired attributes of mined *Sphagnum* peat such as structural stability, high water storage capacity and low nutrient concentrations adjustable to the requirements of individual crops (Schmilewski, 2008; Gaudig et al., 2014) are also provided by cultivated *Sphagnum*. Another important field of application is the use as an inoculum for accelerated vegetation development at degraded bogs under restoration (Quinty and Rochefort, 2003; Hugron and Rochefort, 2018), as in Central Europe donor material is extremely scarce. *Sphagnum* farming might thus turn out to be a long-term amelioration measure, as a regenerating *Sphagnum* cover increases soil moisture in the peat beneath (Price et al., 2003). Although *Sphagnum* species colonizing lawns might be more productive (van Breemen, 1995), hummock species such as *Sphagnum palustre* L. and *Sphagnum papillosum* LINDB. are more resilient to moisture changes, inhibit a large water storing capacity and stable structure and are therefore best suited for *Sphagnum* farming (Gaudig et al., 2014; Gaudig et al., 2018).

1.4 Current challenges for *Sphagnum* farming

Sphagnum farming needs stable water levels close to the peat surface deduced from the ideal growth conditions of *Sphagnum* and the not yet existing buffering characteristics of a functioning acrotelm (Pouliot et al., 2015; Gaudig et al., 2014). However, low hydraulic conductivities of highly decomposed peat at former peat extraction sites could result in insufficient water supply from ditches and reduced moisture contents at the capitula and finally to a reduced *Sphagnum* growth (Clymo and Hayward, 1982; McNeil and Waddington, 2003; Strack et al., 2009). Further, water level amplitudes are higher at sites with highly decomposed peat and a low porosity. In contrast to *Sphagnum* farming attempts on thicker peat layers (Beyer and Höper, 2015) and on less decomposed peat (Günther et al., 2017), the feasibility of large-scale *Sphagnum* farming on highly decomposed sites has yet to be proven (Wichmann et al., 2017).

Different irrigation techniques are available to facilitate water levels close to the capitula while preventing flooding (Gaudig et al., 2018). Possible systems are subsurface pipes, drip irrigation systems at the peat surface or irrigation ditches channeling the water from reservoirs into the cultivation area. Due to the negative climatic water balance in summer (Brust et al., 2018), it is necessary in Northwestern Germany to provide irrigation water during dry periods. However, groundwater and surface waters are most often not accessible or not appropriate for irrigation due to high pH and nutrient load (Gaudig et al., 2018). One possible solution is to store excess winter precipitation at *Sphagnum* farming sites in irrigation polders, neighboring polders that have been restored by ditch blocking but are not used as cultivation sites. In these polders, inundation in winter is allowed and water can be withdrawn in summer. The chosen irrigation technique and the surface area of polders and ditches might considerably contribute to the overall GHG balance of a *Sphagnum* farming site (Günther et al., 2017).

Besides *Sphagnum* spores or shoots from the greenhouse, *Sphagnum* shoots from wild populations (considering conservation status and legal requirements) can be used as donor material for cultivation areas, as *Sphagnum* is able to regenerate already from small parts of the stem (Gaudig et al., 2018; Hugron and Rochefort, 2018). Parts of the cultivation sites investigated in this research were established using *Sphagnum* biomass collected manually from a near-natural bog in close distance. However, besides the fact that the collecting depth should allow a rapid regeneration (Gaudig et al., 2018), little is known about the effect of harvesting donor material on vegetation development and GHG exchange at the donor area.

The vegetation at *Sphagnum* farming sites is in a dynamic successional stage. Vascular plants have been reported to encroach degraded peatlands with disturbed hydrology due to their ability to reach deeper peat layers with their roots in times of drought (Chambers et al., 1999). At *Sphagnum* farming sites, vascular plant species could be introduced via the spread *Sphagnum* biomass or naturally from the surrounding area (Fig. 1.4). The expansion of vascular plants depends on water availability to some extent (Järveoja et al., 2016) and some species might also respond positively to warming (Buttler et al., 2015). When their cover exceeds a certain threshold, they can negatively affect *Sphagnum* growth as less light is reaching the mosses beneath (Pilkington et al., 2021). Further, they can enhance water losses from deeper in the peat profile (Price et al., 2003), which could negatively affect *Sphagnum* development during periods of insufficient water supply. On the other hand, vascular plants could act as ‘shelter plants’ (Pouliot et al., 2011; Guêné-Nanchen et al., 2017), enabling higher *Sphagnum* growth by providing protection and structure for vertical growth. In any case, vascular plants affect *Sphagnum* farming in many ways, are an unwanted by-product in the produced growing media and need to be considered in site management and in the discussion of the GHG balance of *Sphagnum* farming.

Fig. 1.4: Scattered vascular plants act as 'shelter plants' or compete with *Sphagnum* for water and light. In addition, vascular plants possibly affect the GHG balance of *Sphagnum* farming areas (photo by Dominik Düvel).

For the near future, the mean increase in surface temperatures is estimated with high confidence to be 0.2 °C per decade (IPCC, 2018). In addition to warming, a more irregular distribution of precipitation and increased risk of extreme events such as droughts are expected (IPCC, 2018; IPCC, 2021). Consequently, climate change conditions might have major impacts on the existence and functioning of near-natural and cultivated peatlands. The effect of future warming on vegetation development and GHG exchange could threaten the success of *Sphagnum* farming as land use option at degraded peatlands and needs to be understood in more detail.

As the processes in carbon and nutrient cycling at these newly emerging ecosystems are not yet fully understood, GHG measurements are needed for a profound discussion of the climate impact of *Sphagnum* farming. Near-natural and cultivated peatlands emit and sequester GHG. The GHG balance of a peatland area comprises the exchanges of the following three major GHGs.

1.5 The greenhouse gas exchange at near-natural peatlands and *Sphagnum* farming areas

1.5.1 Carbon dioxide

Carbon dioxide is sequestered from the atmosphere by plants during photosynthesis and is finally stored as peat or lost again via respiration or fluvial export. The net ecosystem exchange (NEE) therefore is the sum of gross primary production (GPP), which is the amount of atmospheric CO_2 taken up by plants, and ecosystem respiration (R_{eco}), which is the sum of all autotrophic and heterotrophic respiration. The high importance of this GHG arises from the persistence in the atmosphere of several hundred up to some thousand years (Archer et al., 2009). Water level is a major factor controlling NEE and while pristine peatlands have been long-term sinks for atmospheric CO_2, large emissions to the atmosphere originate at drained degraded peatlands due to dropping water levels and the concomitant aeration of peat (Tiemeyer et al., 2020; Boonman et al., 2022). At *Sphagnum* farming sites, CO_2 losses might be reduced due to raised water levels, stopping further peat decomposition. While GPP is largely controlled by photosynthetically active ration (PAR) (Limpens et al., 2008), R_{eco} is tightly coupled to soil temperature (Lloyd and Taylor, 1994). Both additionally depend on soil moisture or, as a proxy, water level (Strack and Price, 2009; Säurich et al., 2019; Tiemeyer et al., 2020). The different contribution of plant functional traits and single species to processes in the C cycle (Dorrepaal, 2007; Heijmans et al., 2008) makes the vegetation composition at near-natural and *Sphagnum* farming sites a further important driver of NEE. Higher C assimilation on the one hand and higher autotrophic respiration on the other hand have been reported for vascular plants in comparison to *Sphagnum* (Trinder et al., 2008; De Deyn et al., 2011; Järveoja et al., 2016), as well as increased C loss due to the higher decomposability of vascular plant litter (Dorrepaal et al., 2005; Limpens et al., 2008). All the above-mentioned drivers lead to strong seasonal and diurnal variation in NEE (Vargas et al., 2011; Anav et al., 2015).

In a warmer future, the emission of CO_2 to the atmosphere might increase at some areas or decrease at others. It is still under debate whether the response of peatland NEE to warming is dominated by increased C loss due to higher decomposition (Ward et al., 2013; Gallego-Sala et al., 2018) or by increased C sequestration (Johnson et al., 2013; Charman et al., 2013; Philben et al., 2015). Changes in C uptake and loss could also cancel each other out, resulting in a marginal overall effect on NEE (Pearson et al., 2015). Long-term temperature increases might furthermore shift the plant community towards increased covers of vascular plants and reduced bryophyte covers (Weltzin et al., 2003; Walker et al., 2006) with the consequences mentioned above.

1.5.2 Methane

Peatlands constitute a significant source of atmospheric CH_4 (Abdalla et al., 2016), which is produced by archaea during the breakdown of organic matter under water-logged and anaerobic conditions. At *Sphagnum* farming areas, CH_4 emissions might contribute less to the overall GHG balance given a stable water level a few centimeters below the peat surface and the prevention of inundation (Turetsky et al., 2014; Beyer and Höper, 2015). The climate forcing of a GHG relative to that of CO_2 is commonly expressed for a chosen time horizon by its global warming potential (GWP) in CO_2 equivalents (Ramaswamy, 2001) and CH_4 has a 28-fold higher GWP than CO_2 based on a timeframe of 100 years (Myhre et al., 2013). However, it remains in the atmosphere only for about a decade. Methane is transported from the water-saturated zone through the peat column to the atmosphere by diffusion, ebullition or plant-mediated transport. Some of the diffusive flux is converted to CO_2 by methanotrophic bacteria in the aerated peat column before reaching the atmosphere and the measured flux at the peat surface is the sum of these two processes. Consequently, fluxes of CH_4 are temporally and spatially (Kutzbach et al., 2004; Teh et al., 2011; Köhn et al., 2021) highly variable and depend on temperature (Yvon-Durocher et al., 2014), water level (Moore and Roulet, 1993; Limpens et al., 2008) and plant community. Plant-mediated transport through aerenchymous tissues of specialized wetland plants, enabling gas transport between the rooting zone and atmosphere, bypass the consumption of methanotrophs and can considerably contribute to peatland CH_4 exchange (Greenup et al., 2000; Kutzbach et al., 2004; White et al., 2023).

As in the case of NEE, the impact of climate warming on the exchange of CH_4 is not yet fully understood as production and consumption might be enhanced (van Winden et al., 2012). Predicting the response of ecosystem level CH_4 exchange to increasing temperatures is further complicated by changes in plant community structure and water availability (Yvon-Durocher et al., 2014).

1.5.3 Nitrous oxide

Nitrous oxide is produced during the processes of nitrification and denitrification, which is the oxidation of ammonium to nitrate and the reduction of nitrate to molecular nitrogen or N_2O (Butterbach-Bahl et al., 2013; Lin et al., 2022). It is an even more potent GHG considering its GWP of 265 CO_2 equivalents (Myhre et al., 2013) and possibly persists in the atmosphere for more than a century (Volk et al., 1997). Processes involved in N_2O exchange depend on water levels and concomitant oxygen contents (Song et al., 2019) and on temperature (Anthony and Silver, 2021). Pristine peatlands hardly emit N_2O due to low availabilities of oxygen and nitrogen (Regina et al., 1996) or even act as small sinks (Lin et al., 2022). While draining has been reported to result in increased emission of N_2O especially at nutrient-rich peatlands (Martikainen et al., 1993; Regina et al., 1996), rewetting possibly stops further N_2O emission (Lin et al., 2022). At *Sphagnum* farming sites, N_2O might thus especially add to the overall GHG balance in the establishment phase with developing vegetation covers and higher emissions at patches of bare peat (Marushak et al., 2011). Due to interrelated effects of temperature-dependent microbial activity, vegetation development and water availability, warming might lead to increased N_2O loss of peat soils (Voigt et al., 2016).

1.5.4 The greenhouse gas balance

All three GHGs are summed up in a GHG balance as CO_2 equivalents given their GWP. The GHG balance of *Sphagnum* farming is not yet adequately investigated and deviates from near-natural peatland sites due to irrigation management and a not yet fully developed vegetation cover. This will be especially the case at highly decomposed areas. Hydrology is affecting the exchange of all above mentioned GHGs and irrigated *Sphagnum* farming sites with adjusted water levels close to the peat surface could develop into areas of climate protection in contrast to drainage-based land use.

However, only few studies have been investigating the GHG exchange of *Sphagnum* farming in Northwestern Germany so far. Beyer and Höper (2015) and Günther et al. (2017) report an already high C sequestration (2.3–8.6 t CO_2-eq. ha^{-1} yr^{-1}), hinting towards a potentially rapid recovery of the CO_2 sink function, the C export of harvested biomass not yet included. The GHG balance of shallow and highly decomposed former peat extraction areas is not yet investigated on a larger scale. Further, robust conclusions on the GHG mitigation potential of *Sphagnum* farming are only possible if all parts of the production cycle are included. In particular, open water surfaces of the irrigation system might considerably reduce the overall GHG mitigation. Further, the biomass harvested at *Sphagnum* farming sites needs to be included in the overall GHG balance, as most of the sequestered C will eventually be released to the atmosphere again during the application of the growing substrate.

Climate warming will affect the GHG exchanges at near-natural and cultivated peatlands and might complicate restoration measures. In addition to determining the GHG balance of *Sphagnum* farming, it is therefore of high interest in what direction the GHG exchange develops at these areas in a warmer future. Ultimately, increased GHG emissions from peatlands due to climate warming might again accelerate climate change, creating positive self-reinforcing feedback (Friedlingstein et al., 2006; Limpens et al., 2008). However, the impact of climate warming on near-natural peatlands and *Sphagnum* farming sites is complex and cannot easily be predicted as direct effects such as the control of temperature on microbial processes (Dorrepaal et al., 2009; Butterbach-Bahl et al., 2013; Yvon-Durocher et al., 2014) interact with indirect effects such as increased evaporation and changes in plant community structure. Knowledge is particularly scarce for the newly emerging ecosystem of paludiculture, which might be more resilient against warming due to the possibility to adjust water levels by irrigation measures.

Dissolved organic carbon (DOC) is composed of plant exudates and decomposed organic matter and its concentration in the soil pore water is therefore dependent on temperature, plant community (Freeman et al., 2004) and water level (Frank et al., 2014). The production and export of DOC, which is finally decomposed in parts to CO_2 and CH_4 (Evans et al., 2016), needs to be included in the discussion of the GHG balance of *Sphagnum* farming.

1.6 Determination of greenhouse gas balances at peatland sites

1.6.1 Measurement approaches

The GHG exchange is defined as the sum of fluxes between the plant-soil system and the atmosphere. For small-scale parcels of only a few hundred square meters and for investigating differences between neighboring treatments, the determination of GHG fluxes using measurement chambers (Livingston and Hutchinson, 1995; Maier et al., 2022) is most appropriate and preferred to other available methods, such as the eddy covariance technique for large homogeneous areas (Aubinet et al., 1999). In systems with expected high temporal dynamics in GHG exchange, automatic chambers might enable higher measurement frequencies (Pihlatie et al., 2010), although at the cost of increased investment and decreased on-site supervision.

1.6.2 Flux calculation

Following the non-steady-state approach, the increase or decrease in headspace gas concentrations is measured during a constant time period (Hutchinson et al., 2000). Flux calculation aims at estimating the initially undisturbed slope at chamber closure and the appropriate linear or nonlinear calculation scheme must be considered carefully (Kutzbach et al., 2007; Hüppi et al., 2018).

As the GHG exchange between soil, vegetation and atmosphere is reliant on several sensitive parameters, which clearly are affected by covering the soil with a measurement chamber, care must be taken in order to prevent or minimize measurement artefacts (Hutchinson et al., 2000; Kutzbach et al., 2007; Maier et al., 2022) and to improve comparability between studies (Rochette and Eriksen-Hamel, 2008), although the overall excellent suitability of the chamber system was confirmed in crosschecks with eddy covariance results (Drösler, 2005; Lucas-Moffat et al., 2018). Air temperature and humidity increase inside the chambers during employment. Further, chambers impact the natural atmospheric pressure fluctuation and consequently the gas exchange at the soil-atmosphere boundary. Moreover, gas concentrations inside the chambers might increase or decrease in such way that natural emission or uptake rates might be influenced. During closed chamber measurements, the increase or decrease of GHG concentration resulting from diffusive flux is driven by the concentration gradient between soil and chamber air. Depending on chamber size and closure time, this effect could majorly impact flux determination, switching from linear to nonlinear concentration development for example due to a reduced flux resulting from increased gas concentration (Rochette and Eriksen-Hamel, 2008).

The following steps and chamber design elements were implemented in order to circumvent or lessen the above-mentioned drawbacks. First of all, the large area and volume of the measurement chambers used in the present research increased the inertia of chamber headspace conditions and helped to increase flux accuracy by reducing nonlinearity in concentration changes (Rochette and Eriksen-Hamel, 2008; Pihlatie et al., 2013; Maier et al., 2022). While short chamber closure periods during CO_2 flux measurements resulted in close-to-linear concentration changes, partially nonlinear development of gas concentrations during the longer closure periods of CH_4 and N_2O flux measurements was accounted for by a selection scheme between linear and nonlinear regression types based on objective criteria (described in more detail in chapter 3.2.3.2). In addition, barometric pressure differences between the chamber inside and outside (Xu et al., 2006; Rochette and Eriksen-Hamel, 2008) were excluded by rubber stops which were not closed before the chamber rested in its final position and vents connecting the inside and outside air during measurements. Further, all measurement plots were accessible via boardwalks in order to reduce the risk of GHG emission resulting from subsurface shocks during handling. The chambers were fixed on the bases using a rubber seal and clips, the gas-tightness of this system and of all chambers was tested in the laboratory. Finally, fans permanently mixed the chamber air during measurement, in order to homogenize headspace gas concentrations (Drösler, 2005). For transparent chambers, where temperature and humidity increased quickly, additional quality criteria were implemented (as described in chapter 3.2.3.1).

1.6.3 Calculation of annual balances

In order to derive annual GHG balances, the gas exchange during the period between measurement campaigns needs to be estimated either by using simple interpolation between measured fluxes (as for CH_4 and N_2O, chapter 3.2.3.2) or by using functional dependencies of measured fluxes and continuously measured environmental parameters (as for CO_2, chapter 3.2.3.1). At bog ecosystems with a slowly developing vegetation, moderate seasonal and diurnal variability and, above all, an absence of regular cutting or fertilization events, biweekly measurements of CH_4 and N_2O fluxes and monthly measurements of CO_2 exchange has been widely accepted as adequate (Alm et al., 2007; Beyer and Höper, 2015; Leiber-Sauheitl et al., 2014; Günther et al., 2017).

1.7 Simulation of climate warming conditions

The effect of future climate warming on the GHG exchange at *Sphagnum* farming areas can be estimated in a warming experiment. Climate warming conditions can be simulated using active (infrared lamps or heating cables) or passive techniques such as open top chambers (OTC). The advantage of using OTCs is the easy and inexpensive handling, allowing the application in remote or inaccessible areas without power supply (Marion et al., 1997). Inside the transparent chambers, air and soil temperatures increase as a result of a reduced convective heat flow and reflection of infrared radiation. Using OTCs, Voigt et al. (2016) for example found that tundra peatland sites might shift from GHG sinks to sources, governed by increased R_{eco} and increased emissions of N_2O and CH_4. On the other hand, unwanted effects on further environmental parameters in addition to air and soil temperatures complicate a discussion of the warming effect. For example, OTCs have been reported to affect water availability and plant community structure (Dabros et al., 2010; Carlyle et al., 2011), as well as light intensity (Biasi et al., 2008). Further, the warming effect is tightly coupled to solar radiation, resulting in pronounced daily and seasonal fluctuation (Godfree et al., 2011). All these challenges have to be carefully considered when evaluating the warming effect of OTCs.

1.8 Pulse labelling: Tracing the fate of sequestered carbon

Complementing the results of the annual GHG balances of *Sphagnum* farming sites on highly decomposed peat and the results of the warming experiment, C stable isotopes enable a more detailed look at the path of sequestered C to plant biomass and subsequent C pools (Studer et al., 2014). Detailed knowledge on the contribution of *Sphagnum* and vascular plants to C allocation and storage could help to adapt management practices for *Sphagnum* farming sites and for restored bog peatlands in general. Moreover, knowledge on the quantities and longevities of different C pools might improve measures maximizing the GHG mitigation at these sites. This is even more important considering climate warming and the increasing risk of extreme events like droughts, which might strongly affect GHG exchange and C retention at *Sphagnum* farming sites.

Stable isotopes, atoms of the same chemical element but of different mass resulting from different numbers of neutrons, are ubiquitous in nature. Carbon has two stable isotopes with the isotope mass numbers 12 and 13 (Brand and Coplen, 2012), the former being dominant and constituting almost 99% of all C atoms. The heavier ^{13}C isotope has an additional neutron and represents about 1,1% of all natural C. On the one hand, certain isotopic ratios can be attributed to fractionation during biological (Farquhar et al., 1989) and abiotic processes (Amesbury et al., 2015). On the other hand, label material enriched in the less common heavier isotope can be used to visualize biological processes and label allocation from one pool to another (Studer et al., 2014). For example, Raghoebarsing et al. (2005) could demonstrate a rapid oxidation of CH_4 by endophytic methanotrophic bacteria in submerged *Sphagnum* plants exposing them to CH_4 enriched in ^{13}C.

Recent studies on C isotope ratios have already demonstrated the important role of *Sphagnum* in retaining sequestered C (Street et al., 2013) and the risk of a reduced C sink strength of *Sphagnum*-dominated ecosystems as a result of changing environmental drivers promoting graminoids (Woodin et al., 2009). Bryophytes exhibit a slower metabolism und C allocation compared to vascular plants (Ward et al., 2009) but might incorporate significantly more sequestered C in pools resistant to degradation (Trinder et al., 2008; Woodin et al., 2009). Again, results at *Sphagnum* farming sites might differ from those at pristine or restored sites, due to managed irrigation and the successional stage of plant community. In terms of climate protection, it is of interest how bryophyte and vascular plant species affect C allocation and storage.

1.9 Motivation, knowledge gaps and research questions

In this thesis, I address the GHG balance of *Sphagnum* farming on highly decomposed peat including different irrigation treatments and GHG measurements at an inundated irrigation polder. Accompanying GHG measurements at a near-natural bog area allow to compare patterns in GHG exchange between cultivated and near-natural areas and to determine the impact of harvesting *Sphagnum* donor material. I further complete the results of the GHG measurements by setting up simultaneous side experiments investigating the impact of warming on GHG exchange and vegetation development and the fate of sequestered atmospheric CO_2 in bryophyte and vascular plant biomass and subsequent C pools.

The innovative character of the presented research first of all lies in the study area. *Sphagnum* farming as a form of paludiculture at degraded bog areas is a newly emerging and highly dynamic ecosystem and studies investigating the GHG exchange at restored peatlands in general and paludiculture sites in particular are still scarce despite the promising benefits (Chimner et al., 2017; Zhao et al., 2024). In order to rewet and transform degraded peatland areas on a significant scale, large areas with disturbed hydrology and peat properties need to be included in management plans and might act quite differently in terms of biomass production and GHG exchange compared to pilot studies on paludiculture at less degraded sites. In comparison to previous research on *Sphagnum* farming in Northwestern Germany (Beyer and Höper, 2015; Günther et al., 2017) or Canada (Pouliot et al., 2015), the focus of this research is therefore put on large-scale *Sphagnum* farming on highly decomposed peat. Further, studies on multiannual measurements of the full production system, including open water surfaces and dams, are still missing (Daun et al., 2023). This way, the results of my research will enhance the understanding of successful peatland restoration and future *Sphagnum* farming attempts.

The high value of the presented results further lies in the measurement of the three major GHGs (CO_2, CH_4 and N_2O) and major environmental parameters over a time period of two complete measurement years, covering seasonal and interannual variation. Especially for N_2O, balances of peatland sites are scarce (Zhao et al., 2024). Moreover, it is the interdisciplinary approach of GHG measurements combined with vegetation surveys and soil science that encourages me. Finally, the topic of my research is of high current relevance. The results of the warming experiment and the detailed investigation of C allocation using stable isotopes will help to identify challenges in future research on *Sphagnum* farming and peatland restoration (Chimner et al., 2017; Loisel et al., 2021). Due to high GHG emissions of conventional drainage-based peatland use, a ‘business as usual’ is no longer an option for Central European peatlands and I am fascinated by the promising combination of restoring degraded peatland areas while being able to harvest a highly demanded product, a sustainable alternative to ongoing peat extraction.

This research scientifically evaluated the attempt of large-scale *Sphagnum* farming on former peat extraction sites in Northwestern Germany during the first years after establishment (Graf et al., 2017). Following from the knowledge gaps and challenges defined in the preceding chapters, I addressed the following research questions.

1st research question: What is the GHG balance of *Sphagnum* farming on highly decomposed peat?

In particular, I asked to what extent the high decomposition of the shallow residual peat layer affect vegetation development and the exchanges of CO_2, CH_4 and N_2O in comparison to previous studies on less decomposed peat. In order to be able to compare the results to other land use options, I aimed at determining total areal GHG balances, including emissions of the irrigation system, dams and an extractable biomass. I tested drip irrigation, ditch irrigation and a combination of ditch irrigation and previous multiannual inundation in terms of optimal *Sphagnum* growth and GHG mitigation, as well as different *Sphagnum* species (*Sphagnum palustre*, *Sphagnum papillosum* and a mixture of *Sphagnum* species from a neighboring near-natural area). Further, I quantified the impact of harvesting donor material on vegetation development and GHG exchange at this near-natural area.

In addition to the highly decomposed peat at former peat extraction sites, climate warming could have drastic impacts on *Sphagnum* farming sites. Thus, I asked the

2nd research question: In what way do simulated climate warming conditions affect vegetation development and GHG exchange at *Sphagnum* farming sites?

Temperature is an important driver of GHG exchange. However, it is still under debate in what way climate warming will affect GHG balances of peatland ecosystems. Complementing the results of the GHG measurements, I therefore conducted a warming experiment to explore whether OTCs successfully increase air and soil temperatures and in what way vegetation and the exchanges of CO_2, CH_4 and N_2O will be influenced by warming. In particular, the warming experiment was set up to investigate differences in the responses of the near-natural and *Sphagnum* farming area, which might be more resilient due to irrigation and adjustable water levels on the one hand or more sensitive due to a missing functioning acrotelm on the other hand.

The results of the warming experiment will enable a glimpse into the future, a more detailed view on the C cycle at *Sphagnum* farming sites will be gained using stable isotopes. Consequently, I asked the

3rd research question: What is the fate of sequestered atmospheric carbon allocated to plant biomass and subsequent pools at a *Sphagnum* farming site?

For the evaluation of *Sphagnum* farming as climate protection measure it is of further interest, adding to the overall GHG balances, how much of the sequestered atmospheric C is stored in the long term or lost as DOC or as emitted CO_2 and CH_4. Using a pulse labelling approach, I addressed the short-term C allocation within the first three weeks after label addition, as well as the medium-term storage of sequestered C after 140 days at a *Sphagnum* farming site in its establishment phase. In particular, I aimed at elucidating the allocation to plant and soil microbial biomass and to DOC and dissolved and emitted CO_2 and CH_4, as well as the contribution of *Sphagnum* and *Molinia caerulea* as dominant vascular plant. Further, investigating warmed and control plots allowed me to ask to what extent simulated climate warming conditions affect C sequestration and allocation.

As not all measurement sites and methods are used in each of the papers, the research project, the study areas and the applied methods are briefly summarized and visualized before answering the three research questions in detail on the basis of three peer-reviewed publications (bibliography and authors' contributions on page X). These publications were adapted to the format of this thesis without changing the original content.

2 STUDY AREAS AND APPLIED METHODS

2.1 Research project and study areas

The presented research is part of a joint research project of the substrate manufacturer Klasmann-Deilmann GmbH in Geeste, the Institute of Environmental Planning at the Leibniz University Hannover and the Thünen Institute of Climate-Smart Agriculture in Braunschweig. The former was responsible for the preparation and maintenance of the two *Sphagnum* farming areas (project title 'Großflächige Torfmooskultivierung in Niedersachsen als Folgenutzung nach Schwarztorf Abbau und ihr Potenzial zur nachhaltigen Produktion eines Substratausgangsstoffes als Torfersatz'). The Institute of Environmental Planning and the Thünen Institute of Climate-Smart Agriculture investigated flora and fauna and the GHG exchange, respectively. Funding was provided by the Lower Saxony Ministry for Nutrition, Agriculture and Consumer Protection (project title 'Großflächige Torfmooskultivierung in Niedersachsen als Folgenutzung nach Schwarztorf-Abbau und ihr Potenzial für Klimaschutz und Biodiversität') and the German Federal Environmental Foundation (project title 'Auswirkungen großflächiger Torfmooskultivierung nach Schwarztorf-Abbau auf Biodiversität und Treibhausgasfreisetzung').

Balances of GHG exchange were determined at three different study areas in Northwestern Germany (Fig. 2.1). All are located in close vicinity to each other in the Bourtanger Moor-Bargerveen International Nature Park in the communities of Twist and Geeste.

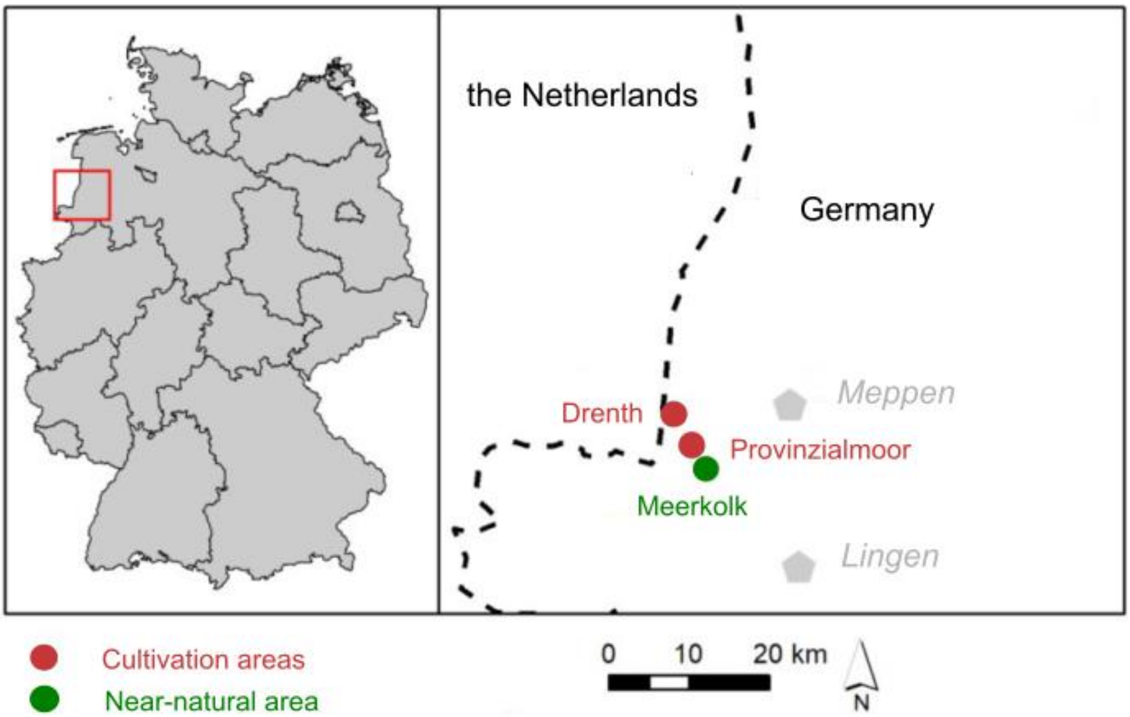

Fig. 2.1: Study areas in Northwestern Germany. The areas are located close to the cities of Meppen and Lingen (Graf et al., 2017, modified).

The Bourtanger Moor once was one of the largest contiguous bog areas in Central Europe (Casparie, 1993), which has been almost completely drained. Beginning with small-scale peat cutting for fuel in the 17th century (Casparie, 1993), draining and colonizing of larger areas continued and culminated in transforming the complete landscape from 1950 onwards as a result of the national 'Emslandplan', funding steam-powered deep ploughing and land reclamation to improve the living standard and food situation of the poor population (Mayhew, 1969). Only small remains could be protected. Today, the area is characterized in large parts by dairy farming and the cultivation of maize, as well as by ongoing peat extraction and rewetted former peat extraction sites. The climate in this region can be described as oceanic. It is influenced by the vicinity to the North Sea, resulting in year-round high humidity, warm summers and moderate winters. Average annual precipitation and temperature are 791 mm and 9.8 °C, respectively (1971–2000, Lingen, German Climate Service).

One study area was the near-natural bog area ‘Meerkolk’, a silting former bog lake with an area of about four hectare and a depth of almost four meters. A dense mat of peat mosses (mainly *Sphagnum papillosum*) and vascular plants (mainly *Rhynchospora alba*, *Vaccinium oxycoccos*, *Erica tetralix*, *Drosera rotundifolia*, *Molinia caerulea*) was floating on water containing dead plant material with its grade of decomposition increasing with depth. As a result, the vegetation surface was able to follow the water level throughout the experiment (Fig. 3.2). This area was never subjected to peat extraction and therefore towered above the surrounding area like a bathtub encircled by dams. It is denoted as near-natural, as it is nevertheless affected by anthropogenic influence. In addition to its artificial hydrological situation, it is surrounded by agriculture and exposed to increased atmospheric deposition of nitrogen (25 kg N ha^{-1} yr^{-1}; Hurkuck et al., 2016) which affects plant species composition and might even reduce *Sphagnum* growth (Berendse et al., 2001).

The other two study areas were former peat extraction areas, ‘Provinzialmoor’ and ‘Drenth’, differing in their irrigation system and land use history (Fig. 2.2). At both areas, peat was industrially extracted to a remaining peat thickness of about half a meter in theory. Practically, peat depth ranged from 0.32 m to 1.00 m (Grobe et al., 2021). *Sphagnum* farming was established according to the moss layer transfer technique (Quinty and Rochefort, 2003; Graf et al., 2017) introduced in chapter 1.3.

Provinzialmoor (net cultivation area 2.3 ha) was inundated as a shallow polder for several years following the termination of peat extraction in 2008 and irrigated by shallow ditches (about 0.3 m deep and 0.5 m wide) connected to surrounding polders saving excess winter precipitation for dry summer months. However, still active drainage pipes were not discovered until the end of the experiment, contributing to prolonged periods of low water levels.

In contrast, Drenth was prepared for *Sphagnum* farming (net cultivation area 2.5 ha) directly after the termination of peat extraction and was irrigated in parts by shallow ditches and in parts by drip irrigation using perforated hoses at the peat surface. Here, irrigation water was withdrawn from a small pond, where groundwater was added in dry summer months. However, problems during the initial phase of site establishment, such as the displacement of *Sphagnum* fragments by ice, a short-term algae infestation and temporary insufficient inundation led to poor growth rates at this area.

At both areas, excess irrigation water was channeled out to prevent inundation. Amongst the *Sphagnum* plants, scattered vascular plants (mainly *Molinia caerulea*, *Erica tetralix*, *Rhynchospora alba*, as well as *Eriophorum angustifolium* and *Eriophorum vaginatum*) grew in different intensities.

Fig. 2.2: Aerial photography of the cultivation areas Provinzialmoor (left) and Drenth (right). While the former was surrounded by rewetted polders, Drenth was an oasis in the midst of ongoing peat extraction (photos by Klasmann-Deilmann GmbH).

In close distance to the measurement sites, vertical soil profiles were dug (Fig. 2.3) and described following the German Manual of Soil Mapping (Ad-hoc-AG Boden, 2005) and the World Reference Base for Soil Resources (IUSS Working Group WRB, 2015). Meerkolk was classified as 'Normhochmoor' (Ad-hoc-AG Boden, 2005) or Ombric Fibric Histosol (IUSS Working Group WRB, 2015). The upper 0.53 m were marginally to weakly decomposed (H1–H3; von Post, 1924) *Sphagnum* peat with strong and very strong rooting, the remaining deeper horizons were highly decomposed (H6–H9) with a high water content and a low bulk density (not determined). The upper 0.18 m were periodically water-saturated (hHw), the soil horizons below permanently (hHr). The concentration of total organic carbon (TOC) increased from 45.9% in the upper horizon to 56.9% at the bottom, total nitrogen (TN) ranged between 0.7% and 1.5% and pH ranged between 3.2 and 4.1.

Both cultivation areas were classified as 'Normerdhochmoor' (Ad-hoc-AG Boden, 2005) or Ombric Hemic Histosols (IUSS Working Group WRB, 2015). Total peat thickness was 0.95 m at the northern part of Provinzialmoor, 0.80 m at the southern part and 0.43 m at Drenth. At Provinzialmoor and Drenth, two soil profiles each were described. At the northern part (sites P-PAP and P-PAL) and southern part (sites P-MIX and P-MIX-W) at Provinzialmoor, highly decomposed (H6–H8) sedge peat (nHr) was overlain by moderately to highly decomposed *Sphagnum* peat with *Eriophorum* (H5–H7). The upper 0.33 m and 0.25 m, respectively, were periodically water-saturated (hHw), followed by a reduced peat horizon (hHr) which was slightly larger in the northern part. Strong rooting was identified in the upper horizon of the southern part, all other horizons showed weak and very weak rooting. Total organic carbon increased with depth from 51.9% to 58.2%, TN ranged between 0.8% and 1.8% and pH ranged between 3.0 and 3.5.

Similar to Provinzialmoor, a moderately to highly decomposed (H5–H7) sedge peat horizon (nHr) was overlain by moderately to highly decomposed *Sphagnum* peat with *Eriophorum* (H5–H8) at the eastern part (site D-DITCH) and western part (sites D-DRIP and D-DRIP-W) at Drenth. The upper 0.15 m and 0.16 m were highly decomposed (H8), affected by peat extraction and site preparation, followed by another 0.12 m and 0.14 m of moderately to highly decomposed (H5–H7) periodically water-saturated peat (hHw). Rooting was very weak to zero. Total organic carbon increased from 50.2% to 59.9%, TN ranged between 1.1% and 1.7% and pH ranged between 2.9 and 3.4.

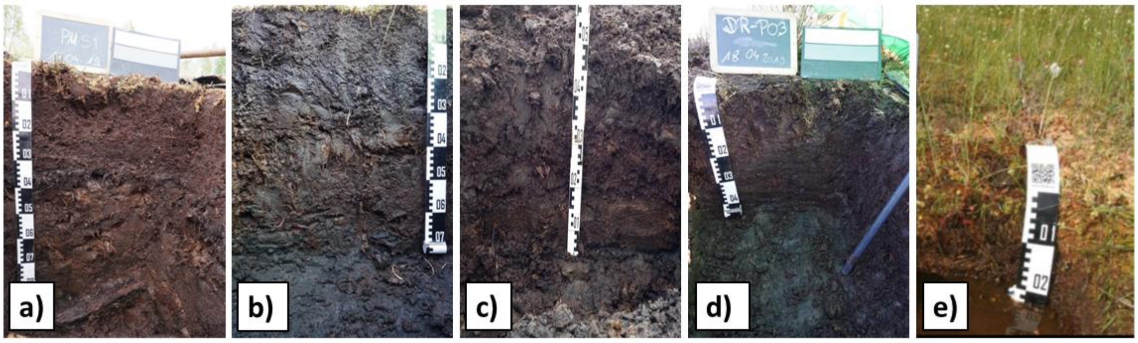

Fig. 2.3: Soil profiles at the study areas. Profiles were dug at a) the northern and b) the southern part of Provinzialmoor, the c) eastern und d) western part of Drenth and e) at Meerkolk.

At the three study areas, eleven study sites, each consisting of three replicate measurement plots were installed (Table 2.1, Fig. 2.4). It is important to note that different parts of the cultivation areas were established in different years and seasons.

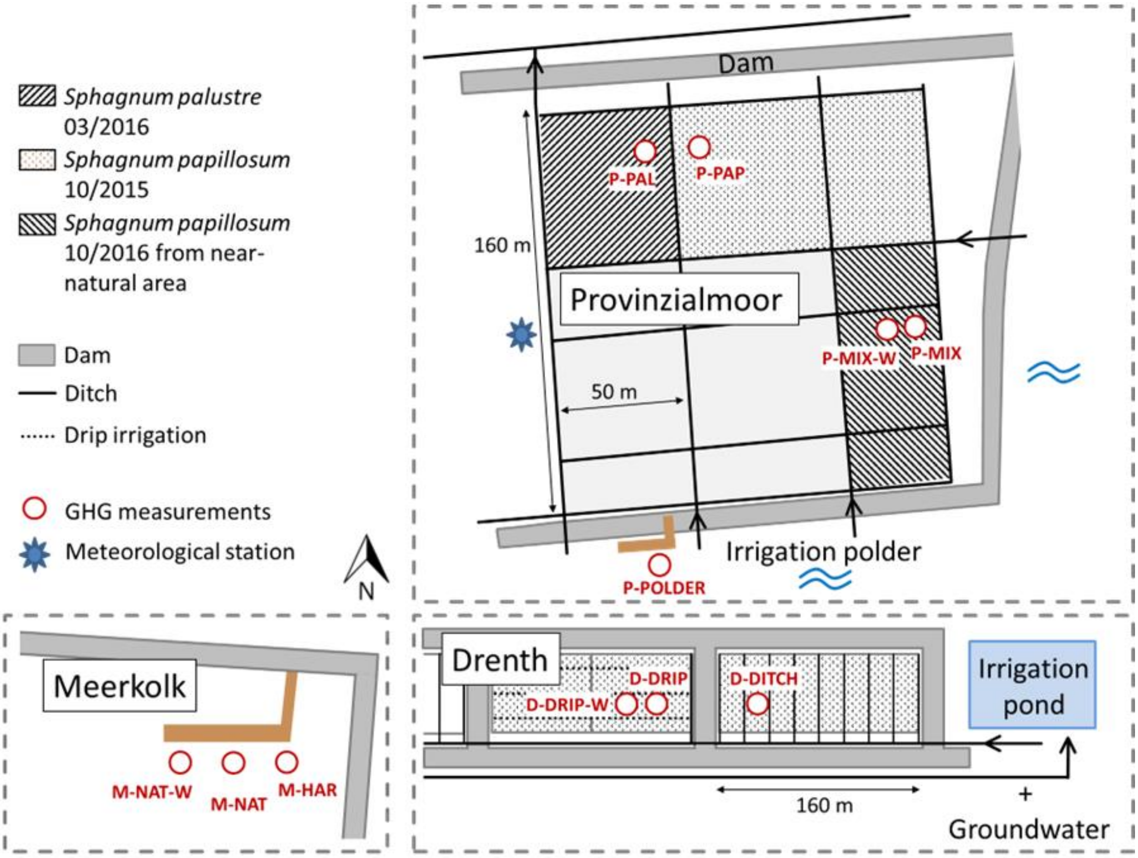

Fig. 2.4: Study areas and sites (Graf et al., 2017, modified). The cultivation areas Provinzialmoor and Drenth were established at different dates using different *Sphagnum* species. Study sites are a reference (M-NAT), warmed (M-NAT-W) and harvested (M-HAR) site at Meerkolk, a ditch irrigation (D-DITCH), drip irrigation (D-DRIP) and warmed (D-DRIP-W) site at Drenth and a reference (P-MIX) and warmed (P-MIX-W) site at Provinzialmoor inoculated with *Sphagnum* biomass from Meerkolk, as well as sites inoculated with *Sphagnum palustre* (P-PAL) and *Sphagnum papillosum* (P-PAP) and the polder site (P-POLDER).

At Meerkolk, *Sphagnum* biomass (mainly *Sphagnum papillosum*) was harvested close to the measurement sites up to a depth of 5 cm and used as an inoculum for the establishment of sites P-MIX and P-MIX-W at Provinzialmoor. This was simulated at the measurement plots of site M-HAR by manually cutting and removing the upper 5 cm of vegetation (Fig. 2.5).

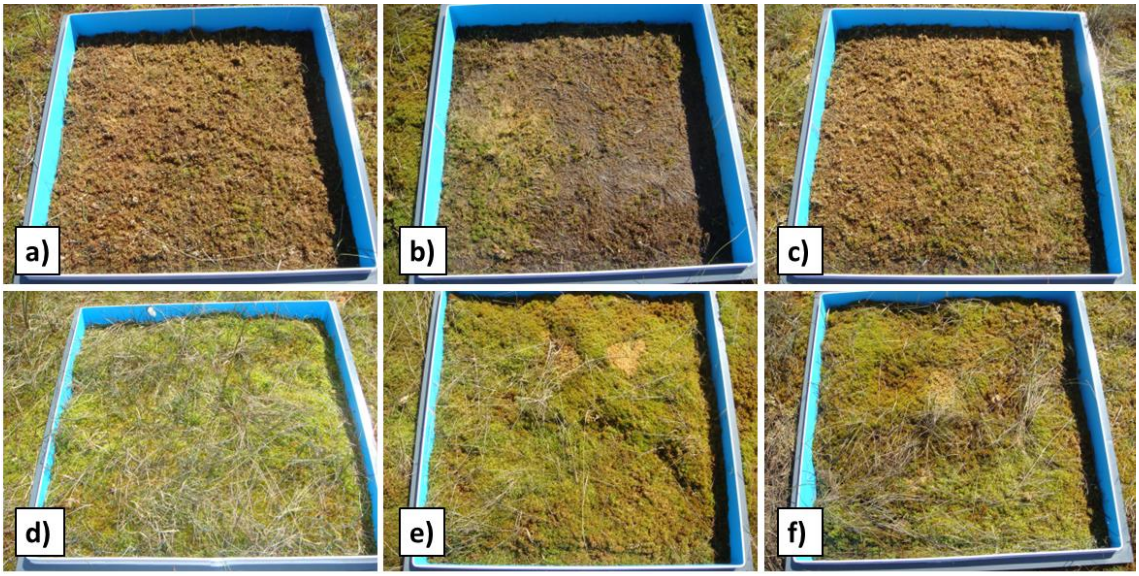

Fig. 2.5: Harvested (M-HAR; a-c) and control (M-NAT; d-f) plots at the near-natural area. The photos were taken one month after cutting. Plot M-HAR 2 (b) did not fully recover until the end of the experiment.

At the Provinzialmoor area, different *Sphagnum* species (*Sphagnum papillosum*, *Sphagnum palustre* and *Sphagnum* biomass from Meerkolk) were investigated in terms of vegetation development and GHG exchange. In addition, the GHG exchange at an adjacent irrigation polder was determined. In Drenth, a drip irrigation site was compared against a ditch irrigation site. At all three study areas, passively warmed sites were installed to investigate the impact of climate warming conditions on vegetation development and GHG exchange.

Table 2.1: Study areas and sites. WTD refers to the mean (± standard deviation) water table depth (m) over the whole study period.

Area	Site	WTD	Publication	Treatment
Meerkolk	M-NAT	-0.05 ± 0.05	1, 2	near-natural, control
	M-NAT-W	-0.09 ± 0.05	1, 2	near-natural, warmed
	M-HAR	-0.01 ± 0.05	1	near-natural, harvested
Provinzialmoor	P-MIX	-0.19 ± 0.17	1, 2, 3	*Sphagnum* farming, ditch irrigation and previous inundation, mix of hummock *Sphagnum* species from Meerkolk, control
	P-MIX-W	-0.18 ± 0.21	1, 2, 3	*Sphagnum* farming, ditch irrigation and previous inundation, mix of hummock *Sphagnum* species from Meerkolk, warmed
	P-PAL	-0.18 ± 0.20	1	*Sphagnum* farming, ditch irrigation and previous inundation, *Sphagnum palustre*
	P-PAP	-0.17 ± 0.20	1	*Sphagnum* farming, ditch irrigation and previous inundation, *Sphagnum papillosum*
	P-POLDER	0.18 ± 0.23	1	irrigation polder
Drenth	D-DITCH	-0.13 ± 0.13	1	*Sphagnum* farming, ditch irrigation
	D-DRIP	-0.10 ± 0.12	1, 2	*Sphagnum* farming, drip irrigation, control
	D-DRIP-W	-0.12 ± 0.14	1, 2	*Sphagnum* farming, drip irrigation, warmed

2.2 Greenhouse gas measurements

Over a period of two complete measurement years, GHGs were measured using manually operated chambers (0.75 m * 0.75 m * 0.50 m) which were placed onto permanently installed bases inserting about 0.10 m into the soil. Details on flux measurements and calculations can be found in chapter 3.2.3.

2.2.1 Carbon dioxide

Fluxes of CO_2 were measured in monthly campaigns, covering the whole diurnal range of soil temperature and PAR from one hour before sunrise until afternoon (Leiber-Sauheitl et al., 2014). Since the interpolation of annual balances is based on the environmental parameter obtained during these campaigns, the timing of the campaigns directly affects the balances (Leiber-Sauheitl et al., 2014). Therefore, days with ranges of soil temperature and PAR typical for the respective season were chosen where applicable.

Concentrations of CO_2 in the chamber headspace air were determined on-site (Fig. 2.6) using a portable measurement device equipped with an infrared gas analyzer (LI-820, LI-COR, Lincoln, Nebraska, USA) in a resolution of one measurement per second. Transparent and opaque measurement chambers were used for NEE and R_{eco} measurements, respectively, with closure times of 120 and 180 seconds. At least four NEE and four R_{eco} fluxes were recorded per plot and campaign day, in total 7621 CO_2 fluxes in 101 measurement campaigns.

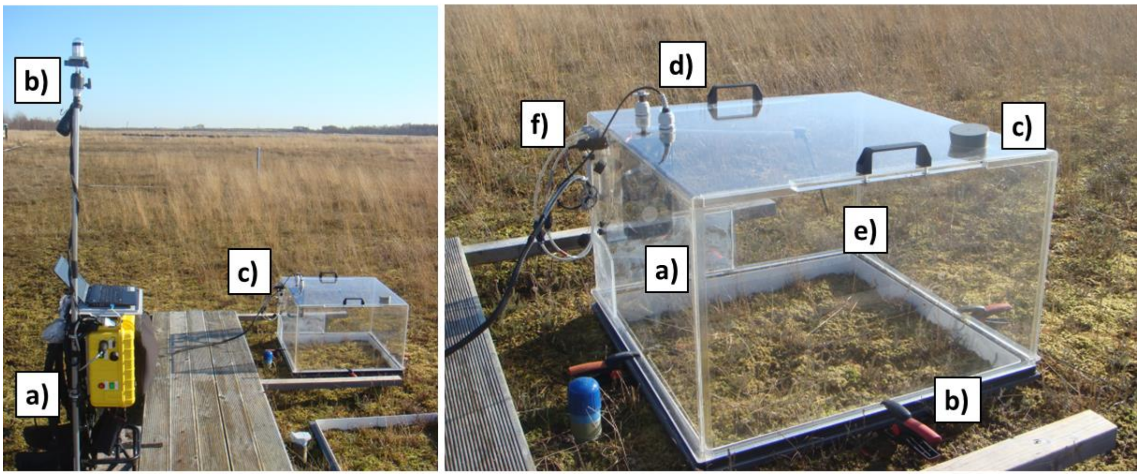

Fig. 2.6: Measurement of net ecosystem exchange (NEE) using a portable infrared gas analyzer and transparent measurement chambers. Left: a) backpack with infrared gas analyzer, power supply and data logger, b) PAR sensor, c) connection to the measurement chamber. Right: a) fans mixing the headspace air, b) clips adjusting the chamber gas-tightly on the base via a rubber seal, c) rubber stops were not closed until the chamber was in its final position, d) temperature and humidity were continuously recorded during measurement, e) air was pumped into the measurement system from the mixed headspace, f) the chamber headspace air was connected to the measurement system via an inlet and an outlet, while a second blind outlet vent enabled pressure balance.

2.2.2 Methane and nitrous oxide

During each fortnightly measurement campaign, five consecutive headspace air samples were taken from opaque chambers (Fig. 2.7) in intervals of 20 minutes (t0, t20, t40, t60, t80). Concentrations of CO_2, CH_4 and N_2O were subsequently measured in the laboratory using a gas chromatograph (Shimadzu, Kyoto, Japan) equipped with an electron capture detector (ECD) for analyzing CO_2 and N_2O and a flame ionization detector (FID) for analyzing CH_4. In total, 1599 valid CH_4 fluxes and the same number of N_2O fluxes were determined, 451 and 34 of them using nonlinear regression.

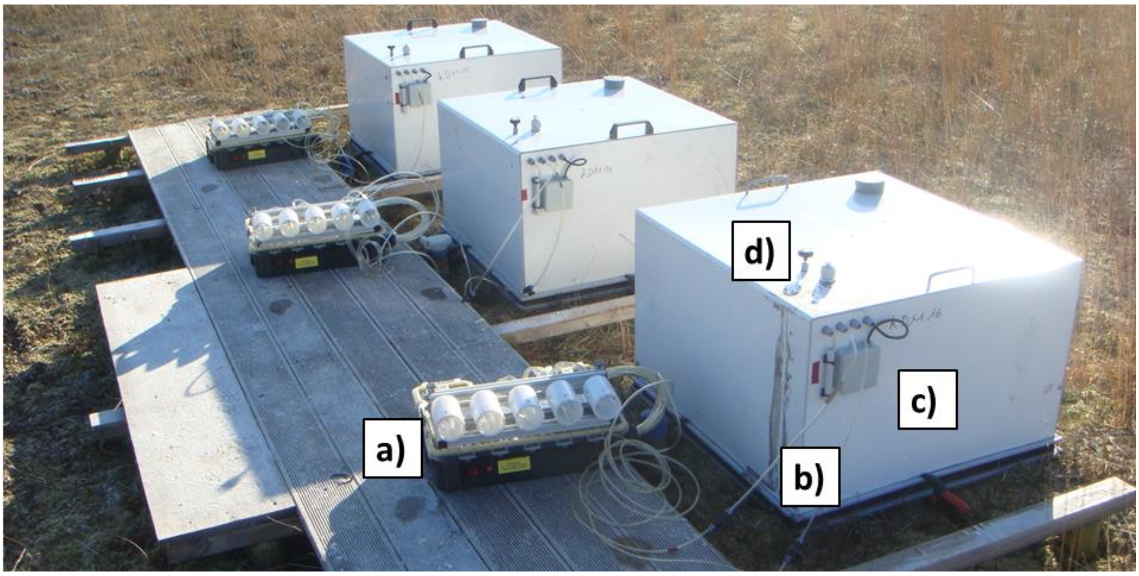

Fig. 2.7: Sampling of methane (CH_4) and nitrous oxide (N_2O). Sampling was conducted using a) semi-automatic measurement devices equipped with five vials, b) inlet, outlet and vent enabling pressure balance, c) power supply for fans, d) the air temperature inside the chambers was recorded at every time interval.

A special challenge were the measurements at the near-natural area and at the irrigation polder at Provinzialmoor. At the former, four-meter-long piles fixed the boardwalk to the bottom of the bog lake. At the latter, buoyant bases following the water surface (fluctuation > 0.70 m) were fixed to the boardwalk via poles during measurement and chambers were placed at u-formed water-filled crowns for gas-tight closure (Fig. 2.8).

Fig. 2.8: Buoyant base and measurement chamber at the polder site at Provinzialmoor.

2.2.3 Environmental parameters

In addition to GHG fluxes, a whole set of environmental parameters was determined (Fig. 2.9). Soil temperatures were recorded at each plot in half-hourly intervals, water table depths (WTD) at every site. At the warmed and control sites, air temperature, humidity and soil moisture were additionally measured. Water was sampled biweekly at each measurement site for the determination of dissolved organic carbon (DOC) contents and concentrations of cations and anions. A meteorological station at Provinzialmoor recorded air and soil temperatures, photosynthetically active radiation, humidity, wind speed and precipitation in half-hourly intervals. In spring and autumn, covers of bryophyte and vascular plant species were estimated using the Londo scale (1976) and mean heights of the peat moss lawn was measured in each plot.

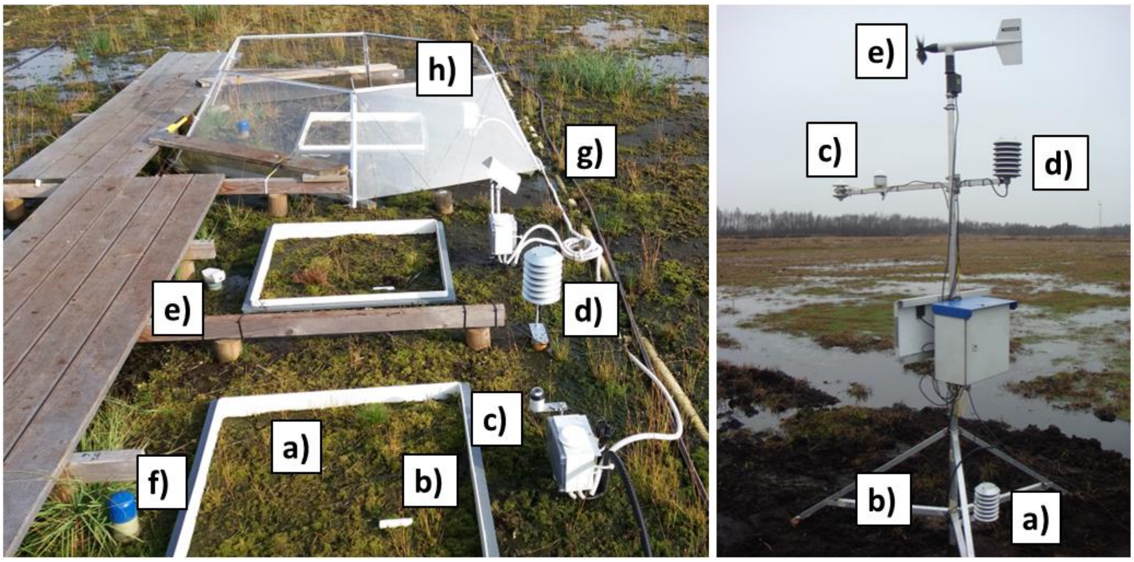

Fig. 2.9: Measured environmental parameters. Data were recorded at the measurement plots (left) for a) soil temperature, b) soil moisture, c) photosynthetically active radiation, d) air temperature and humidity, e) water table depth. Dip wells enabled f) pore water sampling. The respective site was irrigated via g) drip irrigation, one plot was passively warmed using a h) open top chamber. A meteorological station at Provinzialmoor (right) recorded a) air temperature and humidity close to peat surface, b) soil temperature, photosynthetically active radiation, d) air temperature and humidity (2 m), e) wind speed and wind direction.

2.2.4 Site-specific and areal greenhouse gas balances

The contribution of CH_4 and N_2O to site-specific GHG balances [t CO_2-eq. ha^{-1} yr^{-1}] was calculated given their GWPs of 28 and 265 CO_2 equivalents over a timeframe of 100 years (Myhre et al., 2013; equation 2.1). Following the atmospheric sign convention, a negative flux represents a flux from atmosphere to soil (Chapin et al., 2006).

$$GHG\ balance\ (t\ CO_2 - eq.ha^{-1}yr^{-1}) = NEE + 28CH_4 + 265N_2O \qquad [2.1]$$

Total areal GHG balances were estimated including an extractable biomass and emissions of the irrigation system and dams (equation 2.2). Surface areas of dams, irrigation polders and ditches were estimated using aerial images. This way, the contribution of this infrastructure to the total area of the cultivation sites could be determined and compared between the investigated irrigation systems.

$$Areal\ GHG\ balance = GHG_{bal} * a_c + GHG_{polder} * a_w + GHG_{dam} * a_d + harvest \qquad [2.2]$$

Note that GHG_{bal} are the mean GHG balances per irrigation treatment (including both measurement years), a_c is the share of the cultivation area (%), GHG_{polder} is the mean GHG balance at site P-POLDER, a_w is the share of the open water surfaces, GHG_{dam} is the GHG emission of dams (value for peat extraction sites published by Tiemeyer et al., 2020), a_d is the share of dam surfaces and harvest is the estimated extractable biomass (details in chapter 3.2.3.3).

2.3 Warming experiment using open top chambers

At each study area, three replicate plots were equipped with open top chambers (OTC), permanently installed hexagonal enclosures made from transparent polycarbonate. As stressed in chapter 1.7, OTCs possibly affect other environmental parameters in addition to temperature alone. In order to minimize these unwanted concomitant effects, large dimensions were chosen for the OTCs and the measurement plots were positioned right in the center of the upper aperture (Fig. A.1). In addition, water availability and vegetation development were closely monitored and the light reduction inside the OTCs was accounted for during the parametrization of GPP response functions (described in detail in the appendix).

2.4 Carbon isotope measurements and calculations

Samples taken during the pulse labelling experiment were analyzed for their carbon isotopic ratio using isotope ratio mass spectrometry (IRMS). In brief, the sample material is combusted to gaseous products that are passed on to a mass spectrometer using magnets to precisely determine isotope contents. The measured isotopic ratios were expressed using the isotope delta (δ) notation, relative to a standard ratio for better readability and comparability (Brand and Coplen, 2012). The difference between the isotopic ratio in the sample and the standard is divided by the standard ratio and multiplied by 1000, expressing the difference in per mill (‰). The used standard for C isotopic ratios is the Vienna Pee Dee Belemnite (V-PDB, $^{13}C/^{12}C = 0.0111802$). For mass balance calculation, delta values were converted to atom% abundances and the excess atom fraction of each C pool at each campaign day was calculated as the difference between the atom% value of a sample and the respective pre-labelling value. This value then allowed a determination of the mass of recovered label, by multiplying it with the C pool size or flux (Trinder et al., 2008).

3 GREENHOUSE GAS BALANCE OF *SPHAGNUM* FARMING ON HIGHLY DECOMPOSED PEAT AT FORMER PEAT EXTRACTION SITES

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HIGHLIGHTS

Sphagnum farming is possible on highly decomposed peat.

GHG exchange was mainly affected by water table depth and vegetation development.

CH_4 and N_2O may influence GHG balances of inadequately managed sites.

ABSTRACT

For two years, we quantified the exchange of carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) at two different large-scale *Sphagnum* farming sites. At both, peat extraction left a shallow layer of highly decomposed peat and low hydraulic conductivities. One site was characterized by preceding multi-annual inundation and irrigated by ditches, while the other one was inoculated directly after peat extraction and irrigated by ditches and drip irrigation. Further, GHG emissions from an irrigation polder and the effect of harvesting *Sphagnum* donor material at a near-natural reference site were determined. GHG mitigation potentials lag behind the results of less decomposed sites, although our results were also affected by the extraordinary hot and dry summer 2018. CO_2 exchanges ranged between -0.6 and 2.2 t CO_2-C ha^{-1} yr^{-1} and were mainly influenced by low water table depths. CH_4 emissions were low with the exception of plots with higher *Eriophorum* covers, while fluctuating water tables and poorly developing plant covers led to considerable N_2O emissions at the ditch irrigation site. The removal of the upper vegetation at the near-natural site resulted in increased CH_4 emissions and, on average, lowered CO_2 emissions. Overall, best plant growth and lowest GHG emissions were measured at the previously inundated site. At the other site, drip irrigation provided more favorable conditions than ditch irrigation. The size of the area needed for water management (ditches, polders) strongly affected the areal GHG balances. We conclude that *Sphagnum* farming on highly decomposed peat is possible but requires elaborate water management.

3.1 Introduction

Drained and intensively used peatlands emit large amounts of greenhouse gases (GHG) into the atmosphere (Waddington and Price, 2000; Tiemeyer et al., 2020). Rewetting these areas as soon as possible is the most effective measure to mitigate climate warming in the long term (Günther et al., 2020; Wilson et al., 2016b). However, raising water table depths (WTD) hinders conventional land use. Ecological and economic goals could be combined by implementing the concept of paludiculture, that is, the production of biomass under wet and peat preserving conditions using suitable wetland crops (Wichtmann et al., 2016). Under nutrient-poor and acidic conditions, that is, on bog peat, the cultivation of peat mosses (*Sphagnum* farming) is the most promising land use option (Gaudig et al., 2018). Harvested moss fragments can be spread in degraded peatlands in order to accelerate vegetation restoration (Quinty and Rochefort, 2003) or *Sphagnum* fibres can be used as a sustainable resource in horticultural substrates (Emmel, 2008), substituting fossil weakly decomposed peat and this way relieving the pressure of ongoing peat extraction on pristine peatlands.

Besides providing habitat for endangered flora (Gaudig and Krebs, 2016) and fauna (Muster et al., 2015; Zoch and Reich, 2020), rewetting, for example, for *Sphagnum* farming has major impact on the GHG exchange of the cultivation sites. If water tables can be kept close to ground surface, carbon dioxide (CO_2) emissions can be reduced, stopped or even reversed (Wilson et al., 2016a). Previous studies in northwest Germany hint towards a rapid recovery of *Sphagnum* farming sites as sinks of atmospheric carbon (Beyer and Höper, 2015; Günther et al., 2017). On the other hand, quasi-natural hydrological conditions favor the production of methane (CH_4). On average, CH_4 emissions of classically rewetted sites are comparable to those of natural sites (Wilson et al., 2016a). CH_4 emissions from *Sphagnum* cultivation sites have so far been found to be very low (Beyer and Höper, 2015; Günther et al., 2017) due to the strictly controlled water tables and the low abundance of aerenchymous species. Drained peatlands can release relevant amounts of nitrous oxide (N_2O) (Regina et al., 1996; Tiemeyer et al., 2020), whereas the N_2O emissions of *Sphagnum* farming field sites are close to zero (Beyer and Höper, 2015; Günther et al., 2017).

In this study, the cultivation sites were established following the moss layer transfer technique (Quinty and Rochefort, 2003). Data on the effect of harvesting donor material are scarce, but need to be considered when assessing the GHG balance of *Sphagnum* cultivation. It is suggested that harvested sites recover quickly (Silvan et al., 2017; Krebs et al., 2018; Guêné-Nanchen et al., 2019) and might return to their pre-disturbance carbon balance naturally within a few years (Murray et al., 2017), but further research is of special importance in areas such as Germany where near-natural sites are extremely rare.

Peat mosses possess no roots and rely on precipitation and capillary water supply. As moisture controls *Sphagnum* photosynthesis and productivity (McNeil and Waddington, 2003), the adjustment of a high and stable water table is the key factor of a successful cultivation of peat mosses (Pouliot et al., 2015). Previous *Sphagnum* farming trials have been relatively small in scale (0.10 to 1.1 ha; Brown et al., 2017; Beyer and Höper, 2015; Günther et al., 2017), where WTDs are relatively easy to control. Thus, there is still a gap in knowledge on which irrigation technique is most suitable in large-scale peat moss cultivation regarding optimum growth of mosses and maximum GHG mitigation. The most common techniques are subsurface irrigation (Brown et al., 2017; Gaudig et al., 2017) and irrigation ditches (Beyer and Höper, 2015; Brown et al., 2017; Günther et al., 2017), while drip irrigation has not yet been tested.

In contrast to previous studies, this study is the first to explore the feasibility and the GHG exchange of large-scale *Sphagnum* farming on shallow, highly decomposed peat remaining after industrial peat extraction. The high degree of decomposition of the peat imposes new challenges to large-scale *Sphagnum* farming as the concomitant low porosity and hydraulic conductivity (Liu and Lennartz, 2019) cause strong fluctuations of WTDs and poor water supply from ditches. This raises the question whether highly decomposed peat can support *Sphagnum* farming.

A further challenge is the irrigation water: surface and groundwater might be unsuitable due to high nutrient, electric conductivity (EC) and pH levels, while rainwater storage requires space. 'Classical' bog rewetting after peat extraction is frequently done by creating water-filled polders separated by dams, which are to undergo succession towards peatland vegetation (Blankenburg, 2004). Such polders could also be used to store and deliver water to *Sphagnum* cultivation sites, but *Sphagnum* farming on highly decomposed peat need to be included into an areal GHG balance of a *Sphagnum* cultivation system. Such data are important as high emissions have been reported for inundated fens (Franz et al., 2016; Hahn et al., 2015).

Vascular plants emerge even in strongly controlled *Sphagnum* farming systems. They could, on the one hand, compete with *Sphagnum* for resources and are unwanted in the produced substrate. On the other hand, vascular 'shelter' plants have been shown to be beneficial for *Sphagnum* development by creating microhabitats with higher soil moisture and protection from excess solar radiation and wind (McNeil and Waddington, 2003; McCarter and Price, 2015). Further, species composition will influence the GHG exchange, for example, by increasing CH_4 emissions via aerenchymous tissues (Gray et al., 2013).

Consequently, the objective of this study is to determine areal GHG balances of large-scale *Sphagnum* farming on a highly decomposed peat soil including emissions from the irrigation system, dams (using literature data) and projected harvest in comparison with a near-natural bog. Special emphasis is put on the influence of different irrigation techniques (ditch irrigation, drip irrigation and a combination of ditch irrigation and preceding multi-annual inundation) and on the effect of harvesting *Sphagnum* donor material at the near-natural site.

3.2 Materials and methods

3.2.1 Study sites and implementation of the *Sphagnum* cultivation areas

We measured GHGs at two *Sphagnum* cultivation areas ('Provinzialmoor', 52°40' N, 07°06' E and 'Drenth', 52°41' N, 07°05' E) and a near-natural peat bog ('Meerkolk', 52°38' N, 07°08' E) from March 2017 to March 2019 (Fig. 3.1). All sites are situated approximately 20 km northwest of Lingen, Lower Saxony, Germany. The climate is oceanic with an average annual precipitation of 791 mm and an average annual temperature of 9.8 °C (1971–2000, Lingen, German Weather Service).

Meerkolk, a last remainder of a once vast peatland complex, is a former bog pool characterized by partially floating peat moss and cotton grass mats with a peat thickness of about 350 cm. The upper 53 cm are weakly decomposed, and the lower part is highly decomposed with a high water content (Table 3.1). The site can be classified as an Ombric Fibric Histosol (IUSS Working Group WRB, 2015). The dominating plant species are *Sphagnum papillosum*, *Sphagnum pulchrum*, *Sphagnum cuspidatum*, *Rhynchospora alba*, *Molinia caerulea*, *Vaccinium oxycoccos*, *Erica tetralix*, *Drosera rotundifolia* and *Eriophorum angustifolium*. Close to the measurement plots, the upper 5 cm of *Sphagnum* vegetation was harvested and used for the inoculation of parts of Provinzialmoor (P-MIX). As the area is – as nearly all potential donor sites in Germany – strictly protected, mosses were selectively manually harvested. Meerkolk is hereafter referred to as near-natural reference site. GHGs were measured at a control site (M-NAT) and at a harvest site where the upper 5 cm of vegetation were removed in April 2017 (M-HAR).

Both Provinzialmoor and Drenth are former sites of industrial peat extraction with remaining peat thicknesses of about 90 cm and 45 cm, respectively. Both sites are Ombric Hemic Histosols. The lower part of the profile is moderately decomposed fen peat overlying a relictic gley and the upper part moderately to highly decomposed bog peat. The major difference between the two areas is that

Provinzialmoor has been rewetted in 2008 after the termination of peat extraction as a system of large (~ 1.6 to 4.2 ha) shallow polders, while Drenth is a narrow strip of seven polders installed in 2015 directly after terminating peat extraction without any previous rewetting. Thus, Drenth is not surrounded by water bodies and rewetted peatlands but by ongoing peat extraction. The inoculation of *Sphagnum* mosses was performed following the moss layer transfer technique (Quinty and Rochefort, 2003). In brief, small fragments of peat mosses were spread evenly and covered with straw mulch (details in Graf et al., 2017) and developed into new moss plants. Along with the *Sphagnum* mosses, vascular plants were also transferred. In order to prevent negative feedback of dominant vascular plants on peat moss development and substrate quality, the cultivation sites were mowed 1–2 times a year.

In Drenth, water is pumped from two ponds, which were additionally replenished with deeper ground water in dry periods. Excess irrigation water is channeled back to the ponds. The sites were inoculated with *Sphagnum papillosum* in October 2015. Due to the poor growth of mosses, parts were re-inoculated with *Sphagnum palustre* in April 2017. GHGs were measured at two of these polders (0.4 ha each): one irrigated by ditches (D-DITCH) and the other one by drip irrigation (D-DRIP). Drip irrigation was installed in April 2017 and the site was irrigated via subsurface drain pipes until then.

In Provinzialmoor, one of the polders (2.3 ha) was prepared for *Sphagnum* cultivation in 2015 by lowering the water table to the peat surface and profiling the ground. Different parts were inoculated with different peat moss species, that is, with *Sphagnum papillosum* in October 2015 (P-PAP), with *Sphagnum palustre* in March 2016 (P-PAL) and with a mix of *Sphagnum* hummock species from Meerkolk in October 2016 (P-MIX), although *Sphagnum papillosum* was the dominant species (Fig. 3.1). Water is supplied by the surrounding polders and is distributed via shallow ditches. To avoid inundation, surplus water is discharged to a drainage ditch. Unfortunately, drainage pipes (30 m drain spacing) have been discovered and destroyed only after termination of measurements. GHGs were also measured at the southern irrigation polder (P-POLDER) which was subjected to seasonal fluctuations of the water table (-0.21 to 0.56 m). The measurement plots are located approximately 6 m away from the shore, with a sparse cover of submerged peat moss (*Sphagnum cuspidatum*).

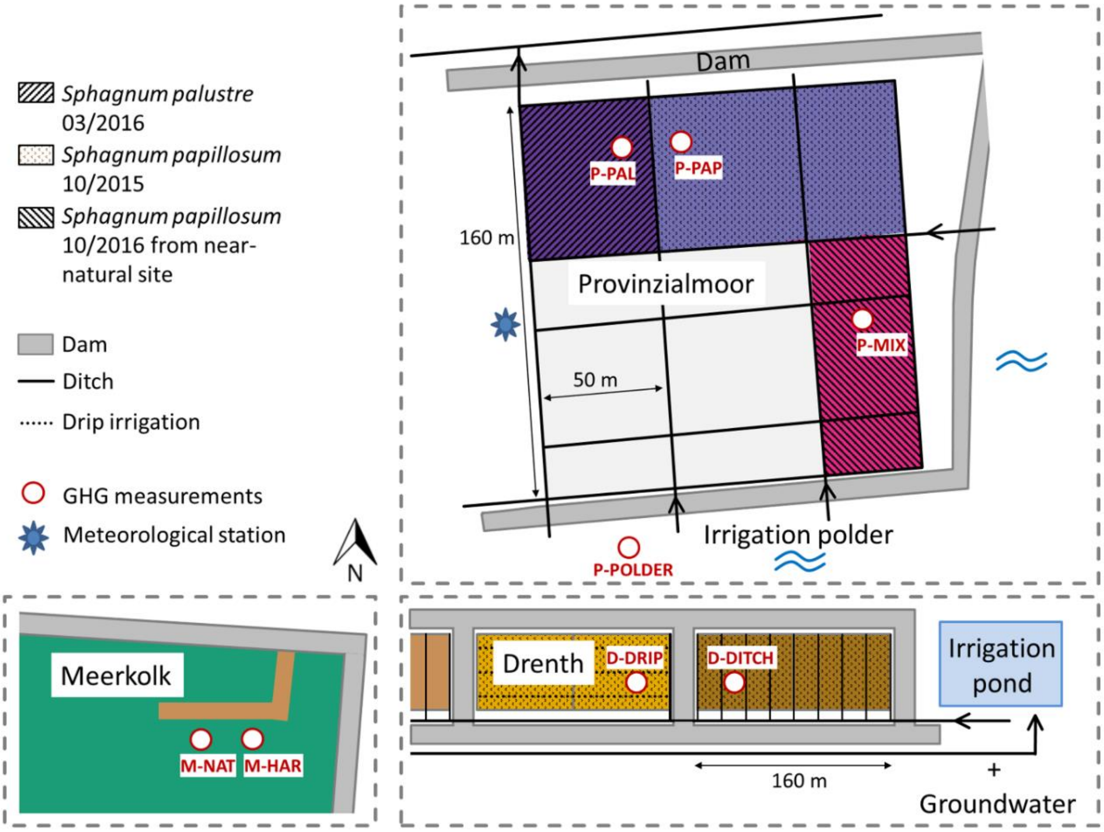

Fig. 3.1: Scheme (not true-to-scale) of study sites (near-natural area Meerkolk and two cultivation areas Provinzialmoor and Drenth) after Graf et al. (2017, modified). The background colors of the respective sites are maintained in all figures.

3.2.2 Environmental parameters

3.2.2.1 Hydrological and meteorological characteristics

A meteorological station in Provinzialmoor (Fig. 3.1) measured soil temperature (2 cm), air temperature and relative humidity (2 m), wind speed, photosynthetic active radiation and global radiation. All hydro-meteorological data were recorded in 30-min intervals. Each GHG measurements site consisted of three replicate plots, and at all plots, soil temperatures (2 cm) were measured from June 2017 onwards. At the meteorological station, 15% of the temperature and 2% of radiation data were missing and filled with data of the German Weather Service (station Lingen, 20 km away). In Meerkolk (M-NAT), 14% of soil temperature values were missing and replaced by meteorological station data. In Drenth (D-DRIP) and Provinzialmoor (P-MIX), it was 29% and 23%, respectively.

At sites M-NAT, D-DRIP and P-MIX, near-surface soil moistures were recorded using GS3 capacitance sensors (Decagon Devices Inc., Pullman, WA, USA). Volumetric water contents h (cm^3 cm^{-3}) were calculated from dielectric permittivities using the standard calibration of the device for potting and peat soils. To exclude the impact of freezing on the dielectric permittivity, values at soil temperature below 2 °C were discarded. Measurements of h were transformed to water-filled pore space (WFPS) by dividing h with the maximum h of the time series. Additionally, relative humidity was measured near the soil surface (IST AG, Ebnat- Kappel, Switzerland). Monitoring wells (slotted PVC tubes) were installed in the peat at all plots. To avoid measurements of deeper groundwater, they were installed in the peat layer only and thus fell periodically dry. Water table depth (WTD) was measured using Mini-Divers in combination with Baro-Divers for atmospheric pressure correction (Eijkelkamp, Giesbeek, the Netherlands). In the following, WTD below ground is noted with a negative sign and vice versa.

Table 3.1: Soil properties of sites.

Area	Sites	Peat depth (cm)	Horizon depth (cm)	Von Post (-)	Peat type	SOC (%)	N_t (%)	CN-ratio (-)	pH	BD (g cm^{-3})	ε (cm^3 cm^{-3})	Field capacity (cm^3 cm^{-3})	K_s (m d^{-1})
Meerkolk	M-NAT, M-HAR	350	0–18	H1	*Sphagnum* peat	45.9	0.72	64.1	3.3	n.d.	n.d.	n.d.	n.d.
			18–30	H2	*Sphagnum* peat	52.9	1.10	48.0	4.1	n.d.	n.d.	n.d.	n.d.
			30–53	H3	*Sphagnum* peat	50.7	1.54	32.8	n.d.	n.d.	n.d.	n.d.	n.d.
			53–65	H6	*Sphagnum* peat	53.3	1.35	39.4	3.2	n.d.	n.d.	n.d.	n.d.
Drenth	D-DITCH	43	0–15	H8	*Sphagnum* peat	51.4	1.20	42.6	3.3	0.19 ± 0.01	0.85 ± 0.04	0.44 ± 0.06	0.18 ± 0.21
			15–27	H5	*Eriophorum*-*Sphagnum* peat	53.8	1.15	46.7	3.4	0.17 ± 0.01	0.88 ± 0.02	0.48 ± 0.02	0.18 ± 0.21
			27–43	H7	Sedge-wood peat	59.9	1.68	35.7	3.0	0.11 ± 0.00	0.91 ± 0.03	0.51 ± 0.07	
Drenth	D-DRIP	40	0–16	H8	*Sphagnum* peat	50.2	1.19	42.1	3.4	0.21 ± 0.01	0.88 ± 0.02	0.55 ± 0.08	n.d.
			16–30	H7	*Sphagnum* peat with *Eriophorum*	54.6	1.13	48.2	2.9	0.18 ± 0.01	0.93 ± 0.04	0.56 ± 0.03	
			30–40	H5	Sedge-wood peat with *Phragmites*	57.8	1.52	38.1	3.3	0.13 ± 0.00	0.95 ± 0.01	0.65 ± 0.04	
Provinzialmoor	P-MIX	80	0–25	H5	*Sphagnum* peat	52.0	1.09	47.7	3.5	0.16 ± 0.01	0.96 ± 0.01	0.59 ± 0.01	0.05 ± 0.05
			25–65	H6	*Eriophorum*-*Sphagnum* peat	56.4	0.86	65.5	3.0	0.10 ± 0.01	0.94 ± 0.03	0.67 ± 0.03	
			65–80	H8	Sedge peat with *Eriophorum*	56.6	1.77	31.9	3.0	0.15 ± 0.01	0.95 ± 0.02	0.71 ± 0.03	
Provinzialmoor	P-PAP, P-PAL	95	0–33	H5	*Sphagnum* peat	51.9	0.98	52.8	3.1	0.12 ± 0.00	0.94 ± 0.03	0.51 ± 0.01	0.09 ± 0.15
			33–80	H7	*Sphagnum*-*Eriophorum* peat	56.2	0.82	68.2	3.1	0.10 ± 0.00	0.97 ± 0.01	0.67 ± 0.05	
			80–95	H8	Sedge-wood peat	58.2	1.50	38.8	3.4	0.13 ± 0.01	0.96 ± 0.01	0.72 ± 0.07	

M-NAT: Meerkolk reference site, M-HAR: Meerkolk harvested site, D-DITCH: Drenth ditch irrigation, D-DRIP: Drenth drip irrigation, P-MIX: Provinzialmoor *Sphagnum* plants from Meerkolk, P-PAP: Provinzialmoor *Sphagnum papillosum*, P-PAL: Provinzialmoor *Sphagnum palustre*, SOC: soil organic carbon, N_t: total nitrogen, BD: bulk density, ε: porosity, K_s: saturated hydraulic conductivity measured with bail tests at water table depths of 0.05 to 0.30 m (Grobe et al., 2021), n.d. = not determined. BD, ε, field capacity and K_s are given as mean ± standard deviation of repeated measurements.

3.2.2.2 Soil properties

At all study sites, soil profiles were dug. If sites were very close to each other, a profile was shared to minimize disturbance of the area (Table 3.1). From each horizon, samples for the determination of physical (six steel rings with a volume of 244.29 cm^3 each) and chemical properties (grab samples) were taken. The degree of humification was determined according to von Post, and carbon (C) and nitrogen (N) contents were measured using an elemental analyzer (LECO Corporation, St. Joseph, Michigan, USA).

Bulk density (BD) and porosity (ε) were determined as part of evaporation experiments with standard mass calculations based on the sample weight at the beginning and end of the experiment. Field capacity (θ at pF 1.8 – θ at pF 4.2; pressure heads h (cm) are expressed as pF = log10(h)) was determined with soil hydraulic properties using the bimodal hydraulic function of van Genuchten (1980) (Durner, 1994) derived by evaporation experiments using the ‘inverse method’ described in Dettmann et al. (2019).

3.2.2.3 Water quality

Biweekly, soil water samples were taken at each site and from the irrigation pond in Drenth and polders in Provinzialmoor. EC and pH values were measured in situ (WTW, Weilheim, Germany). Samples were filtered to 0.45 µm (PES, Merck Millipore, Tullagreen, Ireland), and concentrations of nitrate (NO_3^-), ammonium (NH_4^+), phosphate (PO_4^{3-}), sulphate (SO_4^{2-}) and calcium (Ca^{2+}) were determined by ion chromatography (850 Professional Ion Chromatograph, Metrohm, Filderstadt, Germany). Concentrations of dissolved organic carbon (DOC) were calculated as the difference between total carbon and total inorganic carbon (DimaTOC 2000, Dimatec, Essen, Germany).

3.2.2.4 Vegetation characteristics

Every spring and autumn, vegetation cover (mosses and vascular plants) and species composition were classified according to the Londo scale (Londo, 1976) at each measurement plot. In addition, heights of *Sphagnum* lawns were recorded. The harvested biomass at the donor site (M-HAR) and the mowed vascular plants at the cultivation sites were dried to determine biomass. Subsequently, C and N contents were determined by elemental analysis (LECO Corporation, St. Joseph, Michigan, USA).

3.2.3 Determination of greenhouse gas balances

GHGs were measured using manual static chambers (Livingston and Hutchinson, 1995) at 8 sites (Fig. 3.1, Table 3.1). A ‘site’ represents a management/vegetation type in one of the three study areas ‘Meerkolk’, ‘Provinzialmoor’ and ‘Drenth’ and consists of three ‘plots’ as measurement replicates. GHG measurements were taken for two years. 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. We follow the atmospheric sign convention and emissions of GHG are specified as positive values.

All plots were accessible by boardwalks in order to minimize soil disturbances. During measurements, chambers were placed on permanently installed PVC frames and were fixed gas-tightly via a rubber seal and clamps. Fans mixed the air inside the chambers in order to avoid concentration differences. An opening in the chamber wall, which was closed with a rubber plug after placement, prohibited possible pressure differences during the placement of the chambers. Additionally, a vent tube prevented differences in pressure between inside and surrounding air. When necessary, transparent chambers were cooled with icepacks. At the irrigation polder (P-POLDER), buoyant frames with a water-filled u-shape were deployed. The frames were able to follow the WTD of the polder and held in position by thin steel poles. Before measurements, they were fixed to the poles.

3.2.3.1 Carbon dioxide

Measurement and flux calculation

Fluxes of CO_2 were measured monthly in diurnal campaigns using transparent and opaque chambers (78 x 78 x 50 cm, transparent polycarbonate and PVC) to determine the net ecosystem exchange (NEE) and ecosystem respiration (R_{eco}), respectively.

Campaigns started with one set of R_{eco} measurements before sunrise, followed by one set of NEE measurements at sunrise and then continued in alternation until the maximum light intensity was reached at noon and the maximum soil temperature was reached in the afternoon. If possible, measurements were taken on sunny days to cover the whole range of environmental parameters. A minimum of four transparent and four opaque fluxes was measured per plot and campaign day. The CO_2 concentration of the chamber air was measured with an infrared gas analyzer (LI-820, LICOR, Lincoln, Nebraska, USA) during chamber closure times of 120 (NEE) and 180 (R_{eco}) seconds. Additionally, air temperature and humidity (Rotronic GmbH, Ettlingen, Germany) were recorded and the CO_2 concentrations were corrected for water vapor concentrations (Webb et al., 1980).

Fluxes were calculated using the linear regression of a moving window with the highest coefficient of determination (R^2). The length of the moving window was adjusted according to the solar declination between 40 s at the longest day and 50 s at the shortest day. This was necessary as chamber air temperatures rapidly increased during summer and low fluxes required longer moving windows during winter. Fluxes with $R^2 < 0.75$ were excluded from further calculations unless the increase or decrease of the CO_2 concentration was smaller than 3% of the mean concentration. If the change of photosynthetic active radiation (PAR) exceeded a threshold of 10% of the initial value and/or the change of air temperature inside the chamber was higher than 1.5 °C, no flux was calculated.

Calculation of annual balances

To account for the seasonal development in vegetation response to environmental conditions, we used a campaign-based approach for annual balances (for example, Leiber-Sauheitl et al., 2014).

First, response functions relating R_{eco} to soil temperature were parameterized for each campaign day using the temperature dependent Arrhenius-type model of Lloyd and Taylor (1994):

$$R_{eco}(T) = R_{ref} \times exp\left[E_0 \times \left(\frac{1}{T_{ref} - T_0} - \frac{1}{T - T_0}\right)\right] \quad [3.1]$$

where T is the measured soil temperature, T_{ref} the reference temperature of 283.15 K and T_0 the temperature constant for the start of biological processes (227.13 K) and R_{ref} (respiration at the reference temperature (mg CO_2-C m^{-2} h^{-1})) and E_0 (an activation-like parameter (K)) are the estimated parameters. If the difference between minimum and maximum temperatures was smaller than 1.5 °C during the campaign day, the median of all R_{eco} fluxes was used as R_{ref} in Eq. 3.1.

Secondly, using these parameters and half-hourly data of soil temperature, annual time series of R_{eco} were interpolated for each site (Leiber-Sauheitl et al., 2014). For every time point, R_{eco} was calculated as the distance weighted mean of the two values derived by using the parameters of the previous and subsequent campaign.

Thirdly, gross primary production (GPP) was calculated as the difference between measured NEE and the nearest modelled R_{eco} flux. For each campaign, the rectangular hyperbolic light response equation based on the Michaelis–Menten (Johnson and Goody, 2011) kinetics was parameterized (Falge et al., 2001):

$$GPP\ (PAR) = \frac{GPP2000 \times \alpha \times PAR}{GPP2000 + \alpha \times PAR - \frac{GPP2000}{2000\ \mu mol\ m^{-2} s^{-1}} \times PAR} \tag*{[3.2]}$$

where PAR is the photon flux density of the photosynthetic active radiation (µmol m^{-2} s^{-1}) and GPP2000 (the rate of carbon fixation at a PAR value of 2000 (mg CO_2-C m^{-2} h^{-1})) and α (the light use efficiency (mg CO_2-C m^{-2} h^{-1}/µmol m^{-2} s^{-1}), that is, the initial slope of the fitted curve) are the estimated parameters. The PAR data of the measurement campaigns were corrected by a factor of 0.95 as the transparent chambers slightly reduce light transmission (PS-Plastic, Eching, Germany). If GPP parameters could not be fitted, the respective campaign was combined with the nearest campaign which best resembled the campaign’s environmental conditions, that is, ranges of PAR and GPP. This was especially the case at the polder site (P-POLDER), where fluxes were low and variable and all campaigns were pooled. Annual time series of GPP were interpolated in analogy to Reco using the campaign parameters and half-hourly PAR data. The effect of cutting vegetation on the GPP interpolation of the near-natural donor site (M-HAR) was accounted for by setting the GPP parameters to zero at this day. NEE values were obtained by summing up GPP and R_{eco}.

Finally, annual balances and uncertainties of NEE were estimated by bootstrapping. The response functions for R_{eco} and GPP were fitted again using random resamples of the campaign fluxes with replacement (number of bootstraps = 1000). From the bootstrapped fits, standard errors were calculated.

3.2.3.2 Methane and nitrous oxide

Measurement and flux calculation

Fluxes of CH_4 and N_2O were determined fortnightly using opaque chambers. Over a total closure time of 80 min, five consecutive chamber air gas samples were collected using semi-automatic sampling devices directly after placing the chamber and every 20 min from then on. Concentrations of CO_2, CH_4 and N_2O were measured in the laboratory using a gas chromatograph (Shimadzu, Kyoto, Japan) equipped with an electron capture detector (ECD) for analyzing CO_2 and N_2O and a flame ionization detector (FID) for analyzing CH_4.

Fluxes were determined using robust linear or nonlinear Hutchinson–Mosier (HMR, Pedersen et al., 2010) regressions (R Core Team, 2019; Fuß et al., 2020). Linear or nonlinear fits were selected according to the kappa.max criterion introduced by Hüppi et al. (2018). In brief, the robust linear regression was set as a default. HMR was selected, if the kappa value, that is, the nonlinear shape parameter, did not exceed kappa.max (h^{-1}), that is, the quotient of the linear flux estimate and the minimal detectable flux multiplied by the closure time. This was the case for 28% of CH_4 fluxes and 2% of N_2O fluxes.

Decreases in CO_2 concentration of more than 10 ppm compared to the previous measurement were interpreted as a hint towards a leak of the system or other shortcomings, and the respective data points were discarded. If there were less than four data points per measurement, no flux was calculated. Fluxes indicating an uptake of CH_4 higher than 0.5 mg m^{-2} h^{-1} (n = 6) were regarded as implausible and discarded (Günther et al., 2015; Hütsch, 2001). Finally, fluxes of both CH_4 and N_2O were excluded (n = 54), if the respective CO_2 flux was smaller than 30% of the maximum CO_2 flux of the other two replicates.

Calculation of annual balances

Annual balances of CH_4 and N_2O and uncertainties were estimated using a combination of bootstrap and jackknife procedures (Günther et al., 2015). In brief, one of the three replicate flux estimates was randomly selected for each campaign day. This way, 2000 random time series were generated. Out of these data, balances were calculated via linear interpolation, each time omitting one campaign day. The reported annual estimates and uncertainties represent the means of all jackknife balances and standard errors.

3.2.3.3 Site-specific and areal greenhouse gas balances

Methane and N_2O entered the greenhouse gas balance of sites given their global warming potentials of 28 and 265 t CO_2-eq. ha^{-1} yr^{-1} over a timeframe of 100 years (Myhre et al., 2013).

$$GHG - balance\ (t\ CO_2 - eq.ha^{-1}\ y^{-1}) = NEE + C_{Export} + 25CH_4 + 298N_2O \qquad [3.3]$$

Sphagnum donor material was harvested at MHAR, and the cultivation sites were mowed. The respective C exports (t CO_2 ha^{-1} yr^{-1}) are part of the GHG balance. The C import by *Sphagnum* fragments and straw was not accounted for as the inoculation took place before starting the measurements, and no straw was present during the measurement period anymore.

In order to derive total areal balances of the three *Sphagnum* farming sites differing in their irrigation system, emissions of the irrigation system, of dams and of projected biomass harvest have to be included. To do so, we used the following assumptions:

Size of the irrigation polders: The contribution of GHG emitted from the irrigation systems (polders and ditches) was determined by sizing the respective areas using scans of an aerial drone and assuming that the emission of irrigation ditches equals the measured emission of the P-POLDER site. The exact amount of irrigation water could not be determined in Provinzialmoor. Therefore, a theoretical size of 3.8 ha of an irrigation polder needed to balance water deficits of the cultivation area was estimated based on the maximum irrigation amount determined in Drenth (500 mm in 2018, Köbbing, personal communication) and a theoretical extractable water column of 0.30 m.

Peat dams: Peat dams surrounding the cultivation sites were constructed out of the upper layer of onsite peat and will largely decompose to CO_2. For D-DITCH, D-DRIP and Provinzialmoor, areas of the surrounding peat dams of 0.17 ha, 0.17 ha and 0.31 ha were determined using scans of an aerial drone. We assumed that emissions from peat dams correspond to peat extraction sites in Northwestern Germany (5.2 t CO_2 ha^{-1} yr^{-1}, Tiemeyer et al., 2020).

Re-distribution of Sphagnum fragments: We assumed that all materials harvested at the donor site were spread on the cultivation sites. Therefore, the harvested biomass enters the site-specific GHG balance of M-HAR, but not the areal GHG balances.

Biomass harvest: Over the course of this study, no harvest of *Sphagnum* biomass was conducted. However, we determined biomass and height of mosses at the cultivation sites (Grobe et al., 2021). The linear regression ($R^2 = 0.43$) between biomass and height of these data was used to derive biomasses for each measurement site from the height of mosses in our plots. It was further assumed that 70% of this biomass could be harvested and this estimated extractable biomass was divided by the number of years since the establishment of respective sites and included in the areal GHG balances (t CO_2-eq. ha^{-1} yr^{-1}, Table 3.4). Areal GHG balances of the different irrigation systems were finally standardized per unit of estimated extractable *Sphagnum* biomass (t DM ha^{-1} yr^{-1}, Table 3.4).

3.3 Results

3.3.1 Hydro-meteorological conditions

The early summer of 2017 was unusually dry but extensive rainfalls in the second half of the year resulted in an annual precipitation of 50 mm above the long-term average value of 791 mm in Lingen (German Weather Service). However, in 2018, only 561 mm was measured, which was the lowest value since 1960. With 10.9 °C and 11.7 °C, both years were warmer than the long-term average of 9.8 °C. 2018 was the second warmest year since recording began in 1951.

WTD at the near-natural reference site (M-NAT) was close to the peat surface throughout both measurement years, with annual means of -0.05 ± 0.03 m (mean of daily averages ± standard deviation) in 2017 and -0.07 ± 0.06 m in 2018 (Fig. 3.2A). Even in summer 2018, WTD did not fall below -0.16 m. At the ditch irrigation site (D-DITCH), -0.12 ± 0.13 m and -0.14 ± 0.13 m were measured in 2017 and 2018. As this monitoring well temporarily fell dry in June and July 2018, the true mean of site D-DITCH might be slightly lower. At the drip irrigation site (D-DRIP), annual mean WTDs were -0.09 ± 0.12 m and -0.12 ± 0.12 m, in Provinzialmoor (mean of sites P-PAL, PPAP and P-MIX), -0.11 ± 0.11 m and -0.25 ± 0.22 m. WTDs at all cultivation sites fluctuated strongly and fell below -0.30 m for 51 and 81 days in 2017 and 2018 at D-DITCH, for 39 and 42 days at D-DRIP and for 31 and 135 days in Provinzialmoor. During summer 2018, WTDs in Provinzialmoor even fell below -0.60 m, while water management in Drenth could be largely maintained.

While the incomplete data of 2017 already suggested a lower WFPS in Provinzialmoor, WFPS was considerably higher in D-DRIP (83 ± 12%) than in P-MIX (66 ± 19%), but still lower than in M-NAT (93 ± 4%) in 2018 (Fig. 3.2B). In 2018, WFPS tended to be higher at same WTDs in D-DRIP compared to P-MIX. Humidity near the soil surface was measured in 2018 only and was 79 ± 23% at M-NAT (mean ± standard deviation), 80 ± 21% at D-DRIP and 78 ± 22% at P-MIX.

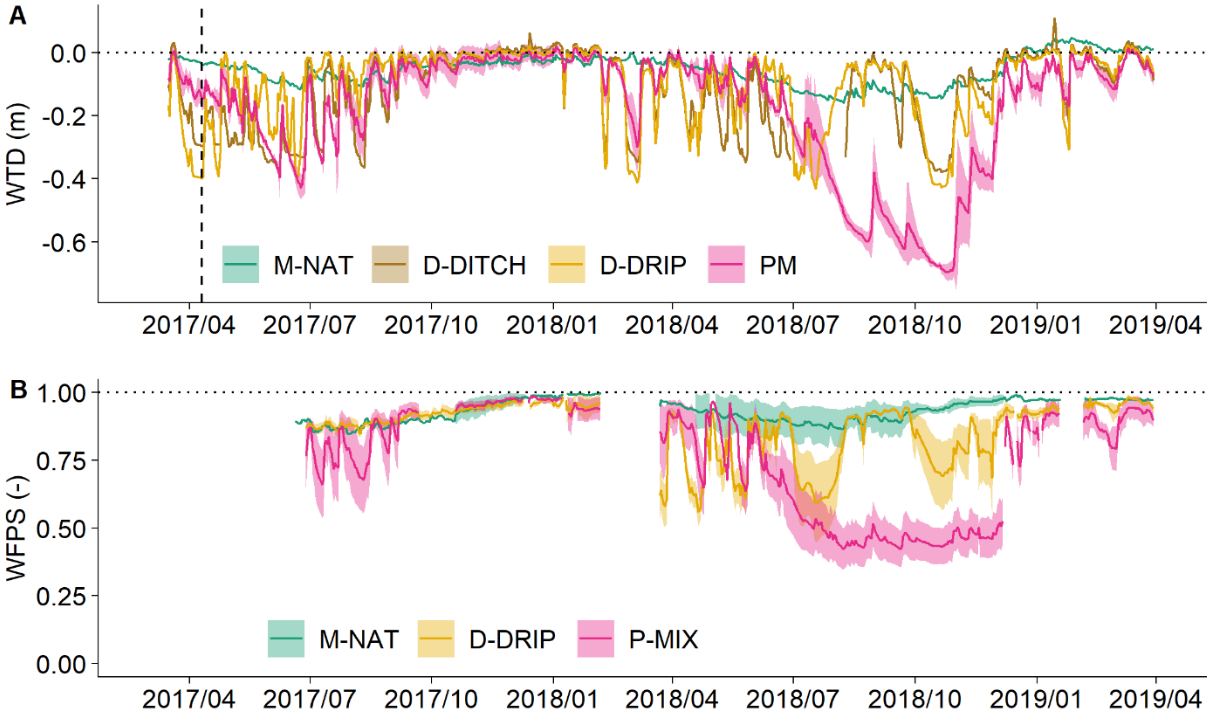

Fig. 3.2: A) Water table depths (WTD) of the near-natural site (M-NAT) and the different irrigation systems ditch irrigation (D-DITCH), drip irrigation (D-DRIP) and a combination of ditch irrigation and previous rewetting (PM, mean and standard deviation of sites P-PAL, P-PAP and P-MIX); and B) water-filled pore spaces (WFPS) of the upper centimeters of M-NAT, D-DRIP and P-MIX. The vertical dashed line denotes the change from subsurface drain pipes to aboveground drip irrigation at D-DRIP. In June and July 2018, WTD of site D-DITCH fell below detection limit and is therefore not plotted.

3.3.2 Water quality

Values of pH and EC as well as solute concentrations were low at the near-natural and at the cultivation sites (Table 3.2). The irrigation water in Drenth showed high pH values and concentrations of Ca^{2+}, especially when ground water was added in dry summer months. However, concentrations of soil pore water at the plots were hardly affected. Maximum pH was 8.7 in the pond water and 5.7 at the measurement plots, and the maximum concentrations of Ca^{2+} were 33.9 mg l^{-1} and 15.9 mg l^{-1}, respectively. At D-DITCH, a peak of NO_3^- concentrations (up to 42.6 mg l^{-1} in comparison with the overall mean of 4.1 mg l^{-1}) was measured in the first summer.

Table 3.2: Values of pH and electric conductivity (EC) as well as solute (DOC = dissolved organic carbon, NO_3^- = nitrate, NH_4^+ = ammonium, PO_4^{3-} = phosphate, SO_4^{2-} = sulphate, Ca^{2+} = calcium) concentrations (mg l^{-1}) of irrigation water and of soil water at the measurement sites (means of biweekly sampling campaigns ± standard deviation).

	Meerkolk Mean of sites	Drenth Irrigation ponds	Drenth D-DITCH	Drenth D-DRIP	Provinzialmoor Irrigation polder	Provinzialmoor Mean of sites
pH	4.6 ± 0.4	5.5 ± 1.3	4.4 ± 0.4	4.3 ± 0.3	4.2 ± 0.3	4.4 ± 0.3
EC	54 ± 16	152 ± 59	159 ± 53	121 ± 23	93 ± 30	117 ± 30
DOC	31 ± 13	51 ± 20	68 ± 20	70 ± 22	43 ± 19	59 ± 26
NO_3^-	0.1 ± 0.1	4.0 ± 4.3	4.1 ± 8.4	0.4 ± 0.4	0.3 ± 0.2	0.3 ± 1.0
NH_4^+	0.5 ± 0.3	0.8 ± 0.7	5.2 ± 2.0	1.4 ± 1.2	0.8 ± 0.7	1.9 ± 1.3
PO_4^{3-}	0.02 ± 0.05	0.07 ± 0.12	0.01 ± 0.02	0.06 ± 0.09	0.02 ± 0.06	0.07 ± 0.19
SO_4^{2-}	0.6 ± 0.3	11.4 ± 0.4	7.4 ± 3.9	4.9 ± 3.0	1.3 ± 0.7	3.8 ± 3.0
Ca^{2+}	0.5 ± 0.6	9.7 ± 8.9	2.3 ± 3.4	2.6 ± 3.0	0.6 ± 1.7	1.3 ± 2.1

3.3.3 Vegetation development

The harvested plots in the near-natural area recovered quickly (Fig. 3.3). In two of the replicate plots, plant cover and species composition resembled the reference plots already one year after harvesting. However, at one replicate plot (M-HAR. 2), remaining mosses were drowned and died off in the subsequent winter. At the cultivation sites, the *Sphagnum* cover increased during the course of this study and spots of bare peat largely closed. However, vegetation developed unequally at the different irrigation treatments (Fig. 3.3). The mean *Sphagnum* cover at the cultivation sites decreased during the dry summer 2018, but mosses slightly recovered until spring 2019. At site DDITCH, mean *Sphagnum* cover decreased throughout the study period. The cover of vascular plants was higher at P-PAL, P-PAP and P-MIX compared to D-DITCH and D-DRIP. Plant species known to play an important role in peatland CH_4 exchange also increased in abundance, especially the cover of *Eriophorum* species increased from 2017 to 2018 at the cultivation sites. *Rhynchospora alba* cover increased in 2018 at the near-natural site and also slightly at the cultivation sites. *Molinia caerulea* was mainly observed at the near-natural sites and at P-MIX and covers decreased in 2018. At P-PAP and P-PAL, higher covers of *Erica tetralix* and *Calluna vulgaris* were recorded which increased in 2018.

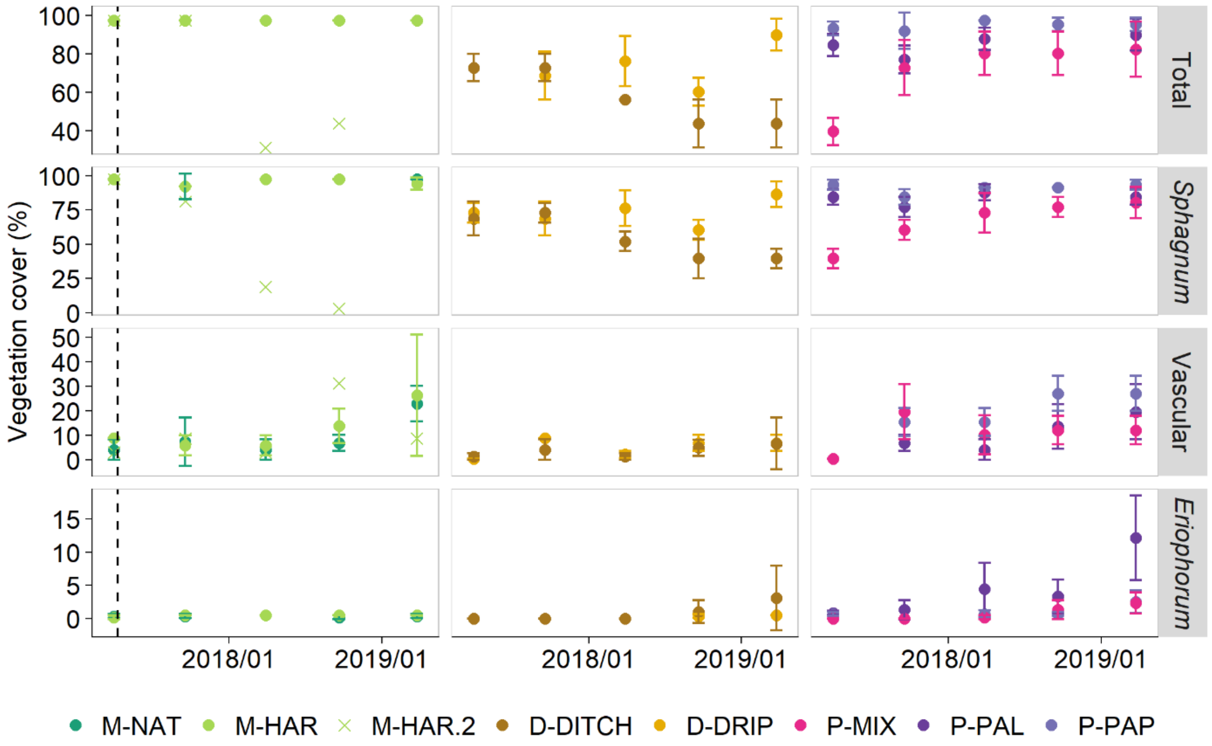

Fig. 3.3: Covers of peat mosses and vascular plants (mean and standard deviations of replicate plots) at the near-natural sites (M-NAT and M-HAR) and at the cultivation sites. One harvested plot (M-HAR.2) did not recover and covers of total vegetation and *Sphagnum* could not be determined in March 2019. *Eriophorum* cover is the sum of *E. angustifolium* and *E. vaginatum* covers, though *E. angustifolium* covers were dominant. The dashed vertical line denotes the date of harvest at M-HAR.

3.3.4 Carbon dioxide

NEE of the near-natural sites was negative (net uptake) in 2017 and positive in 2018 (Table 3.3). Of the cultivation sites, highest CO_2 emissions were determined at D-DITCH, followed by D-DRIP and the sites in Provinzialmoor. P-PAP showed the highest GPP, in its size almost comparable to the near-natural sites, and acted as a CO_2 sink in 2017. Lowest GPPs were measured at D-DITCH. Fluxes of both R_{eco} and GPP were higher at the Provinzialmoor sites compared to the Drenth sites. At the cultivation sites, the extraordinary hot and dry summer 2018 resulted in an earlier GPP peak compared to 2017 (Fig. 3.4). At D-DITCH, GPP even shrank to half during July and August before it increased again in September. This decrease in GPP was considerably less pronounced at the near-natural sites and at D DRIP. CO_2 emissions increased with decreasing WTDs at all sites with the exception of D-DRIP (Fig. 3.5A), as R_{eco} increased in 2018 to a greater extent than the respective GPP values. However, mean WTD only explained changes in NEE between years as in 2018, NEEs of P-MIX and D-DITCH were similar despite different annual mean WTDs and in 2017, similar mean WTDs resulted in different NEEs at the cultivation sites.

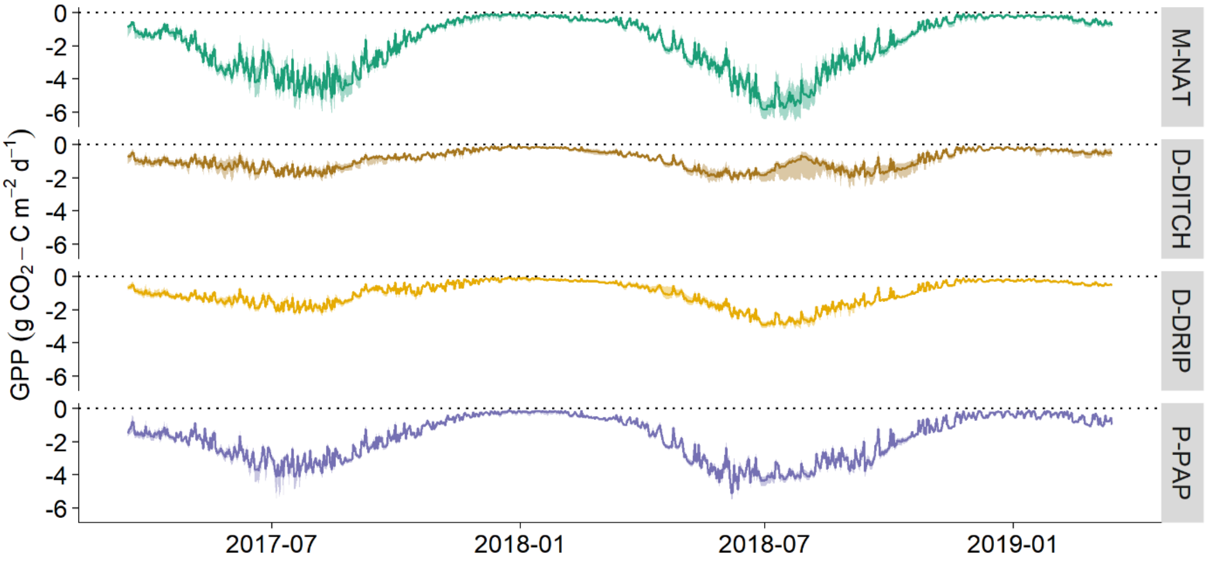

Fig. 3.4: Daily values of gross primary production (GPP) in 2017 and 2018 at the near-natural site (M-NAT) and at the cultivation sites. D-DITCH = ditch irrigation, D-DRIP = drip irrigation, P-PAP (exemplary for Provinzialmoor) = ditch irrigation combined with previous rewetting.

3.3.5 Methane

Highest CH_4 emissions were measured at the near-natural sites and decreased in 2018 (Fig. 3.5B, Table 3.3). Harvested plots (M-HAR) emitted more CH_4, about 20% in 2017 and 10% in 2018. From the irrigation polder in Provinzialmoor (P-POLDER), roughly a third of the amount of M-NAT, that is, 6.9 and 8.9 g CH_4-C m^{-2} yr^{-1}, was released (Table 3.3). At our and other *Sphagnum* farming sites (Beyer and Höper, 2015; Günther et al., 2017), low CH_4 emissions were found. However, CH_4 emissions of the cultivation sites increased in 2018 despite lower WTDs. This increase coincided with an increase of *Eriophorum* cover (*E. angustifolium* and *E. vaginatum*, Fig. 3.6A). Campaign CH_4 fluxes also correlated with daily mean soil temperatures (Fig. 3.6B and C).

Table 3.3: GHG balances of sites.

Site	Year	WTD (m)	NEE ($t\ C\ ha^{-1}\ yr^{-1}$)	GPP ($t\ C\ ha^{-1}\ yr^{-1}$)	R_{eco} ($t\ C\ ha^{-1}\ yr^{-1}$)	CH_4-C ($g\ C\ m^{-2}\ yr^{-1}$)	N_2O-N ($g\ N\ m^{-2}\ yr^{-1}$)	C-Export ($t\ ha^{-1}\ yr^{-1}$)	C balance ($t\ ha^{-1}\ yr^{-1}$)	GHG balance ($t\ CO_2$-eq $ha^{-1}\ yr^{-1}$)
M-NAT	2017	-0.04 ± 0.03	-0.7 ± 0.2	-6.7 ± 0.2	5.9 ± 0.3	36.1 ± 10.8	0.00 ± 0.01		-0.3 ± 0.3	10.9 ± 4.1
M-NAT	2018	-0.06 ± 0.06	1.4 ± 0.3	-7.2 ± 0.2	8.6 ± 0.4	25.1 ± 5.2	0.00 ± 0.01		1.6 ± 0.3	14.5 ± 2.2
M-HAR	2017	0.00 ± 0.03	-0.4 ± 0.2	-4.9 ± 0.1	4.5 ± 0.1	43.8 ± 14.6	0.00 ± 0.01	2.48 ± 0.28	2.5 ± 0.4	23.9 ± 5.6
M-HAR	2018	-0.03 ± 0.07	0.2 ± 0.6	-6.3 ± 0.3	6.5 ± 0.5	27.8 ± 5.0	0.00 ± 0.01		0.5 ± 0.6	11.1 ± 2.8
D-DITCH	2017	-0.12 ± 0.13	1.7 ± 0.2	-3.0 ± 0.1	4.7 ± 0.2	0.0 ± 0.0	1.20 ± 0.83		1.7 ± 0.2	11.1 ± 3.5
D-DITCH	2018	-0.14 ± 0.13	2.2 ± 0.4	-3.5 ± 0.2	5.7 ± 0.4	0.4 ± 0.2	0.38 ± 0.17		2.2 ± 0.4	9.7 ± 1.7
D-DRIP	2017	-0.09 ± 0.12	0.9 ± 0.1	-3.2 ± 0.1	4.1 ± 0.1	0.0 ± 0.1	0.15 ± 0.05		0.9 ± 0.1	3.8 ± 0.6
D-DRIP	2018	-0.12 ± 0.12	0.7 ± 0.1	-4.2 ± 0.1	4.9 ± 0.1	0.1 ± 0.1	0.19 ± 0.06		0.7 ± 0.1	3.5 ± 0.5
P-PAL	2017	-0.10 ± 0.11	-0.0 ± 0.1	-4.1 ± 0.1	4.1 ± 0.1	1.9 ± 0.3	0.05 ± 0.02	0.02 ± 0.01	0.0 ± 0.1	0.8 ± 0.4
P-PAL	2018	-0.25 ± 0.24	0.9 ± 0.2	-5.7 ± 0.2	6.6 ± 0.1	5.3 ± 0.5	0.01 ± 0.01	0.06 ± 0.02	1.0 ± 0.2	5.4 ± 0.7
P-PAP	2017	-0.09 ± 0.12	-0.6 ± 0.2	-5.8 ± 0.1	5.2 ± 0.1	0.7 ± 0.1	0.02 ± 0.02	0.03 ± 0.01	-0.6 ± 0.2	-1.8 ± 0.6
P-PAP	2018	-0.26 ± 0.23	0.1 ± 0.1	-7.2 ± 0.1	7.2 ± 0.1	3.0 ± 0.3	0.00 ± 0.01	0.03 ± 0.02	0.2 ± 0.1	1.7 ± 0.4
P-MIX	2017	-0.13 ± 0.10	0.1 ± 0.2	-4.7 ± 0.2	4.8 ± 0.1	0.3 ± 0.1	0.13 ± 0.07	0.04 ± 0.02	0.2 ± 0.2	1.1 ± 0.8
P-MIX	2018	-0.25 ± 0.21	2.2 ± 0.2	-5.6 ± 0.2	7.7 ± 0.1	1.5 ± 0.2	0.03 ± 0.02	0.04 ± 0.01	2.2 ± 0.2	8.6 ± 0.6
P-POLDER	2017	0.25 ± 0.16	0.9 ± 0.1	-1.6 ± 0.1	2.5 ± 0.1	6.9 ± 5.2	0.01 ± 0.01		1.0 ± 0.1	6.0 ± 2.0
P-POLDER	2018	0.13 ± 0.25	1.0 ± 0.1	-1.6 ± 0.1	2.6 ± 0.1	8.9 ± 4.0	0.00 ± 0.01		1.1 ± 0.1	7.0 ± 1.5

Water table depths (WTD) are means and standard deviation of daily means. Net ecosystem exchange (NEE), gross primary production (GPP) and ecosystem respiration (R_{eco}) are means and standard errors of bootstrap fits, methane (CH_4-C) and nitrous oxide (N_2O-N) are means and standard errors of bootstrap and jackknife balances. C-Export is the *Sphagnum* donor material at M-HAR and the mowed vascular plants at the cultivation sites. In Drenth, C-Export could not be split into D-DITCH and D-DRIP, the combined export was 0.01 t C ha^{-1} yr^{-1}.

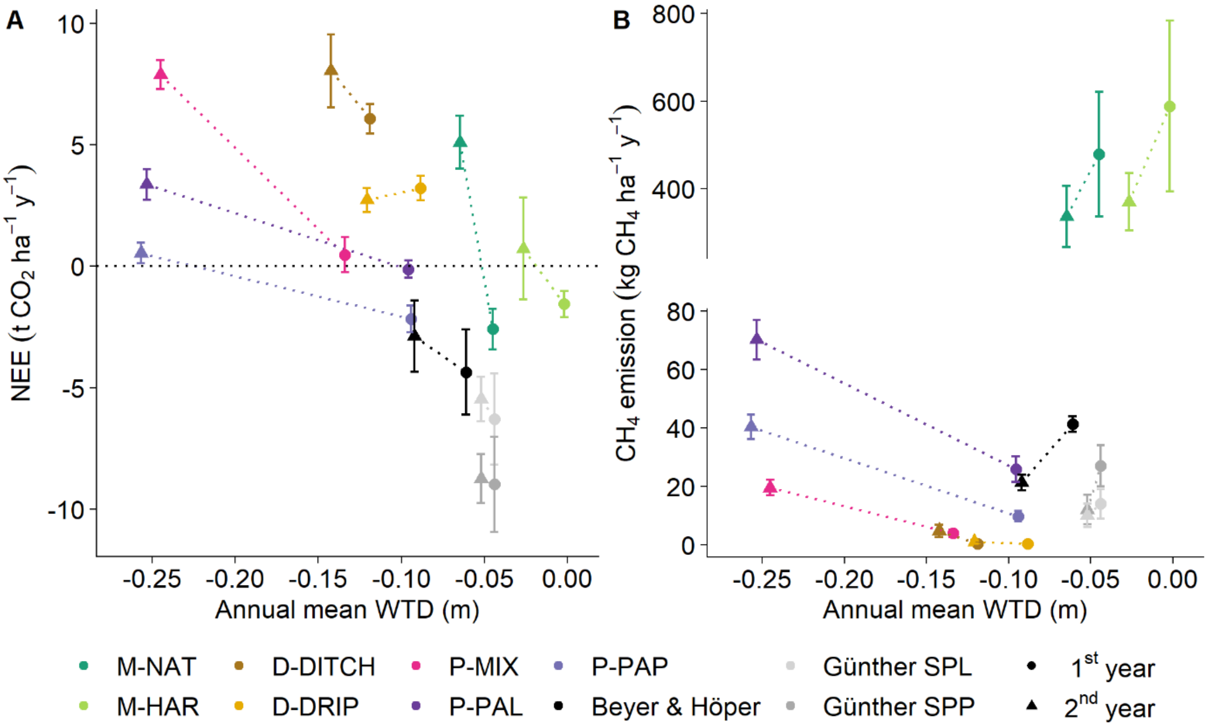

Fig. 3.5: A) Net ecosystem exchange (NEE) and annual mean water table depths (WTD); and B) methane (CH_4) emission and WTD. First and second years are 2017 and 2018 at our sites, 2010 and 2011 (that is, 6 and 7 years after establishment) in Beyer and Höper (2015) and 2012 and 2013 (that is, first and second years after establishment) in Günther et al. (2017; SPL = *Sphagnum palustre*, SPP = *Sphagnum papillosum*). Dotted lines combine both measurement years of each site.

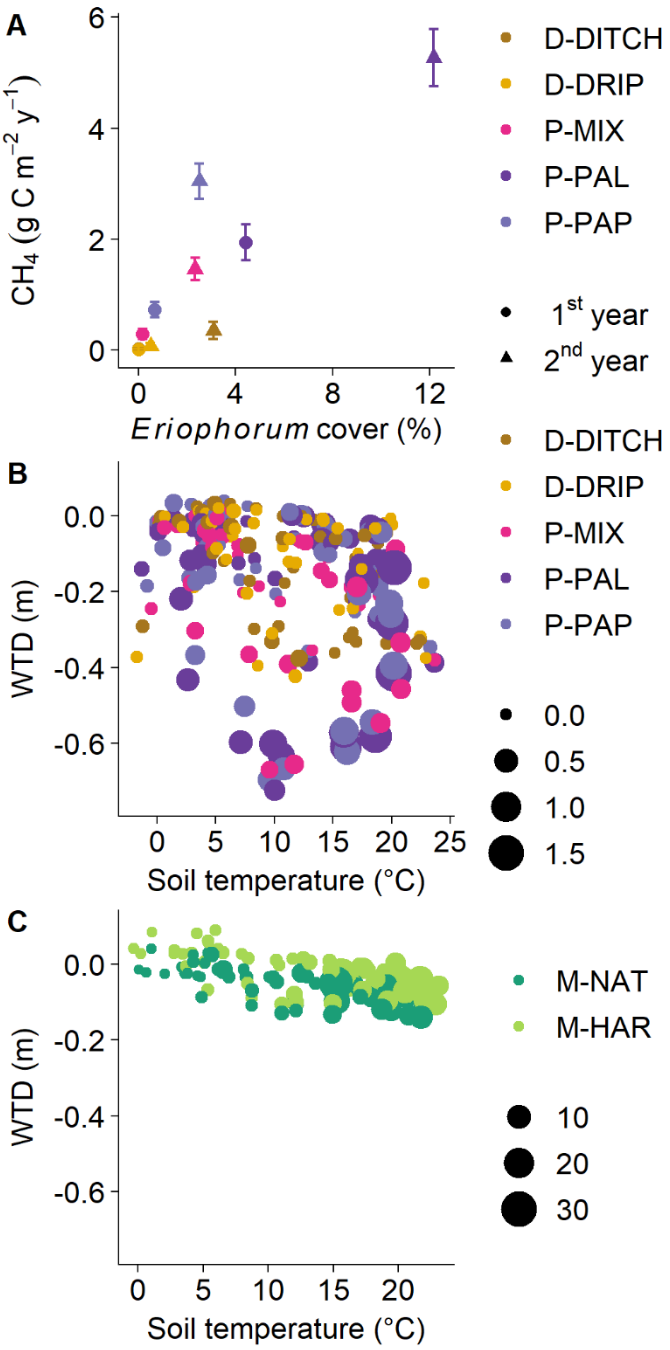

Fig. 3.6: A) Methane (CH_4) emissions and covers of *Eriophorum* (*E. angustifolium* and *E. vaginatum*) at the end of measurement years; B) campaign CH_4 fluxes (mg CH_4-C m^{-2} h^{-1}) and the respective daily mean soil temperatures and water table depths (WTD) at the cultivation sites and C at the near-natural sites.

3.3.6 Nitrous oxide

With the notable exception of D-DITCH, N_2O emissions were low at all sites (Table 3.3). In general, high annual N_2O emissions coincided with low vegetation covers (Fig. 3.7A). The high emissions of D-DITCH could mainly be attributed to a short-term peak in summer 2017 and coincided with a rising WTD after a dry period and high concentrations of NO_3^- in the soil water (Fig. 3.7B and C). The NO_3^- did not seem to originate from the irrigation water, as no elevated concentrations were measured in the irrigation ponds.

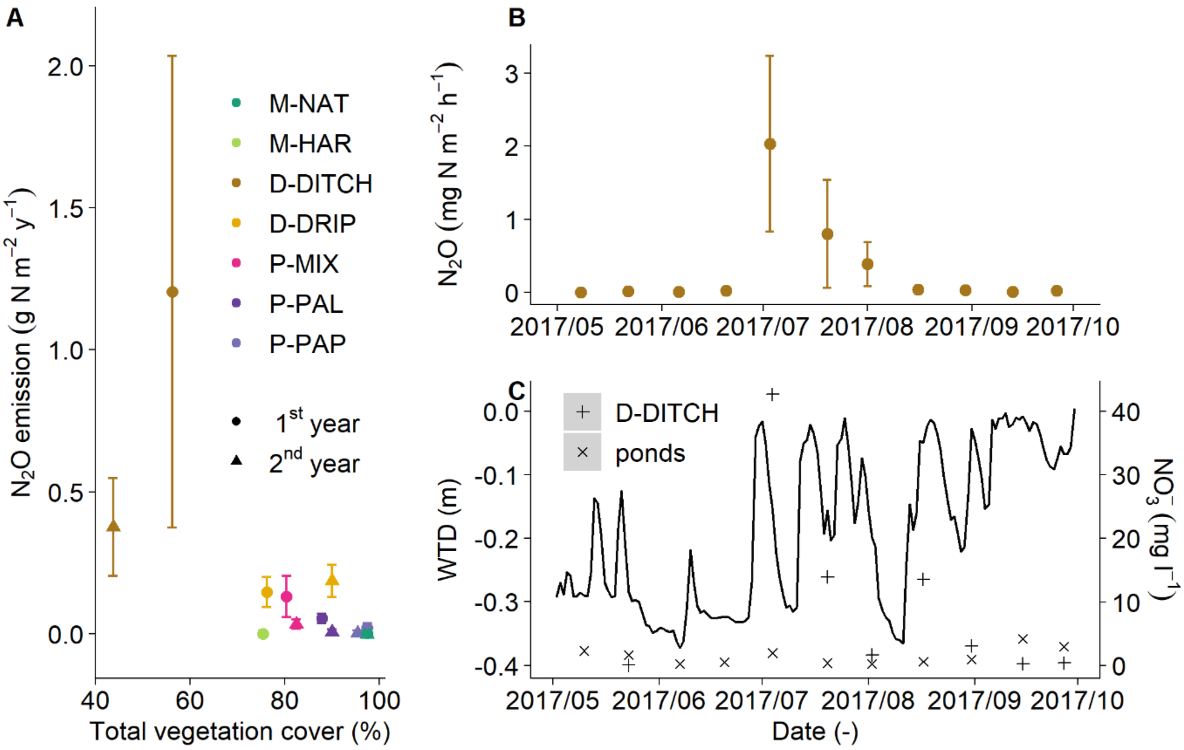

Fig. 3.7: A) Annual nitrous oxide (N_2O) emissions (mean of jackknife balances ± standard error) and total vegetation covers; B) campaigns with peak N_2O fluxes at site D-DITCH (mean of replicates ± standard deviation); and C) the respective water table depths (WTD) and nitrate (NO_3^-) concentrations of the irrigation ponds (ponds) and of the soil water at the measurement plots (D-DITCH).

3.3.7 Site-specific and areal greenhouse gas balances

The GHG balances of the near-natural sites (MNAT, M-HAR) were characterized by high CH_4 emissions, but M-NAT was still accumulating C in 2017 (Table 3.3). At M-HAR, the amount of harvested biomass equals an export of 9.1 t CO_2-eq. ha^{-1} yr^{-1}. In contrast, NEE dominated the GHG balances of the cultivation sites. The only net GHG uptake was calculated for site P-PAP in 2017. High CO_2 and N_2O emissions contributed to the balance of D-DITCH. The GHG balance of the irrigation polder in Provinzialmoor (P-POLDER) was composed of CH_4 and CO_2 emissions, the mean of both years was 6.5 t CO_2-eq. ha^{-1} yr^{-1}. The C-export generated by mowing of vascular plants at the cultivation sites added up to only 0.13 and 0.05 t CO_2-eq. ha^{-1} yr^{-1} for Provinzialmoor and Drenth, respectively, and is therefore not visible in Fig. 3.8 but included in Table 3.4.

In accordance with the different vegetation development, the three irrigation systems produced distinct GHG balances. Mean site-specific GHG balances were highest in D-DITCH, followed by D-DRIP and Provinzialmoor (mean of sites P-PAL, PPAP and P-MIX, Table 3.4). Including emissions of irrigation systems and dams, drip irrigation (D-DRIP) generated the smallest areal GHG balance, whereas irrigation by ditches combined with previous rewetting (Provinzialmoor) produced the lowest GHG emissions per ton of *Sphagnum* biomass.

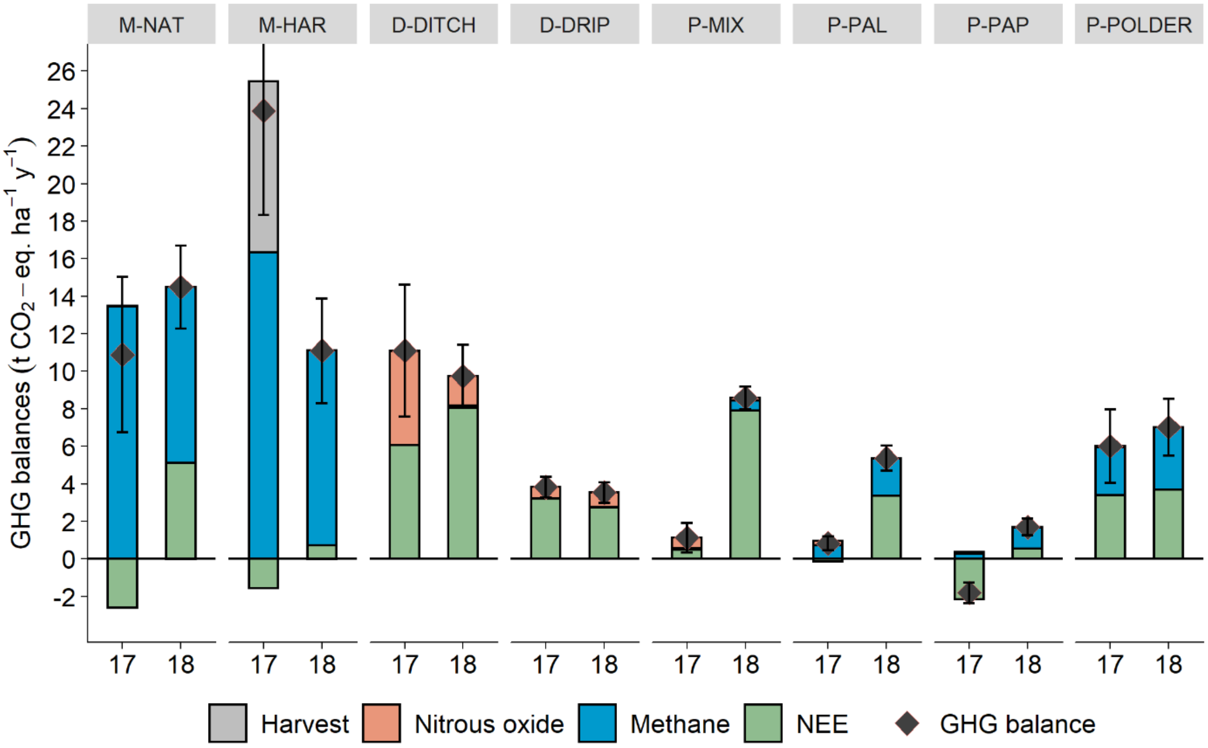

Fig. 3.8: Annual exchange of nitrous oxide, methane and carbon dioxide (NEE) and site-specific GHG balances of the near-natural sites (M-NAT = reference, M-HAR = harvest of *Sphagnum* donor material), of the cultivation sites (D-DITCH = ditch irrigation, D-DRIP = drip irrigation, P-MIX, P-PAL and P-PAP = ditch irrigation combined with previous rewetting) and of the irrigation polder in Provinzialmoor (P-POLDER).

3.4 Discussion

3.4.1 *Sphagnum* farming on highly decomposed peat

In this study, we provide evidence for the general feasibility of large-scale *Sphagnum* farming on highly decomposed peat remaining after peat extraction. Further, results are not only relevant for post-extraction sites, as agriculturally used bog peats may have also already lost the upper horizons due to mineralization and share similar physical soil characteristics. In Germany, this applies to more than half of the total bog area.

However, the highly decomposed peat challenges a successful cultivation of peat mosses. Measured K_s values were small compared to the 1.13 m d^{-1} reported for a nearby *Sphagnum* farming project on less decomposed peat (Brust et al., 2018), and BD was slightly higher compared to the range of 0.07–0.12 g cm^{-3} reported for another nearby site (Gaudig et al., 2017). Over prolonged periods, WTDs at the cultivation sites fell far below the targeted range close to the surface. Price and Whitehead (2001) observed *Sphagnum* recolonization of an abandoned block-cut bog at mean WTD of -0.25 ± 0.14 m and volumetric water contents higher than 50%. WTDs measured at our cultivation sites were higher, but WFPS temporarily dropped below 50% (corresponding to volumetric water contents lower than 50%) in 2018, especially at P-MIX. During these periods of hydrological stress, mosses lost their green color and became visibly inactive.

Although mosses recovered and covers increased again in early 2019, the 2018 drought affected biomass production. The estimated *Sphagnum* biomass in March 2019 was 1.2 t dry mass per hectare at D-DITCH (41 months since inoculation), 2.1 t at D-DRIP (41 months), 3.3 t at P-PAP (41 months) and

2.5 t at P-PAL (36 months) and P-MIX (29 months). A detailed analysis of *Sphagnum* establishment at our sites is available in Grobe et al. (2021), while our data are restricted to the GHG plots only. Biomass production in Drenth was low, but values of the sites in Provinzialmoor are comparable to a neighboring *Sphagnum* farming project (1.0 t ha^{-1} yr^{-1} in the first 3 years, Gaudig et al., 2017). In a greenhouse experiment, Gaudig et al. (2020) found that peat moss productivities can reach up to 7 t ha^{-1} yr^{-1} for *S. papillosum* at a constant WTD 0.02 m below capitulum.

Vascular plants also colonized the cultivation sites and higher *Sphagnum* covers coincided with higher covers of vascular plants (Grobe et al., 2021). This supports the findings of McNeil and Waddington (2003), who observed that vascular plants promote *Sphagnum* growth by providing shadow and suitable moistures, a mechanism especially useful during hydrological stress (Buttler et al., 1998) and after cutting of mosses (Krebs et al., 2018). Vascular plants generally profited from the dry conditions in 2018 and shaded peat mosses remained active longer at the beginning of dry periods compared to spots without shading.

Table 3.4: Areal GHG balances of irrigation systems. D-DITCH = ditch irrigation, D-DRIP = drip irrigation, Provinzialmoor = ditch irrigation combined with previous rewetting, that is, mean of sites P-PAL, P-PAP and P-MIX and product-related GHG balances per ton of extractable *Sphagnum* biomass.

Drenth D-DITCH	Drenth D-DRIP	Provinzial-Moor	
10.4	3.7	2.6	Mean site-specific GHG balance of cultivation sites (t CO_2-eq. ha^{-1} yr^{-1})
6.5	6.5	6.5	GHG balance of polders and ditches (t CO_2-eq. ha^{-1} yr^{-1}) (site P-POLDER)
5.2	5.2	5.2	GHG balance of dams (t CO_2-eq. ha^{-1} yr^{-1}) (Tiemeyer et al., 2020)
5:1	10:1	0.6:1	Ratio cultivation area / irrigation area
2.2:1	2.4:1	7.4:1	Ratio cultivation area / dams
0.05	0.05	0.13	Extracted biomass (mowing) (t CO_2-eq. ha^{-1} yr^{-1})
0.5	0.9	1.4	Estimated extractable biomass (vascular plants + *Sphagnum*) (t CO_2-eq. ha^{-1} yr^{-1})
8.9	5.3	6.6	Areal GHG balance of irrigation system (t CO_2-eq. ha^{-1} yr^{-1})
0.3	0.4	0.7	Estimated extractable *Sphagnum* biomass (t DM ha^{-1} yr^{-1})
29.5	13.2	9.4	GHG balance per extractable ton of *Sphagnum* biomass (t CO_2-eq. t DM^{-1})

3.4.2 Drivers of GHG exchange

3.4.2.1 Carbon dioxide

WTD affected the CO_2 exchange of all sites. At the near-natural site, differences in WTD of only a few centimeters shifted M-NAT from a sink of CO_2 comparable to other near-natural bogs (-2.4 ± 1.2 t CO_2 ha^{-1} yr^{-1}, Helfter et al., 2015) to a considerable source in 2018. The effect of the dry year 2018 on mean WTDs and the accompanying increased CO_2 emissions were particularly pronounced in Provinzialmoor. Fluctuations of WTDs will affect NEEs of *Sphagnum* farming sites, especially when mosses are exposed to periodical desiccation. In a laboratory experiment, McNeil and Waddington (2003) found that respiration of peat columns grown with *Sphagnum* increased shortly after drying and subsequent rewetting, while GPP recovered only after three weeks of water saturation, highlighting the importance of stable WTDs. Brown et al. (2017) also found that water table fluctuation best predicted NEE and that a stable WTD lead to greater uptake of CO_2.

In addition to the hydrology of the sites, the development of the vegetation cover influenced NEE. Lower GPP values at D-DRIP and D-DITCH were consistent with the poor vegetation development, while the decrease of NEE at D-DRIP in 2018 could be explained by an increase in vegetation cover. At sites P-PAP and P-PAL, the restoration of the sites as sinks of atmospheric CO_2 in 2017 can be attributed to the almost completely closed *Sphagnum* lawn. Site P-PAP also showed the highest vascular plant cover of all cultivation sites. In general, higher vascular plant covers went along with increased GPP and R_{eco} fluxes.

In line with peatlands restored with the moss layer transfer technique (Nugent et al., 2018), the time needed for a *Sphagnum* farming site to become a sink of atmospheric CO_2 cannot easily be predicted. Comparing our results to previous neighboring *Sphagnum* farming experiments (Beyer and Höper, 2015; Günther et al., 2017) showed no clear correlation of NEE and GPP with the age of sites, and differences in CO_2 exchange are probably rather explained by the high and stable WTD in those two studies (Fig. 3.5A). In addition, dry years can also turn older restored sites into sources of CO_2 (Strack et al., 2009; Wilson et al., 2016b). Both GPP and R_{eco} values increased from 2017 to 2018. GPP was influenced by growing vegetation covers, while lower WTDs and higher temperatures affected R_{eco}. A higher biomass probably also contributed to the higher R_{eco}, but still the increase in R_{eco} was more than offsetting GPP increases. Possibly, the growing vegetation would have turned the cultivation areas in sinks of atmospheric CO_2 in 2018 under the condition of sufficient water supply. The development of daily GPP values indicates that GPP was strongly affected by the 2018 drought, above all at D-DITCH (Fig. 3.4).

3.4.2.2 Methane

The CH_4 emissions of the near-natural site were high compared to the emission factors for rewetted and near-natural bogs (Wilson et al., 2016a) or temperate wetlands (Turetsky et al., 2014). In addition to the shallow WTD, reasons could be relatively high temperatures compared to both long-term average and other studies summarized by those reviews, the cover of vascular plants or the high N deposition level (about 25 kg N ha^{-1} yr^{-1}, Hurkuck et al., 2016). Meerkolk is surrounded by intensively used agricultural area, which might influence GHG exchange. In a fertilization experiment, Juutinen et al. (2018) could associate increasing CH_4 fluxes with higher N input in a temperate bog. Compared to semi-natural sites in a similar climatic setting, our values are not implausible: Drösler (2005) measured 38 g CH_4-C m^{-2} yr^{-1} in a semi-natural peatland in Bavaria dominated by *Sphagnum cuspidatum*, *Scheuchzeria palustris* and *Rhynchospora alba*, whereas 5–14 g CH_4-C m^{-2} yr^{-1} were reported for a near-natural bog dominated by *Sphagnum fallax* in Northwestern Germany (Tiemeyer et al., 2020).

In general, campaign CH_4 fluxes increased with increasing daily mean soil temperatures and highest fluxes were measured at WTDs close to the peat surface. However, high emissions were observed at the cultivation sites during drought in 2018, which could be attributed to the vegetation composition of the plots. Specialized wetland plants possessing aerenchymous tissues enable a plant-mediated transport of gases between soil and atmosphere (Gray et al., 2013). At the cultivation sites, increasing covers of *Eriophorum angustifolium* and *Eriophorum vaginatum* from 2017 to 2018 resulted in higher CH_4 emissions (Fig. 3.6A) despite drier conditions, a pattern already described in previous studies (Greenup et al., 2000; Tuittilla et al., 2000; Waddington and Day, 2007). *Molinia caerulea* (Leroy et al., 2019; Vanselow-Algan et al., 2015; Rigney et al., 2018) and *Juncus effusus* (Henneberg et al., 2015) have also been associated with higher CH_4 emissions, but their influence seemed to be less important at our sites.

The CH_4 emissions of P-POLDER were higher than emissions of the cultivation sites but significantly smaller compared to the near-natural sites (Table 3.3). They were comparable to emissions of irrigation ditches at a nearby *Sphagnum* cultivation site (4–11 g CH_4-C m^{-2} yr^{-1}, Günther et al., 2017). In contrast, Franz et al. (2016) reported 40 g CH_4-C m^{-2} yr^{-1} for a rewetted rich fen. As in other chamber studies (for example, Günther et al., 2017), we could not determine episodic ebullition fluxes, which might have played a role especially at P-POLDER. Therefore, CH_4 fluxes estimated here probably represent a lower limit of the 'real fluxes'.

3.4.2.3 Nitrous oxide

N_2O emissions were mainly relevant for the GHG balances of the ditch irrigation site (Fig. 3.7A). Annual balances at this site were comparable to those of arable land (Tiemeyer et al., 2020), and even the N_2O emissions of D-DRIP are comparable to low-intensity grassland on bog peat (Leiber-Sauheitl et al., 2014). Emission peaks at D-DITCH (Fig. 3.7B) coincided with a re-rise of WTD after a dry period and high concentrations of nitrate in the soil pore water (Fig. 3.7C). The respective NO_3^- concentrations of the irrigation ponds were not elevated, hinting towards an origin of N in peat mineralization during the preceding dry period. With a rising WTD, NO_3^- was probably converted to N_2O by incomplete denitrification. Unfortunately, it is possible that this peak emission was missed in 2018: A similar re-rise of WTD combined with higher concentrations of NO_3^- in the soil pore water was observed in August 2018, but the respective CH_4/N_2O campaign could not be conducted. A lack of vegetation which could take up N from the soil water also seems to contribute to the observed pattern. High N_2O emissions from bare peat were also reported by other studies (Marushchak et al., 2011), emphasizing the risk of high N_2O emission under suboptimum plant growth conditions even at unfertilized sites.

3.4.3 Greenhouse gas balances

Altogether, the GHG emissions were higher than those of *Sphagnum* farming on less degraded peat soils (Beyer and Höper, 2015; Günther et al., 2017) mainly because of more unfavorable CO_2 exchange in our case and the different degrees of decomposition of the cultivation sites. It also has to be taken into account that 2018 was an extraordinary hot and dry year and that drought substantially affected GHG exchange. Interestingly, the near-natural sites proved to be resilient regarding the WTD due to its ability to oscillate, but to be very sensitive regarding the GHG exchange. Here, the highest annual balances were quantified. This result must not be misinterpreted in a way that near-natural sites should be used as *Sphagnum* farming sites as our cultivation sites have a land use legacy of carbon emissions equivalent to several meters of peat and as near-natural sites are irreplaceable in terms of biodiversity. Further, the temporal dynamic of the radiative forcing impact of natural sites, which is dominated by CO_2 in the long term (Frolking et al., 2006), has to be considered. Despite the high CH_4 emissions, M-NAT was still accumulating C in 2017.

3.4.3.1 Impact of *Sphagnum* harvest at the near-natural site

Harvesting the upper 5 cm vegetation at M-HAR resulted in higher CH_4 emissions and – on average – lower CO_2 emissions. Effectively, it removed the active green *Sphagnum* horizon and moved the peat surface towards the water table, which resulted in a decreased CO_2 uptake in the first year, but lower CO_2 emissions than M-NAT in the dry second year. Reduced oxidation in the shallower *Sphagnum* horizon might be the reason for the increased CH_4 emission. This pattern of higher CH_4 emissions and a reduced CO_2 uptake followed by a rapid plant recovery was also reported by Murray et al. (2017) for a Canadian donor site. However, wetter conditions and flattening of the surface of harvested sites could change plant compositions in the long term (Guêné-Nanchen et al., 2019). M-HAR showed slightly lower *Sphagnum* covers and slightly higher covers of vascular plants (especially *Rhynchospora alba* and *Molinia caerulea*). GPP recovered in 2018, but GPP and R_{eco} were higher at M-NAT in both years. It has to be considered that the 'drowned' replicate (Fig. 3.3) is included in the average GHG values. Silvan et al. (2017) harvested down to a depth of 30 cm and also described a rapid recovery of *Sphagnum* cover and CO_2 sequestration. Under optimum conditions, re-growth of *Sphagnum* could even facilitate yearly harvests (Krebs et al., 2018). However, the depth of cutting needs to be carefully adjusted when harvesting *Sphagnum* farming sites.

3.4.3.2 Impact of different irrigation systems and initial effects

Three different irrigation systems were investigated in this study. In Drenth, drip irrigation (D-DRIP) provided slightly higher WTDs compared to ditch irrigation (D-DITCH), while Provinzialmoor became very dry in 2018 due to a lack of sufficient irrigation water and accidentally continuing drainage. However, despite the apparently hydrological favorable conditions in Drenth, vegetation developed better and CO_2 emissions were lower in Provinzialmoor. In this context, it is important to emphasize that the vegetation development at the GHG plots was in line with the overall vegetation development at the cultivation sites (Grobe et al., 2021). A number of factors might have contributed to these surprising results: differences in soil properties, differences in meteorological conditions, the presence of vascular plants, quality of the irrigation water and initial effects.

Soil properties were slightly more favorable at Provinzialmoor (Table 3.1), which might be the result of the preceding multi-annual inundation (especially the lower BD and higher ε). While this did not prevent dry conditions in the uppermost soil layer, which is relevant for the peat mosses, the vascular plants might have profited from the higher field capacity and in turn positively influenced peat moss development.

The shape of the cultivation areas and the surrounding environment would suggest higher evapotranspiration and lower humidity at Drenth (narrow strip surrounded by ongoing peat extraction) than at Provinzialmoor (square surrounded by rewetted peatlands). However, D-DRIP even showed slightly higher humidity compared to P-MIX in 2018, although this might have been caused by the drip irrigation itself. Furthermore, mean peat thickness was only 45 cm in Drenth compared to 90 cm in Provinzialmoor, which could have affected the ability of mosses to cope with prolonged periods of increased evaporation (Dixon et al., 2017).

The irrigation water used in Drenth during dry summer periods had a lower quality regarding pH and nutrient concentrations than the polders in Provinzialmoor. In particular, higher amounts of calcium were measured. At single dates, concentrations exceeded 20 mg l^{-1}, an amount possibly negatively affecting peat moss health (Vicherová et al., 2015). Higher concentrations were observed only in the irrigation ponds and not in the soil pore water at measurement plots. However, temporal inundation at D-DITCH and aboveground 2017 drip irrigation at D-DRIP could have delivered detrimental amounts.

Especially in the initial phase of *Sphagnum* growth, a sufficient water supply is essential (Pouliot et al., 2015). Before the installation of drip irrigation, site D-DRIP was irrigated via subsurface drain pipes, which did not provide sufficient water in the first months after spreading of moss fragments. It is likely that the well-working drip irrigation could not compensate for damages in the phase of *Sphagnum* establishment. Furthermore, storms and freezing damaged parts of the Drenth area in early 2017, whereas the Provinzialmoor area was hardly affected and also profited from a relatively wet year 2016.

3.4.3.3 Areal GHG balances

Altogether, drip irrigation (D-DRIP) generated the lowest areal GHG balance because the low site-specific emissions in Provinzialmoor were compromised by the large areal contribution of the irrigation polder. However, emissions per ton of extractable *Sphagnum* biomass were lowest in Provinzialmoor due to the better vegetation development.

We need to stress that differences between the investigated irrigation systems (Table 3.4) have to be interpreted with caution. They might be the result of the previous rewetting of Provinzialmoor as well as the result of disturbances in the initial phase in Drenth. In contrast to Provinzialmoor, it was possible to add groundwater in dry periods in Drenth, considerably reducing the areal contribution of the irrigation system.

Furthermore, the assumptions made to derive areal balances induced uncertainties. The water deficit in Drenth (500 mm) and the resulting theoretical polder size for Provinzialmoor were slightly higher than deficits calculated for a neighboring *Sphagnum* farming site. Brust et al. (2018) specified a mean deficit of 160 mm and a deficit of 320 mm in dry years. However, they also recorded a deficit of 636 mm in an extremely dry year, supporting our theoretical polder size. Although emissions from site P-POLDER resemble those from irrigation ditches of this neighboring site (Günther et al., 2017), literature values for emissions from peat dams vary considerably. For example, Vybornova et al. (2019) report 31.5 t CO_2-eq. ha^{-1} yr^{-1} for bare peat dams, two thirds of this emission being CO_2 and about one third being N_2O. This value would be seven times larger than the value used in this study.

To optimize both GHG balances and productivity per area, future designs for *Sphagnum* farming should keep areas of dams and open water as small as possible while avoiding all unnecessary water losses and ensuring a sufficient water supply in dry summer periods. As long as the sites have not yet developed an active acrotelm, irrigation and thus space for water storage will be needed. In Drenth, peat mosses grew better in closer distance to ditches (Grobe et al., 2021) and ditches could be cut in closer distance (5 m, Gaudig et al., 2017). However, this will considerably influence both the maintenance costs and the GHG balance, as emissions of ditches are expected to be higher than the emissions of cultivation areas. Due to the challenging hydrological conditions, the irrigation via ditches seems to be only recommendable for highly decomposed sites if they were inundated before. Drip irrigation might better maintain favorable moisture conditions, but requires water of a better quality than ditch irrigation.

Finally, even though optimum conditions could not be provided, *Sphagnum* farming on former peat extraction sites still offers a considerable GHG mitigation compared to average emissions from cropland (33.7 t CO_2-eq. ha^{-1} yr^{-1}) and grassland (30.4 t CO_2-eq. ha^{-1} yr^{-1}) in Germany (Tiemeyer et al., 2020). In the presented balances, global warming potentials over 100 years were used. When considering longer time frames, the most important goal of peatland restoration and paludiculture projects is to quickly stop the sites from emitting CO_2 to the atmosphere (Günther et al., 2020).

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4 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 (CO_2), methane (CH_4) and nitrous oxide (N_2O) 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 CO_2 and CH_4 increased with warming, dominated by CH_4 at the near-natural bog and by CO_2 at the paludiculture areas, where vegetation was in a successional stage and topsoils temporarily dried out during summer. N_2O 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 CH_4 emissions and improve biomass quality.

4.1 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 characterized 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., 2022a). 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 minimize 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. (2022a). In this paper, we described the annual balances of CO_2, CH_4 and N_2O 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. (2022a). 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.

4.2 Materials and methods

4.2.1 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 4.1). 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 characterized 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 characterized by low hydrologic conductivities.

The cultivation area Provinzialmoor was established in October 2016 and had previously been rewetted as a shallow polder since the termination of peat extraction in 2008, while Drenth was established in October 2015 directly after the 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 *Sphagnum papillosum* at Provinzialmoor and both *Sphagnum papillosum* and *Sphagnum palustre* at Drenth. Vascular plants, e.g. *Molinia caerulea*, *E. angustifolium* and *Erica tetralix* (complete list of plant species in Table A.1), 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. (2022a) and Grobe et al. (2021).

Table 4.1: Study areas and sites.

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 rewetting
	P-MIX-W	Cultivation warming	0.8	Ditch irrigation + previous rewetting
Drenth	D-DRIP	Cultivation control	0.4	Drip irrigation
	D-DRIP-W	Cultivation warming	0.4	Drip irrigation

4.2.2 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. A.1). 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 minimize possible effects on other environmental parameters (e.g. shading and reduced precipitation) at the measurement plots (0.75 m side length) in the center. 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.

4.2.3 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. A.1) and the mean of the three probes was used for further analyses. Near surface volumetric water contents θ (cm^3 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.

4.2.4 Measurement of greenhouse gases and calculation of annual balances

We manually measured GHG exchange using static chambers (0.78 × 0.78 × 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 analyzer (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 analyzer (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., 2022a). 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 parameterize 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., 2022a). 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 analyzing CO_2 and N_2O and a flame ionization detector (FID) for analyzing 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., 2022a). 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., 2022a).

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 kg C ha^{-1} yr^{-1}), no further C inputs and C exports entered the GHG balance.

4.2.5 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 led 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 analyzed 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 ($p < 0.05$).

4.3 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 °C and 11.7 °C, both years were clearly warmer than the long-term average (9.8 °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. A.2 for time series of daily air temperature and precipitation).

4.3.1 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 (± 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 4.3. 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. 4.1). In addition, 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.

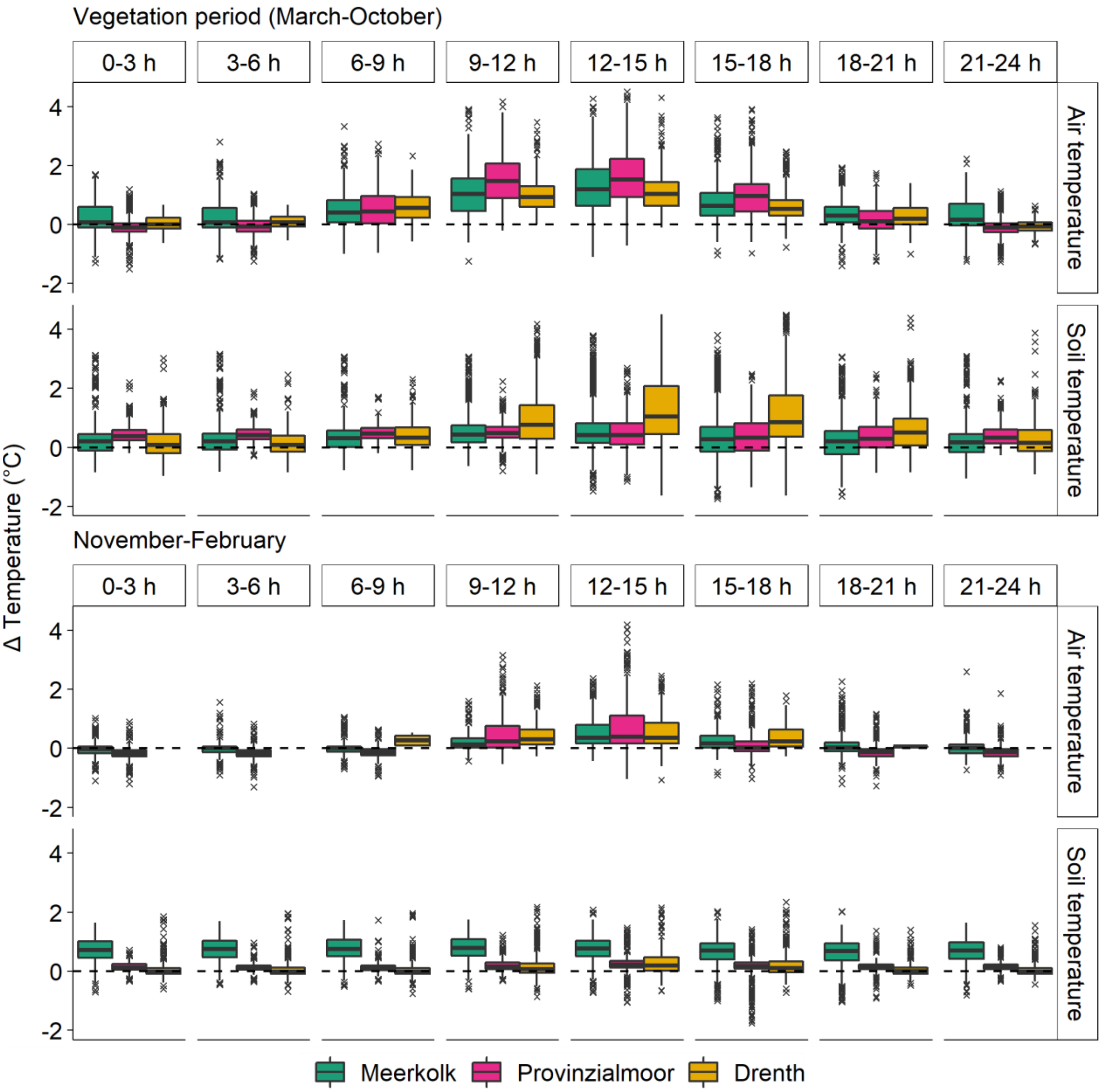

Fig. 4.1: Differences (warmed – control) of hourly air and soil temperatures (°C) at the near-natural area Meerkolk and the cultivation areas Provinzialmoor and Drenth. To improve the readability of the figure, high positive (> 4.5 °C, n = 62, max = 6.0 °C) and high negative (< −2 °C, n = 8, min = −3.4 °C) differences are not plotted; a direct comparison of the different areas is not possible due to differences in data gaps.

4.3.2 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 4.3). Accordingly, the topsoil of the cultivation areas dried out during summer (June–September) and water-filled pore spaces (WFPS ± SD) of 59 ± 10% and 84 ± 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 centimeters (Table 4.3).

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 ± 10% and 87 ± 12% were measured at the warmed and control plots. Similar values were recorded at Drenth, 87 ± 13% and 89 ± 12%, respectively. Differences between mean RH values of warmed and control plots were similarly small. At Meerkolk, 85.5 ± 21.0% and 86.1 ± 21.1% were measured, at Provinzialmoor 83.1 ± 21.4% and 82.9 ± 20.8% and at Drenth 81.3 ± 20.6% and 79.7 ± 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.

4.3.3 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 4.2). 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.

Table 4.2: Means and standard errors of biweekly measurements of pH and electronic conductivity (EC, $\mu S\ m^{-1}$), as well as concentrations ($mg\ l^{-1}$) of dissolved organic carbon (DOC) and ammonium (NH_4^+) of warmed and control sites. Asterisks indicate significance levels of treatment effect at each site (+: $p = 0.06$, *: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$).

	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 ± 5.2^{+}	111.8 ± 3.8	124.9 ± 7.2**
DOC	33.0 ± 2.2	30.3 ± 1.7*	68.5 ± 4.0	93.3 ± 5.3*	61.3 ± 3.3	63.2 ± 2.9
NH_4^+	0.48 ± 0.04	0.72 ± 0.06**	2.06 ± 0.25	2.26 ± 0.29	1.23 ± 0.23	1.56 ± 0.23***

4.3.4 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. 4.2). 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. At Povinzialmoor, 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).

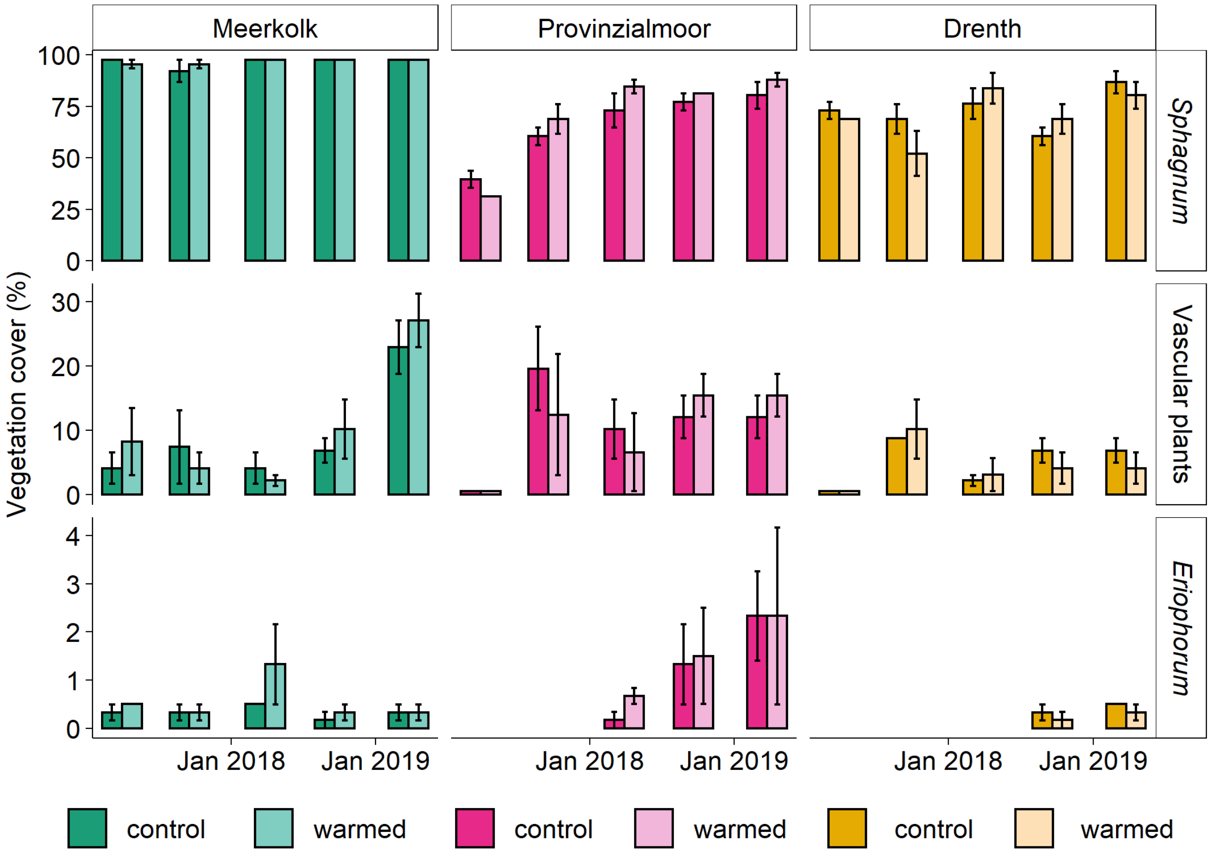

Fig. 4.2: Half-yearly survey of vegetation covers (means and standard errors of the 3 replicate plots) of the near-natural area Meerkolk and the two cultivation areas Provinzialmoor and Drenth. '*Eriophorum*' indicates the sum of *E. angustifolium* and *E. vaginatum*.

4.3.5 Greenhouse gas balances

Open Top Chambers increased total GHG emissions (t CO_2 eq. ha^{-1} yr^{-1}), i.e. the sum of CO_2, CH_4 and N_2O 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. 4.3a). At the near-natural site, this pattern was dominated by differences in the CH_4 exchange of warmed and control plots, while differences in NEE were dominant at the cultivation sites (Fig. 4.3b, 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 difference was higher at Provinzialmoor than at Meerkolk, while Drenth remained largely unaffected.

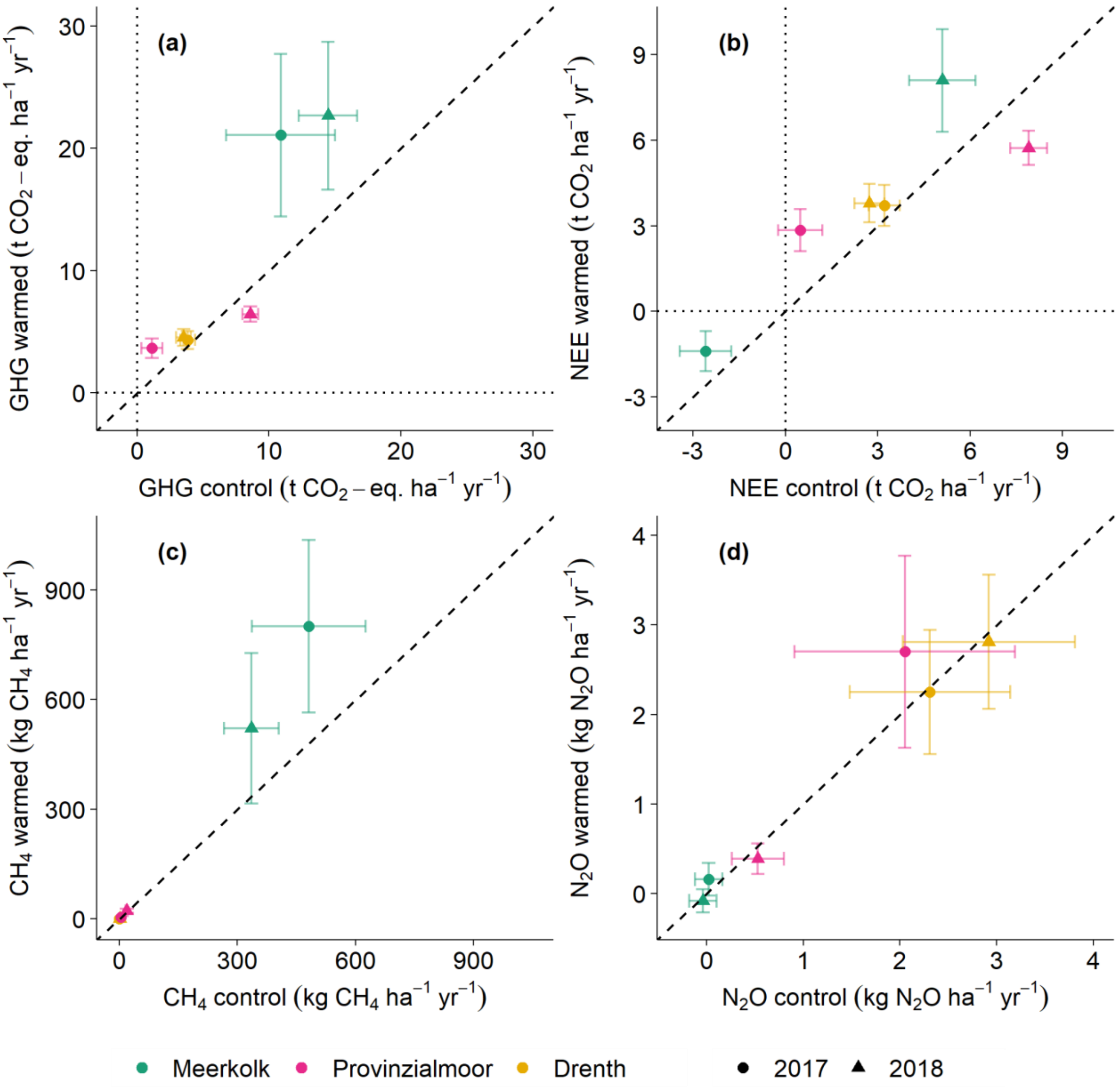

Fig. 4.3: Annual balances of total greenhouse gas exchange (GHG, t CO_2-eq. ha^{-1} yr^{-1}) (a), net ecosystem exchange (NEE, t CO_2 ha^{-1} yr^{-1}) (b), methane (CH_4) emissions (kg CH_4 ha^{-1} yr^{-1}) (c) and nitrous oxide (N_2O) emissions (kg N_2O ha^{-1} yr^{-1}) (d) of warmed and control sites. The dashed lines denote the 1:1 ratio.

4.3.5.1 Net ecosystem exchange

NEE of warmed plots was higher compared to the control plots with the exception of Provinzialmoor in 2018 (Fig. 4.3b). 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 4.3). 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 CO_2 to sources and strongly increased CO_2 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.

Table 4.3: 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	**T_{soil}**	**CH_4**	**N_2O**	**NEE**	**GPP**	**R_{eco}**	**GHG balance**
	m	**°C**	**kg CH_4 ha^{-1} yr^{-1}**	**kg N_2O ha^{-1} yr^{-1}**	**t CO_2 ha^{-1} yr^{-1}**	**t CO_2 ha^{-1} yr^{-1}**	**t CO_2 ha^{-1} yr^{-1}**	**t CO_2 eq. ha^{-1} 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

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 origin from the overall temperature differences than from parametrization (Fig. 4.4). 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.

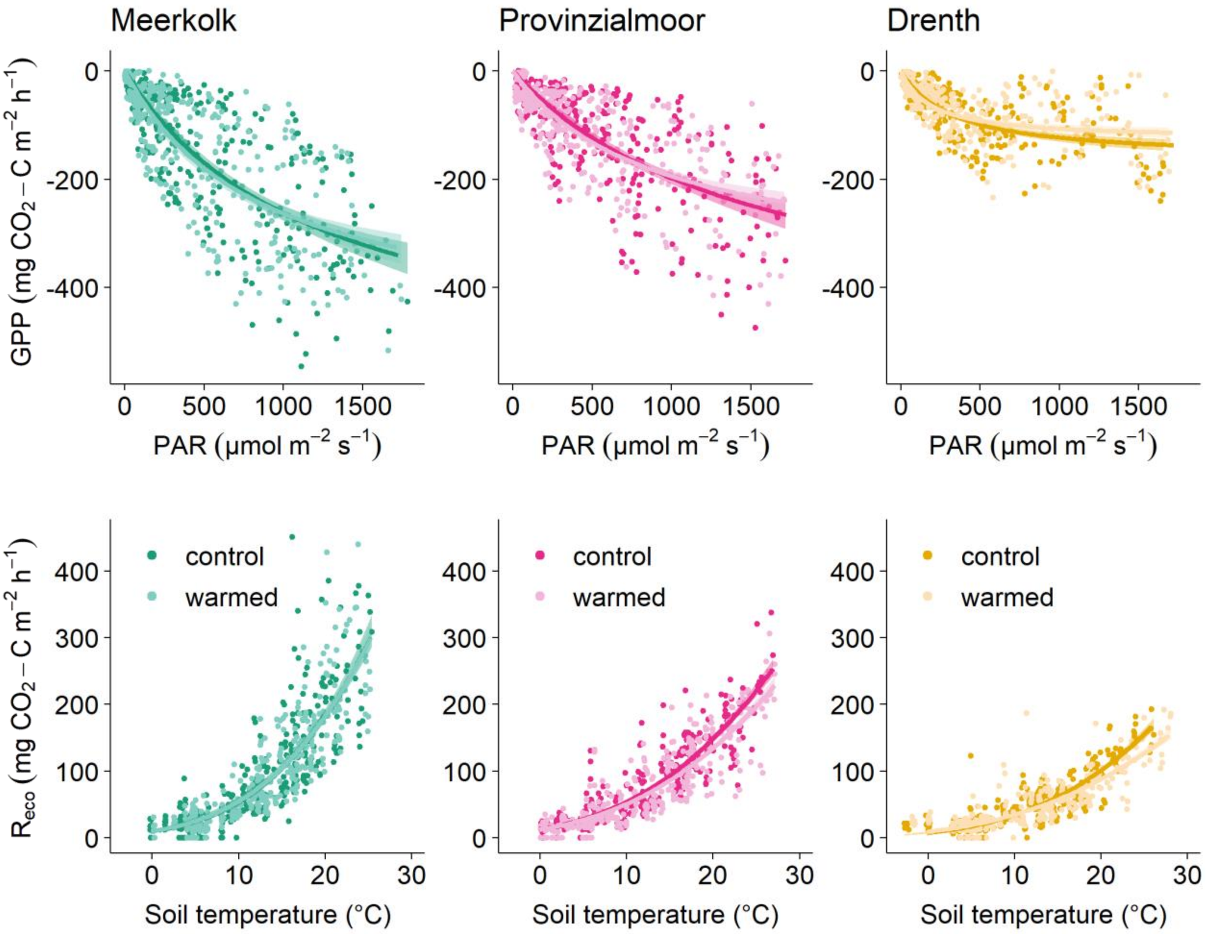

Fig. 4.4: Response functions relating gross primary production (GPP) to photosynthetically active radiation (PAR) and ecosystem respiration (R_{eco}) to soil temperature of warmed and control plots, pooling data of all campaigns. Ribbons indicate 2.5th and 97.5th percentiles of 1000 bootstrap runs; note that final balances were calculated using a campaign-based approach; at Meerkolk, one R_{eco} flux of the control site (639 mg CO_2-C) is not plotted to improve the readability of the figure.

4.3.5.2 Methane and nitrous oxide exchanges

Annual CH_4 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 N_2O exchange remained largely unaffected by warming, though OTCs slightly increased N_2O emissions at Provinzialmoor in 2017 (Fig. 4.3d). At Meerkolk, CH_4 emissions were lower in 2018 compared to 2017, while they clearly increased at Provinzialmoor (Fig. 4.3c, Table 4.3). 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. 4.5). 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. 4.2). 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.

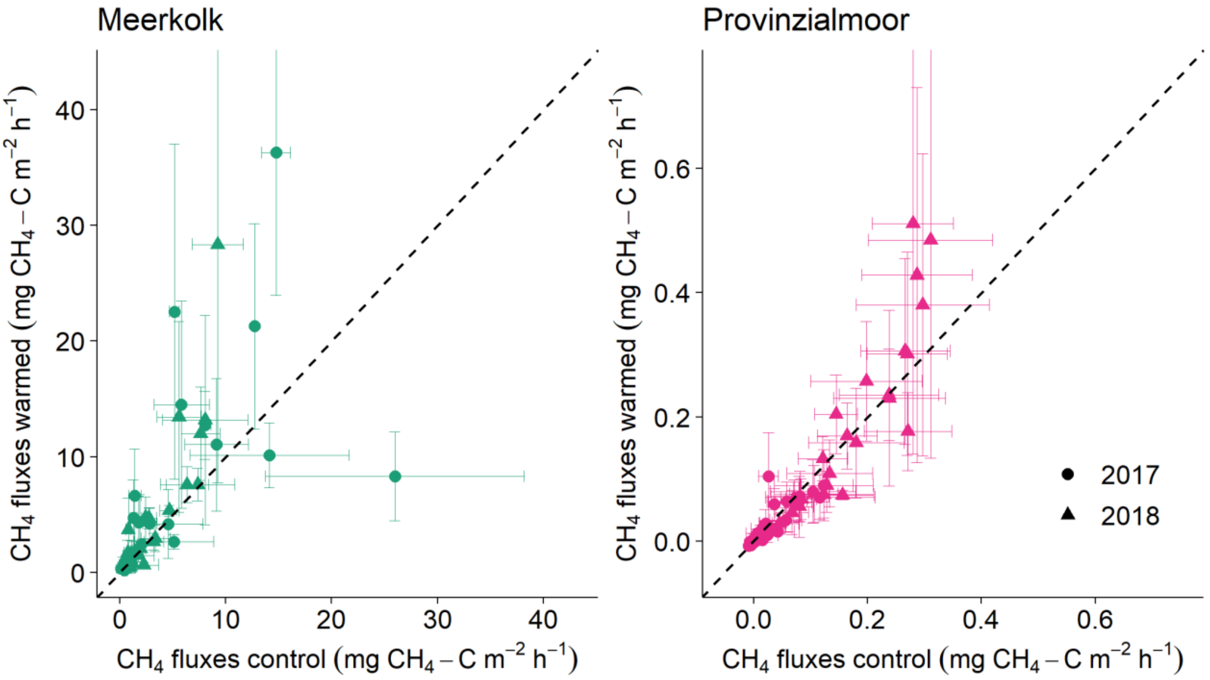

Fig. 4.5 Methane (CH_4) fluxes of warmed and control plots of single campaigns (means and standard errors of the three replicate plots) at the near-natural area Meerkolk and at the cultivation area Provinzialmoor. Fluxes at Drenth were small and are not shown in this figure.

4.4 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, 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 minimized alterations in light and precipitation intensities (Fig. A.1). 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 4.3.2). Finally, the response of R_{eco} and GPP to soil temperature and PAR, respectively, was almost identical at the warmed and control sites (Fig. 4.4), 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.

4.4.1 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 temperate 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 4.3).

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).

4.4.2 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 minimized 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 4.4.3).

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., 2022a), 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.

4.4.3 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 °C (Haraguchi and Yamada, 2011). This raises optimism for *Sphagnum* cultivation in a warmer climate given a sufficient water supply and a functioning acrotelm.

4.4.4 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 characterized 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 multiannual inundation of Provinzialmoor (Grobe et al., 2021). This hampers a comparison of the responses of differently irrigated cultivation sites to warming.

4.4.4.1 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 4.3).

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. 4.4) 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. 4.4). 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.

4.4.4.2 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., 2016a), 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 CH_4 exchange at the soil-atmosphere boundary, e.g. *Eriophorum* sp. (Samaritani et al., 2011; Greenup et al., 2000).

In 2018, CH_4 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 CH_4 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 N_2O emissions. In contrast, the cultivation areas with their developing vegetation and highly decomposed peat (Liu et al., 2019) emitted N_2O, 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 N_2O (Marushchak et al., 2011; Oestmann et al., 2022a).

4.4.5 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 CO_2 and CH_4 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 CH_4 emissions, making the control of vascular plants, which is current management practice for improving biomass quality, a measure for CH_4 reduction at paludiculture sites on ombrotrophic peat soil. Interestingly, increased emissions of CO_2 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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5 SHORT-TERM CARBON CYCLING AT A *SPHAGNUM* FARMING SITE UNDER DROUGHT STRESS

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ABSTRACT

Paludiculture is a new land use option for degraded peatlands, producing biomass under wet and peat preserving conditions. While previous studies indicate a significant greenhouse gas mitigation potential, the impact of bryophyte and vascular plant species on carbon cycling is not yet fully understood, especially under drought stress and climate warming conditions. In July 2018, we conducted a pulse labelling experiment at a *Sphagnum* farming area in Northwestern Germany to trace sequestered carbon dioxide ($^{13}CO_2$) in above-ground biomasses of peat mosses (*Sphagnum*) and dominant vascular plant species purple moor grass (*Molinia caerulea*), soil microbial biomass (C_{mic}), dissolved organic carbon (DOC), as well as dissolved and emitted CO_2 and methane under drought stress induced by summer drought and simulated climate warming using Open Top Chambers (OTCs). We observed fast label allocation to all investigated carbon pools with the exception of DOC. Although label uptake was clearly higher in *Molinia* compared to *Sphagnum*, most carbon was lost via respiration within a few days and the percentage of stored carbon after 140 days was clearly higher in *Sphagnum* and C_{mic}. Differences between warmed and control plots were small, presumably due to the already hot and dry conditions. Our results highlight that carbon uptake and storage processes are maintained even under extreme drought conditions, while further experimental warming using OTCs was less influential. The presented findings confirm the important role of *Sphagnum* in carbon retention and the risk of methane emissions even at low water levels via plant-mediated transport. Consequently, an elaborate irrigation management and control of vascular plants are the key to successful *Sphagnum* farming and GHG mitigation.

5.1 Introduction

Peatlands drained for agriculture and forestry release large amounts of carbon dioxide (CO_2) into the atmosphere (Leifeld and Menichetti, 2018). Paludiculture, which is the production of biomass under wet and peat preserving conditions in re-wetted peatlands aims at combining ecological and economic goals (Wichtmann et al., 2016). For ombrotrophic peatlands, peat mosses (*Sphagnum*) are the most promising paludiculture crop. Harvested *Sphagnum* can be used as substrate in horticulture (Emmel, 2008) or as donor material for peatland restoration (Quinty and Rochefort, 2003).

Due to their recalcitrant litter and the acidification of the surrounding environment, *Sphagnum* mosses play a key role in peat accumulation (Hobbie et al., 2000; Stivrins et al., 2017). However, the vegetation at *Sphagnum* farming sites is in a dynamic successional stage. Especially in the initial phase, this newly emerging ecosystem is highly vulnerable due to a not yet completely closed *Sphagnum* lawn. Vascular plants could intrude depending on site conditions and management. Under optimal conditions, gaps in the Sphagnum lawn close and abundances of vascular plants decrease. Still, *Sphagnum* mosses might be less competitive compared to vascular plants during droughts, as they possess no roots and rely on high and stable water levels (Buttler et al., 2015; Antala et al., 2022). For example, purple moor grass (*Molinia caerulea*) became dominant in some degraded peatlands in north-west Europe (Chambers et al., 2001), with possibly adverse effects on *Sphagnum* due to competition for light (Pilkington et al., 2021).

Greenhouse gas (GHG) balances of *Sphagnum* farming trials in Northwestern Germany indicate that these sites could quickly restore their function as sinks of atmospheric CO_2 under optimal conditions, i.e., high groundwater levels and little interference during the initial growth phase (Beyer and Höper, 2015; Günther et al., 2017; Oestmann et al., 2022a). While CO_2 emissions can generally be expected to decrease with rising water levels (Tiemeyer et al., 2020), methane (CH_4) emissions will increase (Abdalla et al., 2016; Evans et al., 2021), depending on management and vegetation (Wilson et al., 2009; Cooper et al., 2014). However, the longevity of CO_2 in the atmosphere makes a reduction of CO_2 emissions the most important goal of climate protection measures in peatlands (Günther et al., 2020). Nitrous oxide (N_2O) emissions might only play a larger role at poorly vegetated sites (Marushchak et al., 2011; Oestmann et al., 2022a).

The abundance of different plant functional groups affects short-term carbon (C) flux and GHG exchange (Ward et al., 2009; Gong et al., 2020). Vascular plants contribute substantially to C cycling processes (Crow and Wieder, 2005), although this impact depends on the respective process and the aggregation level of plant species and thus is difficult to be generalized (Dorrepaal, 2007). Altogether, they take up and allocate C faster compared to bryophytes and dead plant material is less recalcitrant to microbial decomposition. In addition, specialized vascular plants with aerenchymous tissues could enhance CH_4 emission even at low water level via plant-mediated transport of gases between rhizosphere and atmosphere (Oestmann et al., 2022b; Korrensalo et al., 2022).

As in the case of other ecosystems, the GHG balance of *Sphagnum* farming sites might be affected by climate change. Simulated climate warming conditions using Open Top Chambers (OTC) significantly increased GHG emissions at a near-natural bog and two *Sphagnum* farming areas in Northwestern Germany, governed rather by a decreased primary production than by increased ecosystem respiration, as well as by increased CH_4 emission due to higher abundances of aerenchymous vascular plants (Oestmann et al., 2022b).

More detailed information on C cycling at *Sphagnum* farming sites can be obtained from pulse labelling experiments using stable isotopes. Exposing plants to enriched CO_2 for a short time enables the tracing of sequestered C in plant biomass and subsequent C pools (Trinder et al., 2008; Studer et al., 2014). Trinder et al. (2008) were the first to apply this technique at an abandoned cutover peatland and found that three common vascular plant species (*Calluna vulgaris*, *Eriophorum angustifolium* and *Eriophorum vaginatum*) lost most of the assimilated label via shoot respiration and dissolved organic carbon (DOC), while root and peat respiration were small. For a subarctic tundra site, Street et al. (2013) demonstrated that *Sphagnum* increased ecosystem C use efficiency and retention, highlighting their important role in peat accumulation.

Despite the increasing importance of paludiculture for climate protection, the fate of plant assimilates and the longevity of the different C pools have not yet been closely followed. Understanding the contribution of different plant types to the allocation of fresh photosynthates is a prerequisite for developing adequate restoration measures and for optimizing *Sphagnum* farming. This is especially important during extreme events like droughts, which are expected to happen more frequently due to climate change (IPCC, 2021). In the present study, we are the first to address these questions for a paludiculture site using $^{13}CO_2$ pulse labelling.

The objective of this study was to shed light on the path of sequestered atmospheric C to the pools of bryophyte (*Sphagnum*) and vascular plant (*Molinia*) biomass, soil microbial biomass, dissolved C species in peat pore water and ecosystem respiration during the extreme event of the European heatwave 2018. In addition, the effect of simulated climate warming conditions on C allocation was investigated.

5.2 Materials and methods

5.2.1 Study area

The study area Provinzialmoor (52°40′ N, 07°06′ E) is a former industrial peat extraction site in Northwestern Germany, where the cultivation of peat mosses as a horticultural substrate (*Sphagnum* farming) is recently being tested. The climate is oceanic and average annual air temperature and precipitation are 9.8 °C and 791 mm, respectively (1971–2000, Lingen, German Climate Service). However, in 2018, 11.7 °C and only 561 mm were measured, as the European heatwave 2018 led to an extraordinary hot and dry summer and autumn. A more detailed site description and GHG balances are given in Oestmann et al. (2022a), while the effect of experimental passive warming on the GHG exchange over two years (March 2017 to March 2019) is described in Oestmann et al. (2022b). In brief, experimental warming increased CH_4 emissions in the study area. The overall increase in CO_2 emissions was masked by the cover of vascular plants, which was lower in the warmed plots in comparison to the control plots in the first measurement year (2017) and higher in the second (2018). This resulted in an increased gross primary production at the warmed plots in 2018, while R_{eco} was hardly affected.

The labelling experiment reported in the present study took place at the warmed ('P-MIX-W') and control ('P-MIX') sites of the warming experiment. Both sites consisted of three replicate plots (0.75 m × 0.75 m), which were randomly distributed along boardwalks in distances of about two to 3 m. In each plot, *Sphagnum* and *Molinia* grew in different abundances (Table 5.2). Passive warming was achieved using permanent hexagonal Open Top Chambers (OTC; 0.5 m height and 2.1 m chamber base width; Molau and Mølgaard, 1996), which were constructed from transparent polycarbonate (Makrolon 3 mm, 87% light transmittance, Bayer AG, Darmstadt, Germany) and increased air and soil temperatures by 0.5 ± 0.9 °C and 0.3 ± 0.4 °C (averaged over two years, Oestmann et al., 2022b).

After peat extraction ceased in 2008, the area was rewetted as a shallowly flooded polder. In 2015, the water table was lowered and in October 2016, a large-scale *Sphagnum* farming field trial was established by the moss layer transfer technique (Quinty and Rochefort, 2003). Moss fragments quickly developed into new moss plants and in 2018, the area was almost completely (>80%) covered by a *Sphagnum* lawn (mainly *Sphagnum papillosum* LINDB.) with scattered vascular plants (mainly *Molinia caerulea* L., as well as some *Eriophorum angustifolium* HONCK. and *Erica tetralix* L.). The site was irrigated via shallow ditches connected to several adjacent polders, designed to store excess winter precipitation for dry summer months. The highly decomposed peat layer had a thickness of about 0.8 m and was classified as Ombric Hemic Histosol (IUSS Working Group WRB, 2015).

5.2.2 Environmental conditions and vegetation survey

At each plot, air (0.20 m) and soil temperatures (-0.02 m) were recorded in half-hourly intervals. Water table depths (WTD) were measured at the warmed and control site using Mini-Divers in perforated dip wells close to the measurement plots and Baro-Divers for atmospheric pressure correction (Eijkelkamp, Giesbeek, The Netherlands). A nearby meteorological station (distance approximately 100 m) recorded air and soil temperatures and photosynthetically active radiation (PAR).

Covers of *Sphagnum* and *Molinia caerulea* were estimated using the Londo scale (Londo, 1976) every six months. Here, we use the data of September 2018, when additionally C contents of selected *Sphagnum* plants and *Molinia* leaves were measured by elemental analysis (LECO Corporation, St. Joseph, Michigan, USA). Further, leaf area index (LAI) and plant biomass dry weight (DW) were determined for *Sphagnum* and *Molinia* according to Wilson et al. (2007). First, total numbers of *Sphagnum* capitula and *Molinia* leaves were counted in 25 random sub-sample parcels (0.10 m × 0.10 m) per plot and extrapolated to the total plot area. For *Sphagnum*, leaf and stem areas of ten plants were determined by scanning. These values were extrapolated to the plot area using the total number of capitula per plot and the plot area to derive LAI (m^2 m^{-2}). For *Molinia* LAI, leaves were divided into seven size classes to account for the different individual leaf area per size class, scanned and extrapolated to the plot area. Mean DW were obtained by weighing 20 moss plants and 127 *Molinia* leaves (divided in 7 size classes) and extrapolating to plot area by multiplying with the total number of plants or leaves per plot. Belowground biomasses could not be determined due to ongoing GHG measurements.

5.2.3 Pulse labelling

On July 19th, 2018, i.e., approximately one and a half year after the installation of OTCs, all six plots were exposed to enriched carbon dioxide ($^{13}CO_2$, 99 at%, Sigma-Aldrich, Taufkirchen, Germany) for 5 h using transparent polycarbonate chambers (0.78 m × 0.78 m × 0.50 m). In a preliminary test, it was ensured that PAR was only slightly reduced by raised water vapor levels and that the temperature inside the chamber did not exceed a critical level of 40 °C. During labelling, CO_2 concentration inside the chambers was continuously monitored (LI-820, LI-COR, Lincoln, Nebraska, USA). $^{13}CO_2$ was injected (50 ml $^{13}CO_2$) into the chamber head space using three-way stopcocks and gas-tight syringes when concentrations fell below 350 ppm. As, despite all management efforts, WTDs fell far below optimum conditions for *Sphagnum* growth (partly >0.40 m below soil surface) due to the ongoing drought, plant C sequestration was lower than expected. Consequently, CO_2 concentrations in the chamber head space continuously rose to more than 1000 ppm in the second half of the labelling procedure. Thus, label was added approximately every half hour, in total 500 ml $^{13}CO_2$ per plot, which equals 0.265 g ^{13}C. This high amount of label was regarded sufficient to guarantee an uptake by both bryophytes and vascular plants given a mean daily gross primary production of 3.3 g CO_2-C m^{-2} in July 2018.

5.2.4 Tracing of enriched carbon in the investigated carbon pools

The C isotopic ratios of plant above-ground biomass, ecosystem respiration (R_{eco}), emitted methane (CH_4), soil microbial biomass (C_{mic}), as well as dissolved organic carbon (DOC) and dissolved gases (CO_2 and CH_4) in 10 cm and 30 cm depths were measured before label addition (day -1), 3 h (day 0) and 1, 2, 3, 5, 7, 10, 14 and 21 days after label addition (short-term C turnover), as well as 140 days thereafter (midterm storage of incorporated C). These sampling dates were chosen as the key period of short-term C turnover during which photosynthate is allocated to growth or respiration is about three weeks (Street et al., 2013; Kritzler et al., 2016). Between the end of labelling and the first sampling (day 0), plots were left to aerate for 3 h, to allow back diffusion of label from soil pores and plant interspace before the start of measurements. Sampling was always conducted at the same time of the day and plant biomass and peat were sampled at the end of each campaign. The disturbance of vegetation cover and soil surface was minimal, as only small amounts of plant biomass (about 0.1 g dry mass per sample) and peat (about 12 g dry mass per plot) were needed for analyses. Carbon isotopic signatures ($^{13}C/^{12}C$) of samples measured via isotopic ratio mass spectrometry (IRMS) were expressed using the delta notation ($\delta^{13}C$, ‰), i.e., by comparison to the reference standard (V-PDB).

Two to four single *Sphagnum* plants were sampled randomly from the plot area using tweezers and were further divided into the green living capitula (SPH_{Cap}, the upper 1 cm) and the remaining, less active parts (SPH_{Rem}). In addition, two to three leaves of *Molinia* (MOL) were cut. In December (day 140), MOL leaves were mostly dead and brown. All plant material was stored frozen until further analysis. In the laboratory, it was dried at 105 °C, ground in a ball mill and C isotopic compositions were measured from homogenized material using IRMS (Delta Plus, Thermo Fisher Scientific, Waltham, MA, USA).

For R_{eco} analysis, head space air was sampled from opaque white PVC chambers (0.78 m × 0.78 m × 0.50 m) into exetainers (Labco Ltd., Lampeter, UK) directly after placing the chambers and every 20 min thereafter (t_0, t_{20}, t_{40}, t_{60}, t_{80}). Directly after each CO_2 exetainer, 100 ml glass vials were filled for determining isotopic ratios of emitted CH_4. The C isotopic compositions of CO_2 and CH_4 as well as concentrations of CO_2 were determined at the Centre for Stable Isotope Research and Analysis of the University of Göttingen (KOSI) using IRMS (Delta plus XP, Thermo Fisher Scientific, Bremen, Germany). CH_4 concentrations were later measured from the same exetainers using a gas chromatograph (Shimadzu, Kyoto, Japan) equipped with a flame ionization detector. Isotopic signatures of R_{eco} and emitted CH_4 at the moment of sampling were determined as Keeling plot intercepts of the linear regression of the isotopic composition on the respective inverse value of gas concentration of the five consecutive head space samples (Pataki et al., 2003). In the case of CO_2, regressions with $R^2 < 0.9$ were discarded from further analyses. However, minimum R^2 was set to 0.75 at campaign day 140 (early December) due to low fluxes. For CH_4, minimum R^2 of the Keeling intercepts was set to 0.75 and two intercept values below -100‰ were additionally discarded.

Soil pore water samples were extracted from 10 cm to 30 cm depths using borosilicate glass suction plates (pore size about 1 µm; ecoTech GmbH, Bonn, Germany; connected via Teflon tubes). Subsamples for the measurement of DOC concentrations were stored cool until analysis (DimaTOC, 2000; Dimatec, Essen, Germany). The remaining water was stored frozen and later freeze dried to measure the isotopic composition of DOC using IRMS (Delta Plus). Due to the dry conditions, soil pore water accumulated slowly and the sampled amounts are assumed to represent the water accumulation during the preceding day. Some samples could not be taken at all. Before reaching glass collection bottles, the sampled soil pore water passed a glass vial inside the collection bottle closed with a gas-tight septum via an inlet and an outlet needle. Those were adjusted in such a way that about 9 ml of the 22 ml vial volume were filled with water. From these vials, dissolved CO_2 and CH_4 were extracted by overhead shaking until equilibrium (1 h), extracting 1 ml from the head space air to evacuated and nitrogen flushed exetainers using a gas-tight syringe (SGE, Trajan Scientific, Ringwood, Australia) and measuring isotopic ratios of CO_2 and CH_4 at the KOSI.

For soil microbial biomass, moist peat samples of about 60–80 g (upper 0.10 m) were taken using a cut off syringe and stored frozen. Before further analyses, samples were preincubated for 24 h at 8 °C and 12 h at 15 °C. Subsequently, larger roots were removed with tweezers and samples were roughly homogenized by hand. Extractable soil microbial biomass was determined by chloroform fumigation extraction (CFE), following the protocol of Vance et al. (1987), modified by Helfrich et al. (2008). For each peat sample, the water content of a subsample of about 5 g was determined overnight. The next day, the remaining peat was split in six subsamples, all corresponding to 2 g dry weight. Three of them were fumigated for 24 h using ethanol-free chloroform. The non-fumigated peat samples were diluted in 40 ml 0.05 M K_2SO_4, shaken for 1 h and filtered (8–12 µm, Sartorius, Göttingen, Germany). We used a higher dilution of K_2SO_4 than proposed by Vance et al. (1987) in order to prevent bias of isotopic analyses by salt load. The fumigated samples were treated as the non-fumigated at the next day. Finally, concentrations of organic C in the filtrate were determined (DimaTOC, 2000) and the remaining filtrate freeze-dried for ^{13}C analysis. Carbon contents per gram of dry soil of the fumigated and non-fumigated samples were calculated as follows:

$$\mu g\ C\ g^{-1}\ DS = \mu g\ C\ ml^{-1} * (40\ ml + WC) / DS \qquad [5.1]$$

where WC is the water content of sample (ml) and DS is the amount of dry soil (g). Extractable soil microbial biomass (C_{mic}, µg C per g dry soil) was calculated by subtracting the C contents of the non-fumigated samples from the fumigated samples. No correction factor for determining the exact amount of microbial biomass from extracted C amounts was applied due to the high uncertainty of this factor for organic soils (Joergensen, 1996; Helfrich et al., 2008). Therefore, we use the term extractable soil microbial biomass and stress that values cannot easily be compared with literature but are considered sufficient to compare warmed and control plots. Isotopic signatures of C_{mic} were calculated as:

$$\delta^{13}C_{mic} = (\delta^{13}C_F * C_F - \delta^{13}C_{NF} * C_{NF}) / C_{mic} \qquad [5.2]$$

where $\delta^{13}C$ and C are the isotopic signatures and C contents (µg C per g dry soil) of the fumigated and non-fumigated filtrates, respectively (Helfrich et al., 2008).

5.2.5 Isotopic signatures and mass balance calculations

For mass balance calculations, isotopic ratios were derived from $\delta^{13}C$ values and transformed to ^{13}C atom% values (abundances). Finally, ^{13}C abundances (atom%) before label addition (‘day -1’) were subtracted from each sample and C pool to derive excess 13C abundances (atom% excess).

The quantity of ^{13}C fixed during label addition by *Sphagnum* and *Molinia* plants was calculated by multiplying peak ^{13}C atom% excess values of plant biomass with the respective biomass in each plot (determined in September 2018) and average C contents of 44.2%, 42.6% and 45.1% for MOL, SPH_{Cap} and SPH_{Rem}. Accordingly, the amount of ^{13}C stored in plant and microbial biomass at day 140 was calculated and given as percentage of the initially fixed amount for MOL, SPH_{Cap}, SPH_{Rem} and C_{mic}.

Losses of fixed ^{13}C via R_{eco} were calculated by multiplying ^{13}C atom% excess values with the corresponding daily R_{eco} fluxes (g CO_2-C m^2 d^{-1}; Oestmann et al., 2022b) and summing up daily amounts. Gaps in isotopic ratios at days between sampling dates were filled by linear interpolation. Daily R_{eco} values were derived from monthly measurement campaigns using opaque chambers. The Lloyd Taylor function (Lloyd and Taylor, 1994) was fit to soil temperature and R_{eco} of each campaign. Time series were then interpolated by applying these functions to half-hourly soil temperature data (Oestmann et al., 2022b). Fluxes of CH_4 were determined for each campaign day from the five consecutive CH_4 concentrations using the calculation procedure described in Oestmann et al. (2022a). Daily CH_4 fluxes between campaign days were derived from linear interpolation.

5.2.6 Statistical analyses

Data analysis was conducted using R software (R Core Team, 2021). Differences in isotopic ratios of each C pool and site measured before labelling and at the end of the experiment were investigated using paired t-tests. For differences between two C pools or treatments (warmed, control) at a respective campaign day, Wilcoxon rank sum tests were used.

Further, we used linear mixed effect modelling (package ‘nlme’, Pinheiro et al., 2021) to investigate differences between time series of air and soil temperatures (hourly measurements) as well as of isotopic ratios of investigated C pools (campaign days) at warmed and control plots on a significance level of the likelihood ratio test of 0.05 (Zuur et al., 2009). For each comparison, 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. In both models, an autocorrelation structure of order 1 was applied, as well as a power variance function structure if it improved the model as indicated by a lower AIC value.

5.3 Results

5.3.1 Environmental conditions

The environmental conditions during the experiment were extraordinary hot and dry. Especially during the first 21 days, precipitation amounts were low, while temperatures were high (Fig. 5.1, Table 5.1). Only towards the end of the experiment, higher precipitation led to more favorable conditions for *Sphagnum* growth.

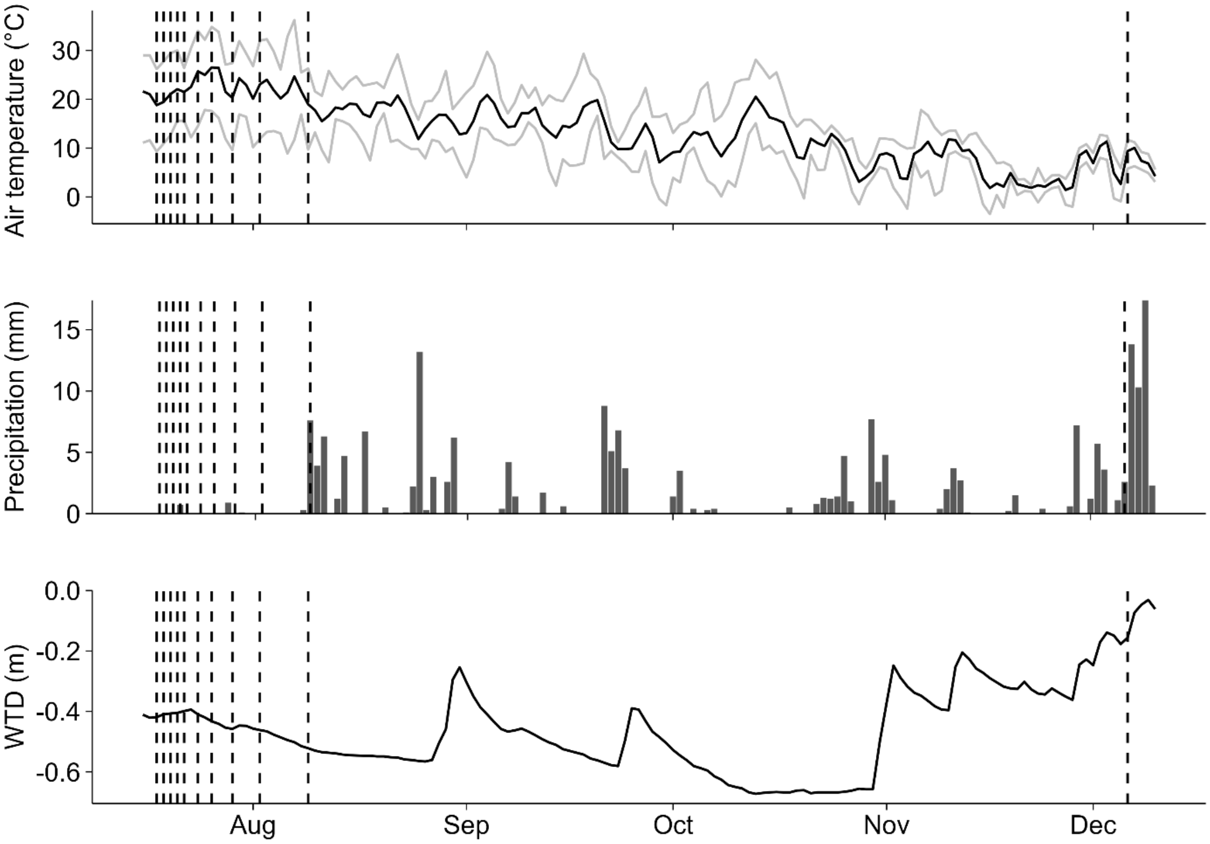

Fig. 5.1: Air temperature at the meteorological station (daily mean, minimum and maximum), precipitation (5 km distance to study area, German Climate Service) and daily mean water table depths (WTD) at the control site in 2018. The vertical dashed lines denote the sampling dates.

The already high air and soil temperatures were even increased in the warmed plots during all considered time spans of the experiment (Table 5.1) and this increase was more pronounced during daytime (PAR >0), when photosynthesis takes place. In contrast to air temperature, the increase in soil temperature was not significant. During the first 21 days, mean daily WTDs at the control site were 0.45 ± 0.04 m below soil surface, in December it was 0.09 ± 0.05 m. In particular, the upper peat layer dried out during summer.

Table 5.1: Air and soil temperatures (°C) of the warmed and control plots (means and standard deviations of hourly measurements) during the experiment (study period from 19th July 2018 to 6th December 2018). $T_{Air, Day}$ refers to daytime air temperatures (PAR >0). Superscript letters a and b indicate statistical significances of each comparison between warmed and control plots.

Time period	Site	T_{Air}	$T_{Air, Day}$	T_{Soil}
First 7 days	Warmed	25.9 ± 8.7^a	30.3 ± 7.2^a	23.4 ± 3.7^a
	Control	25.1 ± 7.9^b	28.9 ± 6.6^a	22.9 ± 3.7^a
First 21 days	Warmed	24.6 ± 9.1^a	29.6 ± 7.0^a	22.7 ± 3.6^a
	Control	23.6 ± 8.4^b	28.2 ± 6.4^b	22.2 ± 3.7^a
Study period	Warmed	14.1 ± 9.4^a	19.7 ± 9.2^a	13.7 ± 6.4^a
	Control	13.6 ± 8.9^b	18.7 ± 8.7^b	13.5 ± 6.4^a

5.3.2 Vegetation

In September 2018, mean (±SE) covers of *Sphagnum* sp., total vascular plants and *Molinia caerulea* in particular were 81 ± 0%, 15 ± 3% and 7 ± 5% at the warmed and 77 ± 3%, 12 ± 3% and 7 ± 2% at the control plots, while in the preceding vegetation survey (March 2018), *Molinia* cover had been lower in the warmed plots than in the control plots (6 ± 5% and 10 ± 4%). Mean leaf area index (LAI) and mean dry weight (DW) of *Sphagnum* was higher compared to MOL (Table 5.2). In contrast to mean covers, LAI_{MOL} and DW_{MOL}, as well as LAI_{SPH} and DW_{SPH}, were clearly lower in the warmed plots.

Table 5.2: Leaf area index (LAI, m^2 m^{-2}) and dry weight (DW, g m^{-2}) of *Sphagnum* (SPH) and *Molinia caerulea* (MOL) at the warmed and control site in September 2018 (means and standard errors of the three replicate plots).

Site	LAI_{SPH}	LAI_{MOL}	DW_{SPH}	DW_{MOL}
Warmed	4.2 ± 0.4	0.1 ± 0.1	149.0 ± 14.1	12.5 ± 7.8
Control	4.7 ± 0.6	0.4 ± 0.2	166.7 ± 20.5	58.2 ± 25.2

5.3.3 Carbon fluxes

In the first 21 days, daily R_{eco} fluxes ranged between 3.7 and 4.9 g C m^{-2} with negligible differences between warmed and control plots. At the end of the experiment, they were lower than 1 g C m^{-2}. In comparison to R_{eco}, CH_4 fluxes contributed only minorly to overall C fluxes (Table 5.3). Cumulative sums of daily R_{eco} and CH_4 fluxes at the warmed and control plots from July to December did barely differ (R_{eco}: 373 and 356 g C m^{-2}; CH_4: 0.9 and 0.7 g C m^{-2}).

Concentrations of DOC in the soil pore water ranged between 37 and 141 mg l^{-1}. They were higher in the upper peat horizon (10 cm) than in 30 cm depth in the first days of the experiment. Extractable soil microbial biomass (C_{mic}) was within a range of 200–1300 µg g^{-1} dry soil. The amounts varied between sampling campaigns from relatively low amounts end of July and early August (on average 320 µg) to higher amounts at days 21 and 140 (>1000 µg). Amounts of DOC and C_{mic} did not clearly differ between warmed and control plots.

Table 5.3: Mean (± SD) interpolated daily R_{eco} fluxes (g C m^{-2}) and daily CH_4 fluxes (mg C m^{-2}) as well as mean (± SD) concentrations of dissolved organic carbon (DOC; mg l^{-1}) in 10 and 30 cm depth and extractable microbial biomass (C_{mic}; µg g^{-1} dry soil) during measurement campaigns (n = number of samples per treatment and period). Several DOC values are missing due to dry conditions.

		R_{eco}	CH_4	DOC_{10}	DOC_{30}	C_{mic}
First 7 days	Warmed	4.7 ± 0.1^a	11 ± 0^a	106 ± 29^a	79 ± 16^a	358 ± 40^a
	Control	4.8 ± 0.1^a	7 ± 1^b	113 ± 18^a	80 ± 2^a	363 ± 87^a
		(n = 7)	(n = 7)	(n = 3)	(n = 3)	(n = 5)
First 21 days	Warmed	4.4 ± 0.3^a	11 ± 1^a	75 ± 37^a	81 ± 12^a	407 ± 237^a
	Control	4.5 ± 0.3^a	7 ± 1^b	86 ± 31^a	80 ± 2^a	424 ± 255^a
		(n = 21)	(n = 21)	(n = 5)	(n = 5)	(n = 8)
Study period	Warmed	2.6 ± 1.2^a	6 ± 2^a	72 ± 34^a	77 ± 14^a	516 ± 365^a
	Control	2.5 ± 1.2^a	5 ± 1^b	79 ± 30^a	75 ± 11^a	528 ± 363^a
		(n = 140)	(n = 140)	(n = 6)	(n = 6)	(n = 9)

5.3.4 Pattern of label uptake and allocation

Before label addition (day -1), the mean (±SE) C isotopic signatures of *Sphagnum* and *Molinia* above ground biomass of all plots was -27.2 ± 0.4‰ and -28.9 ± 0.2‰, respectively. Signatures of DOC and C_{mic} were -25.5 ± 0.2‰ and -23.4 ± 0.2‰, of R_{eco} and CH_4 they were -27.3 ± 0.2‰ and -79.8 ± 4.4‰. In 10 cm depth, signatures of dissolved CO_2 and CH_4 were -22.7 ± 0.1‰ and -30.3 ± 1.1‰, in 30 cm depth -18.4 ± 0.7‰ and -54.5 ± 10.3‰.

Samples of MOL leaves were highly enriched directly after labelling. In contrast, SPH_{Cap} and SPH_{Rem} showed low ^{13}C uptake with indistinct peaks distributed between 3 h and five days after label addition (Fig. 5.2). SPH_{Cap} was more enriched than SPH_{Rem}, although the temporal pattern of label concentration in both plant compartments was similar. The mean quantities of MOL and SPH (capitulum and remaining parts combined) label uptake at the control site were 56 ± 39 mg ^{13}C and 8 ± 1 mg ^{13}C, at the warmed plots it was 14 ± 13 mg ^{13}C and 7 ± 2 mg ^{13}C. The higher uptake of MOL at the control plots is a result of much higher LAI and DW (Table 5.2). In fact, the isotopic enrichment of MOL was higher in the warmed plots.

The concentration of ^{13}C in MOL leaves declined exponentially to about 25% of the initially taken up amount during the first three days and to about 10% in two weeks. In contrast, the decline in SPH ^{13}C enrichment was slow.

The highest R_{eco} ^{13}C abundance was measured 3 h after label addition. Similar to the pattern of MOL biomass, the ^{13}C values declined exponentially for about three weeks, although the enrichment was less than 10% of the peak value already at day 5. During the first 21 days, about 0.14 g ^{13}C was lost as R_{eco} per plot, which is slightly more than half of the applied label. The emitted CH_4 was also enriched in ^{13}C shortly after label addition, although far less than R_{eco}. Unfortunately, 27 of 66 CH_4 isotopic signatures are missing as the Keeling plots did not meet the required quality criterion ($R^2 < 0.75$).

The label reached the soil microbial community (C_{mic}) of the upper peat layer approximately two days after label addition. Label concentration remained relatively low and stable until it dropped to near prelabelling conditions at days 21 and 140.

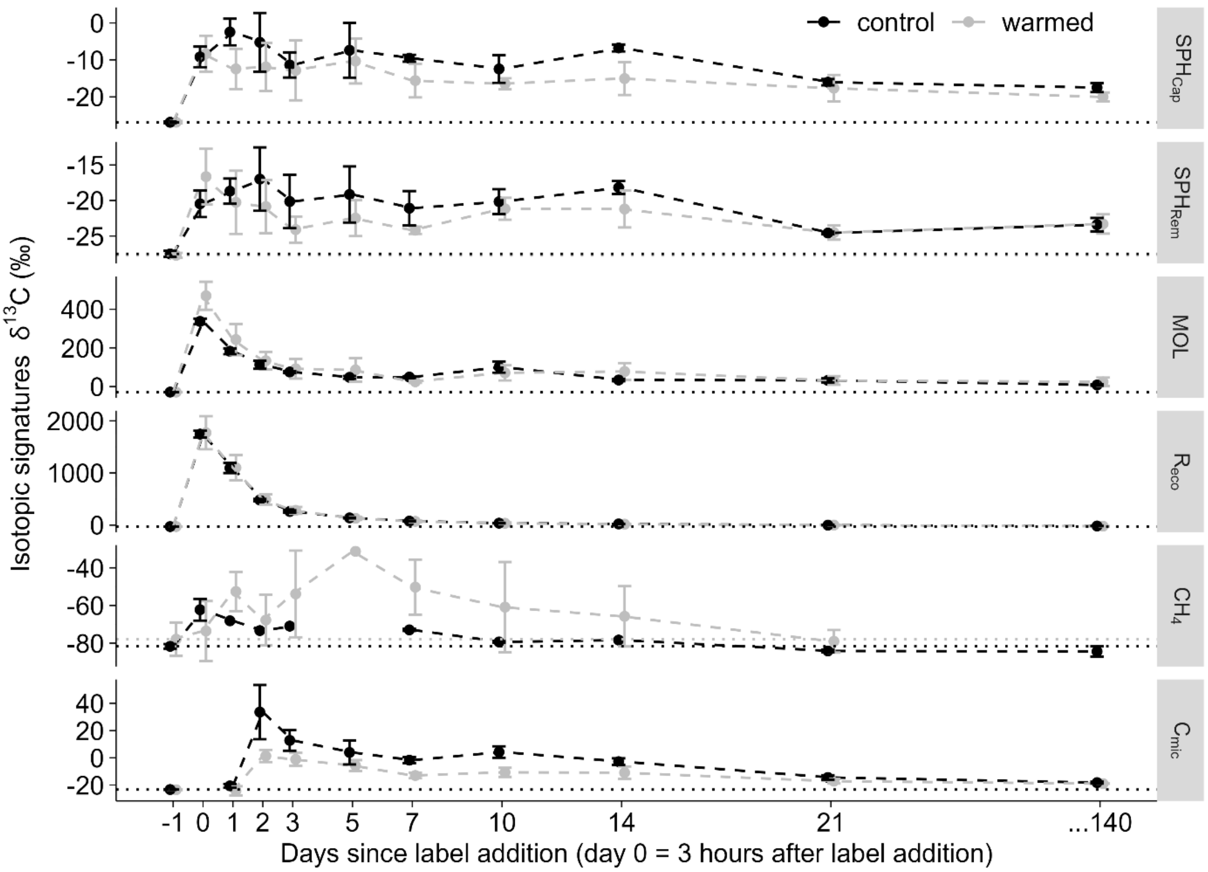

Fig. 5.2: Time series of isotopic signatures (means and standard errors of the three replicate plots) of the carbon pools *Sphagnum* capitulum (SPH$_{Cap}$), *Sphagnum* remaining parts (SPH$_{Rem}$), *Molinia caerulea* (MOL), ecosystem respiration (R$_{eco}$), emitted methane (CH$_4$) and extractable soil microbial biomass (C$_{mic}$). Dotted lines denote the pre-labelling ('day -1') signatures. Day 0 is the sampling directly after label addition (3 h). Note the time interval between sampling days 21 and 140.

The allocation of label to DOC was negligible (Fig. 5.3). However, the enrichment of dissolved CO$_2$ in 10 cm depth roughly followed aboveground patterns with high peaks in the first three days after label addition, while in 30 cm depth, the peak was far less pronounced. Isotopic signatures of dissolved CH$_4$ in 10 cm and 30 cm depth differed clearly from the signatures of emitted CH$_4$. In 30 cm depth, a distinct enrichment is visible during the first days after label addition, while enrichment in 10 cm depth showed no clear pattern.

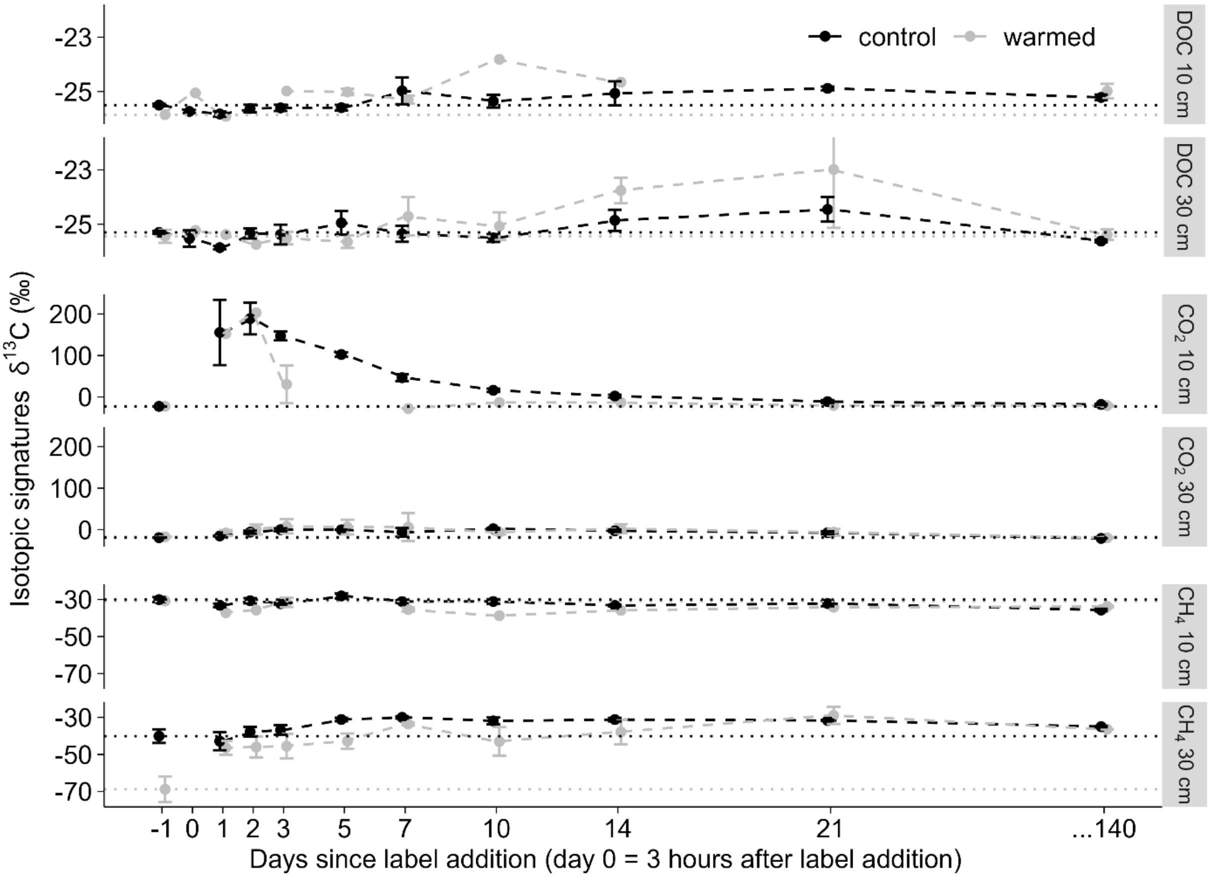

Fig. 5.3: Time series of isotopic signatures (means and standard errors of the three replicate plots) of dissolved organic carbon (DOC), dissolved carbon dioxide (CO_2) and dissolved methane (CH_4) in soil pore water at depths of 10 cm and 30 cm. Dotted lines denote the pre-labelling ('day -1') signatures. Day 0 is the sampling directly after label addition (3 h). Note the time interval between sampling days 21 and 140.

5.3.5 Effect of passive warming

At the warmed plots, SPH_{Cap} and SPH_{Rem} were less enriched compared to the control plots and MOL was more enriched, although differences between replicate plots were high (Fig. 5.4). MOL enrichment is in contrast to the smaller MOL ^{13}C uptake in the warmed plots resulting from the lower MOL biomass. While R_{eco} ^{13}C signatures did not differ between treatments, CH_4 fluxes were slightly more enriched at the warmed plots and C_{mic} clearly less. As shown by mixed effects modelling, differences between time series of isotopic ratios of warmed and control plots were only significant for MOL ($p < 0.05$) and C_{mic} ($p < 0.001$). In the case of SPH, this could be the result of the high variability between sampling days and replicates, while CH_4 could not be tested due to the high number of missing values.

The slightly higher enrichment of DOC in the warmed plots is more likely a result of missing replicate samples due to low WTDs. Dissolved gases in 10 cm depth could not be compared for the same reason. In 30 cm depth, dissolved CO_2 tended to be more enriched at the warmed plots and dissolved CH_4 slightly less (Fig. 5.3).

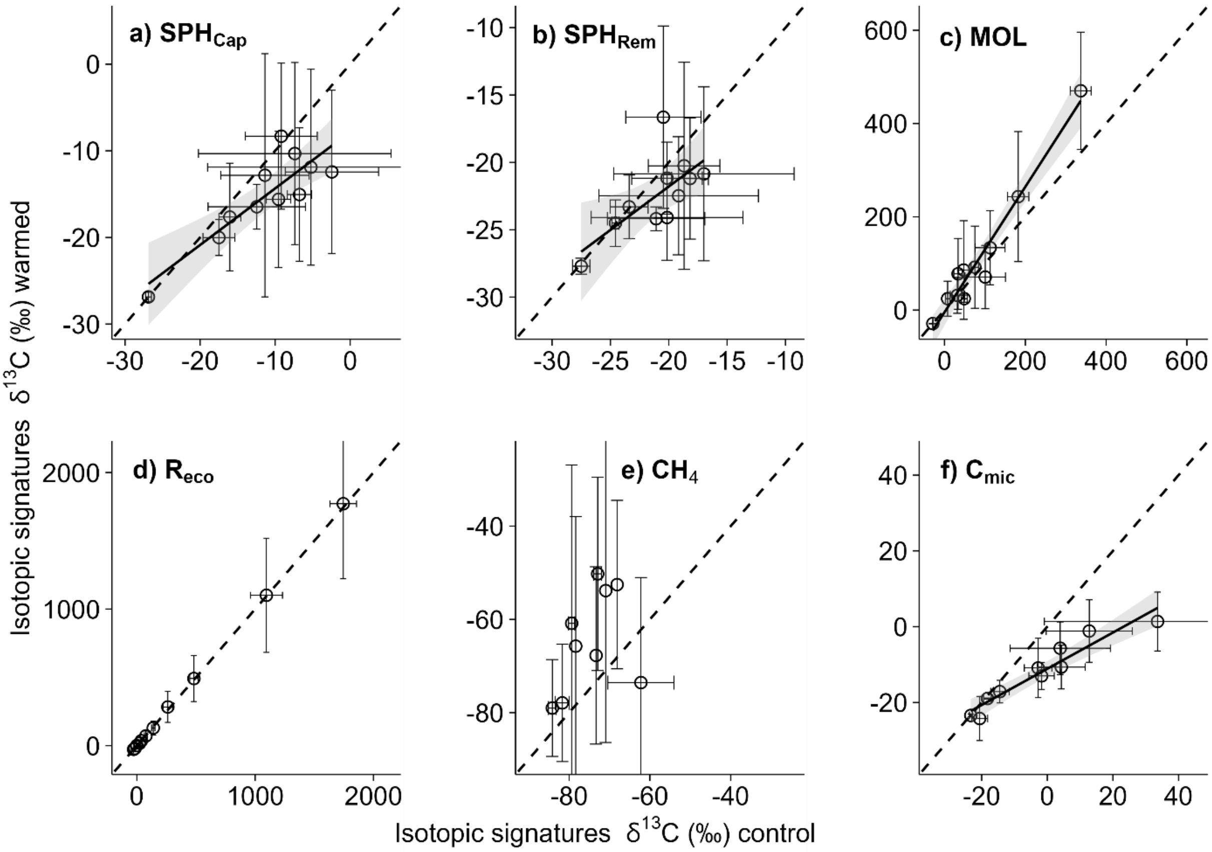

Fig. 5.4: Isotopic signatures (means and standard errors) of warmed and control plots for a) *Sphagnum* capitula (SPH_{Cap}), b) *Sphagnum* remaining parts (SPH_{Rem}), c) *Molinia caerulea* leaves (MOL), d) ecosystem respiration (R_{eco}), e) emitted methane (CH_4) and f) extractable soil microbial biomass (C_{mic}). The dashed lines denote the 1:1 ratio while the solid lines at SPH, MOL and C_{mic} represent a linear regression (confidence interval = 0.95).

5.3.6 Label recovery at the end of the experiment

At the end of the experiment (day 140), MOL, SPH_{Cap}, SPH_{Rem}, R_{eco} and C_{mic} were still significantly enriched compared to pre-labelling conditions (p-value < 0.01). Differences between warmed and control plots were not significant. Methane ratios could not be compared due to missing values.

Assuming a relatively constant biomass over the time course of the experiment, 33 ± 6%, 35 ± 4% and 10 ± 2% of the fixed ^{13}C (peak enrichment) was still incorporated in SPH_{Cap}, SPH_{Rem} and MOL leaves at day 140, respectively (Fig. 5.5). When considering the higher C_{mic} amounts at campaign day 140 compared to the campaigns of peak ^{13}C enrichment (on average 464 and 1267 µg per g dry soil), label recovery in C_{mic} was 53 ± 5% and 33 ± 19% at the warmed and control plots.

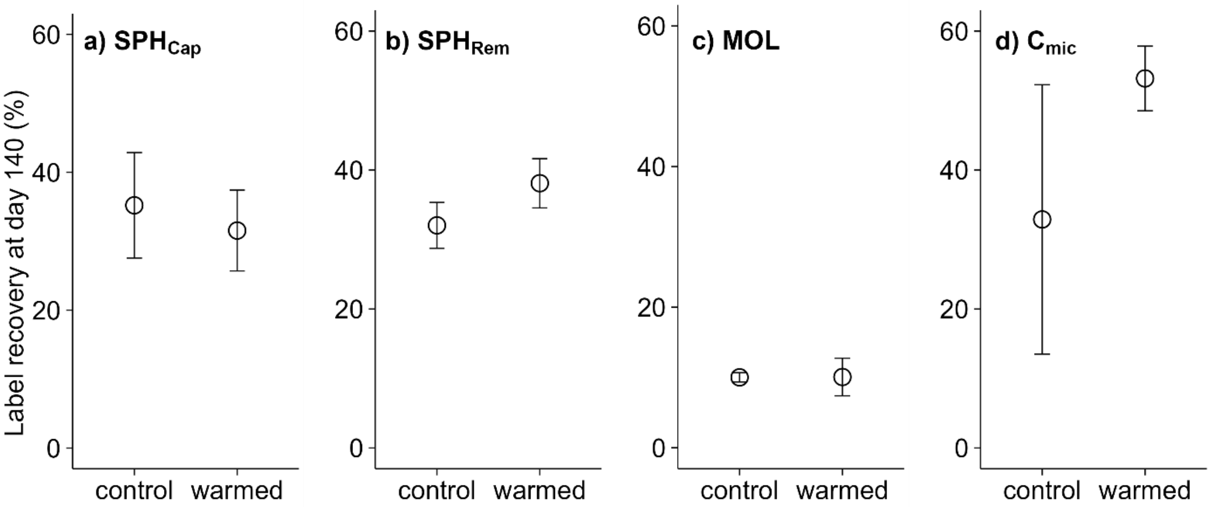

Fig. 5.5: Label recovery (means and standard errors of the three replicate plots) at the end of the experiment as percentage of the initial ^{13}C uptake for a) *Sphagnum* capitula (SPH_{Cap}), b) *Sphagnum* remaining parts (SPH_{Rem}), c) *Molinia caerulea* leaves (MOL) and d) extractable soil microbial biomass (C_{mic}).

5.4 Discussion

5.4.1 Label uptake and allocation

Our results shed light on C allocation in *Sphagnum* farming under drought and heat stress (European heatwave 2018 plus passive warming). Label uptake by Sphagnum (SPH), which temporarily became visibly pale and inactive, was low compared to the uptake by *Molinia caerulea* (MOL). Possessing roots, *Molinia* was able to connect to deeper peat layers with higher moisture and assimilated substantial amounts of $^{13}CO_2$ despite drought conditions. Highest ^{13}C uptake in graminoid leaf tissue and low uptake by bryophytes were also reported in a plant removal study of Ward et al. (2009). However, under controlled laboratory conditions and constant high water levels, Fenner et al. (2004) found considerably higher label uptake in *Sphagnum* capitula, which underlines the severe impact of drought on *Sphagnum* metabolism at our sites. The stable SPH enrichment during the first three weeks in contrast to the exponential decline in MOL might hint towards reassimilation of respired pulse-derived CO_2 (Fenner et al., 2004; Turetsky and Wieder, 1999) or more likely to the allocation of label to more recalcitrant pools. The higher enrichment of SPH_{Cap} compared to SPH_{Rem} fits to the decreasing photosynthesis from *Sphagnum* capitulum to lower parts (Fenner et al., 2004).

A large share of assimilated label was lost via respiration within days. Although the experimental design did not allow for a separation of autotrophic and heterotrophic respiration and the exact contribution of SPH and MOL to R_{eco} remains unknown, the comparison of time series of isotopic ratios clearly indicates a relation of R_{eco} and MOL. It has to be noted here that further plant species in the measurement plots contributed to R_{eco}. Although there might have additionally been back diffusion of label from soil pore spaces during the first hours (Fenner et al., 2004; Subke et al., 2009), this should have been minimized by the aeration of plots after label addition.

Ecosystem respiration is majorly affected by drought conditions, which are complex. At very low moisture contents, plant respiration is reduced (Street et al., 2013). While light droughts increase heterotrophic respiration (Kritzler et al., 2016), severe droughts will additionally reduce microbial growth and activity due to lack of water (Mäkiranta et al., 2009; Moyano et al., 2013). This was also probably the case at our site as C_{mic} increased towards the end when conditions became wetter.

The allocation of label to methanogenesis was low compared to R_{eco} and the results are difficult to interpret due to the high number of missing values and due to the wide range of C isotope ratios in wetland CH_4, resulting from isotope fractionation by methanogens of 20–60‰ (Shoemaker and Schrag, 2010). Hornibrook (2009) reports ratios from -100‰ for CH_4 emitted via aerenchymous transport to -42‰ and higher for dissolved CH_4 remaining after preferential loss of $^{12}CH_4$, which roughly fits to the pre-labelling ratios of dissolved and emitted CH_4 in our study. However, uncertainty in discussing the isotopic ratios of dissolved gases might arise from the fact that the described sampling procedure is novel and lacking comparative studies. In particular, the depletion of pre-labelling ratios of dissolved CH_4 seems to be very low.

Unger et al. (2021) found at a restored temperate fen that the 2018 European drought negatively affected methanogen abundance and increased methanotroph abundance. The relatively fast allocation of C to CH_4 emission within hours is therefore surprising but not implausible as plant-derived C can be converted rapidly to CH_4 (King et al., 2002). The increasing enrichment of dissolved CH_4 in 30 cm depth indicates ongoing methanogenesis in deeper peat layers. The enrichment of emitted CH_4 further hints towards the important role of plant-mediated CH_4 transport during drought (White et al., 2023). As *Molinia* was the dominant vascular plant during the experiment, we chose this species for analyses, but there were other vascular species such as *Eriophorum* in some plots. The plot with the highest *Eriophorum* cover (*E. vaginatum* + *E. angustifolium*) showed highest CH_4 fluxes and highest CH_4 enrichment, at the other plots this relation was inconsistent. In contrast to previous studies (Leroy et al., 2019), *Molinia* seemed to have no effect on CH_4, indicated by higher CH_4 emission and enrichment at the warmed plots despite lower mean LAI.

The production of DOC was obviously decoupled from C allocation in the present study. Above ground plant biomass and soil microbial biomass were significantly enriched after labelling, but DOC was not. This contrast to similar studies (King et al., 2002; Fenner et al., 2004; Trinder et al., 2008) could possibly be explained by the high and stable water level in these studies. However, the most obvious explanation is that bulk DOC at our site is originating from peat mineralization rather than plant derived C. The study site was characterized by a high degree of peat decomposition, which is known to result in high DOC concentrations (Frank et al., 2014) which might result in low amounts of fresh (and labelled) plant exudates being invisible. Further, ^{14}C studies have shown that DOC of highly decomposed peat is ‘old’ compared to DOC in more natural sites and thus not necessarily dominated by recent input (Hulatt et al., 2014; Kalbitz et al., 2000). In contrast to DOC, the enrichment of dissolved CO_2 in 10 cm depth was significant. Peak enrichment in dissolved CO_2 was earlier than in C_{mic}, pointing towards root respiration as main source at least in the first hours while the possible diffusion of label into soil during labelling needs to be also considered. The much less enriched dissolved CO_2 in 30 cm depth might be a result of a low rooting density.

The label reached the microbial biomass of the upper peat layer (C_{mic}) with a delay of about two days. Enrichment remained relatively stable during the first two weeks. The enrichment of C_{mic} is in contrast to the missing enrichment of DOC and might be the result of diffusive flow of label into the soil (Zeh et al., 2021), plant-mediated transport of enriched CO_2 or small amounts of rapidly metabolized plant exudates (Tavi et al., 2013), which were not captured in DOC.

5.4.2 Impact of warming on carbon allocation

When discussing the warming effect, it has to be considered that passive warming via OTCs started one and a half year prior to the labelling experiment (in March 2017) with possible medium-term effects on C cycling processes. Still, the effect of warming on C allocation and storage was rather marginal despite distinct differences in air and soil temperatures. This might be due to the already extraordinary hot and dry conditions in 2018 and the interaction of temperature and soil moisture, i.e., warming effects might have been more pronounced under optimum moisture conditions (Aerts, 2006; Mäkiranta et al., 2009).

The higher enrichment of MOL at the warmed plots in contrast to the lower enrichment of SPH underlines the higher competitivity of *Molinia* during drought and climate warming conditions. Although the special micro environmental conditions created by the OTC panels, i.e., shelter from excess wind, might have additionally affected plant activity, the results highlight that future warming and prolonged dry periods could increase the abundance of vascular plants (Munir et al., 2015) possibly at the expense of reduced *Sphagnum* (Norby et al., 2019).

The warming experiment described in Oestmann et al. (2022b) revealed that warming did not affect or even slightly decreased annual R_{eco} sums at the study area. However, the warming effect was interwoven with ongoing vegetation succession and prolonged dry periods. In addition, the present study found no significant impact of warming on C isotopic ratios of R_{eco} despite slightly higher covers of total vegetation and vascular plants.

Warming might increase CH_4 emission at degraded peatlands even during dry periods (Oestmann et al., 2022b), presumably via plant-mediated transport from the rooting zone to the atmosphere (Dorodnikov et al., 2011). This mechanism could also be the reason for the higher CH_4 enrichment at the warmed plots, as mean covers of vascular plants and *Eriophorum* in particular were slightly higher here.

The lower ^{13}C allocation to C_{mic} at the warmed plots could be a result of the lower amounts of assimilated ^{13}C by MOL and SPH and also fits to the lower enrichment of dissolved CO_2 in 10 cm depth. In addition, Zeh et al. (2021) report that higher temperatures can decrease the path of fresh plant assimilates into the soil due to lower root biomass or reduced belowground allocation.

5.4.3 Longevity of carbon pools

A smaller fraction of applied ^{13}C was incorporated into more stable biomass products. When discussing the high percentage of retained C in C_{mic}, the much lower soil microbial biomass during the first days compared to the end of the experiment has to be considered. However, similar values have been reported for a wide range of biomes (Qiao et al., 2019).

The fast C turnover in MOL as indicated by the high label uptake and subsequent exponential decay is in contrast to the slower turnover and long residence time of sequestered C in SPH. Unfortunately, belowground biomass of MOL could not be determined due to ongoing measurements. *Molinia* develops deep roots and bulbous internodes, which might have also stored sequestered label or translocated it to C_{mic}. Peat mosses nevertheless stand out by the high percentage of fixed C after 140 days, which highlights their important function as ecosystem engineers also at degraded peatlands with a missing functioning acrotelm. Although previous studies (Fenner et al., 2004; Street et al., 2013; Woodin et al., 2009) report higher values under more favorable conditions, our results underline the resilience of *Sphagnum* C retention even under drought and heat stress.

5.4.4 Implications for future *Sphagnum* farming

Altogether, the results of the present study illustrate the need to closely monitor restoration attempts and paludiculture sites with respect to the complex impacts of climate warming. In order to maximize its potential, *Sphagnum* farming as a newly emerging land use option and ecosystem will have to cope with heat events and irregular precipitation. Insufficient water supply will trigger adverse effects, increasing the risk of higher vascular plant abundance (Mäkiranta et al., 2017) and possibly reducing C sink strength (Woodin et al., 2009). However, the recreation of the peat moss lawn half a year after the European heatwave 2018 indicates that *Sphagnum* farming is resilient against extreme climate events to a certain degree. Our results further highlight, that C uptake and storage processes are maintained even under these extreme conditions.

ACKNOWLEDGEMENTS

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6 SYNTHESIS

6.1 Feasibility of *Sphagnum* farming on highly decomposed peat

This research scientifically evaluated the first large-scale attempt of *Sphagnum* farming on highly decomposed peat remaining after industrial peat extraction in Northwestern Germany (Graf et al., 2017). The presented findings on the GHG exchange are an integrative part of the joint project of the substrate manufacturer Klasmann-Deilmann GmbH, the Institute of Environmental Planning at the Leibniz University Hannover and the Thünen Institute of Climate-Smart Agriculture. The findings on the GHG exchange were structured in three individual publications, which are comprehensively consolidated and discussed in the following chapters.

Altogether, the feasibility of *Sphagnum* farming on highly decomposed peat and the ability of *Sphagnum* to rapidly form a dense lawn under these difficult conditions could be demonstrated successfully (Grobe et al., 2021). Grobe et al. (2021) describe the development of plant biomass in detail, although it is important to clarify that their results differ slightly from the vegetation development described in this thesis, as they investigated the whole cultivation area and I focused on the GHG measurement plots only. The low overall biomass development at the cultivation sites of 0.3 to 0.8 tons of dry mass per hectare and year might be interpreted as a result of the adverse hydrological conditions of the highly decomposed peat and temporary insufficient water availability. The additional effect of the extraordinary hot and dry summer 2018 and the implications for *Sphagnum* farming will be summarized in chapter 6.4 and 6.5. Further, the mentioned shortcomings during the initial phase of site establishment at Drenth and undiscovered drainage pipes at Provinzialmoor contributed to the observed low biomass development.

Pouliot et al. (2015) also estimated a relatively low mean *Sphagnum* productivity of about 1.5 tons of dry mass per hectare and year for a Canadian *Sphagnum* farming trial and attributed this to a low water supply. Still, it has to be mentioned here that *Sphagnum* productivity might increase after an initial phase, indicated by lower dry biomass accumulation (mean value 1.0 t ha^{-1} yr^{-1}) during the first three years and higher accumulation (mean value 3.7 t ha^{-1} yr^{-1}) thereafter at another *Sphagnum* farming area in Northwestern Germany (Gaudig et al., 2017).

Further, the establishment of the cultivation areas lead to a reintroduction of typical bog flora (Grobe et al., 2021) and fauna (Zoch and Reich, 2020; Zoch et al., 2023) in addition to the generated GHG mitigation potential. These findings on large-scale *Sphagnum* farming on highly decomposed peat are a new piece of the puzzle in peatland research (Wichmann et al., 2017).

6.2 The greenhouse gas mitigation potential of *Sphagnum* farming on highly decomposed peat

Summing up the main conclusions of the individual publications, I found that *Sphagnum* farming on highly decomposed peat provides a considerable GHG mitigation potential. Peatland restoration is a powerful measure to mitigate GHG emissions (Mander et al., 2024) and beyond doubt, *Sphagnum* farming by spreading *Sphagnum* biomass and regulating water levels accelerates the development of a functioning acrotelm at former peat extraction sites and thus C retention. My results underline that this also holds true on highly decomposed peat. A high degree of peat decomposition affects water transport through the peat layer and water availability to plants (Liu and Lennartz, 2019; Gaudig et al., 2017) and consequently all three parts of the presented research. Therefore, *Sphagnum* development and GHG mitigation were smaller compared to studies on less decomposed peat. In contrast to the uptake between

-2.3 and -8.6 t CO_2-eq. ha^{-1} yr^{-1} reported by Beyer and Höper (2015) and Günther et al. (2017), the site-specific GHG exchange at Provinzialmoor and Drenth ranged between -1.8 and 11.1 t CO_2-eq. ha^{-1} yr^{-1} (Fig. 6.1). This discrepancy is in accordance with lower annual mean water table depths (WTD) at Provinzialmoor and Drenth in comparison to the sites investigated by Beyer and Höper (2015) and Günther et al. (2017) and with the low degree of peat decomposition at the latter (Daun et al., 2023), where a high hydraulic conductivity of the surface peat enabled constant high water levels even during dry periods (Brust et al., 2018; Daun et al., 2023). Beyer and Höper (2015) and Günther et al. (2017) estimate that *Sphagnum* farming will be almost climate-neutral or a small GHG source when including the emissions of dams and open water surfaces and the C export of the harvested biomass. Finally, Daun et al. (2023) report a full-cycle balance of 10.7 t CO_2-eq. ha^{-1} yr^{-1} seven years after establishment for the sites investigated by Günther et al. (2017) and stress that more than half of this amount might be reduced by smaller causeways, roughly confirming the areal balances calculated for Provinzialmoor and Drenth (5.3 to 8.9 t CO_2-eq. ha^{-1} yr^{-1}).

Interestingly, Daun et al. (2023) report an average annual dry mass accumulation corresponding to about 3.3 t CO_2 ha^{-1} yr^{-1}, more than twice as much as estimated for Provinzialmoor (mean of all sites), but a comparably high emission per harvested ton of dry *Sphagnum* biomass as a result of the high contribution of causeways to their overall GHG balance, further highlighting the need to optimize *Sphagnum* farming designs. Altogether, the above cited studies and the results of my measurements show that GHG mitigation will be considerably increased by maximizing the actual cultivation area in minimizing the area of irrigation and dams, as outlined in detail in chapter 6.5.

Using a conceptual model including the most common restoration pathways and considering short-term C uptake and long-term C storage, Mander et al. (2024) even conclude that *Sphagnum* farming potentially shows the highest CO_2 capture, higher than rewetted areas in general. In addition, they found that CH_4 emissions were lower compared to rewetting in general and N_2O emissions were negligible, underlining the potential of *Sphagnum* farming as a peatland restoration and climate protection measure. Considering the rapid development of the northern part of the Provinzialmoor area (in particular site P-PAP) towards a sink of atmospheric CO_2, it could be argued that the GHG exchange of *Sphagnum* farming on highly decomposed peat would more resemble the results at less decomposed sites under more favorable conditions such as better water availability and less disturbance in the initial phase. Nevertheless, more than twenty tons of CO_2 equivalents have been already saved at the cultivation sites per hectare and year compared to conventional agriculture on organic soils (Tiemeyer et al., 2020).

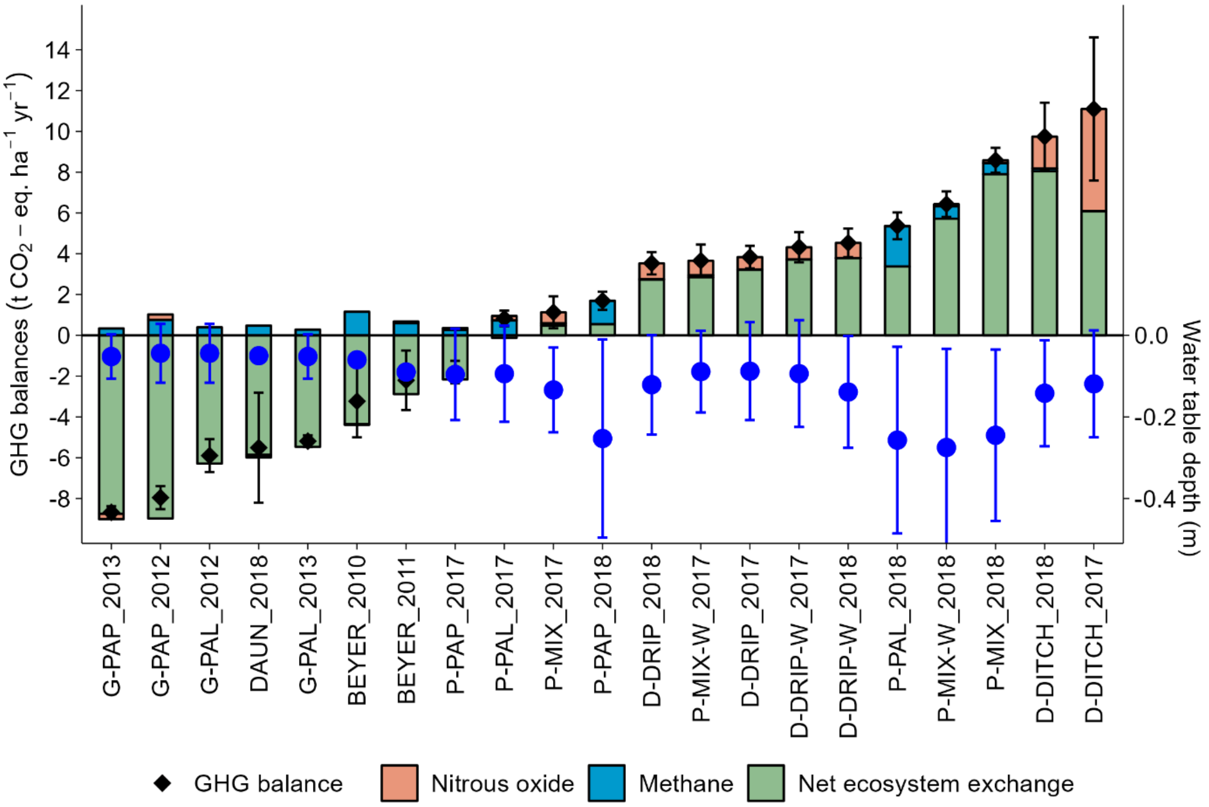

Fig. 6.1: Site-specific greenhouse gas (GHG) balances (± standard error) and respective annual mean water table depths (± standard deviation) of all cultivation sites, as well as of previous studies. D-DITCH, D-DRIP and D-DRIP-W refer to the ditch irrigation, drip irrigation and warmed site at Drenth, while P-MIX, P-MIX-W, P-PAL and P-PAP denote the control and warmed sites at Provinzialmoor, as well as the sites inoculated with *Sphagnum palustre* and *Sphagnum papillosum*. BEYER refers to the results of Beyer and Höper (2015; six and seven years after site establishment), G-PAL and G-PAP refer to the sites investigated by Günther et al. (2017; one and two years after site establishment) inoculated with *Sphagnum palustre* and *Sphagnum papillosum* and DAUN refers to the results of Daun et al. (2023; seven years after establishment). Note the high GHG emissions at D-DITCH despite moderate water levels due to a poor vegetation development, as well as the minor emission at site P-PAP despite low water levels in 2018.

Although the pulse labelling experiment revealed an ongoing C sequestration and storage in *Sphagnum* biomass even during an extreme drought event, the GHG mitigation of *Sphagnum* farming potentially decreases with climate warming, as indicated by generally increased emissions of CO$_2$ and CH$_4$ at the warmed plots. Here, it is worth mentioning that Bockermann et al. (2024) report a stable GHG mitigation potential for a rewetted grassland paludiculture, as experimental warming increased emissions at the rewetted and control site. In contrast to the cultivation sites, the GHG emissions at the near-natural area were surprisingly high (10.9 ± 4.1 t CO$_2$-eq. ha^{-1} yr^{-1} and 14.5 ± 2.2 t CO$_2$-eq. ha^{-1} yr^{-1} at site M-NAT in 2017 and 2018), mainly governed by CH$_4$. Still, site M-NAT was a net C sink in the first measurement year. It has to be further emphasized that the near-natural sites should not be interpreted as a control to the cultivation sites but as independent results complementing the findings at the cultivation sites. Near-natural areas are irreplaceable in terms of biodiversity conservation and C retention.

The GHG balance of *Sphagnum* farming on highly decomposed peat is governed by three main drivers, which are discussed in the following sections.

6.3 The main environmental drivers controlling greenhouse gas mitigation

6.3.1 Water availability

Water availability and the resulting redox potential is the most important driver of GHG emission at peatlands (Limpens et al., 2008) and the key to a successful *Sphagnum* farming and GHG mitigation. While drip irrigation distributed water more evenly compared to ditch irrigation, resulting in higher *Sphagnum* growth and lower GHG emission at Drenth, a multiannual previous inundation seemed to improve conditions for *Sphagnum* development on highly decomposed peat (Fig. 6.1). It still needs to be kept in mind that *Sphagnum* growth at Drenth was negatively affected by inundation with groundwater relatively high in pH in the beginning of the experiment and remaining drainage pipes at Provinzialmoor were discovered only after finalizing the measurements, resulting in a large share of polders to the overall production system which would probably not have been necessary if the drainage system had been effectively destroyed.

Sphagnum activity and C uptake are bound to high water levels or regular precipitation (Robroek et al., 2009) and highest *Sphagnum* growth is reached at stable, near-surface water levels (Brown et al., 2017; Grobe and Rode, 2023). The annual mean WTD between -0.09 m and -0.26 m below peat surface at the measurement sites at Provinzialmoor and Drenth still translate as 'shallow drainage' according to IPCC (2014) and in particular *Sphagnum papillosum* is able to thrive also at moderately low water levels (Robroek et al., 2009). However, WTDs below -0.30 m, and temporarily even below -0.40 m in Drenth and below -0.60 m in Provinzialmoor, largely reduced capillary rise of water to the peat mosses (Ingram, 1982), which is reflected in the results of biomass development and GHG mitigation at the cultivation sites.

Annual CO_2 fluxes clearly increased with deeper mean water levels at the near-natural and at the cultivation sites, well fitting into the general pattern of increased CO_2 loss at decreasing water levels until a threshold of about 0.5 m where further decreasing water levels do not necessarily translate into an increased emission (Tiemeyer et al., 2020). Comparing annual CO_2 exchanges at the cultivation sites to the results of Beyer and Höper (2015) and Günther et al. (2017) illustrates that, excluding all other site conditions and peat properties, the highest sequestration was measured at the sites with the highest water levels and the highest loss at the sites with the lowest water levels (Fig. 6.1). Still, parts of the results are surprising, as lower and more fluctuating water levels at Provinzialmoor should have caused higher CO_2 emission and less *Sphagnum* growth compared to Drenth. This illustrates the complex interaction of all major drivers and conditions during site preparation and before (previous inundation at Provinzialmoor), as discussed in detail in section 3.4.

The share of CH_4 in the site-specific GHG balances reported by Beyer and Höper (2015, 1.6 to 3.1 g CH_4-C m^{-2} yr^{-1}) and Günther et al. (2017, 0.8 to 2.0 g CH_4-C m^{-2} yr^{-1}) was similarly small as at Provinzialmoor (0.3 to 5.3 g CH_4-C m^{-2} yr^{-1}) and Drenth (0.0 to 0.4 g CH_4-C m^{-2} yr^{-1}) despite clearly higher annual mean water levels. This might be interpreted as a hint that CH_4 emissions associated with rewetting will most likely not reduce the overall GHG mitigation potential of *Sphagnum* farming. Beyer and Höper (2015) even conclude from their results that annual mean water levels of about 6–9 cm below peat surface might be deep enough for the oxidation of most of the produced CH_4. In contrast, higher amounts of CH_4 were released at the inundated polder site, making the open water surfaces of the irrigation system hot spots of GHG emission, as also stressed by Günther et al. (2017).

While N_2O emissions decreased with increasing vegetation development, high N_2O losses at D-DITCH in the first measurement year underline the risk of substantial amounts of this potent GHG at poorly vegetated and insufficiently irrigated sites where fluctuating water levels potentially provoke nitrogen release from peat mineralization and subsequent microbial activity.

6.3.2 Temperature

The impact of temperature could be studied both by comparing artificially warmed plots with non-warmed plots and the regular year 2017 with the extremely hot and dry year 2018, i.e., temperature effects with and without additional drought stress. For net ecosystem exchange (NEE), the latter was more pronounced than the warming effect itself, as illustrated by the difference between the two measurement years (Table 4.3, chapter 6.4.1).

In addition to the availability of water, temperature affects the biological processes involved in peatland C cycle (Lloyd and Taylor, 1994; Chang et al., 2020). Consequently, climate warming conditions will clearly affect the GHG exchange of *Sphagnum* farming, which is confirmed by the warming experiment. The high correlation between temperature and single fluxes of ecosystem respiration (R_{eco}) and CH_4 are illustrated in Fig. 4.4 and Fig. 4.5. The obtained results might be a realistic view into a warmer future and are confirmed for a grassland on organic soil by Bockermann et al. (2024). However, in contrast to my expectation, the increase in CO_2 loss was only a result of increased ecosystem respiration at the near-natural area, where water availability was never a limiting factor for microbial activity, and rather a result of a reduced gross primary production at the cultivation areas.

On the other hand, Chiapusio et al. (2022) found in a review of laboratory and in-situ studies that moderate temperature increases (2 to 5 °C) enhanced *Sphagnum* photosynthesis and growth. Further, although the significance of our results is reduced by inhomogeneous covers in the initial phase of the experiment, I found slightly higher *Sphagnum* biomasses at the warmed plots at the cultivation sites, rising hope for a feasibility of *Sphagnum* farming in a warmer future given a sufficient water supply.

The clear rise in CH_4 emission at the warmed plots at Meerkolk and Provinzialmoor reflects the general temperature dependency of CH_4 production (Turetsky et al., 2008; van Winden et al., 2012). The impact of the higher water availability at the near-natural area is further underlined by a high correlation of CH_4 fluxes with the temperature sums of the preceding ten days and a moderate correlation of the fluxes measured at Provinzialmoor (chapter 4.4).

The effect of warming on N_2O exchange seems to be negligible, although Voigt et al. (2016) report increased N_2O emissions from tundra peat soils warmed by open top chambers (OTC). As a by-product of microbial processes, the production of N_2O should be temperature dependent and effects might again have been small at the cultivation sites due to low water levels and aeration of the soil (Butterbach-Bahl et al., 2013) and masked at the near-natural site where a dense vegetation cover took up all nitrogen.

I further asked whether near-natural or cultivated peatlands would be more resilient towards climate warming. The answer to this question is complicated by prolonged periods of insufficient irrigation at the latter and by the high interannual variability at Provinzialmoor. It seems that the warming effect on GHG exchange was – on average – stronger at the near-natural area than at the *Sphagnum* farming areas, considering the high increases in CO_2 (50% less uptake in 2017 and 60% higher loss in 2018) and CH_4 (70% higher in 2017 and 60% higher in 2018) at the former despite similar temperature increases. This indicates a high vulnerability of this ecosystem against climate warming conditions. In contrast, NEE and CH_4 exchange at the cultivation sites seemed to be more resilient towards warming, not as a result of adjustable water levels by irrigation management, as hypothesized, but more likely as a result of the very low water levels and an assumed reduced microbial activity (Säurich et al., 2019).

6.3.3 Vegetation development

The plant species composition and biomass development turned out to be important drivers for the GHG exchange at the *Sphagnum* farming areas and are themselves linked to water levels and temperature (Ward et al., 2013). Swenson et al. (2019) report a correlation between *Sphagnum* cover and gross primary production (GPP), a relation also confirmed by the GHG measurements at Provinzialmoor and Drenth. The important role of *Sphagnum* in ecosystem C retention is underlined by the results of the pulse labelling experiment. In contrast, De Deyne et al. (2011) stress that the abundance of plants exhibiting high C uptake rates is not necessarily beneficial for ecosystem C sequestration if these plants also show high rates of respiration, or even promote the decomposition of organic matter in the rhizosphere via labile exudates (Gavazov et al., 2018). Moreover, the impact of the vegetation development on the measured GHG balances is illustrated by ongoing emissions of CO_2 and N_2O due to poor vegetation development at D-DITCH (Fig. 6.1), or by the contribution of vascular plant covers to interannual NEE variation at the warmed and control plots at Provinzialmoor (Fig. 4.3).

In terms of productivity and GHG mitigation, none of the tested *Sphagnum* species significantly stood out from the others. Grobe et al. (2021) did observe a higher biomass development of *Sphagnum palustre* in comparison to *Sphagnum papillosum* at Provinzialmoor but could not clearly separate differences in *Sphagnum* growth rates from effects of water availability and site establishment. Similarly, comparing only the GHG measurement plots, the site at Provinzialmoor cultivated with *Sphagnum papillosum* (P-PAP) showed the highest GHG mitigation and already developed into a small C sink in the second year after establishment. However, this development in contrast to the other *Sphagnum* species might again be a result of the different dates of site establishment (October 2015 compared to March 2016 and October 2016).

Interestingly, the presented results still highlight the risk of higher CH_4 losses at *Sphagnum* farming sites even during times of low water levels, governed by the abundance of specialized wetland plants possessing aerenchymous tissues for the gas transport from the atmosphere to the rhizosphere and vice versa (Greenup et al., 2000), this way bypassing methanotrophy in the peat column. This effect could potentially override the control of water availability and temperature on CH_4 exchange (Cooper et al., 2014; Abdalla et al., 2016), as indicated by the higher emissions at the Provinzialmoor sites during the 2018 drought, which could be attributed to the increasing abundances of *Eriophorum vaginatum* and *Eriophorum angustifolium*. During drought, an increased methanotrophic activity might be expected (Keane et al., 2021; White et al., 2023). However, White et al. (2023) also report ongoing CH_4 production and emission during drought and emphasize the role of plant-mediated transport of CH_4 to the atmosphere: while the emission of CH_4 was clearly reduced under *Rhynchospora alba* and *Calluna vulgaris* at a Swedish bog during the 2018 heatwave, they remained stable under *Eriophorum vaginatum*.

Reduced N_2O emission due to vegetation development is illustrated by the reduction of annual N_2O fluxes from the first to the second measurement year at the ditch irrigation site at Drenth and at Provinzialmoor. The negligible fluxes reported by Beyer and Höper (2015) and Daun et al. (2023) underline that the risk of increased N_2O losses declines when vegetation gaps close after the initial phase.

6.4 General and methodological limitations of the conducted research

6.4.1 Study period and design

When interpreting the results of this study, it has to be considered that the adverse conditions for *Sphagnum* growth imposed by the high degree of peat decomposition were even worsened by difficulties in delivering enough water to the peat mosses and by prolonged hot and dry periods in early 2017 and especially during the European heatwave 2018 with annual mean temperatures almost 2 °C higher than the long-term average (1970-2000, Lingen, German Climate Service) and only about two thirds of the average precipitation. During these periods, insufficient irrigation amounts could not stop mosses from desiccating and becoming visibly pale and inactive, while even the near-natural area turned from a sink of CO_2 to a source in the second measurement year. On the one hand, this enables a discussion of the impact of extreme climate events on the GHG exchange of *Sphagnum* farming. On the other hand, the distinct interannual variability limits the predictive power of the drawn conclusions and complicates the discussion of the drivers of GHG exchange. Prolonged dry periods as observed in 2018 might accelerate the shift of peatland ecosystems from C sinks to sources (Rinne et al., 2020; Artz et al., 2022), overriding all treatment effects. For example, drought conditions accompanying extreme heat events might be even more influential on NEE development at peatlands than a moderate warming treatment (Alm et al., 1999), while Rinne et al. (2020) found that the temperature dependence of CH_4 fluxes was reduced at lowered water levels.

Further, *Sphagnum* farming on former peat extraction sites still is a very unique system, covering a negligible area to date. Transferring the presented findings to other cultivation areas or to degraded bogs in general needs to be done very carefully even if these areas share similar characteristics such as high compaction and low hydraulic conductivity. If an area selected for *Sphagnum* farming has an agriculturally history, higher nutrient concentrations and the abundance of non-native seeds might affect productivity and GHG exchange (Huth et al., 2022). Here, it is important to note that my results represent the early phase of *Sphagnum* farming (second and third year after establishment) and GHG balances will most likely change in the upcoming years. A fully developed vegetation cover will result in increased C uptake and vertical *Sphagnum* growth (Gaudig et al., 2017; Daun et al., 2023) and the sites will be more resilient towards droughts after the development of a functioning actrotelm. On the other hand, it is difficult to estimate the impact of regular biomass harvest on *Sphagnum* growth, bryophyte and vascular plant community and GHG balances (Silvan et al., 2017; Gaudig et al., 2018).

6.4.2 Greenhouse gas measurements and calculation of balances

Flux measurements using measurement chambers are a common method for determining GHG balances. However, this method exhibits a number of inherent sources of bias and uncertainty that need to be kept in mind. The major sources of bias reported by Kutzbach et al. (2007) and Maier et al. (2022) have been addressed, where possible, in the chamber design and experimental setup. Still, advection and turbulence affect the GHG exchange between soil and atmosphere and are clearly altered during placement of chambers. Further, the gas concentration build-up or reduction itself changes the concentration gradient responsible for the GHG exchange and environmental parameters affecting GHG fluxes change over closure time. Consequently, the given GHG balances are only an approximation of the ‘true’ fluxes. The presented balances further depend on the used gap filling strategy. While the applied procedure of measuring CO_2 from before sunrise to afternoon to capture the complete variation of soil temperature and photosynthetically active radiation (PAR) seems to be most robust and reliable (Huth et al., 2017), the campaign based approach itself could introduce uncertainty, e.g., if the full range of soil temperature and PAR used for the response functions of R_{eco} and GPP are not well covered.

The number of replicates is the minimum number to derive simple statistical measures (Maier et al., 2022) but was regarded sufficient from an ecological point of view due to the large surface area of the measurement plots. However, especially the measurements at the inundated polder site at Provinzialmoor might be prone to a higher uncertainty. Podgrajsek et al. (2014) compared fluxes measured using floating chambers and the eddy covariance technique and state that, although the results generally are comparable, the chamber technique likely misses hot moments such as episodic high flux events at polder sites.

When determining CH_4 exchanges, all transport ways of CH_4 to the atmosphere need to be considered (Bridgham et al., 2013). Diffusive fluxes and plant-mediated transport are captured satisfactorily with measurement chambers given an adequate sampling interval. However, ebullitive fluxes are not well represented and might considerably affect CH_4 balances of *Sphagnum* farming sites on peatland (Tokida et al., 2005; Yu et al., 2014; Bieniada and Strack, 2021) and, above all, emissions from open water surfaces of the irrigation system (Burger et al., 2016; Köhn et al., 2021). Following from this, the reported values might slightly underestimate the 'true' flux of CH_4 to the atmosphere at all sites and at the polder site in particular.

In general, biweekly measurements of CH_4 and N_2O fluxes are the minimum interval for obtaining reliable results. The N_2O losses at Drenth in the first measurement year underline the need to include 'hot spots' and 'hot moments' of N_2O emissions (Butterbach-Bahl et al., 2013) in the GHG balance by a sufficient number of replicates and a sufficient temporal resolution. Where vascular plants with aerenchymous tissues thrive in higher abundance, plant-mediated transport can lead to diurnal variation of CH_4 exchange (Günther et al., 2014; van den Berg et al., 2016). Here, a parameter-based interpolation of CH_4 fluxes might be preferred to linear interpolation (Welpelo et al., 2024), although the fact that Welpelo et al. (2024) found no diurnal cycle of CH_4 emissions from hummocks dominated by *Eriophorum vaginatum* confirms the suitability of my measurement approach for the investigated sites.

The presented areal GHG balances of the tested irrigation systems depend on several assumptions, which might have induced bias. As no GHG measurements were conducted at the dams, literature data was used. I assumed that the emissions of dams would equal those of peat extraction sites in Northern Germany (Tiemeyer et al., 2020). In contrast, Vybornova et al. (2019) measured six times higher emissions of dry bare peat dams largely resulting from substantial CO_2 and N_2O losses and also Daun et al. (2023) adjust the lower values assumed by Günther et al. (2017) upwards to almost 30 tons of CO_2 equivalents based on new measurements, although they did not measure any significant N_2O emissions. Higher emissions of dams would increase the reported areal GHG balances only marginally due to the small area of dams. Still, the given balances might slightly underestimate the 'true' values. A further uncertainty lies in the estimated biomass yield, which is part of the areal GHG balances and was derived from a moderate ($R^2 = 0.43$) correlation between *Sphagnum* height and biomass. Finally, C exports in the form of dissolved organic carbon (DOC) are part of the C balance (Chapin et al., 2006) and need to be considered in discussing GHG balances of peatland systems due to the possible conversion to CO_2 and CH_4 in downstream systems (Evans et al., 2016). However, the study design did not allow for an exact quantification of DOC fluxes and DOC could thus not be included in the areal GHG balances.

When discussing and comparing GHG balances of different ecosystems and land use strategies, it has to be carefully considered that the GWPs of CH_4 and N_2O depend on the time period chosen, which is totally arbitrary for peatlands as ecosystems. The GWPs of CH_4 and N_2O are significantly lower at longer time periods (Günther et al., 2020; Mander et al., 2024) and with this their contribution to the GHG balance and finally their relevance in evaluating the success of peatland restoration or *Sphagnum* farming as climate protection measures.

6.4.3 Warming experiment and pulse labelling

The passive warming using OTCs successfully increased temperatures with negligible effects on further environmental parameters. This method of warming is easy to install also at remote areas but has been criticized in other studies due to a missing or highly variable treatment effect (Kennedy, 1995; Godfree et al., 2011) or due to interrelated effects on water availability and light. In my case, the large dimension of the OTC surrounding the measurement plot well inside the middle of the upper aperture of the OTC reduced unwanted effects on precipitation and shading. Still, the observed changes in the GHG exchange cannot be exclusively attributed to the warming effect alone and need to be interpreted with caution.

The pulse labelling experiment enabled valuable insights in C allocation at a *Sphagnum* farming site during extreme drought. However, not all C pools could be appropriately investigated. *Molinia caerulea* was chosen as dominant vascular plants, other species such as *Eriophorum*, *Erica* or *Juncus* could not be included due to low covers or complete absence in some measurement plots. Especially *Eriophorum* later turned out to be of high interest in CH_4 exchange and is missing in the discussion of C allocation at *Sphagnum* farming sites. Further, belowground plant biomass could not be sampled due to ongoing measurements and might considerably contribute to C allocation and storage (Zeh et al., 2021).

6.4.4 Recommendations for future research

From the above mentioned limitations, new research questions on the GHG balance of *Sphagnum* farming arise. The interrelated effects of environmental parameters on *Sphagnum* growth and GHG exchange, e.g., temperature and water level, have been addressed in recent laboratory and greenhouse experiments (Chiapuso et al., 2022), but large-scale fully factorial studies are scarce. I found that water level had a considerable impact on the GHG exchange but could not directly compare the warming effect on GHG exchange to the effect of water availability. It could be argued that the impact of warming on the GHG balances of the cultivation sites would have been more pronounced at sites with stable water levels close to the peat surface (Aerts, 2006; Mäkiranta et al., 2009; Rinne et al., 2020). An experiment including a treatment with water levels constantly kept near peat surface in comparison to a treatment with lower water levels would add to a more detailed understanding of the response of *Sphagnum* farming areas to climate change.

Further, it should be investigated in subsequent studies how severe and how long-lasting periodical harvest events affect the GHG balance of *Sphagnum* farming. Even if enough *Sphagnum* biomass for a rapid recovery is left behind, it remains of interest whether the resulting gaps in vegetation will again provoke increased emissions of N_2O and to what extent GPP and R_{eco} will be reduced. Emissions of CH_4 might again increase due to the reduction of the aerated peat column.

The high interannual variability of the presented GHG balances generally underlines the need for longer time series for robust conclusions and precise predictions on the GHG mitigation potential and on the impact of climate warming in particular (Elmendorf et al., 2012; Swenson et al., 2019). In contrast to the short-term GHG exchange between the plant-soil system and the atmosphere, which could be satisfactorily determined using the described methods, the long-term C capture and accumulation could not be determined (Mander et al., 2024). This important knowledge gap needs to be addressed especially at rewetted peatland sites with an initial period of potentially higher CH_4 production (Swenson et al., 2019) and at *Sphagnum* farming sites.

Onsite CH_4 measurements using portable laser equipped gas analyzers instead of sampling headspace air for subsequent GC measurement develop to a powerful tool for elucidating more detailed research questions (Zhao et al., 2024). Due to shorter measurement periods, a higher measurement frequency would allow to include more treatments (e.g., *Sphagnum* species, plant communities, management options), a higher number of replicates or a more accurate covering of a possible diurnal variation. This technique will enable a more precise description of the 'hot spots' and 'hot moments' of the GHG exchange at *Sphagnum* farming areas.

6.5 Implications for the large-scale implementation of *Sphagnum* farming

6.5.1 Establishment of future *Sphagnum* farming sites

The presented results are new and relevant for the implementation of a climate-smart management of former peat extraction sites and a wise use of peatlands in general. While the results of the joint project confirm the benefits of *Sphagnum* farming for both GHG mitigation and biodiversity conservation (Grobe et al., 2021; Zoch et al., 2023), several implications for future *Sphagnum* farming arise from the drawn conclusions.

Compared to conventional agriculture at cutover peatlands, Sphagnum farming is a valuable GHG mitigation measure, even at highly decomposed areas and under unfavorable climatic conditions.

At former peat extraction areas assigned to agriculture and at other degraded non-protected bog areas, paludiculture should be fostered from the perspective of climate protection. At degraded peatlands, every rise in WTD in the moist range (Tiemeyer et al., 2024) translates into a reduction of C loss to the atmosphere until a water level of about 0.1 m below the peat surface where increased CH_4 emission could arise (Evans et al., 2021) and a prompt rewetting is the best measure to mitigate GHG emissions (Leifeld and Menichetti, 2018; Günther et al., 2020; Lin et al., 2022). At Provinzialmoor, site-specific GHG balances ranged between -1.8 and 1.1 t CO_2-eq. ha^{-1} in the first measurement year, less than the emission factor for rewetted temperate peat extraction sites of 2.9 t CO_2-eq. ha^{-1} yr^{-1} reported by Wilson et al. (2016a, excluding DOC), although it has to be noted that their emission factor is composed of a moderate CO_2 uptake and higher CH_4 loss in comparison to the pattern observed at Provinzialmoor and Drenth. At Provinzialmoor and Drenth, NEE made up the greatest part of GHG balances and lower NEE values could be assumed for higher water levels based on the results of Beyer and Höper (2015) and Günther et al. (2017).

Although *Sphagnum* turned out to be very resistant and *Sphagnum* plants at Provinzialmoor recovered soon from the European heatwave 2018, disturbances in the initial phase such as insufficient irrigation and displacement of *Sphagnum* fragments by ice and storm resulted in poor *Sphagnum* proliferation at Drenth. The presented results thus underline that especially in the first year after establishment, cultivated *Sphagnum* is fragile and conditions necessary for growth (Gaudig et al., 2018) need to be monitored closely for maximizing productivity and GHG mitigation.

Drip irrigation seems to produce slightly more favorable conditions for Sphagnum growth compared to ditch irrigation.

Water is the key to successful *Sphagnum* farming and needs to be made a top priority in management concepts. The cultivation sites irrigated by ditches dried out with increasing distance to the ditches, also as a result of the low hydraulic conductivity of the highly decomposed peat (Grobe et al., 2021), and even the drip irrigation site desiccated during longer dry periods. The ongoing C loss at the cultivation sites despite increasing C sequestration in *Sphagnum* biomass is in parts a result of the insufficient irrigation which could not stop peat decomposition in the aerated peat column. Water levels clearly below the targeted few centimeters below peat surface negatively affect *Sphagnum* growth and GHG mitigation (Strack et al., 2009; Robroek et al., 2009).

Gaudig et al. (2017) found that ditches delivered more water into the area than subsurface irrigation and Pouliot et al. (2015) found for Canadian bog sites with higher peat thickness that the excess efforts for drip irrigation did not pay off in terms of significant productivity increases. In contrast, drip irrigation supplied water more evenly and resulted in significantly less GHG emission (66% and 64% less in 2017 and 2018, respectively) and higher *Sphagnum* growth compared to ditch irrigation at Drenth, indicating that drip irrigation might be the recommended option for *Sphagnum* farming on highly decomposed peat in the initial phase. Where feasible, automated irrigation systems might save water and prevent desiccation in a warmer future with irregular distribution of precipitation (Pouliot et al., 2015; Gaudig et al., 2018).

Previous inundation and a sufficient remaining peat depth positively affect Sphagnum development.

Mean site-specific GHG balances were lowest at the previously inundated Provinzialmoor area (2,6 t CO_2-eq. ha^{-1} yr^{-1} compared to 10.4 t CO_2-eq. ha^{-1} yr^{-1} and 3.7 t CO_2-eq. ha^{-1} yr^{-1} at D-DITCH and D-DRIP, Table 3.4). In contrast to Drenth, where the cultivation area was prepared directly after termination of peat extraction, seven years of inundation might have improved the peat structure at Provinzialmoor, lessen adverse conditions such as hydrophobicity and reduced hydraulic conductivity resulting from degradation (Roßkopf et al., 2016). Gorham and Rochefort (2003) suggest that peatland restoration should occur immediately after extraction to minimize peat degradation, which could otherwise prolongate the time needed for a dense vegetation cover to develop. For shallow and highly decomposed peat after industrial peat extraction, my results still indicate a positive effect of a preceding inundation as also recommended by Blankenburg (2004) for bog restoration in Lower Saxony, who suggests different stages of water management starting with a prolonged inundation of the peat to enable reswelling.

Further, the promising results at Provinzialmoor might be in parts also a result of a higher peat thickness promoting *Sphagnum* development (Dixon et al., 2017; Grobe et al., 2021). Where possible, *Sphagnum* farming should thus be established on an adequately thick peat layer. Moore et al. (2021) found that *Sphagnum* at shallow (< 0.40 m) peat sites are more vulnerable towards warming and drought compared to deeper (> 0.40 m) peat sites due to reduced ecohydrological feedback maintaining a wet peat surface during drought. Lower bulk densities in the upper peat horizon (0.12 to 0.16 g cm^{-3} at Provinzialmoor in contrast to 0.19 to 0.21 g cm^{-3} at Drenth, Table 3.1) could be interpreted as a hint that the higher peat thickness is in parts a result of the reswelling during inundation.

CH_4 emissions could considerably contribute to the GHG balance even under dry conditions when specialized vascular plants possessing aerenchyma rise in abundance.

I found higher CH_4 emissions (up to 5.3 g CH_4-C m^{-2} yr^{-1}) at the cultivation sites as a result of increasing vascular plant covers and conclude that CH_4 emissions could considerably contribute to the overall GHG balances at inadequately managed sites. At Provinzialmoor, this pattern was particularly pronounced and CH_4 accounted for almost half at site P-PAL and more than half of the total GHG balance at site P-PAP in the second measurement year, respectively. Possible measures to limit CH_4 emission would be keeping water levels about 5 to 10 cm below peat surface (Beyer and Höper, 2015; Evans et al., 2021) while avoiding inundation (Bonn et al., 2014; Anthony and Silver, 2021) and controlling vascular plant abundance.

N_2O emissions can add to the GHG balance even at unfertilized peat soils given a poor vegetation development and strong water level fluctuation.

The relatively short peak emission of N_2O at the ditch irrigation site at Drenth during July and August 2017 resulted in an annual emission of 1.2 ± 0.8 g N_2O-N m^{-2} yr^{-1}. This peak emission could be attributed to strong fluctuations in WTD (-0.33 to -0.03 m) and to a low vegetation cover at this site and is considerable compared to the emission factor for grassland (0.4 g N_2O-N m^{-2} yr^{-1}) or cropland (1.1 g N_2O-N m^{-2} yr^{-1}) on drained organic soils (Tiemeyer et al., 2020). In 2017, N_2O emissions accounted for almost half of the total GHG balance at this site, highlighting the importance of stable water levels and closed vegetation covers especially in the initial phase of *Sphagnum* farming.

As a 'hot spot' of GHG emission, the surface area of the irrigation system should be minimized at Sphagnum farming sites for maximum GHG mitigation.

Higher GHG emissions from the irrigation system (mean annual emission of 6.5 t CO_2-eq. ha^{-1} yr^{-1} at site P-POLDER) stress the need for a reduction of the area of surface waters regarding a maximum GHG mitigation. The key challenge in optimizing future *Sphagnum* farming attempts is to implement an irrigation management robust enough to deliver sufficient amounts of water during dry summer periods but at a minimum surface area of polders and ditches (Günther et al., 2017; Daun et al., 2023). Water deficits of 160 mm or up to 320 mm in dry years in Northwestern Germany (Brust et al., 2018) inevitably translate into considerable dimensions of such polders, significantly contributing to the overall GHG balance (Burger et al., 2016). Ditches in closer distance to each other might thus improve the distribution of water to *Sphagnum* (Gaudig et al., 2017; Grobe et al., 2021) but at the cost of a reduced cultivable area and GHG mitigation.

Vascular plant abundances need to be closely monitored and controlled by mowing.

Grobe et al. (2021) confirmed for Provinzialmoor and Drenth that *Sphagnum* establishment was positively affected by shelter and structure provided by vascular plants, especially during periods of reduced water availability. On the other hand, Grobe and Rohde (2023) found that vascular plant abundance is linked to water availability and that vascular plants might increase dominance at *Sphagnum* farming sites under conditions of insufficient irrigation or inhomogeneous site development. My results underline that, in addition to increased costs for regular mowing and processing of harvested biomass, the abundance of vascular plants affects the GHG balance of *Sphagnum* farming. Moreover, the pulse labelling experiment revealed that vascular plant *Molinia caerulea* lost almost 90% of the sequestered label during the first two weeks while *Sphagnum* still stored up to 40% after 140 days. Consequently, the abundance of vascular plants needs to be monitored and controlled at *Sphagnum* farming sites.

Donor material for new Sphagnum farming sites should be harvested at existing cultivation areas.

The rapid recovery of the harvested plots at the near-natural area and the minor effect on the GHG exchange (36% increase in 2017 and 23% reduction in 2018 compared to the GHG balance of M-NAT) might be interpreted as a hint towards possible repeated harvests at cultivation sites with a closed *Sphagnum* cover (Silvan et al., 2017). However, my results highlight that, when harvesting *Sphagnum* farming sites or when extracting *Sphagnum* biomass as inoculum for new cultivation sites, it is of special importance to leave behind enough *Sphagnum* biomass for a rapid recovery of a dense lawn. In terms of nature conservation, donor material for new *Sphagnum* farming sites should be extracted rather from existing cultivation sites than from near-natural areas. Although the harvested plots at the near-natural area seemed to recover soon in this study, long-term effects such as changes in plant community due to wetter conditions at the harvested area (Guêné-Nanchen et al., 2019) might have remained undiscovered during the short period of two measurement years.

Open top chambers successfully increased air and soil temperatures in the range of predicted climate warming and the emission of CO_2 and CH_4 generally increased at the warmed plots.

Extreme weather events might reduce the productivity of *Sphagnum* farming. While *Sphagnum* farming itself provides GHG mitigation in comparison to drainage-based peatland use, understanding the impact of climate change on *Sphagnum* farming is fundamental in estimating their potential as a climate protection measure. The results of the warming experiment confirm the suitability of OTCs for approximating climate warming conditions in field studies and hint towards the risk of a reduced C sink strength of *Sphagnum* farming in a warmer future. Overall, climate warming and increased rates of evapotranspiration (Brust et al., 2018) even more highlight the importance of an elaborate water management.

6.5.2 Implementing *Sphagnum* farming as a management option on highly decomposed peat

Large-scale pilot studies such as the presented research are important to convince stake holders and landowners of the benefits offered by *Sphagnum* farming and paludiculture as a GHG reduction measure. Comparing expert knowledge on GHG mitigation measures at degraded peatlands with surveys on the opinion of landowners and farmers, Rhymes et al. (2023) stress that the adoption of GHG reduction measures recommended by experts depends on the farmers estimation of practicability and economic impact, leading to a mismatch of ‘effective’ and ‘practical’ measures. They report that in particular *Sphagnum* farming was ranked highly effective by the scientific experts but it was ranked least practical by the farmers. Amongst others, the publications related to my thesis will eventually contribute to an increased public awareness, persuading farmers to invest and policy makers to provide necessary legal framework. A first step, the approval of paludiculture for eligibility of agricultural subsidies, has been made (BMU, 2022), even though it still needs refinements such as not interpreting the establishment of *Sphagnum* farming on grasslands as ‘grassland conversion’ requiring new grassland to be established elsewhere. Temmink et al. (2024) report a high proportion of C stored in recalcitrant *Sphagnum* biomass, further paving the way for *Sphagnum* farming as carbon farming measure.

At the moment, *Sphagnum* biomass from paludiculture is more expensive than peat extracted in Germany or imported from Baltic countries. However, the cultivation of peat mosses in Northwestern Germany can be a profitable land use option in the post drainage age as certain niche products such as orchid potting soils or under certain assumptions such as a 10% price increase for end consumers (Wichmann et al., 2020). The demand for harvested *Sphagnum* is growing. A considerable amount of ongoing peat extraction and the concomitant loss of pristine peatland area could be saved, if half of the abandoned peat extraction area in Northwestern Germany (about 54.000 ha in Lower Saxony, Frank et al., 2021) would be strictly protected for natural succession and the other half would be converted to *Sphagnum* farming (Wichmann et al., 2017), generating a GHG mitigation potential of several million tons of CO_2 equivalents when considering the obtained results of *Sphagnum* farming on highly decomposed peat at former peat extraction sites.

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APPENDIX

Supplementary Information for

EXPERIMENTAL WARMING INCREASED GREENHOUSE GAS EMISSIONS OF A NEAR-NATURAL PEATLAND AND *SPHAGNUM* FARMING SITES

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Supporting methodological information

A major challenge in analyzing CO_2 fluxes of experimental plots warmed by Open Top Chambers (OTC) is separating effects of the increased temperature from effects of the OTC chambers themselves (e.g., reduced wind speed or lower light transmittance). Reduced light intensities and their potential effect on gross primary production (GPP) and thus net ecosystem exchange (NEE) are partially inadequately accounted for in experimental warming studies using OTCs (Sullivan et al., 2008; Johnson et al., 2013). Some authors do mention this issue, but found no significant differences in values of photosynthetically active radiation (PAR) inside and outside the OTC (Bokhorst et al., 2011; Jassey et al., 2019). That might be due to the fact that these studies only comprised spring and summer, where the sun elevation is high and effects are limited to the early morning and late afternoon. Biasi et al. (2008) report a PAR reduction of 10%, but state that differences of this size might most probably be biologically insignificant. In our opinion, the reduction of light intensities has to be considered, especially when measuring year-round. Even large OTCs with ample distance to the central measurement plot can only minimize but not fully prevent PAR losses (Godfree et al., 2011). The approach of fitting light response functions to CO_2 fluxes and PAR values measured outside the OTC would slightly bias GPP at such sites. Therefore, the PAR values used for fitting the response functions need to be corrected. Placing an additional PAR sensor inside the OTC would only partially solve the problem as this would not provide data on how much of measurement plot was shaded. Here, we describe the approach of accounting for the light reduction in the OTC measurement plots entailing the following steps:

1) Analysis of the diurnal pattern of the light transmittance and derivation of half-hourly estimates of the shaded measurement plot area and the light reduction.

2) Parametrization of the response functions of GPP using these reduced light levels (Schneider et al., 2011).

3) Calculation of annual balances of GPP and, subsequently, NEE using light levels outside the OTCs (Schneider et al., 2011).

1) Area shaded by and light transmittance of the OTCs

The correction of PAR values was based on a) an estimate of the shaded plot area and b) on the PAR transmittance of the polycarbonate panel material.

The shaded part of the measurement plot area was estimated on a half-hourly basis using sun elevation data (source: www.sunearthtools.com, accessed 28 August 2020) for Provinzialmoor (52°40’ N, 07°06’ E). The shadow length (*l*), that the upper aperture of the OTC was casting on the measurement plot, was calculated using the tangent function [A.1]:

$$l = \frac{h}{\tan(e)} \qquad \text{[A.1]}$$

where h is the height of the OTC (0.5 m) and e is the sun elevation. For this analysis, the hexagonal shape of the OTC and the quadratic shape of the measurement plot were replaced by circular approximations (Fig. A.3). The radius auf circular approximation r_{plot} was calculated as [A.2]:

$$r_{plot} = (a + c)/2 \qquad \text{[A.2]}$$

where a and c are the apothem and the circumradius of the measurement plot. The radius of the circular approximation of the OTC’s upper aperture (r_{OTC}) was derived accordingly. This simplification enabled a half-hourly calculation of the shaded plot area A_{s} using basic geometric functions [A.3]:

$$A_s = \begin{cases} \pi\, r_{plot}^2,\ if\ l \geq r_{OTC} + r_{plot} \\ 0,\ if\ l < r_{OTC} - r_{plot} \\ {r_{plot}}^2 * \arccos\left(1 - \frac{s}{r_{plot}}\right) - \left(r_{plot} - s\right) * \sqrt{2 * r_{plot} * s - s^2},\ if\ r_{OTC} - r_{plot} \leq l < r_{OTC} + r_{plot} \end{cases} \qquad \text{[A.3]}$$

where s is the height of the segment of the circular plot approximation, i.e. the length of the shadow reaching into the measurement plot (l minus the distance between OTC panel and plot, Fig. A.3). Following this calculation, the shadow of the OTC panels covered the whole measurement plot for large parts of the day during winter, partially all day long. With rising sun elevation, the area and the duration of disturbance decreased and in summer, the measurement plots were only affected in the early morning and late afternoon (Fig. A.4). The plot area was completely shaded in about half of all the time (night-time excluded) and completely unaffected in slightly more than 5% of all time points. The PAR transmittance of the polycarbonate OTC panels (Makrolon 3 mm, Bayer AG, Darmstadt, Germany) was investigated in a supplementary test in summer 2019. A light transmittance of 87% was specified by the manufacturer, but it remained unknown whether the reduction in PAR was dependent on the direction of the sun or light intensity. From July to August, an OTC was equipped with PAR sensors (LI-190R Quantum Sensor, Licor, Lincoln, NE, USA) in the center of the measurement plot at ground level, under the south-eastern panel of the OTC and under the southern panel. Differences to a control PAR sensor outside the OTC were calculated and a mean value of light absorbance by the OTC panels was determined by using a linear model (Fig A.5a). Differences higher than 20%, hinting towards dirt or insects on the sensor, were excluded. The factor of PAR transmittance did not differ between the sensors in the plot center and under the southern (position of the sun at noon) and south-eastern OTC panel. The obtained mean PAR transmittance of 87.5% agreed well with the light transmittance specified by the manufacturer.

In a final step, the percentage (p) of shaded plot area and the factor ($f = 0.875$) of reduced light transmittance were combined to estimate half-hourly values of PAR reaching the measurement plots:

$$PAR_{OTC} = p * PAR_{outside} * f\ +\ (1 - p) * PAR_{outside} \qquad \text{[A.4]}$$

The results are shown in Fig. A.5. The PAR reduction was more pronounced at low to medium PAR values, while high values were less affected. This resulted in a reduction of the mean PAR of all CO_2 measurements using transparent chambers from 489 µmol m^{-2} s^{-1} to 458 µmol m^{-2} s^{-1}, i.e. a mean PAR reduction of 6.3%. For the overall measurement period, the mean PAR reduction was 5.1%.

2) General approach of the parametrization of R_{eco} and GPP response functions

Ecosystem respiration (R_{eco}) was parameterized using the temperature dependent Arrhenius type response function relating CO_2 fluxes of opaque chamber measurements to soil temperature (Lloyd and Taylor, 1994) [A.5]:

$$R_{eco}(T) = R_{ref} \times exp\left[E_0 \times \left(\frac{1}{T_{ref} - T_0} - \frac{1}{T - T_0}\right)\right] \qquad [A.5]$$

where R_{ref} is the respiration (mg CO_2-C m^{-2} h^{-1}) at the reference temperature (T_{ref}, 283.15 K), E_0 an activation-like parameter (K), T_0 the temperature constant for the start of biological processes (227.13 K) and T the measured soil temperature (K). If the difference between minimum and maximum temperature was smaller than 1.5 °C during the campaign day, the median of all R_{eco} fluxes was used as R_{ref} in equation 5. Next, GPP was calculated as the difference between the measured net ecosystem exchange (NEE, transparent chambers) flux and the nearest modelled R_{eco} flux and parameterized in relation to PAR using the rectangular hyperbolic light response function (Falge et al., 2001) based on the Michaelis-Menten kinetics (Johnson and Goody, 2011) [A.6]:

$$GPP\ (PAR) = \frac{GPP2000 \times \alpha \times PAR}{GPP2000 + \alpha \times PAR - \frac{GPP2000}{2000\ \mu mol\ m^{-2} s^{-1}} \times PAR} \qquad [A.6]$$

where *GPP2000* is the rate of C fixation at a PAR value of 2000 µmol m^{-2} s^{-1} (mg CO_2-C m^{-2} h^{-1}), α the light use efficiency (mg CO_2-C m^{-2} h^{-1}/µmol m^{-2} s^{-1}) and PAR the photon flux density of the photosynthetically active radiation (µmol m^{-2} s^{-1}). If GPP parameters could not be fitted, the respective campaign was combined with the nearest campaign which best resembled the campaign's environmental conditions, i.e. ranges of PAR and GPP. For the OTC sites, the corrected PAR values (PAR_{OTC}) were used, while for the control sites, the outside PAR data was applied. In addition to the OTCs, the transparent measurement chambers also reduce the light reaching the vegetation during the measurement procedure, but this has an equal effect on warmed and control plots. For the transparent chambers, a PAR transmittance of 95% was given by the manufacturer (PS-Plastic, Eching, Germany). Both the outside and the corrected PAR data of the measurement campaigns was thus reduced accordingly before fitting the response functions.

3) Calculation of the annual CO_2 balances

The interpolation of the annual GPP fluxes is carried out as described in the main text by using PAR data of the meteorological station. Thus, the CO_2 balances of the OTC treatments do not represent the actual GPP of these plots, but an approximation of the CO_2 balances under the assumption that there was no reduced light transmittance by OTCs. This approach increased GPP by about 0.3 to 0.7 t CO_2 ha^{-1} yr^{-1} compared to an interpolation using reduced light levels, emphasizing that the correction of PAR values is a necessary step in calculating NEE of warmed plots in comparison to control plots.

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Supporting figures and tables

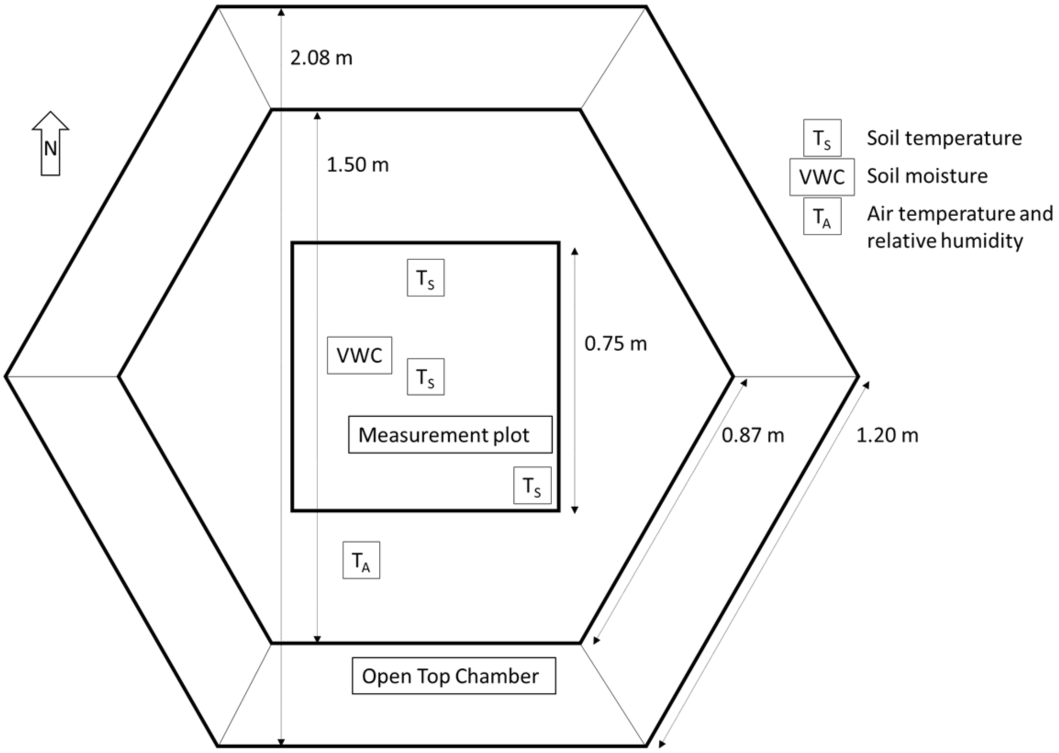

Fig. A.1: Design of Open Top Chambers and installed sensors. OTCs were constructed out of six trapezoid panels with a top side length of 0.87 m and a bottom side length of 1.20 m, resulting in a chamber base width of 2.08 m, an angle between soil surface and panels of 60° and a chamber height of 0.50 m. Soil temperature sensors were installed in the center as well as in the northern (least affected by shadow of OTC panels) and south-eastern (most affected by shadow) corner of the measurement plot.

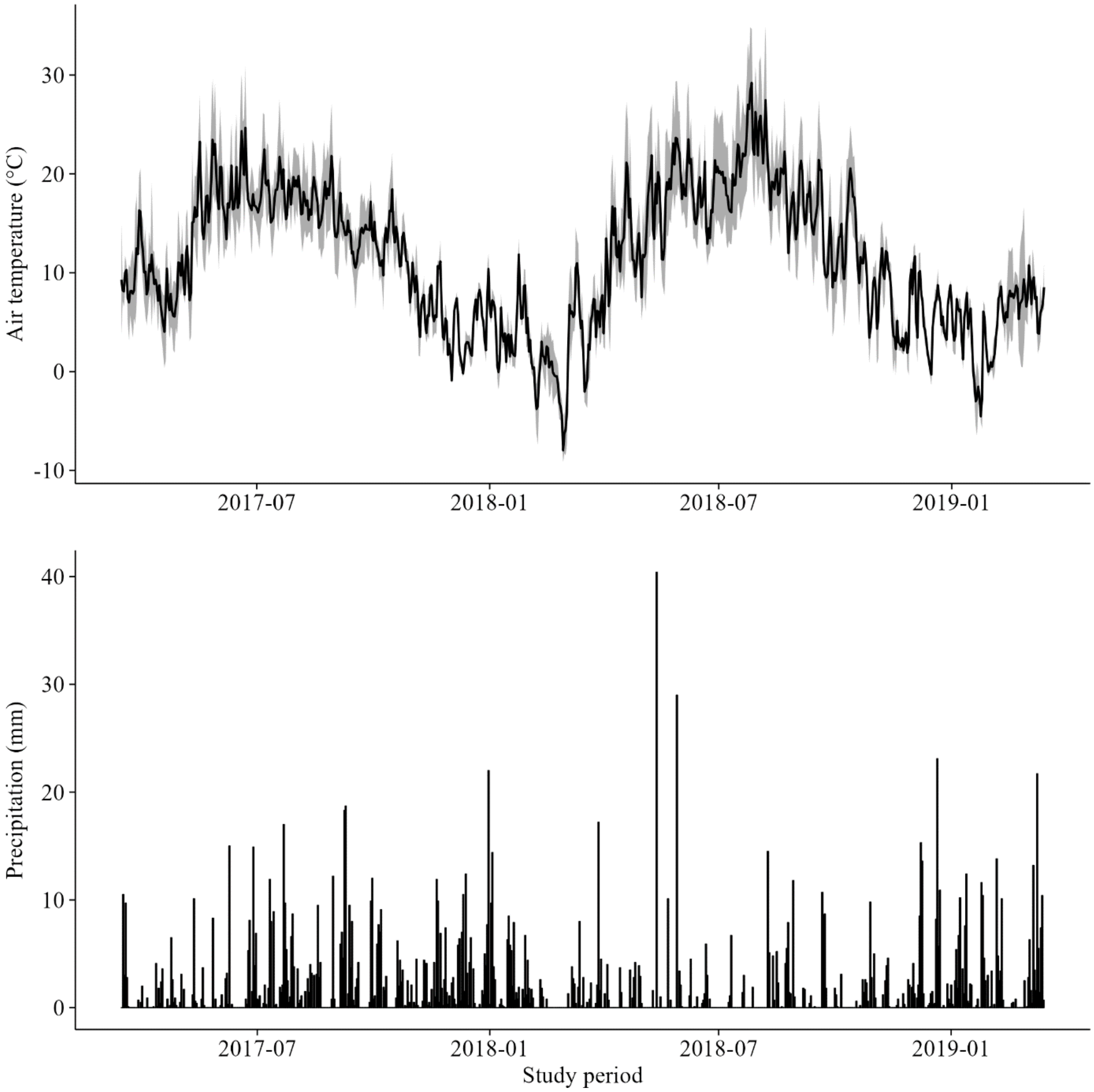

Fig. A.2: Daily mean air temperatures and daily sums of precipitation during the study period from March 2017 to March 2019 (German Climate Service, Station Lingen, 20 km away from study sites). The second measurement year was exceptionally hot and dry, especially during summer and autumn.

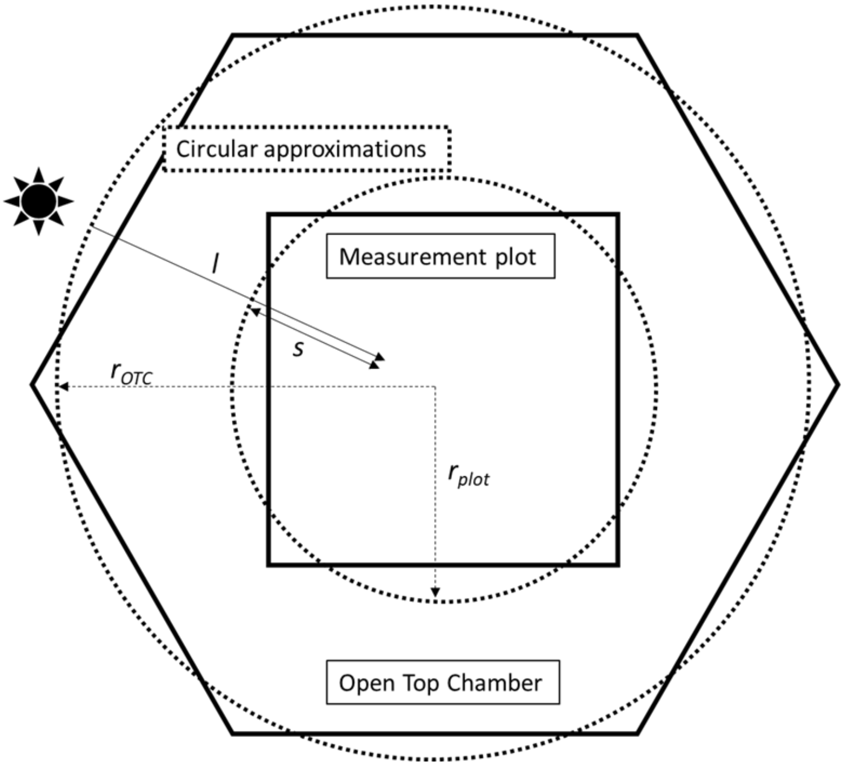

Fig. A.3: Circular approximations of the hexagonal shape of the Open Top Chamber (r_{OTC}) and of the quadratic shape of the measurement plot (r_{plot}). The area of the measurement plot shaded by the OTC was estimated on a half-hourly basis using these circular simplifications, where s is the length of the shadow (*l*) reaching into the measurement plot.

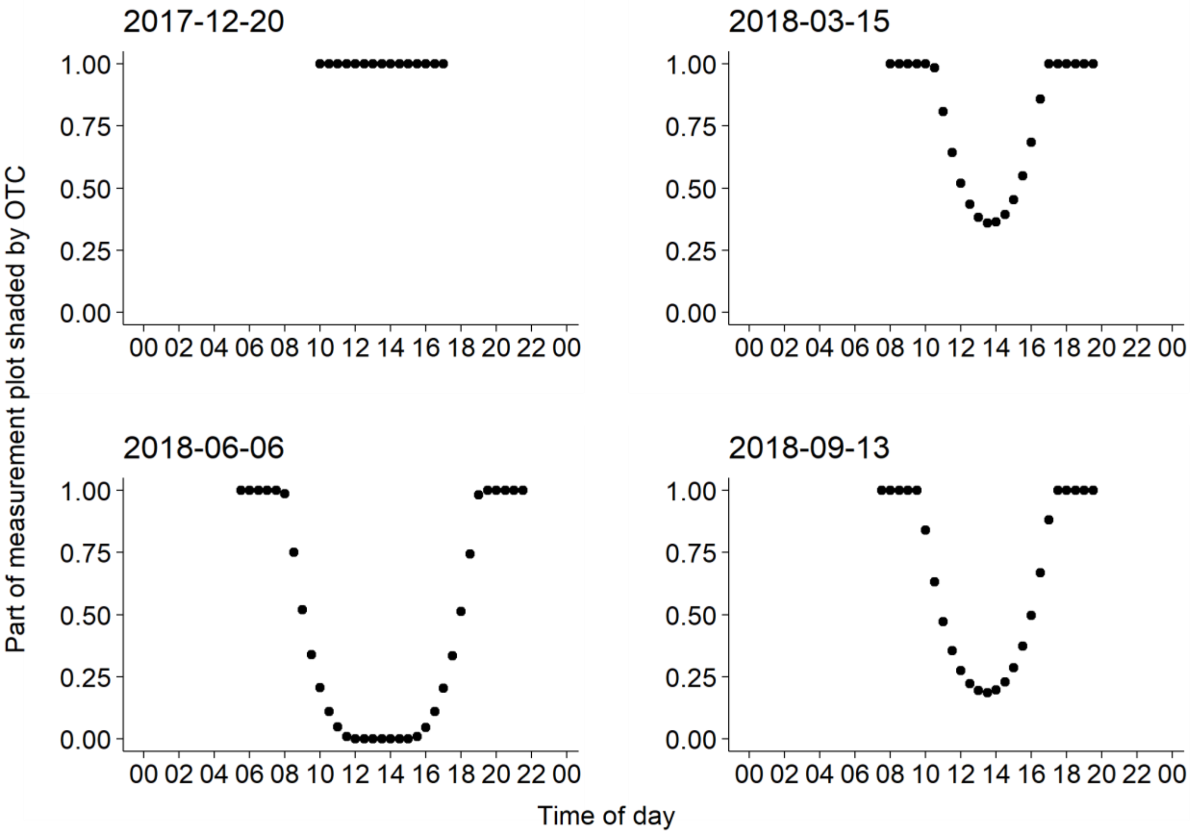

Fig. A.4: Seasonal variation in the reduction of light caused by the Open Top Chambers (OTC). Four examples (CO_2 campaigns in winter, spring, summer, autumn) for the dependence of the area of the measurement plot affected by the OTC panels on sun elevation.

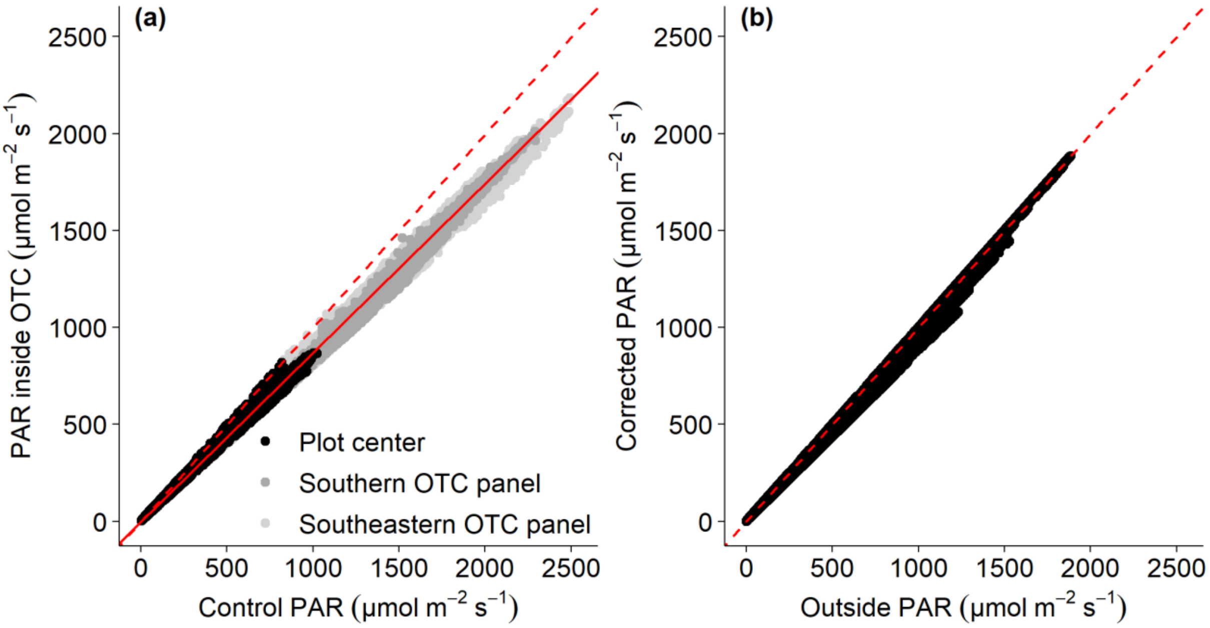

Fig. A.5: Amounts of photosynthetically active radiation (PAR) (a) of the control sensor and sensors inside the Open Top Chamber (OTC) during the supplementary test in 2019 and (b) outside and after the correction procedure described above (reaching the OTC measurement plots) during CO_2 campaigns. The red dashed lines denote the 1:1 ratio, the red line in panel (a) the linear regression. At the plot center, only moderate PAR values were measured, as this sensor was only shaded by the OTC panels in the early morning. During CO_2 measurements, high PAR values were not affected by the correction as they were measured during times when the measurement plots were not shaded by the OTC.

Table A.1: Complete list of plant species found at the measurement sites during the study period. The list is grouped in bryophyte and vascular plant species. An ‘x’ indicates the presence of a species at any of the survey dates.

	M-NAT	M-NAT-W	P-MIX	P-MIX-W	D-DRIP	D-DRIP-W
Bryophyte Species						
Sphagnum papillosum	x	x	x	x	x	x
Sphagnum palustre					x	x
Sphagnum cuspidatum	x	x	x	x	x	x
Sphagnum pulchrum	x	x	x			
Sphagnum medium	x	x	x	x	x	x
Sphagnum fimbriatum					x	
Sphagnum fallax	x	x	x	x		
Campylopus pyriformis			x	x	x	x
Odontoschisma sphagni					x	x
Cladopodiella fluitans				x		
Calliergon stramineum			x			
Campylopus introflexus						x
Dicranella cerviculata			x	x		
Polytrichum strictum	x					
Vascular Species						
Rhynchospora alba	x	x	x	x	x	x
Molinia caerulea	x	x	x	x	x	x
Drosera rotundifolia	x	x	x	x	x	x
Eriophorum angustifolium	x	x	x	x	x	x
Vaccinium oxycoccos	x	x	x	x	x	
Erica tetralix	x	x	x	x	x	x
Calluna vulgaris			x	x		x
Juncus bulbosus			x		x	x
Betula pubescens			x	x	x	
Eriophorum vaginatum			x	x		
Drosera intermedia					x	x
Andromeda polifolia	x					