„Water table and organic substrate as triggers of greenhouse gas emissions from rewetted peatlands"

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Summary

Peatlands are ecosystems comprising a huge carbon reservoir and play an essential role in the exchange of greenhouse gases (CO_2, CH_4 und N_2O) although they only cover $\sim$3 % of the Earth`s land area. Natural peatlands act as CO_2 sinks and CH_4 source – having a neutral net climate impact. Anthropogenic activities, such as drainage and cultivation, significantly modify the exchange of greenhouse gases – leading to an increased CO_2 (and N_2O) release and low CH_4 emissions – having a negative effect on the climate.

Since the reduction of anthropogenic greenhouse gas emissions via rewetting formerly drained peatlands may now be accounted for in the national greenhouse gas reporting under the Kyoto Protocol, rewetting programms are increasingly being implemented in the context of climate mitigation. Under specific conditions, however, CH_4 (or N_2O) emissions may be extremely high and can reduce the positive climate impact of rewetting measures. In order to develop effective rewetting and sustainable management measures, a better understanding of the processes and factors determining greenhouse gas fluxes is needed. Since there a several counteracting processes involved, we need to find a trade-off between CO_2 and N_2O reduction and simultaneous avoidance of high CH_4 emissions.

Within the framework of this PhD theses, four incubation experiments were performed to investigate the most important determinants of greenhouse gas emissions: organic substrate and water table. These laboratory experiments were performed with grassland mesocosms, which represent the most wide-spread land-use on organic soils in Germany. The experiments showed that:

- CO_2 release due to respiration immediately and considerably increased when lowering the water table. Therefore, intermittent dry phases – aiming to avoid high CH_4 emissions – should be kept as short as possible as every wet day saves soil carbon.

- After rewetting, CH_4 production started after a lag-phase until conditions favourable for methanogenesis were established. Aerenchymous plants stabilized the redox potential due to oxygen transport into deeper soil horizons, so that CH_4 production occurred later. Intermittent drainage rapidly recovered the oxidative status of the peat and kept CH_4 emissions very low.

- N_2O emissions were of no importance in our investigations.

- The most positive climatic effect was achieved with a water table slightly below the peat surface – where CO_2 production by respiration was limited, where CH_4 production was still low and CH_4 oxidation could occur in the shallow aerobic layer and where the grassland vegetation was still vital. Rewetting to a water table close to the peat surface increased net GHG uptake in terms of CO_2-equivalents, raising the water table above the peat surface (flooding) clearly reduced the positive climatic effect.

- The amount of readily degradable organic matter determined greenhouse gas production and not the quality of the old peat substrate. It is essential to keep the vegetation vital (i.e. to maintain productivity) and avoid its dying-off (i.e. to avoid the provision of additional readily degradable organic matter as substrate for microbial decomposition) – e.g. allowing for a vegetation transition towards wetness-adapted plant species in practical rewetting.

Zusammenfassung

Moore sind Ökosysteme mit einem riesigen Vorrat an Kohlenstoff und spielen eine bedeutsame Rolle beim Austausch von Treibhausgasen (CO_2, CH_4 und N_2O) obwohl sie lediglich $\sim$3 % der Landfläche unserer Erde einnehmen. Naturnahe Moore fungieren als CO_2 Senke and CH_4 Quelle – ihre Wirkung auf das Klima ist neutral. Anthropogene Aktivitäten, wie Entwässerung und Bewirtschaftung von Mooren, verändern den Austausch von Treibhausgasen maßgeblich – und führen zu erhöhter CO_2 (und N_2O) Abgabe und verminderten CH_4 Emissionen – sie haben eine negative Wirkung auf das Klima.

Da nun die Verminderung von anthropogenen Treibhausgasemissionen durch Wiedervernässung von ehemals entwässerten Mooren im Rahmen der nationalen Treibhausgasberichterstattung unter dem Kyotoprotokoll angerechnet werden kann, werden Wiedervernässungsprogramme mit dem Ziel Klimaschutz in zunehmendem Maße durchgeführt. Unter bestimmten Bedingungen jedoch können CH_4 (oder N_2O) Emissionen extrem hoch sein und folglich die positive Klimawirkung von Wiedervernässungsmaßnahmen erheblich reduzieren. Um effektive Wiedervernässungs- und nachhaltige Managementmaßnahmen zu erarbeiten, ist ein besseres Verständnis jener Prozesse und Faktoren notwendig, die die Treibhausgasflüsse beeinflussen. Da mehrere entgegengesetzte Prozesse stattfinden, muss ein Mittelweg gefunden werden, um CO_2 and N_2O Emissionen zu reduzieren und gleichzeitig hohe CH_4 Emissionen zu vermeiden.

Im Rahmen dieser Doktorarbeit wurden vier Inkubationsexperimente durchgeführt, die die wichtigsten Steuerfaktoren für die Emission von Treibhausgasen untersuchen: organisches Substrat und Wasserstand. Die Experimente wurden mit Grünland Mesokosmen durchgeführt, der häufigsten Landnutzungsform von organischen Böden in Deutschland.

Diese Laborexperimente haben gezeigt, dass:

- Die Abgabe von CO_2 aus der Atmung stieg unmittelbar und erheblich an, wenn der Wasserstand abgesenkt wird. Daher sind zeitweise trockene Phasen – die hohe CH_4 Emissionen vermeiden sollen – möglichst kurz zu halten. Jeder nasser Tag erhält gespeicherten Kohlenstoff.

- Die CH_4 Bildung startete mit einer Verzögerung nach Wiedervernässung bis sich für die Methanogenese günstige Bedingungen eingestellt hatten. Aerenchympflanzen stabilisierten das Redoxpotential durch den Transport von Sauerstoff in tiefere Bodenhorizonte, sodaß die CH_4 Bildung verzögert wurde. Zwischenzeitliche Drainage stellte den oxidativen Zustand des Torfes rasch wieder her und hielt CH_4 Emissionen sehr niedrig.

- N_2O Emissionen spielten in unseren Untersuchungen keine Rolle.

- Die positivste Wirkung auf das Klima wurde durch einen Wasserstand leicht unterhalb der Torfoberfläche erreicht – wo die CO_2 Bildung durch die Atmung eingeschränkt war, wo die Bildung von CH_4 noch gering war und CH_4 Oxidation in der oberflächennahen aeroben Schicht stattfinden konnte und wo die Grünlandvegetation noch vital blieb. Die Wiedervernässung mit einem Wasserstand nahe der Torfoberfläche erhöhte die Aufnahme von Treibhausgasen (ausgedrückt in CO_2-Äquivalente), ein Anheben des Wasserstandes über die Torfoberfläche (Überflutung) reduzierte deutlich den positiven Klimaeffekt.

- Die Menge an leicht abbaubarem organischen Material bestimmte die Treibhausgasbildung und nicht die Qualität des alten Torfsubstrates. Es ist wesentlich, die Vegetation in einem vitalen Zustand zu halten (d.h. die Produktivität zu erhalten) und ein Absterben zu verhindern (d.h. die Zufuhr von leicht abbaubarem organischen Material als Substrat für mikrobiellen Abbau zu vermeiden). Dies kann beispielsweise bei Wiedervernässungsmaßnahmen erreicht werden, indem man einen Übergang zu Pflanzenarten erlaubt, die an nasse Bedingungen angepasst sind.

Chapter 1: Overall introduction

1.1. Peatlands: definition, area and importance

A peatland is an area with a naturally accumulated peat layer at the surface (Joosten 2010a). Peatlands have been defined by their soil type or by their vegetation cover (Ramsar 1971). While the definition by vegetation type is restricted to the presence of peat forming species, the definition by soil type is wide enough to include the managed, drained and degraded peat forms.

Organic soils are defined by their organic matter content together with a depth criterion. The German soil classification system (Ad-Hoc-AG Boden 2005) defines peat as organic soils which have > 30 % organic matter and an organic horizon $\geq$ 30 cm. The minimum peat depth of 30 cm is historically based on the ploughing depth (Joosten 2010a). The *World Reference Base for Soils* (WRB IUSS Working Group 2006) lists histosols as soils with an organic layer > 40 cm formed from organic material and with a carbon content between 20 to 30 %. In contrast, the IPCC definition of organic soils is broader and includes shallow peat soils with an organic horizon of $\geq$10 cm and strongly degraded peat soils with a carbon content $\geq$12 % (IPCC 2006) – and assumes that they also behave like real peat soils regarding GHG (greenhouse gas) fluxes (Leiber-Sauheitl et al. 2014).

In this thesis, the peat soils studied fall under the histosol definition of the German soil classification system (Ad-Hoc-AG Boden 2005) and the W*orld Reference Base for Soils* (WRB IUSS Working Group 2006).

Peatlands are ecosystems in which carbon (C) has been accumulated on the long term as more carbon is fixed through photosynthesis than released through respiration. Therefore, peatlands are a long-term sink for atmospheric carbon dioxide (CO_2) (Gorham 1991; Roulet et al. 2007). Peat forms under wetland conditions, where waterlogging causes oxygen deficiency and organic matter accumulates because decomposition is slowed down and incomplete (Kasimir-Klemedtsson et al. 1997). Peat usually accumulates slowly, at the rate of about a millimetre per year (Keddy 2010).

Peatlands can be classified in terms of their source of water and nutrients into bogs and fens. Bogs are situated higher than the surrounding landscape on a dome-shaped landform and obtain most of their water from rainfall (i.e. are ombrotrophic). Fens are located on slopes, flats, or depressions and get their water from both rainfall as well as surface water – they are known as minerotrophic.

Peatlands provide many ecosystem services including biodiversity, agricultural products, forestry, water resources, flood water retention, recreation, archaeological resource and – the most recently considered – carbon sequestration (Lunt et al. 2010).

Worldwide, peatlands cover ~3 % of the total land area (e.g. (Joosten and Couwenberg 2009). Most peatlands are found in the northern hemisphere (87.5 %) and only 10-12 % in tropical regions (IPS 2008). The carbon accumulated in peatlands corresponds to almost half of the total atmospheric carbon stock (Houghton et al. 1990). They are important carbon stores, representing up to one third (between 250 and 450 Pg; 1 Pg = 1Gt = 1015g) of the World's terrestrial carbon pool (Gorham 1991). But peatlands also influence the global climate via the atmospheric CH_4 budget – they are considered to be the largest single source of atmospheric CH_4 also when considering all natural and anthropogenic emissions.

On the European continent, peatlands cover 5–6 % of the land surface (ca. 515,000 km²) (Drösler et al. 2008) and are concentrated in northern and temperate regions.

In Germany, 3.8 to 5.1 % of the land area is peatlands – depending on the source (Drösler et al. 2011b). Recently gathered information reveals that 16,668 km² of the German land area are peatlands (status of 2008; International Mire Conservation Group Global Peatland Database (IMCG-GPD) (Joosten 2010a) which corresponds to 4.67 % of the total land area.

1.2. Societal context

1.2.1. Peatland use history

Peatlands have long been perceived as wild, dangerous and hostile environments for humans. In temperate regions, making use of peatlands by peat extraction or cultivation was expensive and hard for the first generations and often done as public effort (e.g. colonization of Dutch in N-Germany, „Emslandplan" in the 1960`s, etc.).

In Europe, peat was used early as litter, for soil improvement and in balneology. Since the bronce age, peat has traditionally been extracted for energy supply. It even became essential as fuel in parts of Germany due to shortage of firewood, e.g. during the 18th until the beginning of the 20th century (Succow 2001a). Nowadays, peat is not extracted any more for energy production in Central Europe, but it is still important in Ireland, North- and Eastern Europe and Russia (Joosten and Couwenberg 2001).

For several hundreds of years peatlands were used in an extensive manner. Since the Middle Ages, peatlands were used as pastures. The more intensive agricultural use started at the end of the 19th century. Although peatlands were systematically drained during the first World War these agricultural areas were still extensively used. In Central Europe, it was only in the period between the 1950`s and the 1980`s that the agricultural use was profoundly intensified and extended to the major part of peatland areas (Succow 2001b).

During the last decades, the use and destruction of peatlands in South East Asia became more prominent in the public perception. These peatlands are being deforested, usually accompanied by some form of drainage, and subjected to agricultural use and other forms of land conversion (Hooijer et al. 2012). Major concerns here are land subsidence, leading to damage on infrastructure, and peat fires which easily break out on degraded peat soils and which set free large amounts of carbon (Page et al. 2002; Page et al. 2010). In recent years, carbon losses from drained SE Asian peatlands have been found to contribute substantially to global GHG emissions (Hooijer et al. 2012).

The drainage of peatlands not only leads to ecological consequences – such as degradation of peatlands and carbon losses, loss of biodiversity, nutrient fluxes leading to environmental pollution – but also to economic and social consequences (Succow 2001b).

In Central Europe, the use of peatlands is diminishing due to the socio-economic changes since the 1990´s and ongoing soil degradation (Couwenberg et al. 2008). In some areas, where peatland use has proven unsuccessful, peatlands are being rewetted.

1.2.2. Peatlands in the context of climate change mitigation

More than 30 % of the total global anthropogenic GHG emissions are estimated to originate from the land use sector (Agriculture, Forestry and Other Land Use (AFOLU)) (IPCC 2007a) – a quarter of those are released via peatland fires and degradation of drained peat soils (Couwenberg 2009a).

While globally, drainage and cultivation of peatlands is going on, in particular in South East Asia (Page et al. 2010), the value of peatlands as a carbon reservoir (Gorham 1991; Ramsar 2002) and their role in global climate regulation (Joosten 2010b; Tanneberger and Wichtmann 2011) has been recognized.

After years of international debate, peatland rewetting is now eligible as voluntary activity for reducing GHG emissions in the framework of international commitments, e.g. under the *Kyoto Protocol*, the *REDD+*[1] mechanism or the *EU LULUCF decision*[2]. Rewetting reduces CO_2 and nitrous oxide (N_2O) emissions but reinstates methane (CH_4) emissions that then are defined as anthropogenic and thus must be reported and accounted (Couwenberg 2009a).

Thus, rewetting programmes for degraded peatlands present a new challenge and may be implemented by using the opportunity for climate change mitigation (Joosten 2010b). Challenging rewetting programms are already being implemented with the explicit goal of reducing GHG emissions (Couwenberg et al. 2008), e.g. in Germany, Poland and Belarus[3].

On the global scale, peatland rewetting is expected to reduce GHG emissions in the order of several hundred Mio t CO_2 equivalents per year (Joosten 2010a). For Germany, the hypothetical potential for emission reduction via a climatic friendly management of peatlands – extenxive management and rewetting – is estimated to about 35 Mio t CO_2 equivalents per year, respectively 76 % of the actual emissions (Freibauer et al. 2009).

International conventions for climate change mitigation

The role of peatlands in carbon storage and sequestration and their importance for climate change has been discussed since the 1990s by various international conventions and stakeholders[4] before it was brought to the agenda of the Climate Convention (see UNFCCC below) in 2006 (Joosten 2011a). Large emissions from peatland conversion and fires in SE Asia emphasized the problems of peatland destruction on the global scale.

The *United Nations Framework Convention on Climate Change* (UNFCCC) is an international environmental treaty with the objective to prevent dangerous anthropogenic interference of the climate system. In 1997, the *Kyoto Protokol* to the UNFCCC was adopted which sets binding obligations on industrialized countries (Annex I parties of the UNFCCC) to reduce GHG emissions.

Under the *Kyoto Protocol*, countries are obliged to report on their anthropogenic GHG (greenhouse

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1 Reducing Emissions from Deforestation and Forest Degradation
2 Decision No 529/2013/EU of the European Parlament and of the Council of 21 May 2013 on accounting rules on greenhouse gas emissions and removals resulting from activities relating to land use, land-use change and forestry and on information concerning actions relating to those activities. L 165/80 Official Journal of the European Union 18.6.2013
3 Large-scale rewetting projects are performed in Belarus – where 14 % of the land area are peatlands – and within which funds should bei raised through selling high quality carbon credits on the voluntary market. One of these initiatives is the three-year project "Restoring peatlands and applying concepts for sustainable management in Belarus – climate change mitigation with economic and biodiversity benefits" (for details see (Tanneberger and Wichtmann 2011).
4 e.g. the *Ramsar Convention on Wetlands of International Importance*, the *Convention on Biological Diversity* (CBD), the *Intergovernamental Panel for Climate Change* (IPCC), and global peatland stakeholder groups

gas) emissions including some of the GHG emissions from peatlands. The aim of reporting emissions is to monitor the progress of agreed national emission reduction targets[5]. In the *first commitment period* under the *Kyoto Protocol* (2008-2012), only N_2O emissions from „cultivated Histosols" (i.e. peatlands drained for cropland and grasslands under agriculture) and CO_2 and N_2O emissions from drained peatlands under forestry (if the activity „Forest Management" has been elected) were included. In contrast, a more comprehensive inclusion of anthropogenic GHG emissions from wetland drainage and rewetting is allowed in the *second commitment period* under the *Kyoto Protocol* (2013-2020).

In addition, the *Kyoto Protocol* includes a mechanism for „carbon trading" – the opportunity to offset a country´s emissions by acquiring the reduced emissions of another country (Joosten 2011b).

The 2006 *Guidelines for National Greenhouse Gas Investories* provide the methodology for calculating and reporting national GHG emissions and removals. The *2013 IPCC Kyoto Protocol Supplement*[6] includes guidance on methodologies on how to implement the activity „Wetlands Drainage and Rewetting", which „is a system of practices for draining and rewetting on land with organic soil that covers a minimum area of 1 hectare. It applies to all lands that have been drained since 1990 and to all lands that have been rewetted since 1990 and that are not accounted for under any other activity. Drainage is defined as the direct human-induced lowering of the soil water table and rewetting is the direct human-induced partial or total reversal of drainage" (IPCC 2014).

In order to fill the gaps related to peatland rewetting in the 2006 *Guidelines for National Greenhouse Gas Investories*, the *Wetlands Supplement*[7] has been developed and accepted in 2013 and provides guidance on methodologies on how to estimate GHG emissions from drained and rewetted wetlands.

Under some conditions, voluntary activities for reducing GHG emissions can be accounted for under the *REDD+*[8] mechanism which is still under discussion by the *United Nations Framework Convention on Climate Change* (UNFCCC). The objectives of *REDD+* are climate mitigation by reducing GHG emissions and the removal of GHG through enhanced forest management in developing countries.

In parallel to the global negotiations, the EU has issued the *LULUCF decision*[9], making reporting of CO_2 and CH_4 emissions from cropland and grazing land mandatory from 2013 onwards, although these emissions do not count for any quantitative emission reduction targets. This includes emissions from peatlands drained for agriculture.

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5   reduced emissions compared to the reference year 1990
6   activity „Wetlands Drainage and Rewetting" decided under Decision 2/CMP.7 (Land use, land-use change and forestry) contained in document FCCC/KP/CMP/2011/10/Add.1
7   The 2013 Supplement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories: Wetlands (http://www.ipcc-nggip.iges.or.jp/public/wetlands/background.html)
8   Reducing Emissions from Deforestation and Forest Degradation
9   Decision No 529/2013/EU of the European Parlament and of the Council of 21 May 2013 on accounting rules on greenhouse gas emissions and removals resulting from activities relating to land use, land-use change and forestry and on information concerning actions relating to those activities. L 165/80 Official Journal of the European Union 18.6.2013

1.3. Undisturbed peatlands

1.3.1. The crucial role of the water table position for GHG production and release

Natural peatlands are characterized by a high water table position. The mean annual water table is close to the soil surface with seasonal fluctuations (IPCC 2014) due to a net surplus of water and the effect of the specific vegetation types together with the peat characteristics. Peat bodies consist classically of two layers:

- the acrotelm: a relatively shallow surface layer with a fluctuating water table where aerobic conditions occur; and

- the catotelm: a layer located below the mean water table with anaerobic conditions created by the consumption of oxygen. Anaerobic conditions lead to reduced mineralization and allow the accumulation of organic material.

Thus, the position of the water table determines the thickness of the aerobic and the anaerobic zone in the peat profile (Fig. 1-1) and has the strongest effect on GHG exchange (Augustin 2001). The thickness of the upper aerobic zone is crucial as respiration processes are much more faster under aerobic conditions and methane is oxidized in this upper aerobic zone. A high water table position entails moderate net CO_2 fixation, moderate to high CH_4 emissions and very low N_2O emissions (Augustin 2001). In undisturbed peatlands, the layer with aerobic conditions is usually shallow (Drösler et al. 2008).

The gaseous exchange between the atmosphere and the peat surface (Fig. 1-1) is dominated by the photosynthetic fixation of CO_2 (GPP, gross primary production) and by heterotrophic and autotrophic respiration losses (R_{eco}, ecosystem respiration). The balance between these is known as the net ecosystem exchange (NEE) of CO_2. Respiration processes are an order of magnitude faster under aerobic conditions than under anaerobic conditions (Drösler et al. 2008) as anaerobic degradation provides less energy than aerobic degradation (Koppisch 2001).

CH_4 flux is the result of methane production in the lower anaerobic peat layer and methane oxidation in the near-surface aerobic layer or in the oxic zones of the rhizosphere (see Fig. 1-1). Methane is one of the end products of anaerobic decomposition. Organic matter (e.g. plant litter, root excudates, peat) is rapidly degraded by non-methanogenic microorganisms into low molecular compounds (such as H_2/CO_2 and acetate) that are further reduced by methaongenes into methane (Augustin et al. 2011). First of all, anaerobic conditions have to be established, thereafter, the availability of fresh organic matter is the main determant for CH_4 formation (Couwenberg 2009a). Aerenchymous plants ("shunt" species) affect the CH_4 flux as they enable the transport of O_2 into anaerobic peat horizons where methane is re-oxidized in the oxygenated zone surrounding plant roots (Couwenberg 2009a). They also allow methane transport from deeper peat horizons to the surface by-passing CH_4 oxidation in aerobic layers ("chimney-effect") (Augustin 2001).

Methane production is spatially very variable (Worrall et al. 2010). A literature review of field GHG measurements in temperate European peatlands shows that net CH_4 emissions were negligible at mean annual water table < -20 cm and steeply increased with rising water table (Couwenberg et al. 2008).
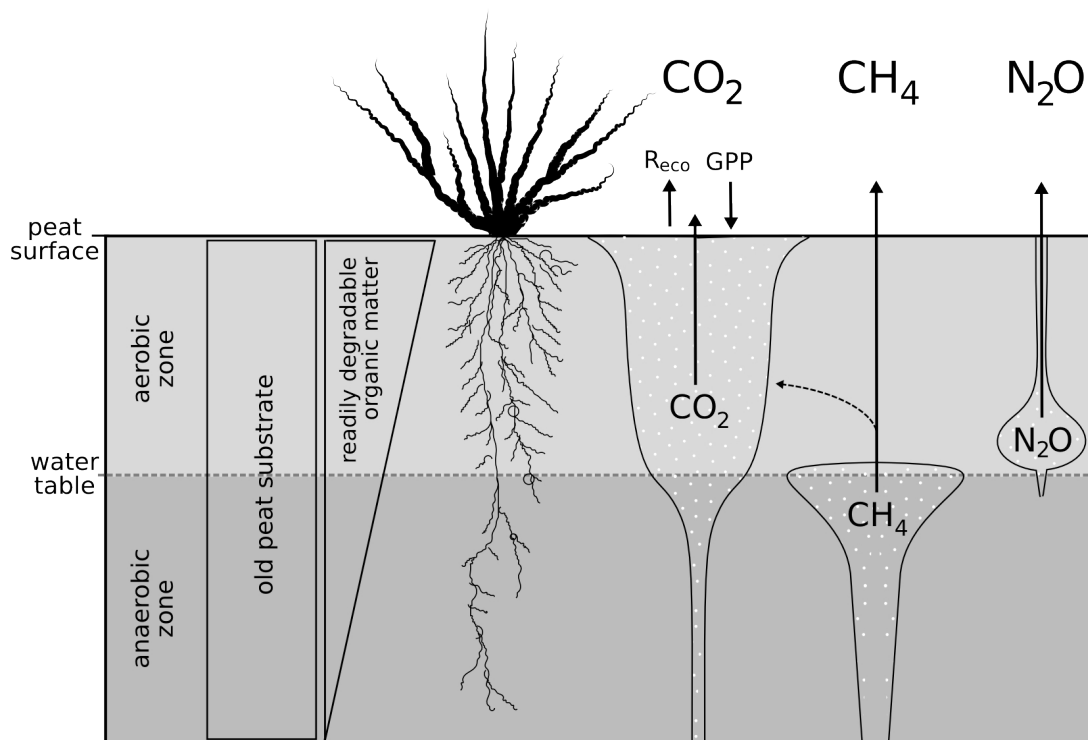
Fig. 1-1: Schematic illustration of a peat profile showing the two determining factors water table and organic matter (left) for microbial production of the greenhouse gases CO_2, CH_4 and N_2O (right). The water table position determines the thickness of the aerobic and the anaerobic zone. Organic matter consists of the old peat substrate (i.e. recalcitrant carbon compounds more resistant to decomposition) and readily degradable organic matter (e.g. from plant litter, root excudates, etc.). The exchange of CO_2 on the peat suface is determined by the two opposing processes ecosystem respiration (R_{eco}, release of CO_2 into the atmosphere) and gross primary production (GPP, fixation of CO_2 via photosynthesis). Gas transport can take place via diffusion, ebulition and plant mediated transport (arrows). Methane may be consumed in the aerobic zone (dashed arrow) or in the oxic zones of the rhizosphere by methane oxidizing microorganisms.

N_2O flux is the result of production and consumption processes by nitrifying and denitrifying bacteria. Nitrification mainly depends on NH_4^+ and O_2 availability, while denitrification is generally controlled by O_2, N-oxides and a suitable reductant which is commonly organic carbon (Firestone and Davidson 1989). The soil water content is the dominant environmental controller as it controls gas transport within the soil (Firestone and Davidson 1989; Davidson et al. 2000). N_2O is produced under sub-oxic condidtions (Fig. 1-1) (Kasimir-Klemedtsson et al. 1997) which occur e.g. in the capillary fringe. In water-saturated (anaerobic) soils, much of the N_2O is further reduced to N_2 by denitrifiers (Davidson et al. 2000). Abrupt changes is soil moisture (e.g. a drastic rise of the groundwater table or strong rainfalls) are considered important for trace N-gas fluxes as they change the controlling factors for nitrification and denitrification (Firestone and Davidson 1989). N_2O production only occurs when ammonium or nitrate are available, e.g. via peat mineralization,

fertilization or N-deposition (Augustin et al. 2011). Natural peatlands usually have a low potential for N_2O emissions due to their N-poor conditions and, therefore, N_2O emissions are often not considered in GHG balance studies (Beetz et al. 2013).

1.3.2. Organic matter quality and quantity and its effects on GHG production

Besides the water level, the quality and quantity of organic matter plays an important role in potential GHG production (Fig. 1-1). It is the presence and amount of fresh, readily decomposable organic matter that determines the magnitude of GHG emissions (Hahn-Schöfl et al. 2011). This is supported by the observation that CO_2 and CH_4 production rates are generally greatest in the surface peat (e.g. (Glatzel et al. 2004; Reiche et al. 2010; Estop-Aragonés and Blodau 2012) as the availability of organic matter decreases with depth (Segers 1998). The old peat plays only a subordinate role as a substrate for GHG production (Couwenberg 2009a; Hahn-Schöfl et al. 2011) and, consequently, the quality of the bulk peat substrate itself is of minor importance.

The decomposability of the organic material is crucial for CO_2 and CH_4 formation and often chemical peat characteristics, nutrient availability, aromaticity (Smolders et al. 2002; Frank et al. 2014) or thermal stability (Reiche et al. 2010) are used to indicate organic matter quality. However, there is currently no common definition of organic matter quality (Reiche et al. 2010).

1.3.3. Climatic relevance of natural peatlands

Within the context of this thesis, we use the atmposhere as reference point: negative gas fluxes mean a removal from the atmosphere and incorporation into the soil and plant (decreasing the atmospheric concentration), positive values indicate gas fluxes from the soil to the atmosphere (increasing the atmospheric concentration).

The impact of peatlands to radiative forcing is twofold. Most natural northern peatlands sequester carbon by accumulating peat – which lowers the atmospheric CO_2 burden – but simultaneously emit CH_4 – increasing the atmospheric CH_4 burden (Frolking et al. 2006). The climatic relevence of peatlands can be assessed depending on the purpose and with regard to different time scales.

On the long term, the carbon balance is the key factor which reflects the functional role of peat growth. The long-term carbon balance (Long-term average carbon uptake rates (LORCA)) is determined as a function of the total mass accumulated and the age of the peat deposit. In northern peatlands, the average long-term carbon uptake is around 25 g C m^{-2} yr^{-1} (Drösler et al. 2008). The longer the time horizon the less important is the radiative forcing of CH_4. Methane has a relatively short lifetime. In contrast to CO_2, a CH_4 pulse input is almost completely removed from the atmosphere within several decades and the atmosphere comes into approximate equilibrium with a new constant CH_4 source or sink (Frolking et al. 2006).

The short-term GHG exchange is important with regard to the anthropogenic activities in peatlands having an impact on climate change (Drösler et al. 2008). In order to assess the relative climate impacts of anthropogenic GHG emissions and to compare the climate impacts of different GHGs, the Global Warming Potential (GWP) methodology was adopted (Frolking et al. 2006). The radiative forcing of a site is determined by CO_2, CH_4 and N_2O fluxes together accounting for their individual global warming potential relative to CO_2 for a 100-year time horizon (IPCC 2007b). In order to assess and compare the climate impact of different peatlands, the GWP methodology is

based on the annual GHG flux rates (Frolking et al. 2006), e.g. as done first for various European peatlands by (Drösler et al. 2008). A negative GWP means that a peatland site is a GHG sink (having a „cooling effect" on the climate), a positive GWP value indicates a peatland as a GHG source („warming effect"). Within the context of this PhD thesis, the short-term GHG exchange is assessed by using the GWP methodology – however, based on GHG flux rates over a defined period and not on annual flux rates.

Within the *Kyoto Protocol*, the GWP methodology provides a mechanism for „trading" among gases. The GWP methodology is a policy tool to evaluate the climate impact of GHG pulses but it does not assess the impact of sustained or variable GHG emissions on radiative forcing at any given time (Frolking et al. 2006).

Natural European peatlands are close to climate neutral (Drösler et al. 2008). They generally take up CO_2, release part of the accumulated carbon as CO_2 and CH_4 due to microbial decomposition processes and are neutral with respect to N_2O (see natural state in Fig. 1-2). However, GHG fluxes from peatlands are very variable in space and time.

1.4. Drainage

Peatlands have been subjected to land use – which is usually associated with draining – for many centuries: for use in agriculture, forestry, and peat extraction. Drainage is the „artificial (human-induced) lowering of the soil water table to levels which are at least temporarily below natural levels, i.e. below the soil surface, but can experience seasonal fluctuations" (IPCC 2014).

Worldwide, 500,000 km² (of the total 4 million km² peatland area) are degraded (Joosten 2010a). Approximately 60 % of European natural peatlands have been destroyed due to anthropogenic activities – such as agriculture (50 %), forestry (30 %) and peat extraction (10 %) – so that only a small area of living, peat-accumulating peatlands still exists (Joosten and Couwenberg 2001). In Germany, the major part of peatlands (71 %) has been drained for use in agriculture – mainly as cropland (31%) and grassland (40 %). Germany turns out as the second largest emitter in Europe despite its relatively small peatland area. The reason for this fact is the intensive use of most of the peatland area as cropland and grassland with intensive drainage (Drösler et al. 2008).

1.4.1. Effect on peat characteristics

Long-term drainage and agricultural use of peatlands cause irreversible chemical, physical and biological changes in peat characteristics (Grønlund et al. 2006).

Drainage leads to an irreversible lowering of the surface (subsidence) (Kasimir-Klemedtsson et al. 1997; Joosten 2010a; Hooijer et al. 2012) which is caused by two different processes: biological oxidation – resulting in carbon loss – and physical volume reduction which is caused by compaction, shrinkage and consolidation (Hooijer et al. 2012). Subsidence occurs in the first years mainly due to consolidation and later due to compaction and peat mineralization (Höper 2007; Hooijer et al. 2012). In the first few years after drainage, carbon loss rates are substantially higher as a finite pool of the most labile carbon compounds decomposes rapidly leaving only recalcitrant carbon compounds that are more resistant to decomposition (Hooijer et al. 2012).

Furthermore, drainage leads to internal eutrophication of the peat soils (Stegmann and Zeitz 2001; Zak et al. 2010). A reduction of macroporosity, increased bulk density and ash content, and reduced

permeability to air and water are also effects from draining (Kasimir-Klemedtsson et al. 1997; Grønlund et al. 2008).

The water content and the water conductivity of the peat are reduced and the amplitude between summer and winter groundwater level is increased (Drösler 2005; Hooijer et al. 2012). In case of agricultural use, ploughing leads to aeration and better incorporation of fertilizer and boosts peat mineralization (Kasimir-Klemedtsson et al. 1997; Freibauer et al. 2004; Grønlund et al. 2006).

1.4.2. Effect on GHG fluxes and climate impact

Drainage can significantly alter carbon cycling within peatlands (e.g. (Roulet et al. 2007) such that peatlands can become a large and persistent source of CO_2 to the atmosphere (see Fig. 1-2) (e.g. (Waddington et al. 2002; Couwenberg et al. 2008; Joosten 2010a), dissolved organic carbon (DOC) to aquatic ecosystems (e.g. (Limpens et al. 2008; Zak et al. 2010) and particulate organic carbon (Estop-Aragonés and Blodau 2012). As the enormous peat carbon pool is gradually but continuously tapped GHG emissions last for many decades (Joosten and Couwenberg 2009).

Various factors are given which may control CO_2 and N_2O emissions from agriculturally used organic soils, such as peat structure, C:N ratio, drainage depth, cultivation practice and climate (e.g. (Kasimir-Klemedtsson et al. 1997). The location of the groundwater table has the largest influence on GHG emissions from peatlands (Augustin 2001). Lowering the groundwater table results – due to aeration – in extremely high net CO_2 release and moderate to high N_2O emissions (Fig. 1-2) (Kasimir-Klemedtsson et al. 1997; Augustin 2001). CH_4 emissions cease as the aerobic zone is enlarged through drainage, increasing methane oxidation (Fig. 1-2). Maximum mineralization rates are observed at groundwater levels of 60 to 90 cm (Höper 2007).

Peatland drainage may also cause substantial emissions of N_2O (Fig. 1-2) (Joosten 2010a) which mainly depend on the groundwater level and fertilizer N application (Kasimir-Klemedtsson et al. 1997; Flessa et al. 1998). Fertilized peatlands have a higher potential for N_2O emissions because of enriched N-pools compared to natural peatlands (Beetz et al. 2013). Perturbations in the soil, e.g drying/wetting or freezing/thawing, affect substrate availability and cause seasonal fluctuations in N_2O emissions (Kasimir-Klemedtsson et al. 1997; Flessa et al. 1998). N_2O emissions have high spatial and temporal variability and should be seen with caution (Kasimir-Klemedtsson et al. 1997).

In the literature, situations when high N_2O emissions can be expected are diverse: The risk for N_2O emissions is highest in nutrient-rich fens with highly variable water table and a mean annual groundwater table of -50 cm (Drösler et al. 2011b). The highest N_2O flux was observed at intermediate soil moisture content (Kasimir-Klemedtsson et al. 1997) (Joosten and Couwenberg 2009) state that N_2O is in general emitted at water levels below -20 cm.

Summarizing, lowering the water level in peatlands differently affects the three GHGs – it leads to an increase in net CO_2 and N_2O release and a decrease in CH_4 emissions. Considering all three GHGs together, managed peatlands are significant sources of GHGs (Drösler et al. 2008).

CH₄   CO₂ CH₄ N₂O   CO₂   N₂O   source

CO₂   CH₄   sink

natural   slight ... deep
state   drainage   drainage
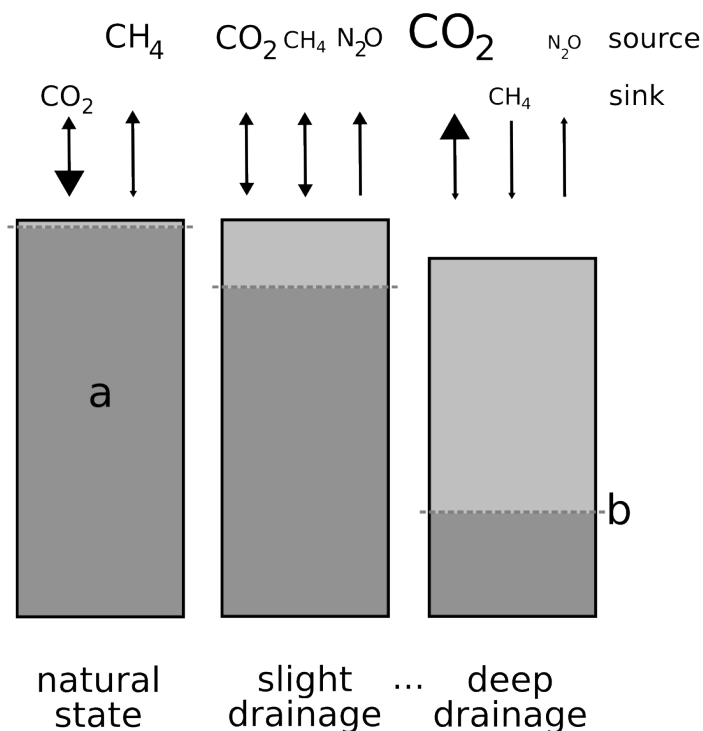
Fig. 1-2: Peatlands in their natural state and under drainage: Direction and relative amount of GHG fluxes (CO_2, CH_4 and N_2O) from peat surface (the arrows indicate the direction of the gas flux, the arrow and font size exhibits the relative amount emitted or taken up); a) peat profile with aerobic (light grey) and anaerobic layer (dark grey), b) position of the water table). (The figure was amended based on those presented in (Drösler et al. 2008).

On the global scale, the amount of CO_2 and N_2O released by peatland drainage corresponds to 2-3 Gt CO_2 equivalents per year (Couwenberg 2009b).

Gobal CO_2 emissions from drained peatlands[10] have strongly increased from 1,058 Mio t in 1990 to 1,298 Mio t in 2008 – this is equivalent to an increase of > 20 % of the 1990 emissions (Joosten 2010a). After Southeast Asia, temperate Europe (EU-27) is the World's second largest emitter of CO_2 from drained peatlands (Joosten and Couwenberg 2009). However, emissions have decreased from 191[11] (in 1990) to 174 Mio t (in 2008) which corresponds to a decrease of ~10% since 1990 (Joosten 2010a).

Drained peatlands represent the largest GHG source in Germany outside the energy sector emitting 5 % of the total German GHG emissions (Umweltbundesamt 2013). This corresponds to 46.0 Mio t CO_2 equivalents per year[12]. So despite its relatively small peatland area, Germany is the second largest emitter of GHGs from peatlands in the European Union because the majority of the peatland area is drained (Drösler et al. 2008).

80 % of German GHG emissions from peatlands originate from fens (Höper 2007) and the

10 CO_2 emissions from peat extraction and fires are excluded
11 CO_2 emissions from peat extraction and fires are excluded
12 all land use types considered including peat extraction

remainder from bogs. In 2011, 60 % of GHG emissions emerged from croplands, 29 % from grasslands, about 5% from settlements, about 5% from peat extraction, and 1.5 % from forestry (Umweltbundesamt 2013). In 2011, drained German peatlands used as cropland and grassland emitted about 25,000 and 11,000 Gg CO_2, respectively, corresponding to approximately 2.7 % and 1.2 % of total anthropogenic CO_2 emissions in Germany (Umweltbundesamt 2013).

1.5. Rewetting of peatlands

Peatland restoration can have different objectives – e.g. re-vegetation, vegetation management, water management (Lunt et al. 2010), conservation of carbon stocks or climate change mitigation (Worrall et al. 2010). In the literature, the term "peatland restoration" is ambiguous as it is defined in different ways depending on the context.

As we focus our work on climate change mitigation, we refer to the definition by the recently adopted *IPCC Wetlands Supplement*: "Wetland restoration aims to permanently re-establish the pre-disturbance wetland ecosystem, including the hydrological and biogeochemical processes typical of water saturated soils, as well as the vegetation cover that pre-dated the disturbance. Normally, the restoration of previously drained wetlands is accompanied by rewetting" (IPCC 2014).

For the assessment of GHG emissions – as done within the framework of this thesis – the term "rewetting" is of importance and the definition given by the IPCC is used: "Rewetting is the deliberate action of raising the water table on drained soils to re-establish water saturated conditions and is accomplished by e.g. blocking drainage ditches or disabling pumping facilities. Rewetting can have several objectives, such as wetland restoration or allowing other management practices on saturated organic soils such as paludiculture. The position of the water table is a major control of the biogeochemical processes responsible for GHG fluxes from wetlands" (IPCC 2014).

„Natural" water levels are closer to the peat surface and show less seasonal fluctuation (Lunt et al. 2010). In practice it is often difficult to establish and maintain the water table at a certain level, so that the water table may be below (partial rewetting) or above an optimum level (permanent flooding).

Peatland restoration represents a new development due to peatland conservation programs. Most peatland restoration measures have happened after peat extraction or on near-natural sites. There is little experience with restoration of deeply drained, fertilized agricultural sites, where the GHG emission reduction per area is highest.

Peatland restoration is an emerging area of GHG research (Drösler et al. 2008). Studies so far have focused on the effect of rewetting on GHGs. While there is a constant growth of annual carbon and GHG observations in the literature, few studies have considered the full GHG budget of CO_2, CH_4 and N_2O. A clear functional relationship between GHG emissions and important physical, chemical and biological drivers is still missing. This makes estimates of GHG emission reductions by peatland restoration projects highly uncertain. The absence of long-term monitoring data is a major problem and limits our knowledge about the success of peatland restoration (Lunt et al. 2010).

1.5.1. Effect on peat characteristics

Rewetting leads to fundamental changes in site characteristics in a transient and dynamic way which are currently inadequately studied (Couwenberg et al. 2008).

In case the swelling and shrinkage capacity of the peat is lost, peat characteristics change irreversibly with drainage (Frank et al. 2014). With rewetting taking place, futher degradation of the peat is prevented and new peat may be formed by peat forming vegetation if established. Depending on drainage and land use history, highly decomposed peat layers are located in the top horizon and less decomposed peat in subjacent layers.

It has been shown that rewetting leads to the release of large amounts of nutrients into the pore water, e.g. phosphorus, ammonium, dissolved carbon and iron (Zak and Gelbrecht 2007; Smolders et al. 2008; Knorr and Blodau 2009; Worrall et al. 2010; Zak et al. 2010; Riet et al. 2013). The *IPCC Wetlands Supplement* provides global default estimates for water-borne dissolved organic carbon fluxes (IPCC 2014).

1.5.2. Effect on GHG fluxes and climate impact

The recently adopted *IPCC Wetlands Supplement* provides guidance on GHG emissions from rewetted organic soils including boreal, temperate, and tropical wetlands occurring in any land-use category (IPCC 2014).
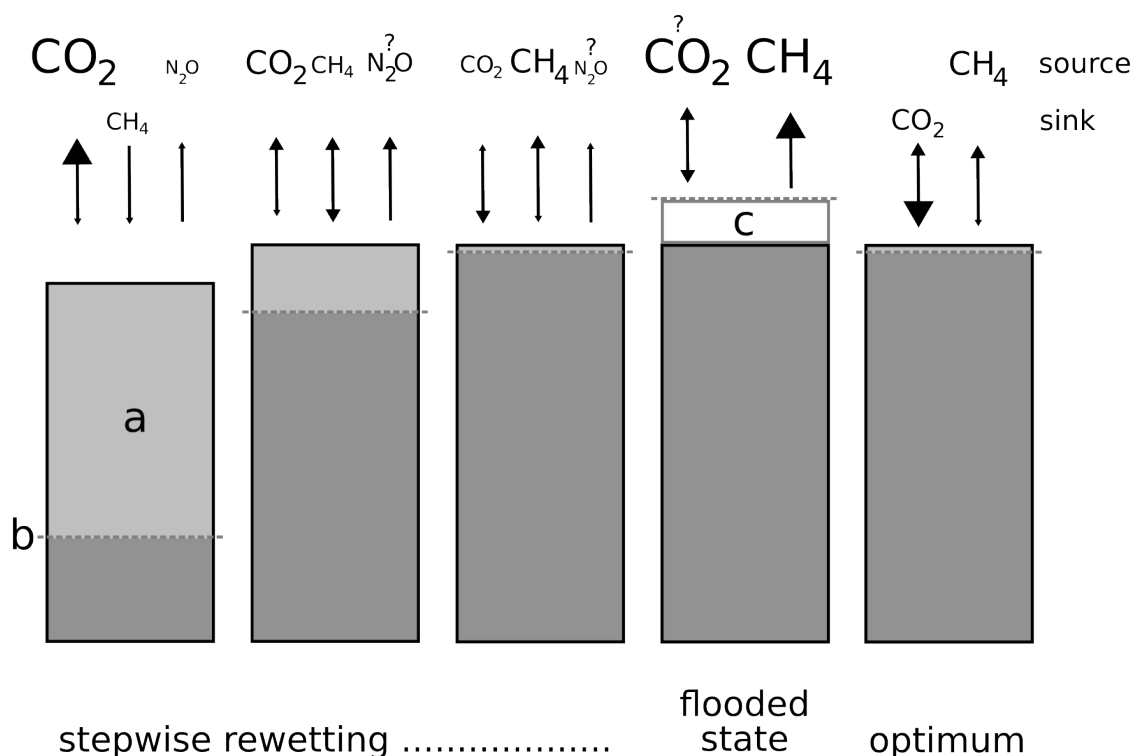
Fig. 1-3: Rewetting of peatlands: Direction and relative amount of GHG fluxes (CO_2, CH_4 and N_2O) from peat surface (the arrows indicate the direction of the gas flux, the arrow and font size exhibits the relative amount emitted or taken up); a) peat profile with aerobic (light grey) and anaerobic layer (dark grey), b) position of the water table, c) supernatant water. (The figure was amended based on those presented in (Drösler et al. 2008).

Raising the water level principally reduces CO_2 emissions (Fig. 1-3) due to a reduction in peat mineralization (Couwenberg et al. 2008; Worrall et al. 2010; IPCC 2014). However, re-establishing water saturated conditions in the peat also re-creates conditions favourable for methanogenesis and may, consequently, lead to an increase in CH_4 emissions (e.g. (Drösler 2005; Hendriks et al. 2007; Drösler et al. 2008; Worrall et al. 2010; IPCC 2014). It has been observed that after rewetting CH_4 emissions increased while simultaneously CO_2 emissions remained at a high level (Augustin and Joosten 2007; Couwenberg et al. 2008; Höper et al. 2008).

Methane has a global warming potential 25 times higher than CO_2 (IPCC 2007b) and, when accounting for this higher GWP, increased CH_4 emissions may considerably reduce the positive climate impact of rewetting measures. Due to their better nutrient supply, formerly agriculturally used peatlands produce much more CH_4 after rewetting than near-natural sites (Höper 2007). In addition, fluctuations of the water table may result in a drastic increase of N_2O emissions (see Fig. 1-3) (Augustin and Joosten 2007; Couwenberg et al. 2008) the GWP of which is 298 times higher compared to CO_2 (IPCC 2007b).

Since rewetting activities have been carried out for a relatively short term, no data are available from long-term studies on rewetted peatlands (Augustin and Joosten 2007; Lunt et al. 2010). Seen on a long term perspective, GHG release from rewetted peatlands is proposed to change in three phases[13] – shifting the climate impact from negative to positive: During the first phase after rewetting, GHG emissions in terms of CO_2 equivalents are expected to be extremely high due to high CH_4 emissions and low CO_2 uptake – a strong negative climatic effect may be expected. In the second phase, the climatic effect turns slightly positive as CH_4 emissions decrease while CO_2 uptake increases. The third phase is comparable to those in pristine peatlands with their neutral climatic effect – based on low CH_4 release and low CO_2 uptake (see optimum in Fig. 1-3).

It has been shown that, on the medium to long term, rewetting definitely leads to a reduction in greenhouse gas emission compared to the situation without rewetting (Augustin and Joosten 2007; Joosten and Couwenberg 2009). However, observed evidence of the existence and length of these three individual phases is lacking. Additionally, we do not know how GHG emissions will develop within and in between these phases.

Thus on the short term, rewetting of drained peatlands also bears its risks – e.g. CH_4-dominated GHG emissions – and may not necessarily turn a peatland into a GHG sink. Effective rewetting measures with respect to climate change mitigation means to raising the water table and find a trade-off between reduced peat mineralization and avoiding an increase in CH_4 release.

1.6. Motivation for performing incubation experiments and research questions

The reduction of anthropogenic greenhouse gas emissions via rewetting drained peatlands may now be accounted for in national greenhouse gas reporting under the *Kyoto Protocol*. As drained agricultural peatlands are hotspots for CO_2 and N_2O, challenging rewetting programms are being implemented in Europe as climate mitigation measure (Joosten 2007; Höper et al. 2008). However, with raising the water table the risk of CH_4 emissions increases but detailed knowledge is still lacking in particular on the long-term time scale.

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13 The possible long-term shift of GHG release is based on currently available evidence from Belarussian mires (Augustin and Joosten 2007).

In order to develop effective rewetting and sustainable management measures we need to better understand the processes and factors determining GHG fluxes after rewetting (Augustin and Joosten 2007). To achieve the goal of reduced GHG emissions, practical guidance is needed to find a balance between reduction of CO_2 and N_2O release and simultaneous avoidance of high CH_4 emissions.

GHG emissions are extremely variable in time and space and may be explained by a multitude of factors: the complexity of processes involved in formation / transformation / release, site characteristics, weather conditions, characteristics of the peat substrate, plant development and peatland management (Augustin 2001). GHG emissions are controlled by parameters which vary considerably within the course of a year, such as water table, temperature, vegetation growth and actual management of a peatland site.

Several field studies have been performed to quantify the annual GHG balance from European peatlands (Drösler 2005; Augustin and Joosten 2007; Hendriks et al. 2007; Höper et al. 2008; Beetz et al. 2011; Drösler et al. 2011a; Beetz et al. 2013; Heinichen et al. 2014; Tiemeyer et al. 2014; Leiber-Sauheitl et al. 2014). The GHG balance – that is determined by measuring annual atmospheric CO_2, CH_4 and N_2O fluxes and accounting for their different Global Warming Potentials (GWP) – may be used to assess and verify the climate mitigation effect of peatland rewetting projects and to account for GHG reduction under the *Kyoto Protocol* and the *EU LULUCF Decision* (529/2013/EU). However, annual GHG fluxes vary considerably between years (e.g. (Drösler et al. 2011a; Tiemeyer et al. 2014) because they are influenced by seasonal weather conditions. Therefore, field studies are not suitable to investigate the effect of the most important determinants for GHG fluxes due to the covariance between factors.

Studying GHG fluxes under controlled conditions in the laboratory allows to purposefully investigate the factors determining GHG exchange, e.g. by systematically manipulate the water table, the duration of flooding / draining and by selecting a specific organic substrate.

The results of both field studies and laboratory experiments together can be used to develop practical guidance for low-GHG rewetting strategies for drained peatlands and to assess their impact on GHG fluxes under defined conditions.

The incubation experiments performed within this PhD thesis aimed to manipulate key drivers of CO_2, CH_4 and N_2O emissions in a range beyond the conditions in the field, so that projections of future GHG emissions could be made based on process understanding under controlled conditions in the laboratory.

This PhD thesis aimed to investigate the role of the organic substrate and the water table under controlled environmental conditions. The main goals of the four incubation experiments were

1. to understand the mechanisms of CO_2 emission reduction by rewetting,

2. to find trade-offs with CH_4 and N_2O emissions after rewetting, and

3. to identify conditions under which CO_2 emission reduction safely outweigh CH_4 emission increase.

The incubation experiments were performed within the framework of the project *„Climate mitigation via peatland management"*[14] (for project details see (Drösler et al. 2011a). Peat samples originated from sites where on-site GHG measurements were performed for several years.

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14 The project was financed by the Federal Ministry of Education and Research and lasted from 2006 to 2010.

The PhD thesis is set out in the form of three publications respectively manuscripts for publication. Consequently, detailed information, materials used and methods applied, results of the incubation experiments and discussions can be found in the respective chapters.

Explanatory notes regarding the set-up of the incubation experiments

Firstly, to investigate the effect of the organic substrate two incubation experiments (see chapter 2) were performed that:

- used mixed samples of different organic substrates;

- excluded living vegetation;

- were performed at constant temperatures in the dark;

- were performed under permanently anaerobic conditions (water table above the surface);

- included regular measurements of CO_2 and CH_4;

- lasted for 363 and 53 days, respectively.

Secondly, to investigate the effect of the water table two incubation experiments (see chapter 3 and chapter 4) were performed that:

- used undisturbed peat mesocosms from drained fen and bog peatlands;

- included living grassland vegetation (testing the response of water-intolerant and wetness-adapted species to changing water table);

- simulated real-world conditions in terms of temperature and radiation allowing for ideal plant growth and microbial activity;

- included regular measurements of all three GHGs (CO_2, CH_4 and N_2O), which is a pre-requisite for assessing the full net GHG balance;

- were performed as long term incubations (lasting 252 and 196 days, respectively).

1.6.1. The effect of the organic substrate for CO_2 and CH_4 emissions

Rewetting principally reduces CO_2 emissions but may lead to an increase in CH_4 release. This was observed at a permanently flooded nutrient-rich fen grassland in Northeastern Germany where extremely high CH_4 emissions were measured in the years following flooding[15] (Augustin and Joosten 2007; Höper et al. 2008). The net climate impact of this site was even higher after flooding than under drained conditions because the ecosystem did not immediately return to its long-term CO_2 sink function. This on-site measurements are in contrast to expectations.

After rewetting, the investigated fen site formed a highly eutrophic shallow lake and the permanently inundated conditions led to the dying-off of the vegetation and the formation of a new sediment layer with a high content of relatively fresh plant litter[16].

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15 The flooding was done within the large-scale nature conservation project „Peene-Haffmoor / Peenetal" by opening the dykes which limited the river Peene.

16 Due to the high nutrient load floating and submerged macrophytes were growing in the open water areas. These aquatic macrophytes have the capability to take up large amounts of nutrients but also contribute to the amount of readily degradable organic matter in the new sediment layer (Steffenhagen et al. 2012).

The two incubation experiments aimed to test the role of fresh plant litter for anaerobic CO_2 and CH_4 production and were performed with material from the phases immediately after flooding and 2.5 years later. The different organic substrates either originated from different depths or included/exluded the newly formed sediment layer. Additionally, pore water chemistry was taken into account.

Research questions:

> *What are the possible sources of the high CO_2 and CH_4 emissions on-site after rewetting? How do organic substrates from different depths or including/exluding fresh plant litter contribute to anaerobic GHG production? We hypothesize that the fresh plant litter can account for a large proportion of the increased CH_4 and CO_2 emissions.*

> *When do conditions favourable for methanogenesis occur?*

These incubation experiments are described and discussed in detail in chapter 2.

1.6.2. The effect of the water table on GHG fluxes: stepwise rewetting and prolonged flooding

The water table position has been identified as the most important factor influencing GHG fluxes. Draining peatlands – as usually done under agricultural management – stimulates CO_2 production, turning peatlands from long-term sinks to significant CO_2 sources, while CH_4 formation decreases. Rewetting – i.e. deliberately raising the water table to re-establish water saturated conditions – principally leads to a reduction of CO_2 emissions but might unintentionally boost CH_4 emissions. Eutrophic fen grasslands are the most frequent peatland and management type in Germany having a risk for high CH_4 (and N_2O) emissions under rewetting depending on the target position of the water table.

Our knowledge of the effect of different water levels on the GHG exchange after rewetting is still restricted. In the literature, a suitable water table minimizing net GHG balance is recommended to be slightly below the peat surface – e.g. around -10 cm (Drösler et al. 2008) repectively -5 cm (Jungkunst et al. 2008). To achieve minimum GHG emissions, the optimum water table must aim to minimize peat mineralization but also to avoid high methane and nitrous oxide release as they have a much higher global warming potential compared to CO_2. It is difficult to determine the functional role of the water table position from field studies due to the seasonal covariance between water table, temperature and vegetation activity.

The effect of the water table position on GHG fluxes (CO_2, CH_4 and N_2O) under controlled environmental conditions was investigated by an incubation experiment simulating gradual rewetting and prolonged flooding. The use of mesocosms from drained fen grasslands with intact vegetation allowed for the assessment of the vegetation effect on GHG fluxes.

Research questions:

> *How does the vegetation react to raising water level and extended flooding (water-intolerant grasses versus water-tolerant sedges)? How does the contribution of autotrophic and hetertrophic respiration change with water table?*

> *Are there water table thresholds for drastic changes in GHG fluxes? At which water table position are net GHG emissions minimal? How are GHG fluxes affected by extended flooding?*

What is the effect of aerenchymous plants? Do sedges boost CH_4 emissions under wet conditions due to plant mediated CH_4 transport?

This incubation experiment is described and discussed in detail in chapter 3.

1.6.3. The effect of the water table on GHG fluxes: alternating wet-dry conditions

Rewetting is being implemented to reduce anthropogenic GHG emissions from peatlands. A high water table reduces CO_2 emissions from peat mineralization, however, it establishes anaerobic conditions favourable for CH_4 production. Flooding might cause high CH_4 emissions, in particular when easily degradable organic matter is present. Thus, rewetting activities should be aimed at minimum CO_2, CH_4 and N_2O release and practical guidance for low-GHG rewetting strategies is needed. The challenge of keeping CH_4 emissions low has been tackled in paddy rice fields[17] by intermittent rather than continuous flooding. In addition, the water table of a rewetted peatland area is expected to fluctuate seasonally as the water table is driven by rain events and water management.

In order to test whether mitigation strategies for rice paddies can also be applied in peatlands, we systematically quantified the GHG response and redox status of fen and bog grassland mesocosms to intermittent wet-dry conditions under constant meteorological conditions.

Research questions:

How do grassland vegetation, photosynthesis, respiration, CH_4 and N_2O fluxes react to a dynamic change in the water table from wet to dry conditions and vice versa? How do wet respectively dry conditions affect the net GHG balance?

Is the response fully reversible when water table switches back to the original position, and repeatable? Is there a memory effect of previous flooding or drainage events?

What length of interim dry periods is needed to effectively reduce CH_4 emissions?

Do wet-dry cycles foster N_2O emissions?

Can alternating water tables work as low-GHG management strategies in peat grasslands?

This incubation experiment is described and discussed in detail in chapter 4.

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17 By alternating wet and dry phases methane emissions were potentially reduced by 48% compared with continuous flooding of rice fields (Siopongco et al. 2013). The water level in the rice field is lowered to 15 cm below the soil surface for a period of 1 to more than 10 days and re-flooded to a depth of around +5 cm.

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Chapter 2: Publication I

Organic sediment formed during inundation
of a degraded fen grassland emits large fluxes
of CH_4 and CO_2

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- assistance in experimental set-up for „organic substrate incubation"; measurement of gas concentration in pore water

- statistical analysis of all data

- graphical presentation

- data interpretation and discussion of results

- planning and writing of the publication

- submission and revision of the publication

contributions by co-authors:

- all data from „peat layer incubation"[18]

- experimental set-up for „organic substrate incubation"[19]; measurement of gas fluxes from peat surface (M. Minke, J. Augustin) and analysis of pore water chemistry (D. Zak, J. Gelbrecht)

- supervision of PhD thesis (A. Freibauer)

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19 The „organic substrate incubation" was planned and performed as a joint activity by ZALF, IGB and MPI-BGC.

Biogeosciences

Organic sediment formed during inundation of a degraded fen grassland emits large fluxes of CH_4 and CO_2

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Abstract. Peatland restoration by inundation of drained areas can alter local greenhouse gas emissions as CO_2 and CH_4. Factors that can influence these emissions include the quality and amount of substrates available for anaerobic degradation processes and the sources and availability of electron acceptors. In order to learn about possible sources of high CO_2 and CH_4 emissions from a rewetted degraded fen grassland, we performed incubation experiments that tested the effects of fresh plant litter in the flooded peats on pore water chemistry and CO_2 and CH_4 production and emission.

The position in the soil profile of the pre-existing drained peat substrate affected initial rates of anaerobic CO_2 production subsequent to flooding, with the uppermost peat layer producing the greatest specific rates of CO_2 evolution. CH_4 production rates depended on the availability of electron acceptors and was significant only when sulfate concentrations were reduced in the pore waters. Very high specific rates of both CO_2 (maximum of $412 \, mg \, C \, d^{-1} \, kg^{-1} \, C$) and CH_4 production ($788 \, mg \, C \, d^{-1} \, kg^{-1} \, C$) were observed in a new sediment layer that accumulated over the 2.5 years since the site was flooded. This new sediment layer was characterized by overall low C content, but represented a mixture of sand and relatively easily decomposable plant litter from reed canary grass killed by flooding. Samples that excluded this new sediment layer but included intact roots remaining from flooded grasses had specific rates of CO_2 (max. $28 \, mg \, C \, d^{-1} \, kg^{-1} \, C$) and CH_4 (max. $34 \, mg \, C \, d^{-1} \, kg^{-1} \, C$) production that were

10–20 times lower than for the new sediment layer and were comparable to those of a newly flooded upper peat layer. Lowest rates of anaerobic CO_2 and CH_4 production (range of $4–8 \, mg \, C \, d^{-1} \, kg^{-1} \, C$ and $<1 \, mg \, C \, d^{-1} \, kg^{-1} \, C$) were observed when all fresh organic matter sources (plant litter and roots) were excluded. In conclusion, the presence of fresh organic substrates such as plant and root litter originating from plants killed by inundation has a high potential for CH_4 production, whereas peat without any fresh plant-derived material is relatively inert. Significant anaerobic CO_2 and CH_4 production in peat only occurs when some labile organic matter is available, e.g. from remaining roots or root exudates.

1 Introduction

Peatlands are recognized as a key player in the atmospheric greenhouse gas (GHG) budget. Although only covering $\sim 3\%$ of the total land area, the carbon accumulated in peatlands corresponds to almost half of the total atmospheric C stock (Houghton et al., 1990; Gorham, 1991). Natural peatlands act as sinks for atmospheric CO_2 and as sources of the methane (CH_4), which has a higher global warming potential than CO_2. The net climate impact of natural peatlands in Europe is nearly zero (Drösler et al., 2008). Drainage of peatland, e.g. for agricultural use, forestry or for peat extraction, turns peatlands from long-term sinks to significant sources of CO_2, while CH_4 emissions cease. This leads to a dramatic increase in the net climate impact (Drösler et al., 2008; Augustin, 2001; Nykänen et al., 1998; Alm et al., 2007). In 2007, drained German peatlands used as cropland and

grassland emitted about 24 000 and 13 000 Gg CO$_2$, respectively, corresponding to approximately 3 % and 2 % of total anthropogenic CO$_2$ emissions in Germany (Umweltbundesamt, 2009). Furthermore, long-term drainage and agricultural use of peatlands cause irreversible chemical and physical changes in peat characteristics, a loss of organic carbon and concurrently internal eutrophication of the peat soils (Zak et al. 2008).

Peatland restoration via rewetting (inundation), i.e. by raising the local groundwater table, is currently being implemented in Germany with the explicit goal of reducing GHG emissions (Höper et al., 2008). Rewetting principally reduces CO$_2$ emissions but can often lead to a sharp increase in CH$_4$ release, as confirmed by field studies in fen (Hendriks et al., 2007; Wilson et al., 2008) and bog ecosystems (Tuittila et al., 2000; Drösler, 2005).

Extremely high CH$_4$ emissions were observed in a flooded fen grassland in NE Germany (up to 205 g C m^{-2} yr^{-1}) in the years following flooding. Contrary to expectations, in this location the net climate impact after flooding was even higher than under drained conditions as the ecosystem did not immediately return to its long-term CO$_2$ sink function (Chojnicki et al., 2007; Höper et al., 2008). As yet, the reason for the excessive CH$_4$ release and the weak CO$_2$ sink function of this flooded fen grassland is not known. However, precise knowledge of these processes is needed to predict if and when a reduction of the expected net climate impact will take place and to propose optimized rewetting measures.

A possible source of the high CH$_4$ production and cause of the weak CO$_2$ sink function after flooding could be the rapid anaerobic decomposition of organic matter in the nutrient-rich upper part of the peat layer. It has previously been shown that this layer releases large quantities of nutrients and dissolved organic carbon once waterlogged conditions have been re-established in peat (Zak and Gelbrecht, 2007). Furthermore, primary production and the deposition of plant litter in the top layer may increase CH$_4$ emissions under anoxic conditions (Tuittila et al., 2000; Juutinen et al., 2003; Wilson et al., 2008), as labile organic matter is a prerequisite for anaerobic CO$_2$ and CH$_4$ formation (Glatzel et al., 2004; Segers, 1998; Conrad, 1989). Raising the water table not only affects GHG exchange but also the vitality and composition of the vegetation (Drösler, personal communication; Clymo, 1984). On the above-mentioned fen grassland in NE Germany, the vegetation, which was dominated by reed canary grass (*Phalaris arundinacea*), died back during the first year of inundation and mixed with sand to form a new sediment layer with a high content of relatively fresh plant litter.

Therefore, we hypothesize that fresh plant litter as a major component of the newly formed sediment can account for a large proportion of the major CH$_4$ emissions and reduced CO$_2$ sink strength as a result of increased CO$_2$ formation. The aim of this study was to quantify the anaerobic CO$_2$ and CH$_4$ production potential of different organic substrates from this highly degraded fen under rewetted condi-

tions. Two incubation experiments were performed to show how GHG emissions differ in pure peat and peat with root litter, compared to the newly formed sediment layer, while also taking pore water chemistry into account. On the basis of the incubation experiments, the risk of high CO$_2$ and CH$_4$ emissions in inundated degraded fen grasslands can be assessed.

2   Material and methods

2.1   Site description

The sampling site "Polder Zarnekow" is located in the valley of the river Peene, 8 km west of the town Demmin (Mecklenburg-Vorpommern, NE Germany; 53°52.5′ N, 12°52.3′ E). The climate is moderately continental temperate with a mean annual air temperature of 8.5 °C and a mean annual precipitation of 544 mm. The mean daily temperature is −0.8 °C in January and 16.7 °C in July (Teterow meteorological station, 24 km south-west of the sampling site). The fen is characterized as a river valley mire system with percolation mires dominated by groundwater flow (Joosten and Succow, 2001).

Drainage of these areas began in the early 18th century and was strongly intensified at the end of the 1960s for agricultural use as intensive grassland (Lenschow et al., 2003). In October 2004, the site was rewetted in the course of an EU-funded conservation project. Since then, field measurements of gas exchange have been performed at this site (see introduction and discussion). Due to substantial peat loss and shrinkage, the Zarnekow polder now appears as a shallow lake permanently inundated with a water level of about +0.1 to +0.5 m (Zak and Gelbrecht, 2007). The subjacent peat layer is up to 10 m thick. Due to peat mineralization during decades of drainage, the upper 0.3 m approximately can be classified as highly decomposed peat (H 10) according to the von Post scale (Puustjärvi, 1970), however, since the soil material is strongly mineralized they are also called "muck-soils" (Okruszko, 1995). Below, slightly to moderately decomposed peat (H 3 to 6) can be found which has either not been affected by the drainage or has been only slightly affected. Long-term drainage and previous agricultural use led to a loss of organic carbon (due to peat oxidation) and, therefore, to an enrichment of P and N with decreasing molar ratios of C:P and C:N in upper soil layers (Zak and Gelbrecht 2007). Concurrently, organic bound P and N was transformed into labile inorganic forms (peat mineralization) supporting the internal eutrophication of the peat soils (Zak et al. 2008).

The former grassland vegetation, dominated by reed canary grass (*Phalaris arundinacea*), died back during the first year of inundation. Since the second year of inundation, the water body of the shallow lake has been dominated by water plants like *Ceratophyllum* and *Lemna* sp. adapted to

Table 1. Selected peat characteristics for peat from different horizons, as well as sediment/peat substrates incubated in two experiments sampled from the Zarnekow polder (mean, $n = 3$).

	Peat layers (m)	dbd (g cm^{-3})	H[c]	OM[d] (%)	C[e] (%)	N[e] (%)	C:N[e]	C:P
Peat layer incubation								
Upper peat layer	−0.1 to −0.2	0.30[a]	10	76	40	3.4	12	320
Middle peat layer	−0.5 to −0.6	0.18[a]	6	84	44	2.8	16	720
Lower peat layer	−1.0 to −1.2	0.12[a]	3	89	48	2.7	18	1550
Organic substrate incubation								
Organic sediment	+0.05 to +0.3	0.2[b]	−	40	13 (s)	1.1 (s)	11 (s)	−
					44 (p)	1.4 (p)	32 (p)	
"Peat with roots"	−0.05 to −0.2	0.4[b]	10	28	16 (s)	1.4 (s)	11 (s)	−
					44 (p)	1.2 (p)	38 (p)	
"Peat only"	−0.1 to −0.2	0.3[b]	10	76	39.8	3.5	11	−

[a] Dry bulk density from Zak and Gelbrecht (2007).
[b] Dry bulk density estimated.
[c] Degree of peat decomposition according to von Post-scale (Puustjärvi, 1970; Zak and Gelbrecht, 2007).
[d] Organic matter in % of dry weight determined by loss of ignition.
[e] Organic substrate incubation: C- and N-content were determined separately for (s) sediment/peat substrate (<2 mm fraction) and (p) plant material.

high nutrient concentrations. An organic sediment layer up to 0.3 m thick was formed at the bottom of the shallow lake with a high content of relatively fresh organic matter from the dying-off of plants. Under the prevailing eutrophic and inundated conditions, the substrate pool is assumed to be continuously refilled by litter from submerged macrophytes and helophytes from the nearby littoral zone.

2.2 Incubation experiments

Two different incubation experiments under simulated flooding were performed to elucidate the impact of different organic substrates on GHG emissions. In the first experiment, peat from different soil depths was incubated (hereafter peat layer incubation) (see Table 2). The second experiment (hereafter organic substrate incubation) focused on three kinds of organic substrates taken from the uppermost layer of the peat. These substrates differed in the amount of fresh plant litter or roots present and in the time elapsed since the flooding of the wetland. In both experiments temperature was kept constant and the anaerobic production potential for CO_2 and CH_4 as well as pore water chemistry were investigated. An overview of selected characteristics of the incubated substrates, including chemical data, is given in Table 1.

2.2.1 Peat layer incubation: experimental set up and chemical analysis

Peat samples were extracted by spade in August 2004 (prior to rewetting on site) from three successive, superimposed soil horizons: upper peat layer (from −0.1 to −0.2 m depth), middle peat layer (from −0.5 to −0.6 m), and lower peat layer (from −1.0 to −1.2 m) (3 replicates each). The ground-

water level at the time of sampling was lower than the deepest sampling depth. Consequently, we assume that aerobic conditions were present for all samples taken from different soil depths. Visible fresh roots were removed by hand from the upper peat layer during peat homogenization. However, it was impossible to remove all fresh plant-derived material. As the upper peat layer was the rooting zone of the grassland vegetation, it can be assumed that some fresh organic matter e.g. from rhizodeposition may be present in the peat.

For incubation, water-tight PVC boxes (0.6 m × 0.4 m × 0.4 m; 96 L) were used. The incubation vessels were filled with ~40 kg mixed peat samples from the different horizons (0.2 m high, ~0.05 m^3). For experimental rewetting of the peat, 3.4 mM sodium chloride solution, equivalent to the average ionic strength of the fen-feeding groundwater, was added. To ensure water-saturated conditions throughout the experiment, the water level was kept 5 cm above the peat surface, and evaporation loss was replaced with deionized water. Incubation lasted for 363 days in a climate chamber at a constant temperature of 20 ± 1 °C under dark conditions to avoid algae growth. The incubation vessels were kept open to the atmosphere except during the brief intervals when gas fluxes were measured.

The rates of CO_2 and CH_4 emitted from the various substrate surfaces were determined using the closed chamber method, measuring the concentration change in the headspace over time (Schinner, 1993). For this purpose, the incubation vessels were closed for one hour by gas-tight lids equipped with plugs for gas sampling. Gas samples were taken from the headspace using evacuated glass flasks (100 mL) at 0, 0.5 and 1 h and were analyzed by the gas chromatograph (GC 145, Shimadzu) (Loftfield et al., 1997). We

Table 2. Overview of the two incubations performed.

	Peat layer incubation	Organic substrate incubation
Duration	363 days	53 days
Substrates incubated (3 replicates each)	Peat taken from different depths (upper, middle and lower peat layer)	Upper peat layer with differing quality of plant litter (organic sediment, "peat with roots", "peat only")
Incubation conditions	$20 \pm 1\,^\circ$C no light, water stagnant conditions	$15 \pm 1\,^\circ$C no light, water stagnant conditions
Incubation vessels	Open PVC-boxes ($0.6 \times 0.4 \times 0.4$ m) with closure lid for gas exchange measurement	Continuously closed PVC-columns ($d = 0.15$ m, $h = 0.35$ m)
Substrate volume	$h = 0.2$ m, $V = 0.05$ m^3	$h = 0.27$ m, $V = 0.005$ m^3
Measurement of gas fluxes	CO$_2$ and CH$_4$ emission from surface (every two weeks/monthly, closed chamber method)	CO$_2$ and CH$_4$ emission from surface (continuously, flow-through system)
Determination of gas concentrations in pore water	–	CO$_2$ and CH$_4$ concentration in silicone probes (every 1–11 days)
Analysis of pore water chemistry	pH, redox potential, soluble reactive phosphorus (SRP), NH$_4$-N, SO$_4^{2-}$, Fe, Ca, dissolved inorganic and organic carbon (DIC, DOC) concentrations in pore water (at beginning and end of incubation)	pH, redox potential, soluble reactive phosphorus (SRP), Fe and Ca concentrations in pore water (at end of incubation)

assumed linearity. Sampling was done every two weeks for the first 8 weeks and monthly thereafter.

Emission rates of CO$_2$ and CH$_4$ related to carbon content of the peat substrate and time (mg C d^{-1} kg^{-1} C) were calculated according to Eq. (1):

$$\text{emission rate} = \frac{M \times p \times V}{R \times T \times A} \times \frac{dc}{dt} \times \frac{1}{\text{Ct}} \qquad (1)$$

in which M is the atomic mass of carbon, p is the air pressure, V the volume of the headspace, R the gas constant, T the temperature, A the area of the incubation vessel, dc the difference of gas concentrations, dt the time interval between gas sampling, and Ct is the carbon content of the peat substrate.

For the analysis of pore water chemistry, rechargeable dialysis samplers were used, as described in detail by Zak and Gelbrecht (2007). Briefly, the one-chamber-sampler ($\sim$0.05 L) was adjusted in the peat at 1–11 cm depth at the beginning of the incubation experiment. For sampling, the chamber water was completely removed with a pipette and directly renewed by oxygen-free deionized water in order to avoid oxygen input into the anoxic peat. Sampling was done every two weeks for the first 8 weeks and monthly thereafter over the 363-day incubation period. To prevent oxidation and subsequent precipitation of redox-sensitive substances, pore water samples were taken quickly and stabilized with hydrochloric acid (2 M HCl). Pore water pH was determined using a pH probe (WTW), the redox potential by a Pt electrode with Ag/AgCl reference electrode, and measured values were adjusted to standard hydrogen potential and pH of

7. Soluble reactive phosphorus (SRP) was analyzed photometrically by the molybdenum blue method, NH$_4$-N was determined photometrically by the indophenol method. Fe and Ca concentrations in the pore water were analyzed by flame atomic absorption spectrometry and sulfate concentrations by ion chromatography. DIC and DOC were measured with a C-Analyzer. Further details on fixation of anoxic pore water samples and chemical analysis can be found in Zak and Gelbrecht (2007).

2.2.2 Organic substrate incubation: experimental set up and chemical analysis

Three different organic substrates were investigated: (1) organic sediment formed post-flooding (from fragmented fresh roots and leaves, which had accumulated to a thickness of up to 0.3 m above the original fen surface over a period of 2.5 years), (2) a highly decomposed peat with intact *Phalaris arundinacea* roots taken from −0.05 to −0.2 m depth (hereafter "peat with roots"), and (3) a highly decomposed peat without any fresh plant material taken from −0.1 to −0.2 m depth and with roots removed (hereafter "peat only"). Samples were taken from the same location as for the peat layer incubation in April 2007 (2.5 years after rewetting). The soil depths given refer to the soil surface prior to rewetting to be comparable. Organic sediment and "peat only" were sampled by inserting a plexiglass tube ($d = 0.13$ m) into the lake bottom, removing the supernatant lake water and obtaining the desired organic substrate. "Peat with roots" was extracted by spade from a place with no overlying organic

sediment and removal of the upper 0.05 m in order to exclude living above-ground plant material. All three substrates were taken from locations under water-saturated soil conditions and therefore we assume that conditions were anaerobic at the start of the subsequent incubation. Each of the three organic substrates was mixed for several minutes by hand and put into the PVC incubation vessels ($h = 0.35$ m, $d = 0.15$ m, substrate 0.27 m high, ~ 0.005 m^3, 3 replicates each). Subsamples of the substrates were taken directly after sampling for chemical characterization (see below). Multi-chamber dialysis samplers were inserted into the upper 10 cm of the soil columns to investigate pore water chemistry (for details see Zak et al., 2010). In addition, silicone probes were inserted at a depth of approximately 0.23 m in the substrate to determine gas concentrations within the substrates (see below). Lake water from the sampling site was added until the substrates were completely covered in order to maintain anaerobic conditions. The incubation vessels were closed with gas-tight lids equipped with ports for gas measurements and incubated at a constant temperature of $15 \pm 1\,°C$ under dark conditions for 53 days.

The carbon dioxide and methane fluxes from the sediment or peat substrates were determined with a steady state flow-through chamber system combined with automated gas analysis equipment. A constant air flow of 6×10^{-3} m^3 h^{-1} was adjusted in the open headspace of the incubation vessels. The measurements of the inflow/outflow (ambient air/headspace air) concentrations was carried out continuously over the entire incubation period. The gas concentrations were analyzed by a photoacoustic infra-red multi-gas monitor (INNOVA 1312, INNOVA AirTech Instruments, Ballerup, Denmark). Since the gas monitor does not fully compensate for cross-interference of CH_4 and water vapour at high concentrations, the air was partially dried at $5\,°C$ by a gas conditioning system (Rosemount) to reduce water vapour concentrations before measurement. The measurement frequency was three times per hour per incubation vessel with three replications each.

Gas fluxes related to carbon content of the sediment or peat substrate and time (mg C d^{-1} kg^{-1} C) were calculated according to Eq. (2):

$$\text{emission rate} = \frac{M \times p \times v}{R \times T \times A} \times \frac{dc}{\text{Ct}} \qquad (2)$$

in which M is the atomic mass of carbon, p is the air pressure, v the air flow, R the gas constant, T the temperature, A the area of the incubation vessel, dc the difference of gas concentrations, and Ct is the carbon content of the peat substrate.

As a further indicator for the intensity of the gas production processes, CO_2 and CH_4 concentrations in the pore water of the substrates were determined using adapted silicone probes according to Kammann et al. (2001). A silicone probe consisted of a curled-up silicone tube (OD = 8 mm, ID = 6 mm, $L = 1.0$ m) connected with a stainless steel capil-

lary tube (OD = 1.6 mm, ID = 0.75 mm, $L = 0.32$ and 0.21 m) and a 3-port-valve at each end as well as an injection port at one end. Gas exchange takes place between the interior space of the probe and the substrate only by diffusion through the walls of the silicone tube until equilibrium is reached. Gases within the silicone tube reached 95 % equilibrium with the surrounding atmosphere within several hours (Kammann et al., 2001).

For sampling, the air in the silicone tube was moved to the end with the injection port by inserting water into the silicone probe and taking a gas sample using a gas-tight syringe. Silicone probe samples were diluted with N_2 to concentrations which were in the measurement range of the GC, filled into evacuated 100 ml glass flasks and analyzed with the gas chromatograph (Shimadzu GC-14B, ECD for CO_2, FID for CH_4) (Loftfield et al., 1997). After sampling, the water and air in the silicone probes were removed and the probes flushed with N_2 to ensure anaerobic conditions. Samples were taken in 1 to 11 days intervals.

For the analysis of pore water chemistry, the dialysis samplers were removed at the end of incubation, cleaned with deionized water, and the water of the soil chambers was obtained using pipettes. The pore water was analyzed for pH, redox potential, soluble reactive phosphorus (SRP) and Fe and Ca concentrations as described above.

For solid C and N analysis, subsamples of the substrates were taken prior to incubation, sediment/peat substrates and plant material were separated by sieving (2 mm), dried at $40\,°C$ (sediment/peat substrate) or $70\,°C$ (plant material) for 5 days, ground and then analyzed (Elementar CN analyzer vario MAX; combustion at $1100\,°C$; thermal conductivity detector). Measured solid C and N values for the sediment/peat substrates were corrected for water content when dried at $105\,°C$.

2.3 Statistics

Repeated measures analysis of variance by fitting linear mixed-effects models with Tukey post-hoc comparisons were performed with R 2.10.0 (R, 2009) to compare the time series of gas emissions (significance level of $p < 0.001$). SPSS 17.0 was used for one-way ANOVA and Tukey post-hoc comparisons to compare means of pore water chemistry analysis and cumulative gas fluxes (significance level of $p < 0.05$).

3 Results

3.1 Peat layer incubation

The lowest carbon content and the highest nitrogen and phosphorus contents were found in the uppermost peat layer compared to underlying peat samples (see Table 1). Consequently, lowest C:N and C:P ratios – both indicators for substrate degradability – were observed in the upper peat layer
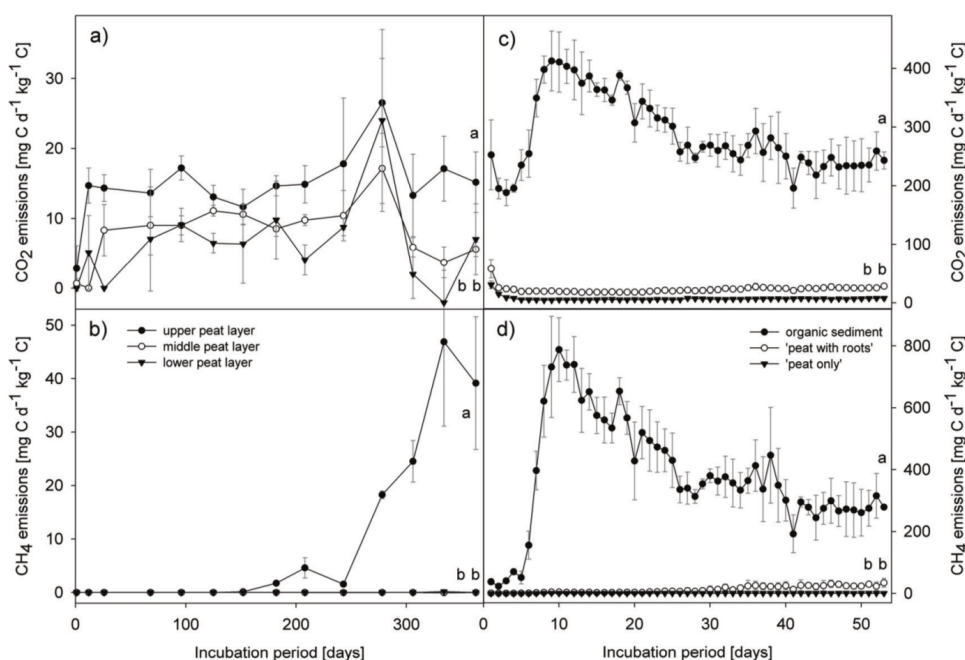
Fig. 1. CO$_2$ and CH$_4$ emissions from the surface for the peat layer incubation (**a, b**) and for the organic substrate incubation (**c, d**) at constant temperature (20 °C and 15 °C) (mean ± SD, $n = 3$; different letters on the left indicate significant differences, $p < 0.001$).

(12 and 320), whereas the lower peat layer had the highest values (18 and 1550).

In accordance with the peat characteristics, peat samples from different horizons differed significantly in their CO$_2$ emissions ($F_{2,6} = 12.6$, $p = 0.0072$). Anaerobic CO$_2$ production was highest ($p < 0.001$) at the top of the soil profile. A strong increase in CO$_2$ production in the upper peat layer was found during the first 14 incubation days and, after approximately 150 days, emission rates increased until day 278 (see Fig. 1a). Anaerobic CO$_2$ production in the middle peat layer was lower than in the upper peat layer but little higher than in the lower peat layer. In the middle peat layer, an increase in anaerobic CO$_2$ production was detected two weeks later than in the upper peat layer. It stayed relatively stable thereafter and decreased at the end of incubation. In the lower peat layer, anaerobic CO$_2$ production showed some fluctuations over the entire incubation period. The cumulative CO$_2$ fluxes over 363 days for the incubation of the material from the upper peat layer were 1.7 times higher than for the incubation of the material from the middle peat layer and 2.3 times higher than for the incubation of the material from the lower peat layer (see Table 4).

CH$_4$ emissions from the middle and lower peat layer were zero over the entire incubation period. The upper peat layer emitted no CH$_4$ until day 152. From day 243 onwards, CH$_4$ emissions increased strongly and reached a plateau at the end of incubation (maximum of 46.9 mg C d^{-1} kg^{-1} C)

(see Fig. 1b). Cumulative CH$_4$ fluxes over 363 days were 3.4 g C kg^{-1} C in the upper peat layer and around zero for the middle and lower peat layer.

During the 363 incubation days, a small fraction of the initial C in the soil organic matter was respired as CO$_2$ or CH$_4$ (Table 4), e.g. from the upper peat layer only 0.55 % and 0.4 % of the initial C were respired as CO$_2$ and CH$_4$.

The experimental rewetting caused a reduction in the redox potential and an increase in pH in all treatments (see Table 3). Sulfate concentrations were generally high at the beginning of the rewetting period. In the upper peat layer, sulfate concentrations decreased rapidly during the first weeks of incubation and stayed around 0.1 mM after day 125 (see Fig. 3). Sulfate concentrations decreased slowly in the middle peat layer but increased in the lower peat layer over the entire incubation period. Fe concentrations increased strongly in the upper peat layer and to a much smaller extent in the middle peat layer. In the lower peat layer, Fe concentrations in the pore water were low overall and showed only a marginal increase over time. The highest concentrations of soluble reactive phosphorus (SRP), ammonium, dissolved inorganic and organic carbon, and calcium were generally found in the pore water of the upper peat layer. These concentrations were 2 to 200 times higher than in underlying peat (Table 3, for single results see Zak and Gelbrecht, 2007).

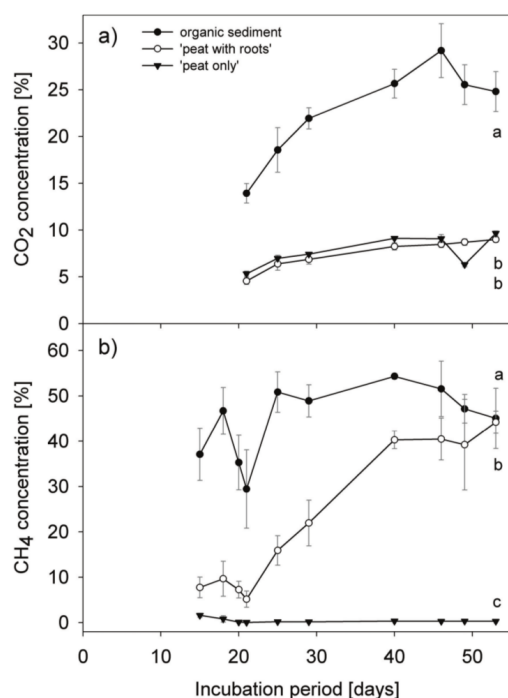M. Hahn-Schöfl et al.: CH$_4$ and CO$_2$ emissions from degraded fen   1545

Fig. 2. Organic substrate incubation: CO$_2$ **(a)** and CH$_4$ **(b)** concentrations in the silicone probes over a 53-day period at constant temperature of 15 °C (mean ± SD, $n = 3$). Three organic substrates (organic sediment, "peat with roots" and "peat only") taken from the uppermost peat layer are compared (different letters indicate significant differences, $p < 0.001$, 1 % = 10 000 ppm).

3.2 Organic substrate incubation

The C and N content were determined separately for the <2 mm fraction of the sediment/peat and the plant material. The C content of the sediment/peat was surprisingly low in the organic sediment and in the "peat with roots" but three times higher in the "peat only" (see Table 1). This fact was explained by sand present in the organic sediment and "peat with roots" samples. The sand intrusion is due to erosion from an adjacent bank built for agricultural machinery. All three sediment/peat substrates had similar C:N ratios, those of the plant material in the organic sediment and the "peat with roots" were three times higher (Table 1).

The differences in CO$_2$ emissions between the three sediment/peat substrates were much more pronounced than for the peat layer incubation ($F_{2,6} = 600.5$, $p < 0.0001$, see Fig. 1c). Anaerobic CO$_2$ production was highest in the organic sediment, with a strong increase at the beginning of incubation (maximum of 412 mg C d^{-1} kg^{-1} C) and a continuous decline after day 8. CO$_2$ production in the "peat with roots" was more than 10 times lower than in the organic sediment ($p < 0.001$) and increased slowly over the incubation period (range of 17–28 mg C d^{-1} kg^{-1} C). In the "peat only",
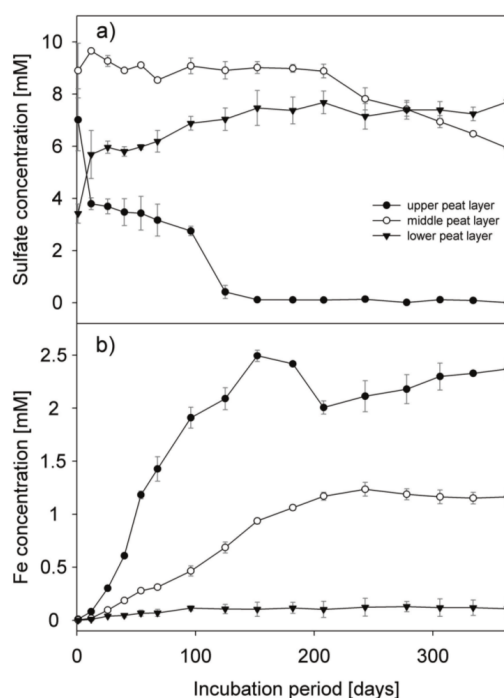
Fig. 3. Peat layer incubation: Sulfate **(a)** and iron **(b)** concentrations in the pore water of the upper, middle and lower peat layer over the 363-day incubation period (mean ± SD, $n = 3$).

CO$_2$ emissions were even lower than in the freshly rewetted upper peat layer of the peat profile incubation and stayed in the range of 4–8 mg C d^{-1} kg^{-1} C over the entire incubation period. Cumulative CO$_2$ fluxes for 53 days were one order of magnitude higher in the organic sediment than in the "peat with roots" and the "peat only" (see Table 4).

CO$_2$ concentrations in the substrate pore water sampled via silicone probes (see Fig. 2) were high in all substrates. The release of gas bubbles was observed on several sampling occasions. Analogous to gas emissions from the surface, CO$_2$ concentrations were significantly higher in the organic sediment and increased strongly over the incubation period until day 46 (up to 29 %), with a decrease thereafter. The CO$_2$ concentrations in "peat with roots" and "peat only" did not differ significantly and increased slowly over time (up to approximately 9 %).

With regard to CH$_4$ production, there were fundamental differences between the three sediment/peat substrates that were incubated (see Fig. 1d). CH$_4$ emissions from the organic sediment were higher compared to the two other substrates and increased strongly from day 6, reaching a maximum on day 10 (788 mg C d^{-1} kg^{-1} C), followed by a continuous decrease until the end of incubation. In contrast, the "peat with roots" showed low CH$_4$ emissions until day 7 and increased slowly thereafter to a maximum of 34 mg C d^{-1} kg^{-1} C at the end of incubation. Thus, the same

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Table 3. Characterization of pore water chemistry for the peat layer incubation and the organic substrate incubation (letters indicate differences between the treatments, $p < 0.05$).

Incubation[z]	pH Start	pH End	Redox potential E_7 (V) Start	Redox potential E_7 (V) End	SRP (µM) Start	SRP (µM) End	NH_4-N (mM) Start	NH_4-N (mM) End	Sulfate (mM) Start	Sulfate (mM) End	Fe (mM) Start	Fe (mM) End	Ca (mM) Start	Ca (mM) End	DIC (mM) Start	DIC (mM) End	DOC (mM) Start	DOC (mM) End
Peat layer incubation																		
Upper peat layer	6.0^a	6.7^a	0.51^a	0.14^a	0.13^a	144^a	0.02^a	1.86^a	7.01^a	0.00^a	0.01	2.37^a	3.43^a	11.9^a	2.80^a	29.2^a	6.58^a	44.4^a
Middle peat layer	5.9^a	6.8^a	0.57^{ab}	0.17^b	0.13^a	0.48^b	0.02^a	0.35^b	8.90^a	5.93^b	0.00	1.16^b	6.93^b	12.1^a	1.42^b	15.1^b	4.69^b	23.2^b
Lower peat layer	5.5^b	6.6^a	0.59^b	0.27^c	0.13^a	0.68^b	0.05^b	0.03^c	3.42^b	7.70^c	0.00	0.11^c	4.75^c	6.45^b	0.64^c	0.69^c	1.49^c	1.20^c
Organic substrate incubation																		
Organic sediment		6.7^a		0.17^a		1085^a		–		–		0.35^a		9.06^a		–		–
"Peat with roots"		7.0^b		0.18^a		35.7^b		–		–		1.38^b		9.11^a		–		–
"Peat only"		6.9^a		0.14^a		129^c		–		–		1.50^c		15.3^b		–		–

[z] Data given for the peat layer incubation: Start on day 1, End on day 363, further data and details see in Zak and Gelbrecht (2007); in the organic substrate incubation data are available for the end of the incubation (on day 53). Letters a–c indicate significant differences between substrates, $p < 0.05$.

level was reached as that found for the upper peat layer in the peat layer incubation (see Fig. 1b), whereas CH_4 emissions from "peat only" stayed low over the entire incubation period ($<1\,\mathrm{mg\,C\,d^{-1}\,kg^{-1}\,C}$). Cumulative CH_4 fluxes in the organic sediment were 2–3 orders of magnitude higher than in the "peat with roots" and "peat only" (Table 4).

Fundamental and significant differences between the three organic substrates were also observed for CH_4 concentrations in the silicone probes ($F_{2,6} = 246.1$, $p < 0.0001$, see Fig. 2). CH_4 concentrations were highest in the organic sediment where they remained relatively constant after day 25 (range of 45–54 %). In contrast, in the "peat with roots" CH_4 concentrations started low but increased strongly from day 21 onwards until they reached the same level as the organic sediment at the end of incubation. CH_4 concentrations in the "peat only" were lower than in the other two organic substrates (maximum of 1.6 % at the start of incubation) and even decreased over the incubation period.

Despite the high gas flux rates from the organic sediment, only 3.5 % of the initial total carbon was respired as either CO_2 or CH_4 during 53 days of incubation. From "peat with roots" and "peat only" the fraction respired was 1–2 orders of magnitude lower (see Table 4).

Comparing the gas fluxes of the two incubation experiments, the organic sediment emitted most CO_2 and CH_4 compared to all peat substrates – both peat from different horizons in the peat layer incubation and "peat with roots" and "peat only" in the organic substrate incubation (Fig. 1 and Table 4). The "peat with roots" showed emissions for both gases that were similar to those of the upper peat layer, and emissions from the "peat only" were identical to those of the lower peat layer from the first incubation experiment (see average flux per day in Table 4).

The redox potential (measured at the end of the incubation period) was similar in all three organic substrates (see Table 3). The pH was slightly higher in the "peat with roots". The concentration of soluble reactive phosphorus (SRP) in the pore water was by far highest in the organic sediment. Fe concentrations were highest in the "peat only" and the "peat with roots" and one order of magnitude lower in the organic sediment. Ca concentration was highest in "peat only" compared to the other two substrates.

4 Discussion

Despite the fact that the two incubations were performed at different temperatures (20 vs. 15 °C), incubation periods (363 vs. 53 days), and time since flooding (immediately after versus 2.5 years later) their respective findings can be regarded as complementary and some general conclusions can be drawn regarding the effect of different kinds of substrates on the anaerobic production of GHGs. The upper peat layer (from peat layer incubation) and the "peat with roots" (from the organic substrate incubation) are comparable substrates, since both consist of highly decomposed peat taken from a depth of −0.1 to −0.2 m with some remaining plant-derived material. Both show similar CO_2 and CH_4 production rates (Fig. 1 and Table 4).

4.1 Anaerobic CO_2 production – indication of microbial activity

Anaerobic CO_2 production is an indicator for instantaneously available organic substrates from peat and fresh organic matter over a wide range of substances and energetic quality (Freibauer and Augustin, 2009). The organic

Table 4. Cumulative CO_2 and CH_4 fluxes over the incubation period (363 days for peat layer incubation; 53 days for organic substrate incubation), average per day (mean $\pm$ SD, $n = 3$), total C in incubation vessels and C respired during incubation (given as total C and in % of total C) (letters indicate differences between the treatments, $p < 0.05$).

	Cumulative flux over entire incubation period		Average flux per day		Total C at incubation start	Total C respired during incubation	% of total C respired during incubation	
	CO_2 flux ($g\,C\,kg^{-1}\,C$)	CH_4 flux ($g\,C\,kg^{-1}\,C$)	CO_2 flux ($g\,C\,d^{-1}\,kg^{-1}\,C$)	CH_4 flux ($g\,C\,d^{-1}\,kg^{-1}\,C$)	(g C)	(g C)	as CO_2 (%)	as CH_4 (%)
Peat layer incubation (363 days)								
Upper peat layer	5.5 ($\pm$ 0.8)[a]	3.4 ($\pm$ 0.4)[a]	0.02 ($\pm$ 0)	0.01 ($\pm$ 0)	4500	40.2 ($\pm$ 5)	0.55	0.34
Middle peat layer	3.2 ($\pm$ 0.4)[b]	0[b]	0.01 ($\pm$ 0)	0	3500	11.1 ($\pm$ 1.3)	0.32	0
Lower peat layer	2.4 ($\pm$ 1.3)[b]	0[b]	0.01 ($\pm$ 0)	0	2500	5.9 ($\pm$ 3.2)	0.24	0
Organic substrate incubation (53 days)								
Organic sediment	15.2 ($\pm$ 1)[a]	20.3 ($\pm$ 2.3)[a]	0.3 ($\pm$ 0.02)	0.4 ($\pm$ 0.04)	126[z]	4.5 ($\pm$ 0.4)	1.52	2.03
"Peat with roots"	1.2 ($\pm$ 0.1)[b]	0.7 ($\pm$ 0.3)[b]	0.02 ($\pm$ 0)	0.01 ($\pm$ 0)	296[z]	0.6 ($\pm$ 0.1)	0.12	0.07
"Peat only"	0.4 ($\pm$ 0.1)[b]	0.03 ($\pm$ 0)[b]	0.01 ($\pm$ 0)	0	613[z]	0.2 ($\pm$ 0.03)	0.04	0.003

[z] Estimated.

sediment consisted mainly of fresh plant litter mixed with sand, and microbial degradation emitting CO_2 was, as hypothesized, substantially higher than in the other organic substrates (see Fig. 1c and Table 4). CO_2 emissions from the surface of the organic sediment showed a substrate-limited reaction (hyperbolic function with two parameters; $R^2 = 0.87$; Paul and Clark, 1996) from day 9 onwards. The gas accumulated in the substrate matrix, as demonstrated by the gas concentrations in silicone probes (up to 29 % CO_2 in the organic sediment, see Fig. 2). In all other substrates with peat from both experiments, specific rates of anaerobic CO_2 production were significantly lower. However, significant differences were also recorded between these substrates (Fig. 1). The upper part of the peat profile released significantly more CO_2 than peat from deeper down the profile. This could be due to some residual fresh plant-derived material (e.g. from rhizodeposition) which was presumably present in the uppermost peat layer and which could not be removed entirely before incubation. In the situation in which fresh plant roots were present in the peat substrate ("peat with roots"), microbial degradation processes releasing CO_2 were more active compared to peat without fresh organic matter ("peat only"). However, the differences were not statistically significant (see Fig. 1c). Anaerobic decomposition depleating "labile" substrates could have occured 2.5 years longer in the peat in the organic substrate incubation. Despite this fact, CO_2 production in "peat only" (taken 2.5 years after rewetting) was in the same range than those in the lower peat layer and "peat with roots" was comparable to maximum CO_2 emissions from the upper peat layer.

These findings are in accordance with those of another study which reported rates of CO_2 and CH_4 production that were generally greatest in the surface peat where a strong cover of vegetation had developed and the content of fresh or slightly decomposed plant litter was highest (Glatzel et al., 2004). This suggests that it is the availability of readily degradable plant material that determines CO_2 and CH_4 production rates, whereupon it only accounts for a small fraction of the total C pool. In our study, only 0.9 % of the initially existing C from the upper peat layer and 3.5 % from the organic sediment were lost as CO_2 or CH_4 (see Table 4). Kiikkilä et al. (2011) showed that dissolved organic carbon (DOC) derived from fresh plant material was clearly more degradable and contained a greater amount of labile compounds than DOC derived from the humus layer of a forest soil. Cumulative CO_2-loss from forest humus DOC was up to 21 % and was twofold from plant DOC in a 110 days incubation.

Anaerobic CO_2 production depends not only on the availability of labile organic substrates but also on the availability of oxidizing substances such as nitrate, ferric iron and sulfate. The concentration of nitrate in the pore water was low throughout the incubation (data not shown). The strong increase in iron concentrations and the depletion of sulfate in the pore water of the upper peat layer indicated that an excess of labile organic substances were available there, in contrast to peat deeper down the profile (Fig. 3). Microbial activity was lower in the middle and lower peat layer as there was a lack of suitable substrate for degradation processes due to the absence of fresh material and the humified nature of the peat. Hence, sulfate concentrations in the pore water decreased only slowly or even increased (see Fig. 3 or Table 3), and favourable conditions for CH_4 production were not established throughout incubation.

4.2 Onset of methanogenesis and magnitude of CH$_4$ emissions

The production of CH$_4$ indicates the instantaneous availability of fresh and energy-rich substrates, and it often decreases with depth as does the availability of organic matter (Segers, 1998).

CH$_4$ emissions from the upper peat layer started after a 182-day lag-phase. This retarded onset of methanogenic activity, as well as the zero CH$_4$ emissions from the middle and lower peat layer, can be explained by competition for organic substrates with iron or sulfate reducers. Thus, it took 125 incubation days before sulfate was almost completely gone (see Fig. 3) and methanogenesis started in the upper peat layer (see Fig. 1b). Therefore, we assume that methanogens were inhibited by competition with iron-reducing or sulfate-reducing bacteria (Smolders et al., 2002). The slow recovery of methanogenesis during the first weeks under waterlogged conditions in the upper peat layer could also be caused by aerobic conditions in the field before sampling. Aerobiosis could damage a methanogenic population either directly by poisoning or indirectly by C-starvation due to competition for substrates with aerobic microorganisms (Segers, 1998). However, Knorr and Blodau (2009) found that methanogenesis recovered locally quite quickly from aeration. Finally, decomposition of organic matter and subsequent production of GHGs can also be inhibited by the presence of organic electron acceptors such as humic substances (Segers, 1998; Blodau, 2002), which might be the case in the humified middle and lower peat layer (Zak and Gelbrecht, 2007).

The substrates used for the organic substrate incubation were under anaerobic conditions in the field for a longer period (waterlogged conditions for 2.5 years). We assume therefore that methanogens were not inhibited by aerobiosis in this experiment. Conditions favourable for methanogenesis were established quickly in the organic sediment with its large amount of labile, fresh plant material. Here, CH$_4$ emissions started immediately, increased rapidly and were extremely high. From day 10 onwards, CH$_4$ production showed a substrate-limited reaction (hyperbolic function with two parameters; R^2=0.89; Paul and Clark, 1996).

In accordance with the substantially lower release of GHGs, the microbial degradation of organic matter was significantly lower in the two peat substrates ("peat with roots" and "peat only"). However, differences in decomposition rates could also clearly be seen between these substrates. Microbial activity in the "peat with roots" with its fresh root material was generally higher and methanogenesis started quickly and increased continuously until the end of incubation. The CH$_4$ formed was not emitted continuously through the surface but accumulated in the substrate up to concentrations of 44%, as shown by the silicone probe results (see Fig. 2). This finding indicates that CH$_4$ production in the peat was higher than detected in the surface emissions. The

"peat only" – consisting of peat substrate without any fresh organic matter – showed, as anticipated, very low microbial decomposition and methanogenesis stayed very low over the entire incubation period (Figs. 1d and 2).

Our findings confirm the results by Tuittila et al. (2000), who observed extremely low CH$_4$ emissions from highly decomposed bog peat at an abandoned cut-away site and emphasized the importance of fresh plant litter and root exudates as substrates for methanogenesis. A pulse-labeling experiment showed that recently-assimilated carbon was translocated to the roots and available to soil microbial community as root exudates and emitted as CH$_4$ quickly (King and Reeburgh, 2002). The low availability of appropriate organic substrate for methanogens caused the lack of CH$_4$ production from a Dutch cut-over bog remnant; peat with relatively low lignin and phenolic content, and with a low C:N, C:P and C:K ratio had a higher potential for CH$_4$ production (Smolders et al., 2002). The highest rates of anaerobic CH$_4$ production occurred in samples close to the soil surface with fresh peat accumulation and a high water table (Glatzel et al., 2004). The largest anaerobic CO$_2$ and CH$_4$ production were found in peat samples close to the soil surface (Reiche et al., 2010). Our findings show that it is not the quality of the bulk peat substrate itself but the presence of fresh organic matter that determines anaerobic GHG production.

Plants no longer growing on a site can be an important control of CH$_4$ production rates – the highest CH$_4$ production occurred at a bog site where sedges had been growing in the recent past and the decomposition of sedge residues in the peat below the surface supported CH$_4$ production (Yavitt et al., 1997). Field measurements on our sampling site revealed extremely high CH$_4$ emissions (up to 205 g C m^{-2} yr^{-1}) in the years following rewetting (Chojnicki et al., 2007; Höper et al., 2008). The reed canary grass (*Phalaris arundinacea*) at the Zarnekow site – due to its high productivity even under flooded conditions – produced, prior to its dying-off during the first year of inundation, a sufficiently large C pool for CH$_4$ production (accumulation of 650 g C m^{-2} yr^{-1}). The main part thereof was presumably transferred to the organic sediment layer. In addition, the substrate pool is assumed to be continuously refilled with labile organic matter by litter from submerged macrophytes and helophytes from the nearby littoral zone under the prevailing eutrophic and inundated conditions.

5 Conclusions

Although laboratory incubations are not considered suitable for assessing the actual relevance of peatlands as a source or sink for CO$_2$ and CH$_4$, they can be used as an indicator for the production potential of CO$_2$ and CH$_4$ in a certain substrate.

Depending on drainage and land use history after rewetting of fens, highly eutrophic shallow lakes can be formed. The bottom of these lakes is typically characterized by highly

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decomposed peat layers at the top and less decomposed peat layers up to several metres below. The original grassland vegetation is not adapted to inundated conditions and therefore dies back, forming an organic sediment layer. This fresh organic substrate has an extremely high potential for CH_4 production. Consequently, the release of CH_4 could be high at least as long as eutrophic and inundated conditions last.

In contrast, pure peat without fresh plant-derived material seems to be relatively inert. Significant methane emissions cannot be expected from pure peat layers under permanently inundated conditions in the field as long as readily degradable substances are lacking.

To some extent, GHG production may occur when some labile organic matter is available, e.g from rhizodeposition or fresh litter from plant roots. However, depending on the availability of alternative electron acceptors (e.g. iron and sulfate), CH_4 production will start after an extended lag-phase, and the available C pool is more limited than in the newly formed sediment layer.

The risk of high CO_2 and CH_4 emissions after restoration is limited to waterlogged conditions and the simultaneous presence of readily degradable and energy-rich substrates for microbial decomposition processes (i.e. eutrophic peat, fresh plant litter, or newly formed organic sediments, e.g. from plants that are not adapted to flooding). In the future, it should be investigated if the expected colonization of flooded areas by adapted plant species such as *Typha* sp., reeds or sedges might also reduce this potential risk as their litter is slowly decomposed (Brinson et al., 1981).

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Chapter 3: Publication II

Experimental rewetting of peat grasslands:
critical water table thresholds for
greenhouse gas emissions and vegetation responses

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own contributions:

- design and implementation of experimental set-up

- design and construction of all devices

- calculation of CO_2 flux rates from raw data

- modelling of daily CO_2 flux rates

- statistical analysis of all data

- graphical presentation

- data interpretation and discussion of results

- planning and writing of the publication

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- supervision of the experiment during maternity leave of M. Hahn-Schöfl (A. Thuille)

- calculation of CH_4 and N_2O flux rates from raw data (A. Thuille)

- development of a procedure for CO_2 flux calculation from raw data (G. Schöfl)

- support in development of linear mixed effects models for GHG flux data (G. Schöfl)

- supervision of PhD thesis (A. Freibauer)

Abstract

The rewetting of formerly drained peat grasslands is considered as an effective measure to reduce greenhouse gas (GHG) emissions and is already implemented in Germany. Deliberately raising the water table re-establishes water saturated conditions, principally reduces CO_2 emissions but might unintentionally boost CH_4 formation. A water table for optimum net GHG balance must aim to minimize peat mineralization but also to avoid high methane and nitrous oxide release. In order to investigate the functional role of the water table position on GHG fluxes (CO_2, CH_4 and N_2O) we performed an incubation experiment under controlled environmental conditions simulating gradual rewetting and prolonged flooding of fen mesocosms with intact vegetation.

Gradually raising the water table from -30 cm up to 0 cm reduced vegetation vitality and increased net CO_2 uptake due to reduced gross primary production (GPP) and ecosystem respiration (R_{eco}). CH_4 and N_2O emissions were low. In summary, gradual rewetting had a positive climate impact – net GHG uptake increased by 0.6 (segdes) to 0.8 (grasses) g CO_2-equivalents m^{-2} d^{-1} per cm water table raise. In contrast, raising the water table above the peat surface (+5 cm) caused a partial dying-off of the grassland vegetation, significantly reduced GPP and simultaneously increased R_{eco} and CH_4 emissions as a consequence of higher substrate availability. In grasses, flooding nearly cancelled the positive climatic effect as the lower net CO_2 uptake was more than compensated by CH_4 emissions in terms of CO_2-equivalents. In segdes, CH_4 never risked to compensate the net CO_2 uptake – the positive climatic effect was halved after flooding. The most favourable water table positions for minimal GHG fluxes range from -10 cm to 0 cm. Under wet conditions, sedges did not boost CH_4 emissions but stabilized the redox potential so that CH_4 production occurred later and was lower compared to grasses.

1. Introduction

Natural peatlands act as a sink for atmospheric carbon dioxide (CO_2) but are, simultaneously, a source of methane (CH_4) as the water table is near the land surface. Conversion of peatlands to human uses changes the hydrology and plant community and consequently, carbon and nutrient cycling and GHG emissions (Drösler et al. 2008; Laine et al. 2009). Water table position has been identified as the most important determinant of CO_2, CH_4 and nitrous oxide (N_2O) fluxes (Augustin 2001; Jungkunst et al. 2008) in hydromorphic soils. If the aerobic peat layer is enlarged by drainage, peat mineralization and consequently CO_2 production is stimulated but CH_4 formation decreases. Deeply drained peat soils as found under agricultural management shift from a carbon sink to a carbon source (Drösler et al. 2008; Laine et al. 2009).

Rewetting former drained peat grasslands has therefore been suggested as effective measure to mitigate greenhouse gas (GHG) emissions from peat soils (Hendriks et al. 2007; Beetz et al. 2013). But, rewetting might unintentionally cause a shift from CO_2 towards CH_4-dominated emissions (Riet et al. 2013). In Germany, peatland restoration via rewetting is implemented with the explicit goal of reducing GHG emissions (Höper et al. 2008). However, restoration is often performed by flooding so that the net GHG effect of reduced peat mineralization and increased methane release remains unclear (Höper 2007). This is due to the fact that flooding can boost CH_4 emissions (Laine et al. 2009), in particular when plants die that are not adapted to excessive water stress (Hahn-Schöfl et al. 2011). The optimum water table to minimize the net GHG balance seems to be located around -5 cm (Jungkunst et al. 2008) respectively -10 cm (Drösler et al. 2008) below the soil

surface.

Vegetation composition reacts sensitively to water level changes both by the shift of dominance structures of the different species and by the vitality of the vegetation layer (Drösler et al. 2008). Plants not adapted to wet conditions may die off providing fresh organic matter for decomposition processes (Hahn-Schöfl et al. 2011), which is a primary substrate for methanogenesis. In rewetted grassland, the original lowland meadow grasses are replaced by water-tolerant sedges (e.g. (Hendriks et al. 2007). Sedges have aerenchyma, which act as chimney for CH_4 in wet conditions. Plant mediated CH_4 transport dominates CH_4 transport in natural peat vegetation communities (Schimel 1995). It remains unclear whether fresh substrate from died-off vegetation or the vegetation shift to sedges produces more CH_4 emissions.

Many field studies have suffered from the seasonal covariance between water table, temperature and vegetation activity so that the functional role of the water table position could not be singled out. Several laboratory experiments have been performed with peat mesocosms under controlled conditions with systematic manipulation of water table, substrate and duration of flooding (Berryman et al. 2009; Reiche et al. 2010; Hahn-Schöfl et al. 2011; Riet et al. 2013). To our knowledge, no incubation study has so far (1) included grassland vegetation before and after shift to wetness-adapted species, (2) simulated real-world conditions in terms of temperature and radiation, and (3) included all three GHG species (CO_2, CH_4 and N_2O), which is a pre-requisite for assessing the full net GHG mitigation effect of peatland rewetting measures. Additionaly, laboratory experiments are often performed without accounting for the CO_2 fixation by vegetation (Jungkunst et al. 2008; Berryman et al. 2009; Riet et al. 2013) which is an essential part of the GHG budget.

The aim of this study was to determine the effect of the water table position on GHG fluxes (CO_2, CH_4 and N_2O) in fen grassland mesocosms with intact vegetation (water-intolerant grasses and water-tolerant sedges). Gradual and complete rewetting was simulated under controlled environmental conditions simulating late spring conditions for 252 days.

Our main questions were:

- How does the vegetation react to raising water level and extended flooding (water-intolerant grasses versus water-tolerant sedges)? How does the contribution of autotrophic and heterotrophic respiration change with water table?

- Are there water table thresholds for drastic changes in GHG fluxes? At which water table position are net GHG emissions minimal? How are GHG fluxes affected by extended flooding?

- What is the effect of aerenchymous plants? Do sedges boost CH_4 emissions under wet conditions due to plant mediated CH_4 transport?

The results of the incubation experiments contribute functional knowledge for recommendations and risk assessment in practical rewetting.

2. Material and Methods

2.1. Site description

The sampling site "Freisinger Moos" (FSM) is located in the vicinity of the town Freising (South Germany, 48°37.2'N, 11°68.6'E, 470 m a.s.l.). The climate is temperate with a mean annual air temperature of 7.5°C and a mean annual precipitation of 788 mm (source: Agrarmeteorologie Bayern). The fen "Freisinger Moos" was extensively managed as pasture until 200 years ago. Nowadays, it is mainly used as grassland and for crop production. The groundwater level has been lowered in 1880 and thereafter several times during the 20th century (Kaufmann, 2004).

For the experiment, we selected two drained locations within less than 50 m distance with different plant composition and differing management intensity (for details see Table 1):

1) a grassland site with predominant grass vegetation (water-intolerant) which is intensively managed for dairy farming (TG5-F8 and TG5-F9, see also in (Drösler et al. 2011a)): we refer to this site as "grasses"; and

2) a site with water-tolerant sedge vegetation, a former peat cut site, which is extensively managed (TG5-F6 and TG5-F7, see also in (Drösler et al. 2011a)), we refer to this site as "sedges".

The peat substrates differed significantly in bulk density, ash content, estimated carbon density and pore volume (Tab. 3-1). Bulk density was typical for highly degraded peat (grasses 0.37 and sedges 0.18 g cm^{-3}) (Zeitz 2001). The pH was in the range of 5.9 to 5.6.

2.2. Experimental set up

In April 2008, at the early stage of vegetation development, intact soil mesocosms with vegetation were taken from the "grasses" and the "sedges" site in the Freisinger Moos (6 replicates each, for site characteristics see Tab. 3-1). A mesocosm was extracted by completely inserting a PVC tube (inner diameter = 16 cm, h = 50 cm) into the soil with a hydraulic drill and removing it by spade.

The mesocosms with vegetation were incubated in the climate chamber (York Deutschland GmbH, Mannheim, Germany) for 252 days under controlled temperature, air humidity, radiation and a 12/12 hours light/dark phase. Conditions in the climate chamber were set to typical temperature and radiation of a sunny spring day at the field site (see Fig. 3-2) and aim to give an idea of the potential CO_2 production respectively fixation and CH_4 formation. Air temperature and photosynthetic active radiation (PAR) were continuously logged at 5 minutes intervals at a central location in the climate chamber as well as at each mesocosm to monitor climate chamber performance and spatio-temporal variability. Measurements of soil temperature and redox profiles in the mesocosms are described in section 2.3.5. Maximum PAR in the climate chamber did not exceed 1200 µmol m^{-2} s^{-1} for technical reasons. Therefore, daily sum of PAR was lower in the climate chamber (32.1*10^6 µmol m^{-2} d^{-1}) than on the field site (52.1*10^6 µmol m^{-2} d^{-1}). Radiation was reduced by 9 to 15% within the variability of PAR in the climate chamber during the 252 days incubation period. The mean air temperature was comparable to the field site (16 °C). The mean soil temperature in 2 cm depth was slightly higher in the climate chamber (16.5 °C) and soil temperature in 30 cm depth slightly lower in the climate chamber (10.2 °C) compared to the field site (14.2 and 11.2 °C).

A basin (transparent acrylic glass; 35 x 35 x 7 cm³) attached and sealed to the top of each PVC tube acted as catchment basin for the supernatant water during flooding (referred to as inundation tank, Fig. 3-1). During flux measurements, the measurement chamber was attached to the bottom of the inundation tank.

The water table was manipulated by means of water canisters connected to the lower end of the mesocosms and applying the principle of communicating tubes. The water table in the mesocosms was raised every 29 days (-30, -20, -10, -5 and 0 cm) and was held at +5 cm for 109 days.

2.3. Measurements and data analyses

Terminology and definitions

CO_2 fluxes are defined as negative when CO_2 is removed from the atmosphere and incorporated into the plant/soil. Positive values indicate a release of CO_2 from the ecosystem into the atmosphere. Net ecosystem exchange (NEE) is the result of CO_2 uptake by photosynthesis and the simultaneous release of CO_2 by respiration: $NEE = GPP + R_{eco}$. Gross primary production (GPP) is a measure for CO_2 uptake by photosynthesis and depends on PAR (Michaelis and Menten 1913). Strongly negative GPP values indicate a high capacity to fix CO_2.

Ecosystem respiration (R_{eco}) is the sum of heterotrophic and autotrophic respiration and a temperature driven process (Lloyd and Taylor 1994). Strongly positive R_{eco} values indicate an elevated release of CO_2 from the plant/soil into the atmosphere.

Environmental conditions and soil parameters

Soil temperatures and redox potentials as well as air temperature and PAR within the climate chamber were logged every 5 minutes over the entire duration of the experiment (AM25T solid state multiplexer and Campbell Scientific data logger (both from Campbell Scientific Ltd., Logan, USA)).

Temperature probes (105T thermoelement probes, Campbell Scientific Ltd., Logan, USA) were permanently installed in -2, -5, -10 and -30 cm depths in each mesocosm. The redox potential in -5, -10, -15, -20, -30 cm depth of each mesocosm was measured via platin electrodes (construction based on (Fiedler et al. 2003) and an Ag/AgCl reference electrode (Mettler Toledo GmbH, Giessen, Germany) which was joined to the soil solution via a gel electrolyte bridge to avoid contamination (see mesocosm set-up in Fig. 3-1). The measured values were corrected by +210 mV at 5 cm depth, +214 mV at 10 and 15 cm depth and +217 mV at 20 and 30 cm depth according to the mean soil temperatures and the molarity of KCl solution in order to get the redox potential in relation to a standard hydrogen electrode (Calmano 2010).

Each mesocosm was insulated and connected to a soil cooling system (Minichiller, Huber GmbH, Offenburg, Germany) to ensure soil temperatures similar to that in the field (Fig. 3-1). Air and soil temperatures were simulated comparable to those of the sampling site (see Fig. 3-2).

Precipitation was simulated by adding 150 ml (for the first 50 incubation days) and 90 ml (thereafter) tap water on 5 days per week. Precipitation was independent of the regulation of the water table but was necessary to avoid drying-out of the topsoil.

For determination of pore volume, samples of a defined volume were taken in 5 respectively 10 cm intervals from the mesocosms and dried at 105°C. Dry weight was determined and samples were subsequently heated to 550° for 5 hours to incinerate all organic matter. The pore volume was

calculated as follows (according to (TGL 31222/03 1985)):

$$PV = 100 - \frac{BD * 207.6 - RI}{287.6} * 100$$

In which PV is the pore volume [%], BD the bulk density at 105°C [g cm^{-3}] and RI is the residue on ignition at 550°C [mass%].

Vegetation

The vegetation was regularly checked for pest infestation and treated with biological pest control when necessary. Vegetation development was documented by means of photos (Sony DSC-F828, f= 50mm, Sony Europe Ltd., Berlin, Germany). General vegetation development was assessed on the basis of the photos to account for the change in vegetation density and height over the incubation period and allocated to three categories: "old": vegetation as from sampling with very small new shoots, "new": upgrowth of the new shoots while old vegetation died-off successively, and "growth": very strong growth of the new shoots with simultaneous dying-off and accumulation of old vegetation, growth of algae in inundation tank of grasses. At the end of experiment leaf area index and dry weight were determined for the above ground biomass.

CO$_2$ exchange

Gas flux measurements and calculations in the mesocosms were performed according to the same methods as used for GHG flux measurements on various field sites (Drösler 2005; Drösler et al. 2011a; Beetz et al. 2013; Leiber-Sauheitl et al. 2014).

Measurement method

NEE and R$_{eco}$ were measured using a dynamic closed chamber system with a CO$_2$ infra-red gas analyser (model LI-6262, LI-COR Biosciences, Lincoln, USA,), a membrane pump (flow 3 l/min) and a data logger (Campbell Scientific Ltd., Logan, USA).

Transparent (NEE) and opaque (R$_{eco}$) chambers (Fig. 3-1) were constructed according to (Drösler 2005) (30 x 30 x 40 cm, volume ~ 36 liters, material: 3 mm thick acrylic glass and white PVC, purchased from SKV GmbH, Jena, Germany) and equipped with two vents, a radiation-protected temperature sensor (Pt 100, LKM Electronic GmbH, Geraberg, Germany) and a PAR sensor (LI-COR Biosciences, Lincoln, USA,). Cooling packs (7.5 x 1.8 x 16.3 cm) and the adjustment of the air stream direction in the chamber kept the temperature at the desired level during measurements. The transparent chamber had a light transmission rate of approximately 95 %. Gas tightness of the chamber was assured by a rubber tube sealing at the chamber bottom and was tested before the start of the experiment. Pressure equilibration was done by a cable gland, which was closed after placement of the chamber before each measurement.

The chamber was attached with elastic bands to the inundation tank and the air stream of the vents adjusted. A measurement lasted for at least 3 minutes after checking the stability of the temperature (± 0.5°C) inside the chamber. CO$_2$ concentration, temperature and PAR data were logged in 2 second intervals (Campell Scientific Datalogger, Campbell Scientific Ltd., Logan, USA).

The experiment lasted for 252 days during which CO$_2$ flux measurements were performed 30 times at the 13, 16, 18, 19, 23°C temperature levels and additionally 58 times at the 16°C temperature level.

Procedure for CO_2 flux calculations

CO_2 flux rates [mg C m^{-2} h^{-1}] were calculated according to the following formula (Flessa et al. 1998; Drösler 2005):

$$CO_2 \; flux = \frac{M \times T_n}{V_n \times (T_n + T_s)} \times \frac{V}{A} \times \frac{d_c}{d_t} \times 10^{-3}$$

in which M is the molar mass of carbon [= 12.0107 g mol^{-1}], V_n the molar volume [= 22,4136 l mol^{-1}] under standard conditions (T_n=273.15°K), T_s is the mean temperature in the chamber during measurement [°C], V is the volume of the chamber [liter], A the surface area of the mesocosm [~0.02 m^{-2}] and dc*dt^{-1} is the concentration change in the chamber atmosphere over time [ppm h^{-1}].

A procedure for semi-automated quality-controlled CO_2 flux calculation from raw data was developed and implemented as R script (R Core Team 2010). The concentration change in the chamber atmosphere over time (dc*dt^{-1}) was calculated by applying a quadratic function (y = a+bx+cx^2+e) to a selected section of the three-minute-measurement. The section of the curve was selected by taking into account the steepest part of the curve, the function fit (indicated by the residual standard error), the length of the selected section (indicated by the Akaike Information Criterium), as well as autocorrelation and normality of residuals (tested by Durbin Watson and Shapiro Wilk test).

To avoid potential interference of CO_2 concentration with photosynthesis, only the first part of the NEE measurement with a maximum change of concentration of 30 ppm was used for slope calculation.

Calculation of daily sum of R_{eco}, GPP, NEE

For each measurement day on which flux measurements were made at all temperature levels the response of R_{eco} to (air and soil) temperature was calculated by the equation according to (Lloyd and Taylor 1994) and fitted taking into account minimum residuals and maximum R^2. The parameters R_{ref} and E_0 were calculated according to:

$$R = R_{ref} \times e^{E_0 \left(\frac{1}{T_{ref} - T_0} - \frac{1}{T_{soil} - T_0} \right)}$$

in which R_{ref} is the respiration rate at the reference temperature [mg C m^{-2} h^{-1}], E_0 the activation energy [°K], T_{ref} the reference temperature: 283.15 [°K], T_0 the temperature constant for the start of biological processes: 227.13 [°K] and T_{soil} is the air/soil temperature of best fit with the dataset [°K].

Based on the parameter R_{ref} and E_0, R_{eco} was modelled with the air/soil temperatures measured during NEE measurements and GPP calculated. These GPP and the observed PAR data were fitted to the rectangular hyperbola equation according to (Michaelis and Menten 1913) and the parameter GP_{max} and α calculated for each measurement day as follows:

$$NEE = \frac{GP_{max} \times \alpha \times PAR}{\alpha \times PAR + GP_{max}} - R$$

in which PAR is the photon flux density of the photosynthetic active radiation [μmol m^{-2} s^{-1}], GP_{max} is the maximum rate of carbon fixation at PAR infinite (i.e. slope of zero) [mg C m^{-2} h^{-1}], α the maximum slope of GPP versus PAR at zero PAR [mg C m^{-2} h^{-1} / μmol m^{-2} s^{-1}] and R are flux rates

from the respiration model [mg C m^{-2} h^{-1}].

Daily R$_{eco}$, GPP and NEE [g C m^{-2} d^{-1}] were calculated as follows: R$_{eco}$ and GPP were modelled in 5-minute-steps with the parameter R$_{ref}$, E$_0$, GP$_{max}$ and α based on the logged air and soil temperatures and radiation in the climate chamber. NEE was calculated as the sum of R$_{eco}$ and GPP. These modelled values for 5-minute-intervals were added up to daily R$_{eco}$, GPP and NEE values.

Contribution of heterotrophic (R$_h$) and autotrophic (R$_a$) respiration

We calculated R$_h$ based on R$_a$:GPP ratio reported in the literature (Schulze et al. 2009) – which is indicated to be relatively stable between 0.44 and 0.53 independent of ecosystem type. As these calculations would partly produce negative R$_h$ values, which is biologically impossible, we used R$_h$ > 0 as constraint. In these calculations it is additionally assumed that the ratio R$_a$:GPP remained the same throughout the experiment and, because R$_a$ is determined by GPP, autotrophic respiration was gradually reduced during rewetting.

CH$_4$ and N$_2$O emissions

The emissions of CH$_4$ and N$_2$O from the mesocosm surface were determined using the static closed chamber method. Six opaque chambers (Fig. 3-1) without ventilation were attached to the inundation tank on top of the mesocosms and fixed with an elastic band. Gas samples were taken manually from the headspace by pumping headspace air through 20 ml glass flasks 0, 30, 60 and 90 minutes after closure. The temperature inside one of the chambers was recorded when sampling (Pt100, LKM Electronic GmbH, Geraburg, Germany). Sampling was done 25 times (at 13°C) and 32 times (at the 19 and 23°C temperature levels of the climate chamber) during 252 experimental days.

Gas samples were stored at room temperature and analysed with a gas chromatograph CP-3800 (Varian Inc., Walnut Creek, USA), equipped with a Quma QHSS-111 headspace sampler (Quma Elekronik und Analytik GmbH, Wuppertal, Germany), a flame ionization detector (FID) (300°C) for CH$_4$ detection and an electron capture detector (ECD) (390°C) for N$_2$O measurement, packed column (70°C), using N$_2$ as carrier gas.

CH$_4$ [mg C m^{-2} h^{-1}] and N$_2$O [mg N m^{-2} h^{-1}] flux rates were calculated as follows :

$$flux = \frac{M \times p_s \times T_n}{V_n \times p_n \times (T_n + T_s)} \times \frac{V}{A} \times \frac{d_c}{d_t}$$

in which M is the molar mass of carbon in CH$_4$ or nitrogen in N$_2$O [= 12 or 28 g mol^{-1}], V$_n$ the molar volume [= 22,4136 l mol^{-1}] under standard conditions (p$_n$=1013 hPa, T$_n$=273.15°K), T$_s$ is the temperature when sampling [°C], p$_s$ the air pressure when sampling [hPa], V is the volume of the chamber [m^3], A the surface area of the mesocosm [~0.02 m^2] and dc*dt^{-1} is the concentration change in the chamber atmosphere over time.

CO$_2$ equivalents

The GHG fluxes were converted to CO$_2$ equivalents [g CO$_2$-equ. m^{-2} d^{-1}] based on the 100-year global warming potentials (GWP) (IPCC 2007) relative to CO$_2$. For CO$_2$ we used daily NEE modelled with soil temperature in -2 cm depth, 1 g CH$_4$ = 25 g CO$_2$-equ., and 1 g N$_2$O = 298 g CO$_2$-equ. The GHG balance is the sum of CO$_2$ equivalents of the three GHGs.

2.4. Statistical analysis

All data manipulation, modelling and graphics were done using the R statistical environment (R Core Team 2013).

Differences in biomass dry weight and peat characteristics between grasses and sedges were tested using the Wilcoxon rank-sum test.

The flooding period was three times longer than other water table positions. For the graphical display and the modelling of GHG fluxes over the incubation period, these data were split into three phases corresponding to differences in ecosystem response to flooding: phase I: immediate response to flooding conditions up to emergence of methanogenesis (incubation days 144-162), phase II: transient response with vegetation adaptation (incubation days 163-232) and phase III: stabilized response to flooding (incubation days 233-252).

Linear mixed-effects model for GHG fluxes

The effects of water table position and plant composition on R_{eco}, GPP, NEE and CH_4 fluxes over the incubation period were estimated by linear mixed-effects models using the R package *nlme* (Pinheiro and Bates 2000).

Fixed effects were modelled for CO_2 fluxes as

$$E\left(R_{eco}\,resp.\,NEE|WT,PC,VD\right)=\beta_0+\beta_1 WT+\beta_2 PC+\beta_3 VD+\beta_4\left(WT\times PC\right)+\epsilon \quad,$$

$$E\left(GPP|WT,PC,VD\right)=\beta_0+\beta_1 WT+\beta_2 PC+\beta_3 VD+\beta_4\left(WT\times PC\right)+\beta_5\left(PC\times VD\right)+\epsilon \quad,$$

and for methane as

$$E\left(CH_4|WT,PC,VD\right)=\beta_0+\beta_1 WT+\beta_2 PC+\beta_3 VD+\beta_4\left(WT\times PC\right)+\epsilon$$

where WT is the water table position [-30 to +5 cm], PC is the plant composition [grasses or sedges], VD is the vegetation development [in three categories: old, new, growth], WT×PC the interaction between water table position and plant composition and PC×VD the interaction between plant composition and vegetation development.

For CO_2 fluxes, two crossed random effects were used to account for global random differences due to temperature/PAR levels and differences between individual mesocosms; additionally, random differences in mesocosms nested within temperature/PAR levels were modelled over the incubation period. For CH_4 fluxes, random differences between individual mesocosms were modelled over the incubation period and random differences in mesocosms per temperature/PAR level over the incubation period were considered.

Systematic differences in the variance structure between water table positions were accounted for by using the varIdent variance model implemented in nlme. The temporal dependence of observations over the incubation period was modelled by incorporating an autoregressive moving average (ARMA) model with 2 autoregressive terms and 2 moving-average terms for R_{eco} and GPP and a moving average model with 2 autoregressive terms for NEE.

The variability in biomass between mesocosms was included in the linear mixed-effects models as random effect.

3. Results

3.1. Controlling factors of greenhouse gas fluxes

Vegetation development and mass

The vegetation in the sedges replicates was composed of sedge plants (74%), herbs (17%), grasses (6.5%), rushes (1.8%) and some moss. The vegetation in the grasses consisted solely of grass species except for mesocosm G-4 in which a large clover plant was growing.

Aboveground vegetation composition at incubation end clearly differed between grasses and sedges (see Fig. 3-3) although total dry weight (dw) was not significantly different (sedges: 2.06 ± 0.5 kg dw m^{-2}; grasses: 2.01 ± 0.5 kg dw m^{-2}). The fraction of green biomass was more than three times higher in sedges (range from 1.3 to 2.2 kg dw m^{-2}, on average 81 % of total sedges biomass) than in grasses (0.5 to 0.7 kg dw m^{-2}, 26 % of total grasses biomass). The fraction of brown (dead) biomass was 5 times higher in the grasses (0.5 to 2.0 kg dw m^{-2}, 58 % of total grasses biomass) compared to sedges (0.1 to 0.3 kg dw m^{-2}, 11 % of total sedges biomass). Algae, which grew in the inundation tank, were observed in the grasses only and accounted for 15 % of the total biomass. Other dead matter – which consisted of biomass other than leaves, e.g. leaf sheaths, dead roots and shoots, etc. – was observed in the sedges (8% of total sedges biomass) and in one of the grasses mesocosms.

We observed a positive correlation between the amount of dead leaves and algae and respiration rates.

Leaf area index (LAI) at incubation end mirrored the differences in biomass and was clearly higher in sedges (8.8 – 16.3 m^2 m^{-2}) compared to grasses (5.4 to 7.5 m^2 m^{-2}). While LAI of sedges was dominated by green leaves (85% green and 15 % brown leaves), brown leaves prevailed in grasses (32% green and 67% brown leaves).

Redox potential

Factors influencing the redox potential are pH, the presence of complexing ions, moisture and organic/inorganic matter. Therefore, it is only possible to define a qualitative value representative of a soil state (Pansu and Gautheyrou 2006). When examining the redox potential in connection with CH$_4$ production it is essential to consider the time when the redox potential falls below a defined threshold (Fiedler 1999). We set the threshold for methanogenesis at 0 mV. According to the assumption by (Pansu and Gautheyrou 2006), at a redox potential below 0 mV, conditions in the peat are considered anaerobic but not necessarily methanogenic, while below -150 mV, conditions are considered strictly anaerobic and consequently favourable for CH$_4$ production. The phase between 0 and -150 mV was quickly passed in our mesocosms.

Grasses and sedges strongly differed in the redox profile and in the reaction of redox potential to gradual rewetting. The redox potentials in grasses started with a homogeneous value above +600 mV in the entire soil profile at a water table of -30 cm (Fig. 3-4). When the water table was raised, redox potentials decreased homogeneously in the profile and passed the threshold for methanogenesis in -20 cm and -10 cm depth when water table was at -10 cm. After a few days of full rewetting to 0 cm the redox potentials dropped to values of -300 mV after flooding.

The redox potentials in sedges showed a persistent redox gradient in the profile until the soil was flooded for a week. Redox potentials rapidly reacted to water table changes and were stabilized at the new level within days, however with high daily fluctuations. The redox potentials of the topsoil (-5 cm) in sedges remained stable above +500 mV up to complete rewetting to 0 cm. Only with

flooding (+5 cm) conditions in the topsoil became favourable for methanogenesis. The redox potential in -10 cm depth slowly declined with raising water table and passed the threshold for methanogenesis a few days after full rewetting (0 cm). At -20 cm conditions turned favourable for methane production already at a water table of -20 cm (Fig. 3-4). During the flooding period redox potential was similar in the entire soil profile and never dropped below -230 mV.

3.2. CO_2 exchange

CO_2 fluxes reacted instantaneously – within one to a few days to changes in the water table position (data not shown). In periods of constant water table position, an equilibrium in CO_2 fluxes was established and therefore the measurements per water table were considered as replicates (see averaged CO_2 fluxes in Fig. 3-5 and results of linear mixed effect model in Tab. 3-2).

Plant composition and water table position had clearly discernible effects on CO_2 fluxes (Fig. 3-5, Tab. 3-2). Grasses and sedges reacted in similar direction, but with different thresholds to rewetting. The most pronounced changes in CO_2 fluxes were observed at the change from -30/-20 cm to -10 cm and at the change from 0 cm to +5 cm water table position (Fig. 3-5).

Daily R_{eco} decreased continuously by 55 % in grasses and by 67 % in sedges until the 0 cm water level water level (Fig. 3-5 top). The decrease started earlier in sedges than in grasses. During the flooding period, daily R_{eco} increased immediately and significantly in sedges and grasses back to the R_{eco} levels of -10 cm (grasses) and -5cm (sedges). Daily R_{eco} was consistently higher by 2.4 – 7.8 g C m^{-2} d^{-1} (19 – 42 %) in grasses than in sedges.

Daily GPP gradually decreased by 15 % in grasses and sedges with raising water table until the 0 cm water level (Fig. 3-5 centre). In this period, daily GPP was about 9 % higher in grasses than in sedges. At the change from the 0 cm to +5 cm water table position a decrease of daily GPP by further 15 % (grasses) and 18 % (sedges) was observed. The capacity to fix CO_2-C recovered in sedges during the flooding period while it remained low in grasses (Fig. 3-5). Sedges grew new shoots during the +5 cm period while grasses were clearly stressed by the high water table position, turned yellow and partly died. The died-off plant material decayed, the grass tussocks were raised above the water table and only few new shoots were produced. In the grasses mesocosms, algae grew in the inundation tank (see Fig. 3-3) and were responsible for the slight recovery of GPP in phase III of the flooding period.

NEE is the result of CO_2 uptake for photosynthesis (GPP) and the simultaneous release of CO_2 due to respiration (R_{eco}). Measurements in this experiment were mainly negative, because photosynthesis exceeded ecosystem respiration. Negative NEE is expected in grassland ecosystems on sunny warm spring days, which were continuously present in our mesocosms. At incubation start, daily NEE was clearly negative in sedges while it was close to zero in grasses. Gradual rewetting reduced R_{eco} more than GPP leading to more negative values for daily NEE in sedges and grasses with raising water table until the 0 cm level (Fig. 3-5 bottom). Maximum daily net carbon uptake was observed at the 0 cm water level. With flooding, daily NEE was immediately and strongly reduced to values below -5 g C m^{-2} d^{-1} in grasses and remained low, similar to the NEE at the drained start. In sedges, however, daily NEE only dropped in the first phase of flooding and recovered to a maximum net carbon uptake of -10 g C m^{-2} d^{-1} due to adaptation and recovery of the sedge vegetation.

The linear mixed-effects models allow a quantitative assessment of the impact of various parameters on CO_2 fluxes. The water table position had by far the largest effect on all CO_2 fluxes (Tab. 3-2). In the R_{eco} and NEE models the plant composition (PC) together with the interaction of plant composition and water table (PC:WT) had a much smaller effect while vegetation development (VD) had the least impact. In the GPP model, VD and PC:VD had a medium effect, the interaction PC:WT was significant although relatively small and PC alone had no significant effect. For the sake of convenience, Tab. 3-2 lists only the effects of the two most important parameters – water table position and plant composition.

Predicted mean R_{eco} in sedges was lower (74 %) relative to grasses averaged over all water table positions (for further explanation see Tab. 3-2). Estimated R_{eco} decreased to 42 % in grasses and 29 % in sedges until the 0 cm water level water level (Tab. 3-2). With flooding, estimated R_{eco} significantly increased immediately by 21 – 27 %. During extended flooding, estimated R_{eco} in sedges decreased much stronger in sedges than in grasses.

The relative mean GPP was equal for grasses and sedges. Estimated GPP gradually decreased to 86 to 88 % until the 0 cm water level (Tab. 3-2). The decrease started slightly earlier in sedges, but was slightly stronger in grasses as a reaction to flooding .During extended flooding, estimated GPP stayed continuously low.

Estimated NEE increased in sedges and grasses with raising water table to a maximum net carbon uptake of ~ 133 % at the 0 cm water level (Tab. 3-2). The flooding event strongly reduced estimated NEE to ~ 91 % in both grasses and sedges. While the net carbon uptake was further reduced in grasses (to 85 %) during extended flooding it recovered in sedges up to 122 %.

3.3. CH_4 emissions

CH_4 emissions showed a slow but continuous reaction to changes in water table position (data not shown).

In the linear mixed-effects model for methane, the water table position and the interaction WT: PC had by far the largest effects on the CH_4 flux. The effect of PC alone was not significant. The vegetation development had a medium effect on the emissions in the mixed-effects model.

CH_4 emissions were zero at the -30, -20 and -10 water table positions and started to increase at the -5 cm water table in both sedges and grasses and strongly increased with further water table raise (Fig. 3-6). Despite different redox profiles and buffering or chimney effects of aerenchymous plants, there was no difference in the start of detectable CH_4 emissions between grasses and sedges. During the 0 cm water level phase and the subsequent flooding, CH_4 emissions increased strongly, reached a maximum in the middle of the flooding period (estimated mean of 16.1 for grasses and 9.8 mg C m^{-2} h^{-1} for sedges in phase II) and slightly decreased towards the end. During flooding, methane emissions were always significantly higher in the grasses than in sedges (Fig. 3-6).

Effect of vegetation development (VD): CH_4 emissions were zero to small from -30 to the 0 cm water table position when the vegetation was still in its early development stage (VD=old). Predictions of CH_4 emissions were in general higher by 3.6 mg C m^{-2} h^{-1} when when the vegetation was fully developed and dead organic matter accumulated in the mesocosms (VD=growth).

3.4. N_2O emissions

N_2O emissions were under the level of 0.2 mg N m^{-2} h^{-1} during the entire incubation period (data not shown). In agricultural soils, a level of 0.2 – 0.4 mg N m^{-2} h^{-1} is generally considered as background, therefore no further statistical analysis was performed.

At the -30 cm water table position N_2O was taken up by the peat in the same order of magnitude for grasses and sedges (on average -0.36 mg N m^{-2} h^{-1}). No N_2O emissions occured at subsequent water table positions.

3.5. GHG as CO_2 equivalents and ratio of all three GHG

The GHG balance was dominated by net CO_2 exchange. Methane contributed mainly during the flooding period and N_2O had a small impact at the water table position of -30 cm only.

Grass mesocosms were a moderate net GHG sink of -10 g CO_2-equ. m^{-2} d^{-1} when drained and jumped to a stronger net GHG sink of around -30 g CO_2-equ. m^{-2} d^{-1} at water table positions between -10 and 0 cm. Flooding immediately and drastically reduced the net GHG sink to values below -6 g CO_2-equ. m^{-2} d^{-1}. Under extended flooding the GHG balance of grasses turned into GHG neutral and even positive with 4.6 g CO_2-equ. m^{-2} d^{-1} because low net CO_2 uptake was more than compensated by CH_4 emissions in terms of CO_2-equivalents.

Sedge mesocosms remained a net GHG sink throughout the experiment, starting with values of -22 g CO_2-equ. m^{-2} d^{-1} at -30 cm, which increased during rewetting and doubled at complete rewetting (0 cm). The net GHG balance decreased to -20 g CO_2-equ. m^{-2} d^{-1} as immediate response to flooding and turned back to -30 g CO_2-equ. m^{-2} d^{-1} after vegetation had adapted to flooding. Methane emissions compensated 17 – 28 % of net CO_2 uptake in terms of CO_2-equivalents in long-term flooded conditions.

The ratio CO_2 : CH_4 : N_2O was 100 : 0 : 43 in grasses and 100 : 0 : 23 in sedges at -30 cm water table. CO_2 was the only relevant GHG at water table positions -20 to -5 cm (100 : 0 : 1 in both grasses and sedges). At 0 cm water table the ratio was 100 : 4 : 1 in grasses and 100 : 1 : 1 in sedges. During the flooding period the fraction of CH_4 increased and the ratio was 100 : 40-143 : 4 in grasses and 100 : 7-28 : 1 in sedges.

4. Discussion

4.1. Response of vegetation vitality and respiration to changes in water table position

Vegetation response

The capacity for CO_2 fixation (GPP) could be used as an indicator for assessing the vitality of the aboveground vegetation. The vegetation growing in the mesocosms reacted with reduced vitality to a water table raise from -30 cm up to 0 cm (see Fig. 3-5, centre). Sedges had in general a lower photosynthetic capacity (i.e. lower productivity) than grasses.

The water table raise from 0 cm to +5 cm obviously imposed a shock on the vegetation, which reacted with immediate and significant reduction of GPP. Sedges are adapted to wet conditions and can grow and survive under anaerobic conditions. They reacted to flooding by forming new leaves and growing vigorously and recovered after several weeks of wetness stress and adaptation (GPP increased during prolonged flooding). In contrast, grasses are not adapted to flooded conditions and reacted by forming mounds, yellowing of leaves and partial die-off of the very productive vegetation, GPP remained low during prolonged flooding. At incubation end, more than half of the total grasses biomass consisted of dead biomass (Fig. 3-3). During flooding, a shallow nutrient-rich lake was formed which allowed the growth of algae.

Permanent flooding led to increased availability of readily degradable matter from recently died-off plants, which is a major factor for methane production (Couwenberg 2009). This caused an increase in R_{eco} and CH_4 emissions – which was significantly higher in grasses. A similar accumulation of dead organic matter was observed in the field at a rewetted fen site where a mud layer under permanent anaerobic conditions was formed producing high CO_2 and CH_4 emissions (Hahn-Schöfl et al. 2011).

Contribution of heterotrophic (R_h) and autotrophic (R_a) respiration

Auto- and heterotrophic respiration (R_{eco}) were gradually reduced in both grasses and sedges. In general, R_{eco} was lower in sedges. Water saturation, anaerobiosis and the accumulation of decomposition products may lead to a near shut down of hetero- and autotrophic respiration in ombrotrophic peat soils (Limpens et al. 2008).

Maximum possible R_a:GPP ratios were 0.30 for the sedges and 0.47 for the grasses which is close to the values given in the literature (Schulze et al. 2009). The proportion of R_h to R_{eco} was initially higher in sedges (0.6) than in grasses (0.5) and was gradually decreased to nearly zero at the 0 cm water table position. During prolonged flooding R_h was around 0.4 in both grasses and sedges with a further decrease in sedges. R_h under flooding likely resulted from decay of died-off vegetation parts.

4.2. The water table position and its influence on GHG fluxes – thresholds for drastic changes and minimal GHG fluxes

Gradual rewetting

CO_2 fluxes changed gradually during stepwise rewetting from -30 cm up to 0 cm. We observed a linear response of reduced GPP by 0.1 g C m^{-2} d^{-1} per cm water table raise in both grasses and sedges and of reduced R_{eco} by 0.3 (segdes) to 0.4 (grasses) g C m^{-2} d^{-1} per cm water table raise. Consequently, net CO_2 uptake increased by 0.2 (segdes) to 0.3 (grasses) g C m^{-2} d^{-1} per cm water table raise, which was equivalent to the reduction in R_h from peat mineralization. Our results agree with field observations on a histic Gleysol where R_{eco} decreased linearly with rising groundwater level and annual NEE budgets were positively correlated to mean annual water table levels (Leiber-Sauheitl et al. 2014).

Methane emissions were around zero from -30 to -5 cm water table position (Fig. 3-6) when the small amount of recently died-off plant material was small and the redox conditions in the surface peat layer were unfavourable for methanogenesis (Fig. 3-4).

N_2O emissions were in the range of background at all water table positions with very small N_2O uptake at the -30 cm water table only. This result agrees with the literature (Riet et al. 2013). The rate of N_2O release (resulting from denitrification, nitrification and N_2O reduction) depends on the water saturation of the soil and has a maximum at a water content of 70-80% of the pore volume (Meyer 1999). Redox potentials in topsoil were favourable for denitrification up to a water table of -10 cm. Denitrification might have produced N_2 in later phases of the incubation.

When all GHG fluxes are considered the linear response was even more pronounced (Fig. 3-7). Each cm water table raise increased the net GHG uptake by 0.6 (segdes) to 0.8 (grasses) g CO_2-equivalents m^{-2} d^{-1}.

Flooding

The most drastic change in GHG balance occurred at the step from complete rewetting (water table at 0 cm) to flooding (+5 cm) in both grasses and sedges (Fig. 3-5 and Fig. 3-6). Flooding caused a significant reduction of GPP and simultaneous increase in R_{eco} and CH_4 emissions due to increased substrate availability.

In this incubation experiment with eternal spring conditions, flooding led to an immediate extra GHG emission of 27 g CO_2-equivalents m^{-2} d^{-1} in grasses and 22 g CO_2-equivalents m^{-2} d^{-1} in sedges (Fig. 3-7). Gradual rewetting and the step from completely rewetted to flooded has to our knowledge not been studied in such temporal detail and systematic way so far, and in some cases the CO_2 fixation by the vegetation was not included in the GHG budget. A peat mesocosm experiment with abrupt permanent flooding resulted in significantly reduced R_{eco} fluxes and increased CH_4 emissions – which is in line with our findings –, however, the increase in CH_4 emissions expressed as CO_2-equivalents was much smaller than the reduction in R_{eco} emissions (Riet et al. 2013). In contrast, CH_4 was the main contributor to total GHG emissions in soil cores from a wetland after rewetting and contributed 60 to 80 % to total cumulative GHG emissions (Berryman et al. 2009). Field measurements showed that Dutch drainage ditches are important sources of CH_4 – emitting up to two times more methane than grasses under flooded conditions in our experiment – and that the contribution of CH_4 to the climatic effect in terms of CO_2-equivalents is significant (Schrier-Uijl et al. 2010).

Thresholds for minimal GHG fluxes

Net CO_2 uptake was strongest at -10 cm to 0 cm water table positions while respiration was lowest at 0 cm water table (Fig. 3-5). CH_4 emissions were zero from -30 to -5 cm water table position (Fig. 3-6). N_2O emissions were very low and unaffected by the water table.

When taking into account all three GHGs, the most favourable water table positions in terms of mitigating climate change range from -10 cm to 0 cm, which corresponds to the typical water table range of natural peatlands. Our finding for an optimum water table position corresponds to other studies. (Drösler et al. 2011b) recommends an annual mean water table around -10 cm as the optimum with respect to GHG mitigation. (Jungkunst et al. 2008) suggests an optimum water table around -5 cm to minimize the net GHG balance.

When the explicit goal of peatland rewetting is the reduction of GHG emissions it should aim to avoid an increase in CH_4 emissions as methane has a global warming potential 25 times higher than CO_2 (IPCC 2007). (Drösler 2005) observed marginal release of CH_4 to the atmosphere at water tables of -10 cm and lower and emphasized the importance of the aerobic layer for CH_4 oxidation (Drösler et al. 2008). A comprehensive literature review of field GHG measurements in temperate

Europe shows that net CH_4 emissions were negligible at mean water table below -20 cm and steeply increased with rising water table, while net CO_2 emissions considerably decreased with a mean water table higher than -30 cm and were nearly zero when the water table was close to the surface (Couwenberg et al. 2008).

As the availability of substrates for CO_2 and CH_4 production, such as fresh plant litter and root exudates, is highest in the uppermost peat layer this layer will contribute most to CO_2 and CH_4 production while peat depths >10 cm marginally contribute to peat respiration and are irrelevant for methanogenesis (Estop-Aragonés and Blodau 2012).

The risk of high CO_2 and CH_4 emissions after restoration is limited to continuously flooded conditions and the simultaneous presence of readily degradable organic matter (Hahn-Schöfl et al. 2011). In contrast, if vegetation is adapted to wet conditions, shallow flooding will not turn the net GHG sink into a source. Raising the water table above the peat surface (flooding) has nearly cancelled the positive climatic effect in grasses (Fig. 3-7) because the lower net CO_2 uptake was more than compensated by CH_4 emissions in terms of CO_2-equivalents. In segdes, CH_4 never risked to compensate the net CO_2 uptake – the positive climatic effect was halved after flooding.

The drastic effect on vegetation and GHG emissions has strong implications for peatland rewetting for GHG mitigation in practice. Degraded peat does not swell and buffer excess water so that rewetting can easily produce flooded conditions. An active vegetation not adapted to these flooded conditions may die-off producing readily degradable and energy-rich substrates for microbial decomposition processes (as showed in grasses). With flooding the GHG sink is drastically reduced or even turned to a GHG source if flooding persists for several weeks.

4.3. The effect of aerenchymous plants – do sedges boost CH_4 emissions?

Plants with aerenchyma, e.g. sedges and rushes, are capable of transporting CH_4 from deeper, anaerobic peat horizons to the surface avoiding CH_4 oxidation in aerobic layers ("chimney-effect") (Augustin 2001; Couwenberg 2009). These "shunt" species are responsible for high CH_4 emissions at a high water table. In our study, we did not observe this "chimney-effect" under flooded conditions in sedges.

However, aerenchymous plants enabled the transport of O_2 into deeper soil horizons which stabilized the redox potential in deeper zones of the sedges mesocosms (see Fig. 3-4). Redox conditions favourable for CH_4 production occurred later and consequently led to a lower CH_4 production in sedges – CH_4 never risked to compensate the net CO_2 uptake. In the topsoil, conditions favourable for methanogenesis occured ~30 days later in sedges than in grasses.

Methane concentrations in fen peat mesocosms were elevated only after electron acceptors were completely depleted which occurred within 50 days of permanently wet conditions (Knorr and Blodau 2009).

5. Conclusions

We present data on the functional role of the water table position on GHG exchange in incubated peat mesocosms from managed fen grasslands. Peatland rewetting with the aim to reduce GHG emissions should take into account the following recommendations which are based on our findings:

Gradually raising the water table up to 0 cm has a positive climatic effect – it increases net GHG uptake in terms of CO_2-equivalents because net CO_2 uptake increases while emissions of CH_4 and N_2O remain low. However, vegetation vitality is affected by the re-established water saturated conditions.

Flooding, in contrast, significantly reduces or may even cancel the positive climatic effect because of increased CO_2 loss from respiration and increased CH_4 emissions – depending on the vegetation and its adaptation to water saturated conditions. Flooding bears the greatest risk for high GHG emissions. Aerenchymous plants do not necessarily boost CH_4 emissions – they contribute to the stabilization of the redox potential retarding the onset of methanogenesis and lowering CH_4 production under wet conditions.

To achieve minimal GHG fluxes in rewetting, a near-natural water table position is recommended (i.e. between -10 cm to 0 cm). A water table slightly below the soil surface limits CO_2 loss from heterotrophic respiration, allows for CH_4 oxidation in the shallow aerobic layer and is favourable for vegetation vitality. Rewetting measures should support a vegetation transition towards wetness-adapted species.

Acknowledgements

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Tables and Figures

Tab. 3-1: Characterization of the sampling sites in the Freisinger Moos: dominant vegetation, management and soil characteristics[*])

	Grasses	**Sedges**
Name of site in other literature [**]	Intensively managed grassland (TG5-F8, TG5-F9)	Extensively managed grassland with sedges (TG5-F6, TG5-F7)
Dominant vegetation	mainly *Festuca pratensis*, *Poa trivialis*, *Alopecurus pratensis* and *Dactylis glomerata*	mainly *Carex elata, Mentha pulegium*
Management[***]	Middle intensity management: 2-3 cuttings per year, low water table, fertilization	extensive management within the framework of nature protection: hay meadow for litter, 1 cut in autumn, litter is removed, drained, no fertilization; former peat cut site
	carbon export: 470 (2007) and 192 (2008) g C m^{-2} yr^{-1}	carbon export: 106 (2007) and 21 (2008) g C m^{-2} yr^{-1}
	carbon import: 135 (2007 and 2008) g C m^{-2} yr^{-1}	
Mean water table at the site[**]	< -60 cm	-30 to -60 cm
Soil type	Sapric Histosol	Sapric Histosol
Bulk density [g cm^{-3}][*]	0.37 (± 0.11)[a]	0.18 (± 0.01)[b]
Ash content [%][#*]	38.6 (± 4.5)[a]	26.0 (± 3.7)[b]
Carbon density [kg C m^{-3}][##*]	177.6 (± 51.6)[a]	90.7 (± 5.3)[b]
Pore volume [%][*]	77.6 (± 7.3)[a]	88.8 (± 0.7)[b]
pH[*]	5.9 (± 0.3)[a]	5.6 (± 0.3)[a]

[*] soil characteristics determined from mesocosms at incubation end (mean ± SD, n = 6; different letters indicate significant differences, p<0.05, Wilcoxon test)

[**] (Drösler et al. 2011a)

[***] personnal communication with Mathias Drösler

[#] determined by loss on ignition at 550°C

[##] belowground carbon estimated based on bulk density according to (Warren et al. 2012)

Tab. 3-2: Relative change in CO_2 fluxes as an effect of plant composition and water table position[*] calculated from predictions derived from linear mixed-effects models for R_{eco}, GPP and NEE:

	R_{eco}		GPP		NEE	
	grasses	sedges	grasses	sedges	grasses	sedges
Effect of plant composition[**] [%]						
Relative mean CO_2 flux	100.0	74.1 ± 9.1	100.0	100.0 ± 7.9	100.0	110.0 ± 15.2
Effect of water table position[***] [%]						
-30 cm	100.0	79.4	100.0	101.2	100.0	112.9
-20 cm	94.6	64.3	98.0	94.9	101.4	115.5
-10 cm	64.9	55.5	92.6	90.1	120.1	113.0
-5 cm	55.0	39.5	89.5	86.7	124.8	122.7
0 cm	41.8	28.8	88.3	86.5	132.3	134.6
phase I: 5 cm	62.7	55.7	79.2	84.9	91.5	90.5
phase II: 5 cm	48.2	33.1	74.2	74.0	94.6	110.6
phase III: 5 cm	51.8	32.7	75.5	78.3	85.1	121.9

[*]   All percentages were calculated based on prediction means derived from the respective linear mixed-effects models for R_{eco}, GPP, and NEE (compare App-Fig. 3-1 in the Appendix; for details on linear mixed-effects models see App-Tab. 3-1 to 3-4).

[**]   Percentages express the reduction in the predicted mean CO_2 flux of sedges relative to grasses averaged over all water table positions. The confidence limits reflect the uncertainty due to differences between water table positions and not the uncertainty in model prediction.

[***]   Percentages express the relative reduction in the predicted mean CO_2 flux compared to grasses at the -30 cm water table (compare App-Fig. 3-1 in the Appendix for prediction intervals).

Fig. 3-1: Mesocosm set-up in the climate chamber:

> a) PVC tube contained peat core with vegetation which was equipped with b) insulation and c) cooling system. In each of the 12 mesocosms d) redox probes were installed in 5 depths (including an e) Ag/AgCl reference electrode) and f) soil temperature probes in 4 depths. Water table manipulation was assured via water supply at the mesocosm bottom (g). An h) inundation tank served as basin for supernatant water during flooding and to place the i) measurement chamber. The transparent / opaque measurement chamber had j) two vents, k) a radiation-protected temperature sensor and l) a PAR sensor. Air temperature was held constant via m) cooling packs. Gas sampling was done via n) two ports (flow-through to an infra-red gas analyser) or manually via o) a septum.
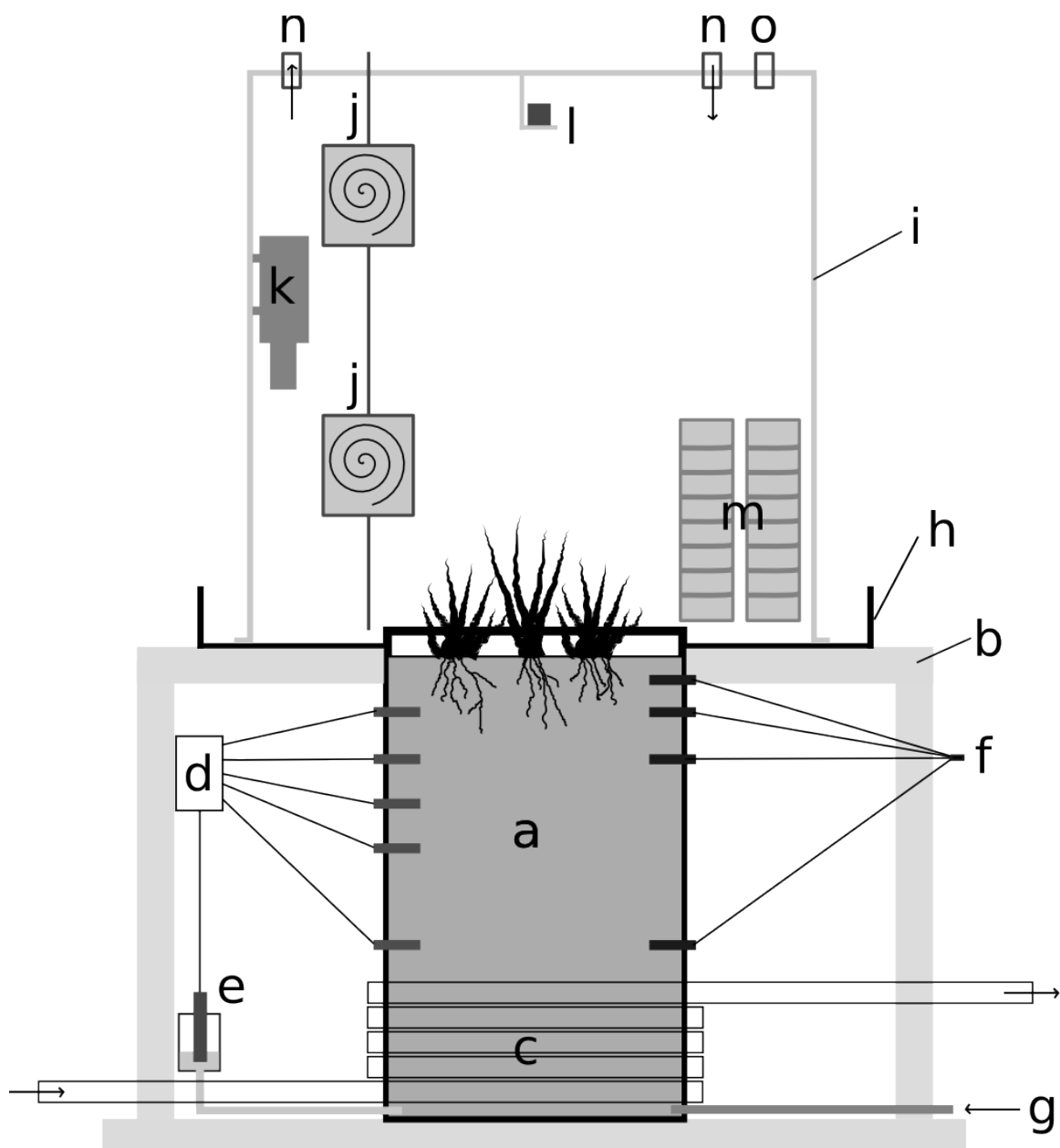
Fig. 3-2: Diurnal radiation and temperature conditions in the climate chamber (black line) and at the sampling site (grey line): photosynthetic radiation (PAR, top), air temperature (centre) and soil temperature in -2 cm depth (bottom). The dotted line indicates the desired temperature level.
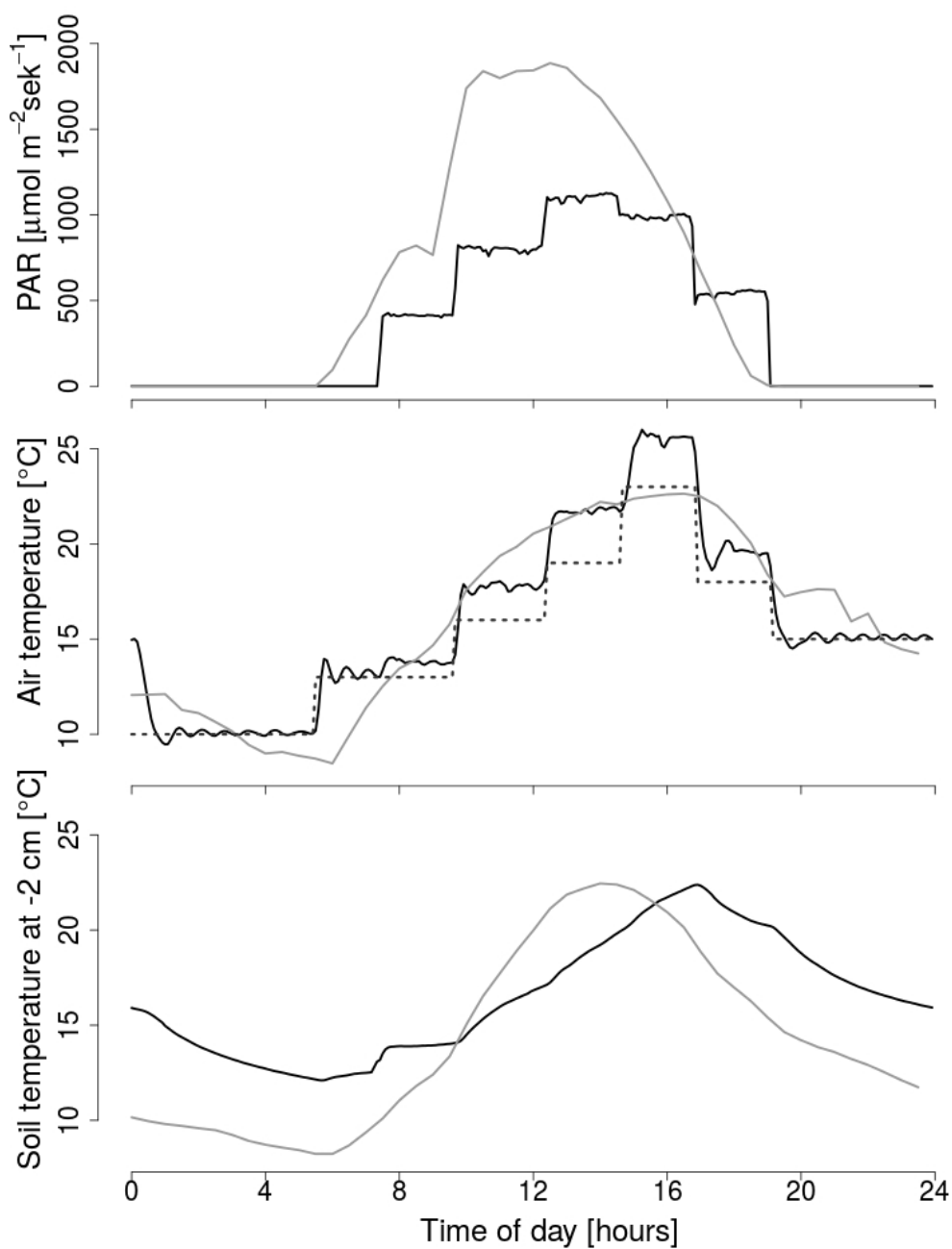
Fig. 3-3: Biomass per area in mesocosms in grasses (left) and sedges (right) at incubation end (separated in fraction green leaves, brown leaves, algae present in the inundation tank and other dead matter (such as leaf sheaths, dead roots and shoots, etc.))
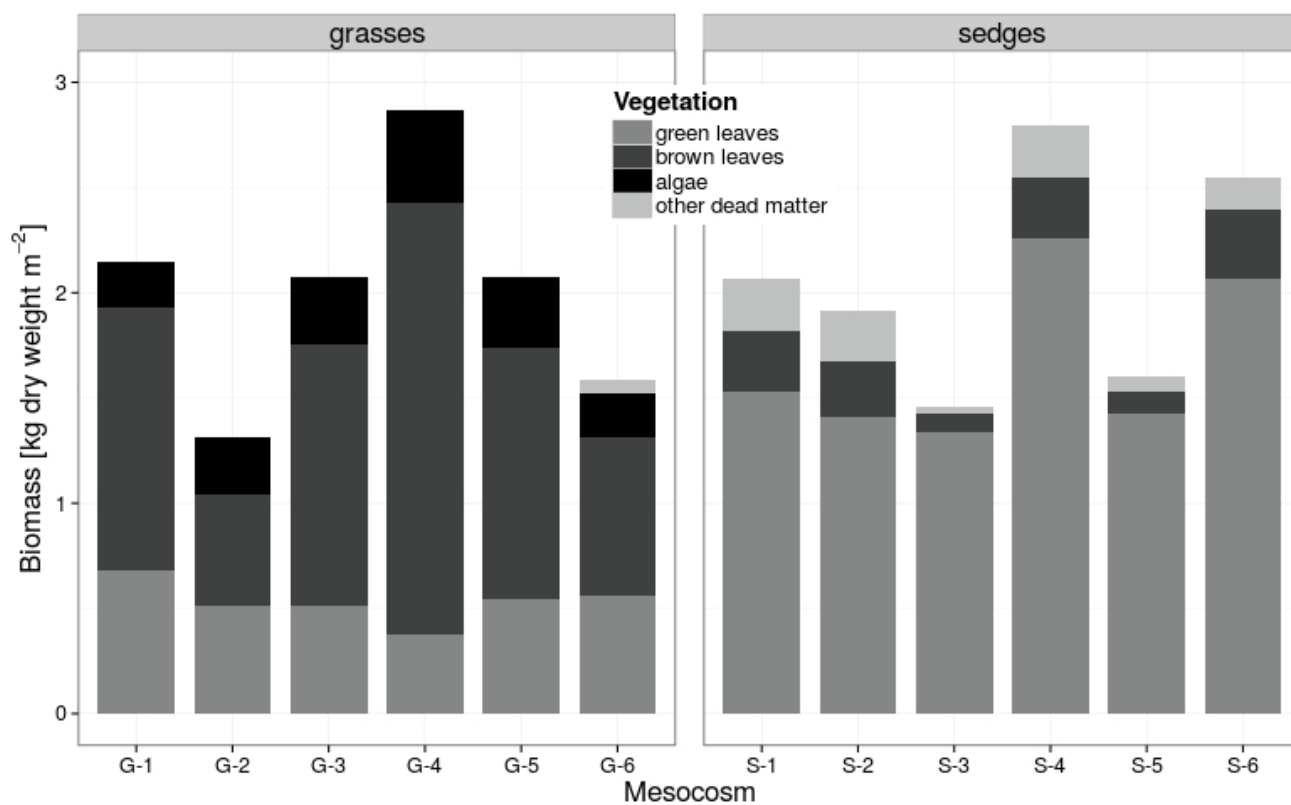
Fig. 3-4: Redox potential over the course of the experiment in grasses (top) and sedges (bottom) measured in -5, -10 and -20 cm depth (daily mean of 6 replicates, n=1728). The dotted line indicates the threshold for methanogenesis.

Fig. 3-5: Daily R_{eco} (top), GPP (centre) and NEE (bottom) in grasses (black) and sedges (grey) at raising water table positions (modelling is based on fitting measurements to Lloyd & Tayler and Michealis & Menten function; crossbar shows mean ± standard deviation, n= 3 to 11). The water table position at +5cm has been split into 3 phases corresponding to differences in ecosystem response to flooding (for details see section 2.4).

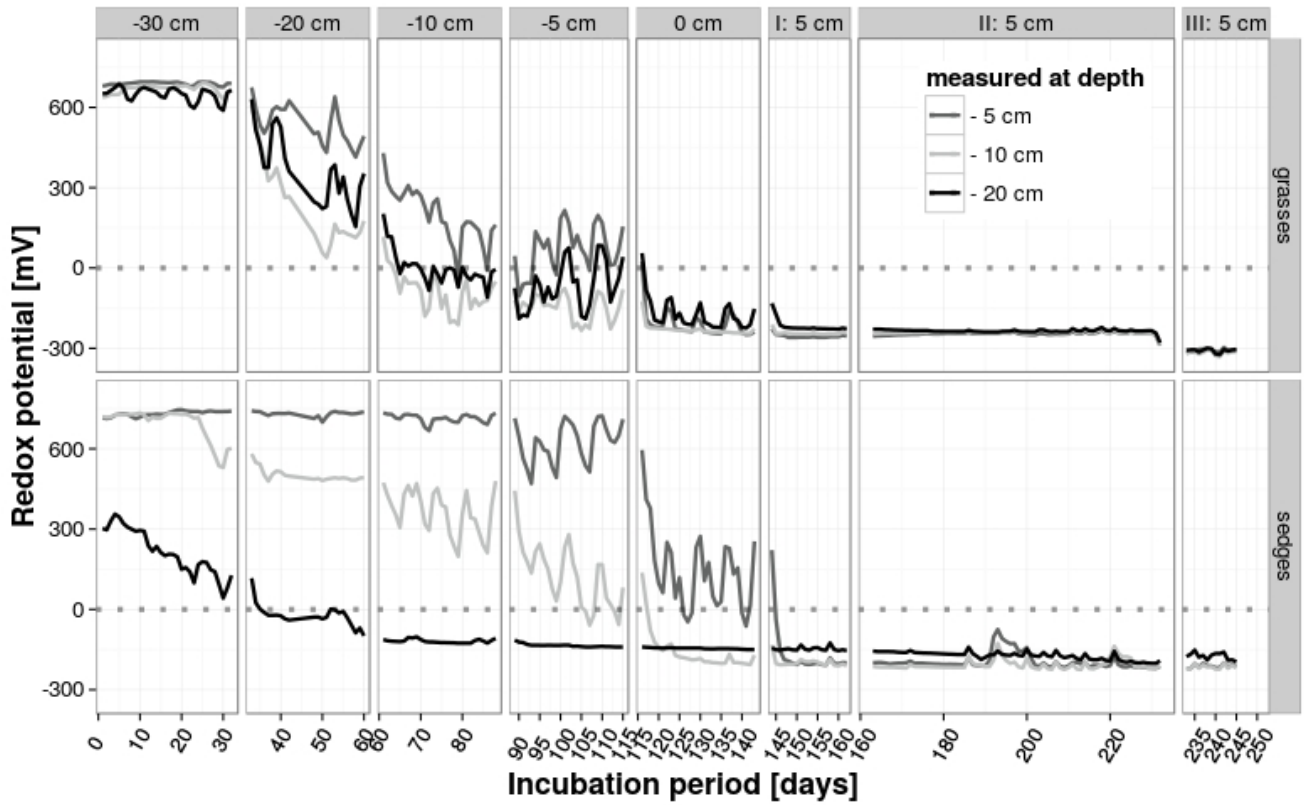Fig. 3-6: Estimated CH$_4$ flux based on the linear mixed-effects model in grasses (black) and sedges (grey) at the different water table positions (± 95% prediction interval). The water table position at +5cm has been split into 3 phases corresponding to differences in ecosystem response to flooding (for details see section 2.4). Predictions are given only for those vegetation development categories (as solid, dashed or dotted lines) which occurred during the incubation experiment.
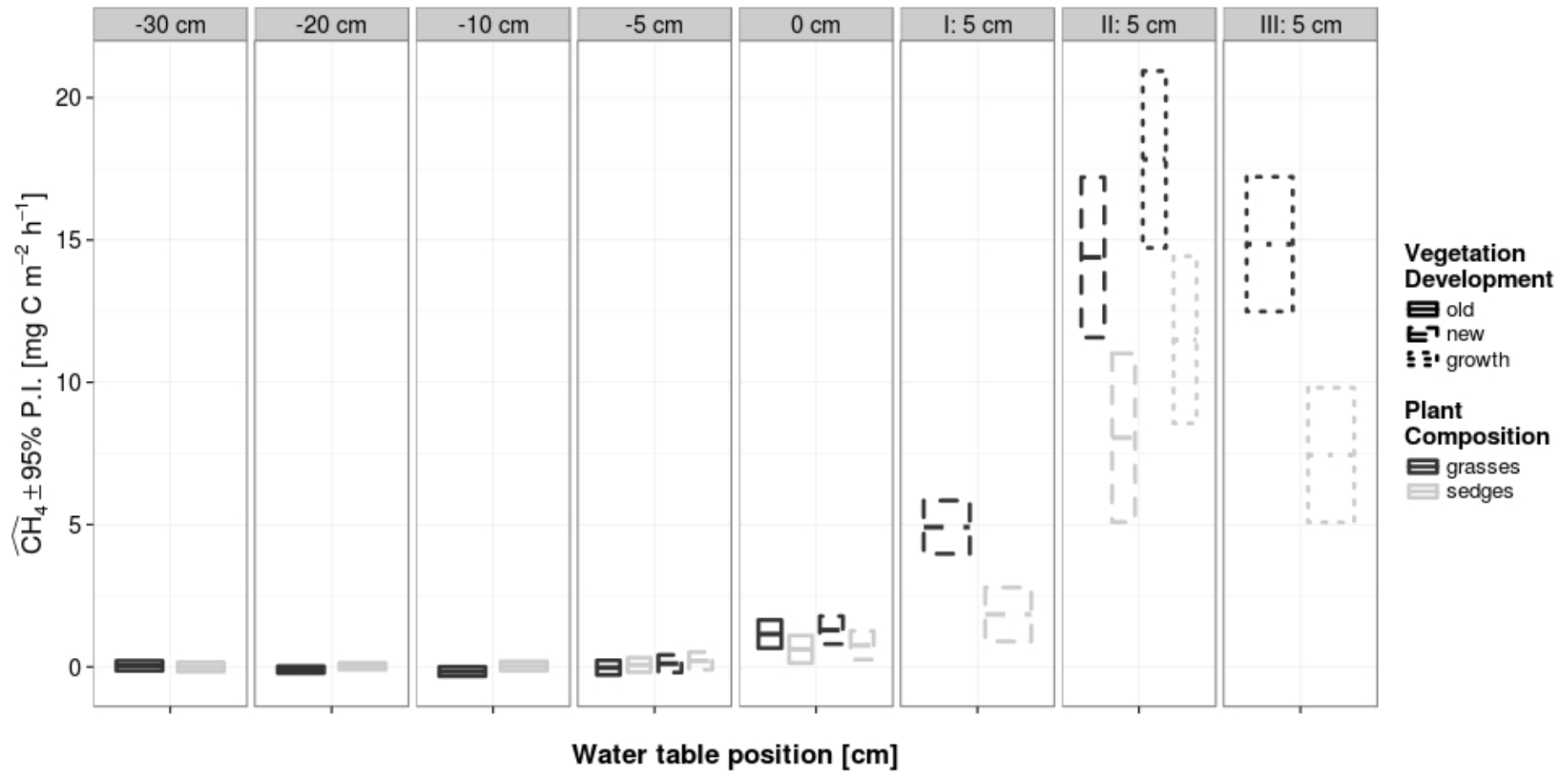
Fig. 3-7: CO_2 equivalents of the three greenhouse gases at different water table positions of grasses (black) and sedges (grey). Arrows indicate the general trend.
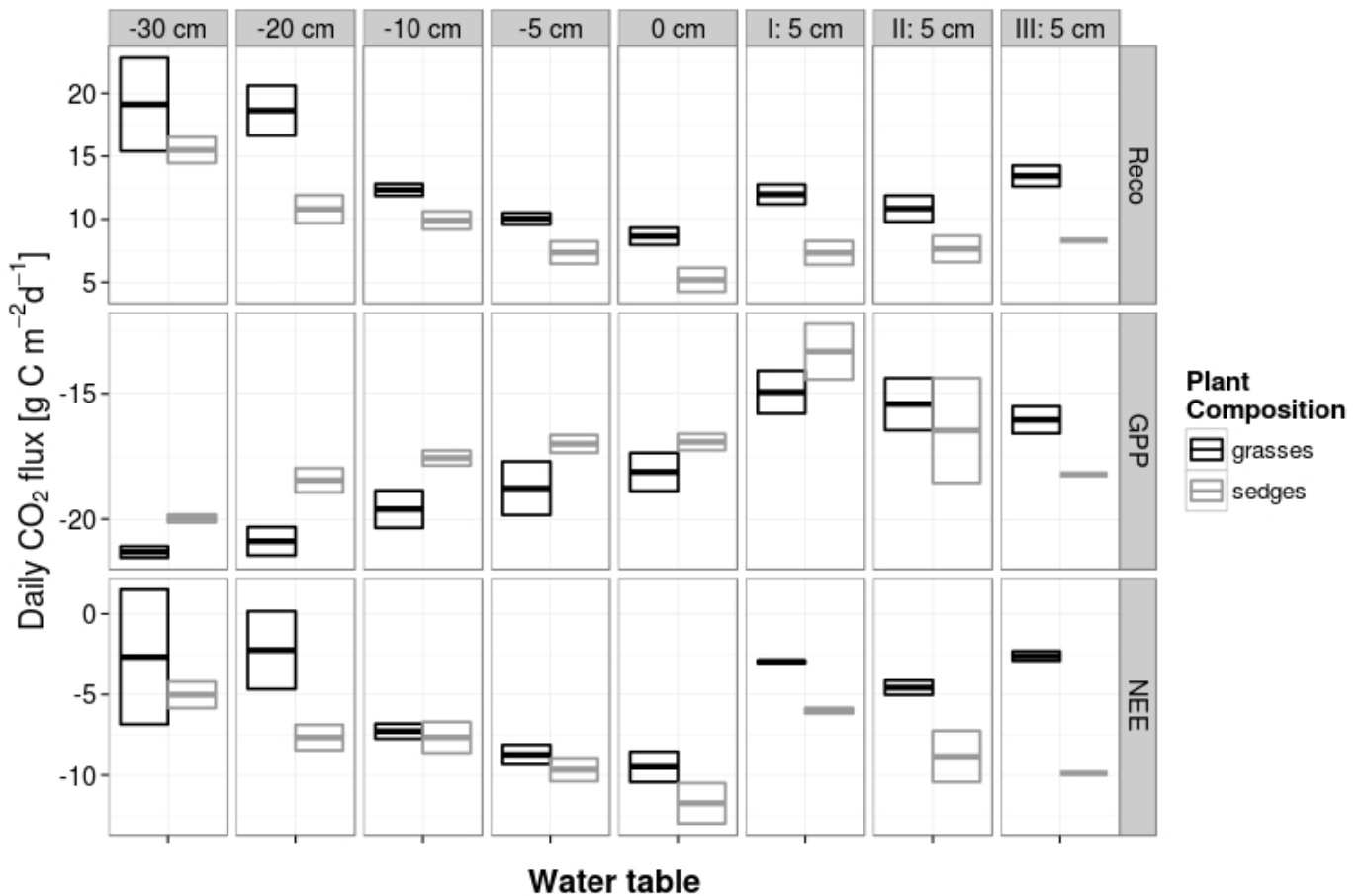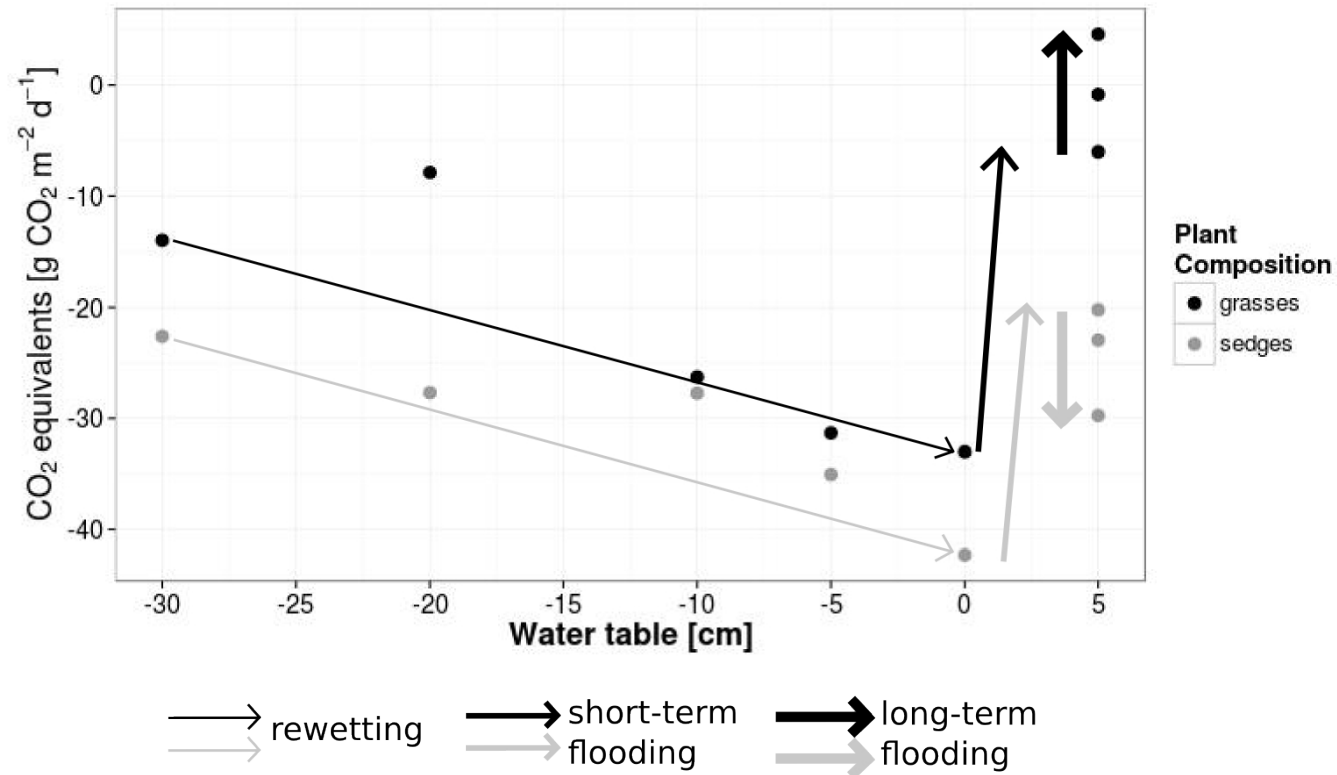
Appendix

App-Fig. 3-1: Estimated CO_2 flux based on the linear mixed-effects model in grasses (black) and sedges (grey) at the different water table positions (± 95% prediction interval; top: R_{eco}, centre: GPP, bottom: NEE). The effect of vegetation development was relatively small and consequently estimations for the three vegetation development categories were averaged.
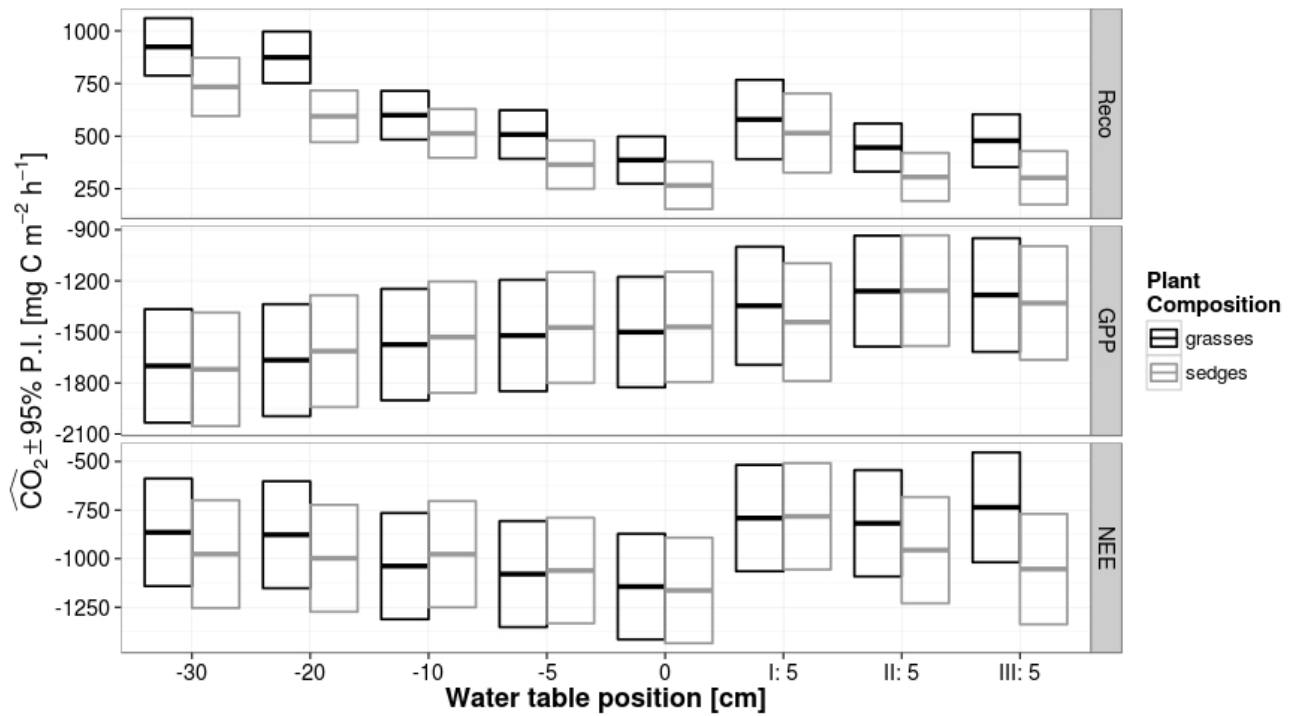
Linear mixed-effects model developed for GHG flux data

In the following tables the linear mixed-effects models developed for GHG flux data are described in more detail. The following abbreviations were used:

fSetTemp	temperature level as set in the climate chamber [13, 16, 18, 19, 23°C]
Col	mesocosm number [1 to 12]
IncDay	day of incubation [1 to 252]
tmpcol	crossed random effects between temperature level and mesocosm to account for global random differences due to temperature/PAR levels and differences between individual mesocosms
WT2	water table positions with the flooding period split into 3 phases as used for the CO_2 flux data [-30, -20, -10, -5, 0, I: +5, II: +5 and III: +5 cm]
WT3	water table positions as used for the CH_4 flux data [<0, 0, I: +5, II: +5 and III: +5 cm]
PC	plant composition [grasses or sedges]
VD	vegetation development [in the categories: old, new, growth]
WT×PC	interaction between water table position and plant composition
PC×VD	interaction between plant composition and vegetation development
const	a dummy variable used to express crossed-block designs in *nlme* (Pinheiro & Bates, 2000)

App-Tab. 3-1: Linear mixed-effects model of R_{eco} vs. water table position, plant composition and vegetation development

```
Linear mixed-effects model fit by REML
Data:
AIC      BIC     logLik
  28802.35 29003.03 -14366.18

Random effects:
 Composite Structure: Blocked

 Block 1: fSetTemp13°C, fSetTemp16°C, fSetTemp19°C, fSetTemp23°C, fSetTemp18°C
 Formula: ~fSetTemp - 1 | const
 Structure: Multiple of an Identity
         fSetTemp13°C fSetTemp16°C fSetTemp19°C fSetTemp23°C fSetTemp18°C
StdDev:     98.07363     98.07363     98.07363     98.07363     98.07363

 Block 2: Col1, Col2, Col3, Col4, Col5, Col6, Col7, Col8, Col9, Col10, Col11, Col12
 Formula: ~Col - 1 | const
 Structure: Multiple of an Identity
            Col1     Col2     Col3     Col4     Col5     Col6     Col7     Col8     Col9    Col10    Col11    Col12
StdDev: 84.09787 84.09787 84.09787 84.09787 84.09787 84.09787 84.09787 84.09787 84.09787 84.09787 84.09787 84.09787

 Formula: ~IncDay | tmpcol %in% const
 Structure: General positive-definite, Log-Cholesky parametrization
            StdDev       Corr
(Intercept) 2.962900e-02 (Intr)
IncDay      7.212417e-05 0
Residual    2.725497e+02

Correlation Structure: ARMA(2,2)
 Formula: ~IncDay | const/tmpcol
 Parameter estimate(s):
        Phi1         Phi2       Theta1       Theta2
 0.237112369  0.739119596 -0.007708513 -0.695887596
Variance function:
 Structure: Different standard deviations per stratum
 Formula: ~1 | WT2
 Parameter estimates:
    -30 cm     -20 cm    -10 cm      -5 cm       0 cm   I: 5 cm  II: 5 cm III: 5 cm
1.0000000 0.7249145 0.4576698 0.4154718 0.2931540 2.0946100 0.4506357 0.7401908
```

```
Fixed effects: Reco ~ WT2 + PC + VD + WT2:PC
                         Value Std.Error   DF    t-value p-value
(Intercept)           879.2087  68.76806 2226  12.785132  0.0000
WT2-20 cm             -49.8203  30.84637 2226  -1.615111  0.1064
WT2-10 cm            -324.3685  35.65210 2226  -9.098160  0.0000
WT2-5 cm             -415.9649  38.14346 2226 -10.905274  0.0000
WT20 cm              -537.5184  39.83208 2226 -13.494612  0.0000
WT2I: 5 cm           -344.7728  81.89057 2226  -4.210165  0.0000
WT2II: 5 cm          -478.2361  42.39649 2226 -11.280087  0.0000
WT2III: 5 cm         -445.4347  50.23666 2226  -8.866725  0.0000
PCsedges             -189.9956  75.97910   58  -2.500630  0.0152
VDnew                  35.1296  10.40136 2226   3.377408  0.0007
VDgrowth               98.4599  15.86092 2226   6.207705  0.0000
WT2-20 cm:PCsedges    -89.7658  46.21191 2226  -1.942483  0.0522
WT2-10 cm:PCsedges    103.4935  52.29199 2226   1.979146  0.0479
WT2-5 cm:PCsedges      46.7592  55.46997 2226   0.842964  0.3993
WT20 cm:PCsedges       69.9097  57.01844 2226   1.226089  0.2203
WT2I: 5 cm:PCsedges   125.8748 115.75435 2226   1.087430  0.2770
WT2II: 5 cm:PCsedges   50.4133  59.78878 2226   0.843190  0.3992
WT2III: 5 cm:PCsedges  13.6652  70.83499 2226   0.192916  0.8470
 Correlation:
                     (Intr) WT2-20cm WT2-10cm WT2-5cm WT20cm WT2I:5cm WT2II:5cm WT2III:5cm PCsdgs VDnew  VDgrwt WT2-20c: WT2-10c:
WT2-20 cm            -0.439
WT2-10 cm            -0.532  0.831
WT2-5 cm             -0.537  0.781    0.931
WT20 cm              -0.554  0.754    0.912    0.932
WT2I: 5 cm           -0.194  0.357    0.413    0.448   0.483
WT2II: 5 cm          -0.528  0.710    0.861    0.878   0.941  0.533
WT2III: 5 cm         -0.444  0.599    0.726    0.740   0.794  0.463    0.851
PCsedges             -0.537  0.397    0.482    0.486   0.504  0.178    0.481     0.407
VDnew                -0.013 -0.008   -0.032   -0.036  -0.172 -0.083   -0.216    -0.185     -0.002
VDgrowth             -0.014 -0.005   -0.020   -0.024  -0.115 -0.097   -0.188    -0.251     -0.008  0.671
WT2-20 cm:PCsedges    0.293 -0.667   -0.555   -0.521  -0.503 -0.239   -0.474    -0.400     -0.585  0.006  0.003
WT2-10 cm:PCsedges    0.363 -0.566   -0.681   -0.635  -0.622 -0.283   -0.587    -0.496     -0.703  0.025  0.018  0.843
WT2-5 cm:PCsedges     0.369 -0.537   -0.639   -0.686  -0.636 -0.307   -0.598    -0.504     -0.712  0.000 -0.001  0.797    0.938
WT20 cm:PCsedges      0.388 -0.526   -0.634   -0.648  -0.686 -0.333   -0.642    -0.542     -0.742  0.053  0.035  0.778    0.926
WT2I: 5 cm:PCsedges   0.139 -0.252   -0.292   -0.316  -0.333 -0.696   -0.361    -0.302     -0.270  0.003 -0.035  0.378    0.431
WT2II: 5 cm:PCsedges  0.376 -0.502   -0.606   -0.617  -0.641 -0.364   -0.673    -0.567     -0.718  0.002 -0.006  0.742    0.885
WT2III: 5 cm:PCsedges 0.317 -0.424   -0.511   -0.520  -0.541 -0.314   -0.571    -0.671     -0.605  0.003  0.032  0.626    0.747
                     WT2-5c: WT20c: WT2I:5c: WT2II:5c:
```

```
WT2-20 cm
WT2-10 cm
WT2-5 cm
WT20 cm
WT2I: 5 cm
WT2II: 5 cm
WT2III: 5 cm
PCsedges
VDnew
VDgrowth
WT2-20 cm:PCsedges
WT2-10 cm:PCsedges
WT2-5 cm:PCsedges
WT20 cm:PCsedges        0.949
WT2I: 5 cm:PCsedges     0.468   0.490
WT2II: 5 cm:PCsedges    0.905   0.943  0.539
WT2III: 5 cm:PCsedges   0.764   0.796  0.460    0.845


Standardized Within-Group Residuals:
        Min        Q1        Med         Q3         Max
-3.6759655 -0.5581056 -0.1555401  0.3558352  7.6213929


Number of Observations: 2302
Number of Groups:
            const tmpcol %in% const
                1                60
```

App-Tab. 3-2: Linear mixed-effects model of GPP vs. water table position, plant composition and vegetation development

```
Linear mixed-effects model fit by REML
Data:
AIC      BIC      logLik
  30774.49 30986.59 -15350.25

Random effects:
 Composite Structure: Blocked

 Block 1: fSetTemp13°C, fSetTemp16°C, fSetTemp19°C, fSetTemp23°C, fSetTemp18°C
 Formula: ~fSetTemp - 1 | const
 Structure: Multiple of an Identity
         fSetTemp13°C fSetTemp16°C fSetTemp19°C fSetTemp23°C fSetTemp18°C
StdDev:      318.6713     318.6713     318.6713     318.6713     318.6713

 Block 2: Col1, Col2, Col3, Col4, Col5, Col6, Col7, Col8, Col9, Col10, Col11, Col12
 Formula: ~Col - 1 | const
 Structure: Multiple of an Identity
            Col1     Col2     Col3     Col4     Col5     Col6     Col7     Col8     Col9    Col10
StdDev: 193.8827 193.8827 193.8827 193.8827 193.8827 193.8827 193.8827 193.8827 193.8827 193.8827
            Col11    Col12
StdDev: 193.8827 193.8827

 Formula: ~IncDay | tmpcol %in% const
 Structure: General positive-definite, Log-Cholesky parametrization
             StdDev        Corr
(Intercept) 3.108603e-03 (Intr)
IncDay      5.999073e-04 -0.003
Residual    2.697821e+02

Correlation Structure: ARMA(2,2)
 Formula: ~IncDay | const/tmpcol
 Parameter estimate(s):
       Phi1        Phi2      Theta1      Theta2
 0.22946731  0.71902027  0.04407699 -0.66868691
Variance function:
 Structure: Different standard deviations per stratum
 Formula: ~1 | WT2
 Parameter estimates:
    -30 cm     -20 cm     -10 cm      -5 cm       0 cm   I: 5 cm   II: 5 cm III: 5 cm
 1.0000000 0.8271283 0.7226829 0.6450219 0.5103796 1.9140388 0.8132554 1.0213585
```

```
Fixed effects: Gpp ~ WT2 + PC + VD + WT2:PC + PC:VD
                            Value Std.Error   DF    t-value p-value
(Intercept)            -1700.6340 167.33714 2223 -10.162920  0.0000
WT2-20 cm                 33.7321  34.75885 2223   0.970460  0.3319
WT2-10 cm                125.0547  39.49419 2223   3.166407  0.0016
WT2-5 cm                 178.3352  42.04479 2223   4.241552  0.0000
WT20 cm                  198.8501  44.80543 2223   4.438080  0.0000
WT2I: 5 cm               353.0893  77.74395 2223   4.541694  0.0000
WT2II: 5 cm              439.4027  51.69214 2223   8.500378  0.0000
WT2III: 5 cm             416.3922  67.59096 2223   6.160471  0.0000
PCsedges                  98.1803 124.84820   58   0.786397  0.4348
VDnew                     24.8917  26.84257 2223   0.927323  0.3539
VDgrowth                 -22.7884  45.63318 2223  -0.499382  0.6176
WT2-20 cm:PCsedges        73.2600  52.13255 2223   1.405264  0.1601
WT2-10 cm:PCsedges        64.2640  57.83319 2223   1.111197  0.2666
WT2-5 cm:PCsedges         67.6866  60.78289 2223   1.113580  0.2656
WT20 cm:PCsedges          50.4594  63.06677 2223   0.800094  0.4237
WT2I: 5 cm:PCsedges      -75.6494 111.19040 2223  -0.680359  0.4963
WT2II: 5 cm:PCsedges      23.0777  74.54436 2223   0.309583  0.7569
WT2III: 5 cm:PCsedges    -26.8536  95.91956 2223  -0.279960  0.7795
PCsedges:VDnew          -105.6191  37.78537 2223  -2.795239  0.0052
PCsedges:VDgrowth       -249.6037  61.12795 2223  -4.083298  0.0000
 Correlation:
                      (Intr) WT2-20cm WT2-10cm WT2-5cm WT20cm WT2I:5cm WT2II:5cm WT2III:5cm PCsdgs
WT2-20 cm             -0.161
WT2-10 cm             -0.181  0.758
WT2-5 cm              -0.186  0.679    0.823
WT20 cm               -0.183  0.627    0.746    0.801
WT2I: 5 cm            -0.102  0.368    0.448    0.496   0.644
WT2II: 5 cm           -0.160  0.541    0.643    0.676   0.844  0.651
WT2III: 5 cm          -0.123  0.413    0.490    0.513   0.640  0.464    0.742
PCsedges              -0.368  0.216    0.243    0.249   0.245  0.137    0.215     0.165
VDnew                 -0.006 -0.030   -0.091   -0.107  -0.425 -0.284   -0.487    -0.378      0.008
VDgrowth              -0.004 -0.019   -0.058   -0.071  -0.265 -0.238   -0.428    -0.591      0.005
WT2-20 cm:PCsedges     0.108 -0.667   -0.505   -0.453  -0.418 -0.245   -0.361    -0.276     -0.326
WT2-10 cm:PCsedges     0.124 -0.518   -0.683   -0.562  -0.510 -0.306   -0.439    -0.335     -0.364
WT2-5 cm:PCsedges      0.129 -0.470   -0.570   -0.692  -0.554 -0.343   -0.467    -0.355     -0.374
WT20 cm:PCsedges       0.130 -0.445   -0.530   -0.569  -0.710 -0.457   -0.600    -0.455     -0.375
WT2I: 5 cm:PCsedges    0.071 -0.257   -0.314   -0.347  -0.451 -0.698   -0.456    -0.325     -0.206
WT2II: 5 cm:PCsedges   0.111 -0.375   -0.446   -0.469  -0.585 -0.451   -0.694    -0.515     -0.320
WT2III: 5 cm:PCsedges  0.087 -0.291   -0.345   -0.362  -0.451 -0.327   -0.523    -0.705     -0.249
PCsedges:VDnew         0.004  0.021    0.065    0.076   0.302  0.201    0.346     0.269     -0.010
PCsedges:VDgrowth      0.003  0.014    0.043    0.053   0.198  0.178    0.320     0.441     -0.008
                      VDnew  VDgrwt WT2-20c: WT2-10c: WT2-5c: WT20c: WT2I:5c: WT2II:5c: WT2III:5c:
```

```
WT2-20 cm
WT2-10 cm
WT2-5 cm
WT20 cm
WT2I: 5 cm
WT2II: 5 cm
WT2III: 5 cm
PCsedges
VDnew
VDgrowth              0.588
WT2-20 cm:PCsedges    0.020  0.013
WT2-10 cm:PCsedges    0.062  0.039  0.778
WT2-5 cm:PCsedges     0.074  0.049  0.705    0.838
WT20 cm:PCsedges      0.301  0.188  0.666    0.774    0.844
WT2I: 5 cm:PCsedges   0.199  0.167  0.385    0.459    0.523   0.646
WT2II: 5 cm:PCsedges  0.338  0.297  0.561    0.649    0.705   0.835  0.663
WT2III: 5 cm:PCsedges 0.266  0.416  0.435    0.503    0.545   0.644  0.485    0.750
PCsedges:VDnew       -0.711 -0.418 -0.020   -0.060   -0.114  -0.341 -0.285   -0.480    -0.380
PCsedges:VDgrowth    -0.440 -0.747 -0.014   -0.042   -0.082  -0.232 -0.266   -0.441    -0.548
                             PCsdgs:VDn
WT2-20 cm
WT2-10 cm
WT2-5 cm
WT20 cm
WT2I: 5 cm
WT2II: 5 cm
WT2III: 5 cm
PCsedges
VDnew
VDgrowth
WT2-20 cm:PCsedges
WT2-10 cm:PCsedges
WT2-5 cm:PCsedges
WT20 cm:PCsedges
WT2I: 5 cm:PCsedges
WT2II: 5 cm:PCsedges
WT2III: 5 cm:PCsedges
PCsedges:VDnew
PCsedges:VDgrowth      0.626


Standardized Within-Group Residuals:
        Min          Q1         Med          Q3          Max
-4.47736930 -0.52792792  0.06070962  0.65242000  6.09674203


Number of Observations: 2301
Number of Groups:
            const tmpcol %in% const
                1               60
```

App-Tab. 3-3: Linear mixed-effects model of NEE vs. water table position, plant composition and vegetation development

```
Linear mixed-effects model fit by REML
Data:
       AIC      BIC     logLik
  31583.56 31774.31 -15758.78

Random effects:
 Composite Structure: Blocked

 Block 1: fSetTemp13°C, fSetTemp16°C, fSetTemp19°C, fSetTemp23°C, fSetTemp18°C
 Formula: ~fSetTemp - 1 | const
 Structure: Multiple of an Identity
        fSetTemp13°C fSetTemp16°C fSetTemp19°C fSetTemp23°C fSetTemp18°C
StdDev:      291.784      291.784      291.784      291.784      291.784

 Block 2: Col1, Col2, Col3, Col4, Col5, Col6, Col7, Col8, Col9, Col10, Col11, Col12
 Formula: ~Col - 1 | const
 Structure: Multiple of an Identity
           Col1     Col2     Col3     Col4     Col5     Col6     Col7     Col8     Col9    Col10    Col11    Col12
StdDev: 98.48247 98.48247 98.48247 98.48247 98.48247 98.48247 98.48247 98.48247 98.48247 98.48247 98.48247 98.48247

 Formula: ~IncDay | tmpcol %in% const
 Structure: General positive-definite, Log-Cholesky parametrization
            StdDev     Corr
(Intercept) 153.090041 (Intr)
IncDay        1.354528 -0.982
Residual    204.204147

Correlation Structure: ARMA(2,0)
 Formula: ~IncDay | const/tmpcol
 Parameter estimate(s):
      Phi1      Phi2
0.2649724 0.5237186
Variance function:
 Structure: Different standard deviations per stratum
 Formula: ~1 | WT2
 Parameter estimates:
    -30 cm     -20 cm     -10 cm      -5 cm       0 cm   I: 5 cm  II: 5 cm III: 5 cm
 1.0000000 1.0263520 0.9015053 0.7607270 0.7097454 0.9124931 0.9227550 1.1028512
```

```
Fixed effects: Nee ~ WT2 + PC + VD + WT2:PC
                          Value Std.Error   DF    t-value p-value
(Intercept)           -846.9533 139.98114 2335 -6.050481  0.0000
WT2-20 cm              -12.4858  29.42494 2335 -0.424327  0.6714
WT2-10 cm             -173.8104  31.63231 2335 -5.494712  0.0000
WT2-5 cm              -214.7512  34.30480 2335 -6.260093  0.0000
WT20 cm               -279.1706  39.27464 2335 -7.108165  0.0000
WT2I: 5 cm              73.4113  46.69054 2335  1.572295  0.1160
WT2II: 5 cm             46.7366  50.40090 2335  0.927296  0.3539
WT2III: 5 cm           128.7508  66.78759 2335  1.927766  0.0540
PCsedges              -111.8900  72.39522   58 -1.545544  0.1277
VDnew                   22.4122  18.85621 2335  1.188587  0.2347
VDgrowth               -75.3426  28.93350 2335 -2.603992  0.0093
WT2-20 cm:PCsedges      -9.2505  43.13842 2335 -0.214438  0.8302
WT2-10 cm:PCsedges     173.1122  45.74360 2335  3.784402  0.0002
WT2-5 cm:PCsedges      130.0009  48.91614 2335  2.657628  0.0079
WT20 cm:PCsedges        92.2080  53.21037 2335  1.732896  0.0832
WT2I: 5 cm:PCsedges    120.5596  62.50064 2335  1.928934  0.0539
WT2II: 5 cm:PCsedges   -26.5836  67.58520 2335 -0.393334  0.6941
WT2III: 5 cm:PCsedges -206.0051  90.42299 2335 -2.278239  0.0228
 Correlation:
                    (Intr) WT2-20cm WT2-10cm WT2-5cm WT20cm WT2I:5cm WT2II:5cm WT2III:5cm PCsdgs VDnew  VDgrwt WT2-20c: WT2-10c: WT2-5c:
WT2-20 cm           -0.133
WT2-10 cm           -0.165  0.616
WT2-5 cm            -0.177  0.541    0.709
WT20 cm             -0.181  0.507    0.655    0.731
WT2I: 5 cm          -0.170  0.454    0.600    0.670   0.833
WT2II: 5 cm         -0.179  0.452    0.612    0.694   0.845  0.851
WT2III: 5 cm        -0.157  0.372    0.517    0.598   0.730  0.729    0.816
PCsedges            -0.253  0.257    0.318    0.342   0.354  0.333    0.355     0.320
VDnew               -0.008 -0.025   -0.067   -0.072  -0.326 -0.350   -0.335    -0.254     -0.002
VDgrowth            -0.013 -0.007   -0.027   -0.024  -0.192 -0.220   -0.265    -0.348     -0.024  0.678
WT2-20 cm:PCsedges   0.090 -0.682   -0.420   -0.369  -0.347 -0.311   -0.312    -0.262     -0.389  0.024  0.029
WT2-10 cm:PCsedges   0.113 -0.425   -0.691   -0.489  -0.452 -0.414   -0.426    -0.368     -0.473  0.047  0.053  0.641
WT2-5 cm:PCsedges    0.124 -0.377   -0.491   -0.695  -0.489 -0.445   -0.468    -0.418     -0.518 -0.016  0.020  0.571    0.723
WT20 cm:PCsedges     0.134 -0.370   -0.473   -0.527  -0.690 -0.565   -0.581    -0.522     -0.548  0.101  0.102  0.555    0.691    0.783
WT2I: 5 cm:PCsedges  0.128 -0.331   -0.429   -0.480  -0.535 -0.654   -0.551    -0.492     -0.521 -0.002  0.030  0.498    0.631    0.720
WT2II: 5 cm:PCsedges 0.136 -0.331   -0.440   -0.501  -0.551 -0.549   -0.663    -0.543     -0.549  0.005  0.021  0.496    0.644    0.748
WT2III: 5 cm:PCsedges 0.119 -0.272   -0.373   -0.433  -0.486 -0.478   -0.535    -0.661     -0.479  0.007  0.038  0.407    0.544    0.647
                     WT20c: WT2I:5c: WT2II:5c:
```

```
WT2-20 cm
WT2-10 cm
WT2-5 cm
WT20 cm
WT2I: 5 cm
WT2II: 5 cm
WT2III: 5 cm
PCsedges
VDnew
VDgrowth
WT2-20 cm:PCsedges
WT2-10 cm:PCsedges
WT2-5 cm:PCsedges
WT20 cm:PCsedges
WT2I: 5 cm:PCsedges    0.813
WT2II: 5 cm:PCsedges   0.834  0.839
WT2III: 5 cm:PCsedges  0.732  0.729    0.808

Standardized Within-Group Residuals:
          Min          Q1          Med          Q3          Max
-3.830207970 -0.611773096  0.000192129  0.558488180  5.007098497

Number of Observations: 2411
Number of Groups:
          const tmpcol %in% const
              1               60
```

App-Tab. 3-4: Linear mixed-effects model of CH_4 vs. water table position, plant composition and vegetation development

```
Linear mixed-effects model fit by REML
Data:
       AIC      BIC    logLik
  3303.917 3461.916 -1618.958

Random effects:
 Formula: ~IncDay | Col
 Structure: General positive-definite, Log-Cholesky parametrization
            StdDev       Corr
(Intercept) 0.292191835 (Intr)
IncDay      0.007020128 -1

 Formula: ~IncDay | fSetTemp %in% Col
 Structure: General positive-definite, Log-Cholesky parametrization
            StdDev       Corr
(Intercept) 0.227610400 (Intr)
IncDay      0.004785474 -0.999
Residual    0.363842637

Correlation Structure: ARMA(2,2)
 Formula: ~1 | Col/fSetTemp
 Parameter estimate(s):
       Phi1       Phi2     Theta1     Theta2
  1.8431830 -0.9186435 -1.6667139  0.7596506
Variance function:
 Structure: Different standard deviations per stratum
 Formula: ~1 | WT3
 Parameter estimates:
        <0         0        5.1        5.2        5.3
  1.000000  3.068926  6.820151 27.242741 17.012223
```

```
Fixed effects: CH4 ~ PC + VD + WT2 + PC:WT2
                           Value Std.Error  DF    t-value p-value
(Intercept)             0.039971 0.0896764 859   0.445726  0.6559
PCsedges               -0.043391 0.1237732  10  -0.350566  0.7332
VDnew                   0.139914 0.0963477 859   1.452180  0.1468
VDgrowth                3.580568 1.3644280 859   2.624226  0.0088
WT2-20 cm              -0.136627 0.1029527 859  -1.327081  0.1848
WT2-10 cm              -0.202344 0.1441368 859  -1.403830  0.1607
WT2-5 cm               -0.067713 0.1908816 859  -0.354736  0.7229
WT20 cm                 1.113327 0.2981111 859   3.734604  0.0002
WT2I: 5 cm              4.731494 0.5113256 859   9.253388  0.0000
WT2II: 5 cm            14.211985 1.4432698 859   9.847075  0.0000
WT2III: 5 cm           11.234992 1.6484884 859   6.815330  0.0000
PCsedges:WT2-20 cm      0.162184 0.1428932 859   1.135000  0.2567
PCsedges:WT2-10 cm      0.236707 0.2027851 859   1.167278  0.2434
PCsedges:WT2-5 cm       0.140806 0.2693466 859   0.522770  0.6013
PCsedges:WT20 cm       -0.491458 0.4167731 859  -1.179198  0.2386
PCsedges:WT2I: 5 cm    -3.023769 0.7117999 859  -4.248060  0.0000
PCsedges:WT2II: 5 cm   -6.295474 1.9132067 859  -3.290535  0.0010
PCsedges:WT2III: 5 cm  -7.364509 1.6908929 859  -4.355396  0.0000
 Correlation:
                       (Intr) PCsdgs VDnew  VDgrwt WT2-2c WT2-1c WT2-5c WT20cm WT2I:5c WT2II:5c WT2III5c PC:WT2-2c PC:WT2-1c PC:WT2-5c PC:WT20c
PCsedges               -0.723
VDnew                  -0.029 -0.022
VDgrowth               -0.016 -0.001  0.058
WT2-20 cm              -0.799  0.580 -0.034  0.041
WT2-10 cm              -0.841  0.612 -0.056  0.041  0.813
WT2-5 cm               -0.802  0.582 -0.035  0.020  0.724  0.892
WT20 cm                -0.622  0.459 -0.173 -0.043  0.508  0.687  0.803
WT2I: 5 cm             -0.375  0.280 -0.165 -0.108  0.307  0.404  0.516  0.595
WT2II: 5 cm            -0.083  0.066 -0.049 -0.359  0.146  0.119  0.135  0.101  0.288
WT2III: 5 cm           -0.150  0.117 -0.038 -0.685  0.173  0.205  0.224  0.179  0.152   0.420
PCsedges:WT2-20 cm      0.574 -0.793  0.065  0.022 -0.720 -0.586 -0.522 -0.375 -0.232  -0.125  -0.159
PCsedges:WT2-10 cm      0.595 -0.845  0.105  0.023 -0.578 -0.712 -0.635 -0.501 -0.303  -0.105  -0.181    0.812
PCsedges:WT2-5 cm       0.568 -0.816  0.028  0.005 -0.512 -0.632 -0.708 -0.570 -0.368  -0.103  -0.172    0.729     0.891
PCsedges:WT20 cm        0.447 -0.655  0.074 -0.022 -0.364 -0.491 -0.573 -0.705 -0.413  -0.052  -0.092    0.524     0.696     0.810
PCsedges:WT2I: 5 cm     0.273 -0.405  0.059 -0.053 -0.224 -0.293 -0.372 -0.413 -0.696  -0.158  -0.020    0.323     0.415     0.525     0.585
PCsedges:WT2II: 5 cm    0.069 -0.102  0.027 -0.091 -0.125 -0.105 -0.109 -0.063 -0.180  -0.625  -0.069    0.174     0.141     0.150     0.092
PCsedges:WT2III: 5 cm   0.155 -0.230  0.020  0.032 -0.195 -0.227 -0.231 -0.150 -0.083  -0.182  -0.539    0.284     0.323     0.326     0.208
                       PC:WT2I:5c PC:WT2II:5c
```

```
PCsedges
VDnew
VDgrowth
WT2-20 cm
WT2-10 cm
WT2-5 cm
WT20 cm
WT2I: 5 cm
WT2II: 5 cm
WT2III: 5 cm
PCsedges:WT2-20 cm
PCsedges:WT2-10 cm
PCsedges:WT2-5 cm
PCsedges:WT20 cm
PCsedges:WT2I: 5 cm
PCsedges:WT2II: 5 cm   0.271
PCsedges:WT2III: 5 cm  0.109        0.254

Standardized Within-Group Residuals:
        Min          Q1          Med          Q3          Max
-4.50038831 -0.41983925 -0.04052017  0.27097536 13.82819651

Number of Observations: 905
Number of Groups:
            Col fSetTemp %in% Col
            12              30
```

Chapter 4: Publication III

High heterotrophic respiration but low methane and nitrous oxide emissions from peat grassland mesocosms under alternating wet-dry conditions

authors:

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status:

draft manuscript, submission planned

own contributions:

- design and implementation of experimental set-up

- design and construction of all devices

- calculation of CO_2 flux rates from raw data

- modelling of daily CO_2 flux rates

- statistical analysis of all data

- graphical presentation

- data interpretation and discussion of results

- planning and writing of the publication

contributions by co-authors:

- peat sampling and installation in climate chamber (A. Thuille)

- supervision of the experiment during maternity leave of M. Hahn-Schöfl (A. Thuille)

- calculation of CH_4 and N_2O flux rates from raw data (A. Thuille)

- development of procedure for CO_2 flux calculation from raw data (G. Schöfl)

- supervision of PhD thesis (A. Freibauer)

Abstract

The rewetting of drained peatlands should aim at a minimum CO_2 and CH_4 release. In order to test if alternating water tables are suitable low-GHG management strategies we performed a mesocosm experiment with bog and fen grasslands quantifying the short-term response of CO_2, CH_4 and N_2O to alternating water tables, observing the response time and the memory effect of previous stress.

The vegetation of the mesocosms was not adapted to permanently flooded conditions but coped remarkably well with the strong water stress. While gross primary production (GPP) was unaffected by water table changes, ecosystem respiration (R_{eco}) reacted very fast with a duplication to triplication under dry conditions due to decomposition of the accumulated plant litter and probably stimulated peat mineralization. Net ecosystem exchange (NEE) was dominated by water-table driven variation in heterotrophic soil respiration. Intermittent dry conditions for a one week fully recovered the oxidative status in the peat soils and, consequently, CH_4 flux rates were low despite the large amount of dead biomass and warm conditions. N_2O emissions remained low and were unaffected by water table changes. Peat grasslands were a GHG sink under wet conditions (+5 cm), however, dry conditions (-45 cm)urned the grasslands into a GHG source due to increased heterotrophic respiration t. There was no legacy effect regarding redox potential and CH_4 fluxes. CO_2 emissions showed a small legacy effect of previous wet-dry cycles by mobilization of easily oxidizable carbon.

1. Introduction

50 % of European peatlands have been drained for agriculture (Augustin 2001; Joosten and Couwenberg 2001; Drösler et al. 2008), mainly as grassland for forage production. Drained agricultural peatlands are hotspots of CO_2 and N_2O emissions (Augustin 2001; Drösler et al. 2008; Joosten 2010). In Europe, drained peatlands are increasingly restored by rewetting, i.e. by raising the groundwater table, with the explicit goal to reduce anthropogenic greenhouse gas (GHG) emissions (Höper et al. 2008). It remains controversial, however, how much of the CO_2 emission reduction by slowed down peat mineralization is compensated by increased methane release in wet conditions (Höper 2007; Couwenberg et al. 2008). Flooding can boost CH_4 emissions, in particular when plants die that are not adapted to excess water stress (Joosten and Couwenberg 2009; Hahn-Schöfl et al. 2011). Thus, rewetting activities should aim at a minimum CO_2 and CH_4 release.

Peat oxidation requires aerobic conditions and tends to increase with drainage depth (Joosten and Couwenberg 2009). Ecosystem respiration was linearly correlated with water table level in histic Gleysols (Leiber-Sauheitl et al. 2014). Highest N_2O emissions have been found at intermediate soil moisture content (Kasimir-Klemedtsson et al. 1997) at intermediate drainage levels around -50 cm below surface (Drösler et al. 2011); N_2O emissions only occur at mean water table below -20 cm below surface (Couwenberg et al. 2008) when both nitrification and denitrification processes can occur. In contrast, methanogenesis occurs at strictly anaerobic conditions (Kasimir-Klemedtsson et al. 1997; Dalal and Allen 2008; Drösler et al. 2008). In practice, water table fluctuates seasonally and is driven by rain events and water management. High field CH_4 emissions were observed in warm conditions with highly active vegetation. The reasons confirmed by laboratory studies include high biological activity under a period of extended flooding for several weeks or more, and active formation of an organic sediment layer from dead, easily degradable plant material (Hahn-Schöfl et al. 2011; Hahn-Schöfl et al. 2014).

A challenge comparable to the rewetting of drained peatlands has been tackled in paddy rice fields where intermittent rather than continuous flooding has significantly reduced CH_4 emissions (UN-FAO 2010; Uprety et al. 2012; Siopongco et al. 2013). Intermittent drainage restores the redox equivalents in soils (Estop-Aragonés and Blodau 2012) so that it takes weeks of flooding before the soil returns to conditions suitable for methanogenesis. On the other hand, strong water table fluctuations may mobilize organic matter in soil by drying and rewetting (Kasimir-Klemedtsson et al. 1997), making the peat more vulnerable to decomposition. In an intermittent wet-dry regime the soil remains for long periods in a redox state optimal for denitrification and consequently, at high risk of N_2O emissions, e.g. as found in mineral soils (Flessa et al. 1998).

Guidance for low GHG rewetting strategies requires improved knowledge about the dynamic response of vegetation with low flooding tolerance and of the GHG forming and consuming processes in soil in reaction to changing water table and redox status (Fig. 1).

To test whether mitigation strategies for rice paddies can also be applied in peatlands, this study aimed at systematically quantifying the GHG response of peat grasslands to periodic, intermittent wet-dry cycles. We performed a mesocosm experiment under constant meteorological conditions and compared two lowland grassland communities on fen and bog peat under short and long water table alternation cycles. In particular, we addressed the following questions:

1. How do grassland vegetation, photosynthesis, respiration, CH_4 and N_2O fluxes react to a dynamic change in the water table from wet to dry conditions and vice versa? How do wet respectively dry conditions affect the net GHG balance?

2. Is the response fully reversible when water table switches back to the original position, and repeatable? Is there a memory effect of previous flooding or drainage events?

3. What length of interim dry periods is needed to effectively reduce CH_4 emissions?

4. Do wet-dry cycles foster N_2O emissions?

5. Can alternating water tables work as low-GHG management strategies in peat grasslands?

2. Material and Methods

2.1. Site description

For the experiment we selected two drained and intensively managed grassland sites on peat soils.

Bog grassland

The peat bog complex Ahlen–Falkenberger Moor is located approximately 80 km northwest of the city of Hamburg (Northern Germany, 53°41' N and 8°49' E). The climate is humid atlantic-temperate with an average annual precipitation of 925.7 mm and an average annual temperature of 8.5 °C (source: German Weather Service). The bog is 3.3 m deep. The uppermost 15 cm comprise a strongly humified degraded bog peat, the subjacent layer consists of 1.25 m poorly humified "white" bog peat and thereunder lies a strongly humified "black" bog peat. The sampling site is an intensively managed grassland for dairy farming, fertilized and cut 4-5 times per year (for site characteristics see Table 1). The mean water table is located ~60 cm below the surface. The samples were taken on the same intensive grassland field as in (Beetz et al. 2013; Frank et al. 2014).

Fen grassland

The fen grassland samples were taken in the "Freisinger Moos". The site is located in the vicinity of the town Freising (Southern Germany, 48°37'N and 11°69'E) and has a temperate climate with an average annual precipitation of 788 mm and an average annual air temperature of 7.5°C (source: Agrarmeteorologie Bayern). The fen grassland is intensively managed for dairy forage, fertilized and cut 2-3 times per year (more details see Table 1). The mean water table is approximately 60 cm below the surface. Samples from this site have been used in previous incubation experiments ("grasses" treatment in (Hahn-Schöfl et al. 2014).

2.2. Experimental set up

Six intact soil mesocosms with vegetation were taken from the two above described sites at the end of March 2009. Each mesocosm was extracted by completely inserting a PVC tube (inner diameter = 16 cm, height = 50 cm) into the soil with a hydraulic drill and removing it by spade.

The incubation lasted for 196 days in a climate chamber (York Deutschland GmbH, Mannheim, Germany) at temperature and radiation conditions of a sunny spring day which aimed to give an idea of the potential CO_2 production respectively fixation and CH_4 formation. Conditions were the same as in (Hahn-Schöfl et al. 2014). In brief, diurnal cycles ranged from 13°C to 23°C for air temperature with a mean of 16°C and 0 to 1200 µmol m^{-2} s^{-1} for photosynthetic active radiation (PAR). Daily sum of PAR was about 32.1*10^6 µmol m^{-2} d^{-1} with some spatio-temporal variation.

During flooded periods, a basin (transparent acrylic glass; 35 x 35 x 7 cm) attached and sealed to the top of each PVC tube contained the supernatant water (referred to as inundation tank). During flux measurements, the measurement chamber was attached to the inundation tank (Fig. 4-2).

The water table in the mesocosms was maintained at +5 cm by means of sensor-controlled pumps connected to water canisters which ensured a continuous supply of tap water. The water level was manually lowered to -45 cm by means of vacuum pumps (Mobile Oil and Fluid Extractor TP69, Sealy Power Products, UK). Three replicates from each of the grassland sites were subjected to two different dynamic water regimes:

- short cycles: the water level was maintained at +5 cm for 7 days (referred to as wet phase thereafter) followed by a 14 days dry phase (water level at -45 cm). These wet-dry phases were repeated 9 times.

- long cycles: the water level was kept at +5 cm for 42 days (wet phase) followed by 7 days at -45 cm (dry phase). These wet-dry phases were repeated 4 times. When comparing the two water regimes the long cycles regime is referred to as extended flooding.

2.3. Measurements and data analysis

Terminology and definitions

Net CO_2 exchange is the sum of CO_2 uptake by photosynthesis and the simultaneous release of CO_2 by auto- and heterotrophic respiration: Net ecosystem exchange (NEE) = gross primary production (GPP) + ecosystem respiration (R_{eco}). Negative CO_2 fluxes signify the removal of CO_2 from the atmosphere and its incorporation into the plant/soil – i.e. a positive climatic effect. Positive NEE values indicate a release of CO_2 from the ecosystem into the atmosphere – i.e. a negative effect with

respect to its climate impact.

Environmental conditions and soil parameters

The experimental set up and measurements methods were identical to (Hahn-Schöfl et al. 2014) and were repeated here using samples from other peatland sites. They are described briefly in this publication, for further details consult (Hahn-Schöfl et al. 2014). The mesocosms were insulated and cooled to ensure soil temperature profiles similar to those of the Freising field site (experimental set-up illustrated in Fig. 4-2). To avoid drying-out of the topsoil, the mesocosms received 90 to 300 ml tap water depending on the water table position.

Air temperature and photosynthetically active radiation (PAR) within the climate chamber as well as soil temperatures and redox potentials in the mesocosms were logged over the entire incubation duration. The measured redox potentials were converted to the potential in relation to the standard hydrogen electrode (Calmano 2010), however, not corrected for pH.

The redox potential gives a qualitative value representing the soil state (Pansu and Gautheyrou 2006) and indicates suitable conditions for methane production (Fiedler 1999). Hence, redox data may be used for the interpretation of CH_4 emissions. We assume that at a redox potential of -150 mV the conditions are favourable for CH_4 production[20].

The vegetation developed during the 7 weeks pre-incubation (air temperature 17 to 21 °C) and was cut to a uniform length of 10 cm at incubation start. This cut strongly influenced the vegetation development during the first 2 to 3 weeks and had its effect during further 6 to 8 weeks. The vegetation was regularly checked for pest infestation and treated with biological pest control when necessary. Vegetation development was documented by means of photos (Sony DSC-F828, f= 50mm, Sony Europe Ltd., Berlin, Germany). Bulk density and pore volume of the peat soil as well as dry weight and leaf area index of above ground biomass were determined at incubation end.

CO_2 exchange

Gas flux measurements were performed using a dynamic closed chamber system and a CO_2 infrared gas analyser (model LI-6262, LI-COR Biosciences, Lincoln, USA) for in-situ measurement. The measurement method, chamber design and procedure for semi-automated quality-controlled CO_2 flux calculations are described in detail in (Hahn-Schöfl et al. 2014). This measurement method has also been used for field measurements on various German field sites (Drösler 2005; Drösler et al. 2011; Beetz et al. 2013; Leiber-Sauheitl et al. 2014).

The experiment lasted for 196 days and CO_2 flux measurements were performed at the 13, 16, 18, 19, 23°C temperature levels with a total of 180 (short cycles) and 135 (long cycles) measurements per grassland site.

Daily R_{eco}, GPP, NEE were modelled based on the equation according to (Lloyd and Taylor 1994) and (Michaelis and Menten 1913) as well as the actual air and soil temperatures and PAR logged in the climate chamber.

CH_4 and N_2O emissions

The static closed chamber method combined with analysis by gas chromatography was used for measurement of CH_4 and N_2O emissions from the mesocosm surface (methodology described in detail in (Drösler 2005; Drösler et al. 2011; Hahn-Schöfl et al. 2014). Gas sampling was done at the

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20 In a previous experiment (Hahn-Schöfl et al. 2014), the phase between 0 and -150 mV was quickly passed and, therefore, the threshold for methanogenesis was assumed at 0 mV.

19°C temperature level at short cycles (total of 77 measurements per grassland site) and at the 13 and 23°C temperature levels at long cycles (total of 73 measurements) due to logistical reasons. A previous experiment (Hahn-Schöfl et al. 2014) showed only a small inconsistent temperature response of CH_4 and N_2O fluxes.

CO_2 equivalents

The calculation of CO_2 equivalents was done using the 100-year global warming potentials (GWP) relative to CO_2 (IPCC 2007) (CO_2 = daily NEE modelled with soil temperature in -2 cm depth, 1 g CH_4 = 25 g CO_2-equ., and 1 g N_2O = 298 g CO_2-equ.). Adding up the CO_2 equivalents of the three GHGs results in the GHG balance. The first wet-dry phase was excluded from graphical display as it cannot be compared to later wet-dry phases due to vegetation growth (Fig. 4-12; see also vegetation results).

2.4. Statistical analysis

CO_2 flux calculations, modelling of daily R_{eco}/GPP/NEE, general data manipulation and all graphics were done using the R statistical environment (R Core Team 2013).

Differences between bog and fen were tested with Wilcoxon rank-sum test for all parameters with more than 6 values. Cumulative and static parameters were observed in three replicates, which were considered a too small number to robustly apply statistics.

3. Results

3.1. Vegetation

Vegetation in bog and fen mesocosms was mainly composed of grass species typical for intensively used lowland meadows but not adapted to high water table (Tab. 4-1).

After a pre-incubation for 7 weeks the vegetation was cut to a length of 10 cm shortly before incubation start as vegetation in the 12 mesocosms had developed differently. This cut affected vegetation growth at incubation start. The vegetation was still in an intensive growth phase in the first 2 to 3 weeks of the experiment and was still growing during the subsequent 6 to 8 weeks.

Short cycles

Total dry weight (dw), living and dead biomass at incubation end tended to be higher in bog (1.0 ± 0.2 kg dw m^{-2}) than in fen grassland (0.6 ± 0.3 kg dw m^{-2}) (see Fig. 4-3; for detailed data see App-Tab. 4-1 in the Appendix). Both grasslands were dominated by brown biomass (bog: 61 %; fen: 62 %) while green biomass accounted for one third of biomass (bog: 31 %; fen: 37 %). The amount of other dead matter – mainly dead roots – was higher in bog mesocosms (on average 8 % of total bog biomass) than in fen (1 % of total fen biomass). Algae were observed in one bog mesocosm only (0.03 % of total bog biomass).

Leaf area index (LAI) measured at incubation end confirmed the biomass results. LAI in bog mesocosms was 7.2 ± 0.3 m^2 m^{-2} and was dominated by died-off leaves (68 % brown and 32% green leaves). In the fen mesocosms, LAI was 4.7 ± 2.6 m^2 m^{-2} with the same green/brown distribution as in bog (68 % brown and 32% green leaves).

Long cycles

The total dry weight (dw) at incubation end was four times higher in bog (1.3 ± 0.4 kg dw m^{-2}) than in fen grassland (0.3 ± 0.1 kg dw m^{-2}) (Fig. 4-3). Green biomass was similar in bog and fen grassland. Consequently, the fraction of green biomass in bog mesocosms (20 % of total bog biomass) was half of the one in fen mesocosms (44 % of total fen biomass). 10 times more brown biomass was present in bog mesocosms (61 % of total bog biomass) than in fen mesocosms where the brown leaves fraction (41 % of total fen biomass) was approximately the same as the green leaves fraction. The amount of other dead matter – mainly dead roots – was 16 % in bog and 15 % in fen mesocosms. Algae growing in the inundation tank were present only in the bog mesocosms and accounted for 3 % of total bog biomass.

Leaf area index (LAI) at incubation end was four times higher in the bog grassland (7.8 ± 1.4 m^2 m^{-2}) and dominated by died-off leaves (78 % brown and 22 % green leaves). In fen grassland, mean LAI was 2.5 ± 1.0 m^2 m^{-2} with 46 % brown and 54 % green leaves. The LAI results confirmed the biomass results.

3.2. Redox potentials

Redox potential measurements are, amongst others, influenced by pH. As the E_h/pH slope varies within different chemical systems and the pH dependent error highly varies between authors, the correction of redox data for pH is controversial (Fiedler et al. 2007)(personnal communication with Sabine Fiedler). Therefore, we did not correct the measured redox potentials for pH. Based on the Nernst equation, lower E_h is predicted at higher pH values (Schüring et al. 1999; Fiedler et al. 2007). The bog grassland had a significantly lower pH (see Tab. 4-1) and redox potentials were in general more positive compared to the fen grassland (see Fig. 4-4 and 4-5). Due to their differences in pH the redox potentials in bog and fen grassland cannot directly be compared.

The redox potential quickly reacted to dry and wet phases with most changes happening in the first week after water regime shift. The temporal patterns and the magnitude of redox shifts were surprisingly well reproduced in the nine (short cycles) or four (long cycles) wet-dry cycles so that there was no indication of legacy effects or pool depletion of redox substances.

Short cycles

The redox potential rapidly decreased during wet periods and increased even faster during dry periods. The fluctuations between dry and wet periods in both grasslands were smaller at incubation start but became more pronounced and recovered more rapidly with proceeding incubation (Fig. 4-4). At -5 cm depth, the redox potential decreased during wet periods to around 0 mV (bog) and to 0 to -170 mV (fen) and increased in dry periods to 600 to 700 mV (bog and fen).

In the fen grassland the redox potentials were mainly above the methanogenesis threshold of -150 mV except for two occasions during wet phases.

Long cycles

In the wet periods, the redox potentials rapidly decreased during the first week after rewetting followed by a long phase of slowly decreasing or stable redox potential (Fig. 4-5). During dry weeks the redox potentials rapidly rose back to the level of the preceding dry phase or even beyond.

The redox potential at -5 cm depth was generally higher in the bog grassland. In the first wet phase, redox potentials at -5 cm were 500 to -75 mV in the bog and 0 to -220 mV in the fen. During dry

phases, they reached values around 600 mV in the bog while in the fen, redox values were around 0 mV during the first two dry phases and increased to a maximum of 460 mV during the last dry period (see Fig. 4-5). In the topsoil of the fen grassland conditions were favourable for methanogenesis within 20 days or less after onset of the wet phase.

The redox potential at -20 cm depth was also lower in the fen grassland. In the bog, the redox potential at -20 cm started at 500 mV and continuously decreased to -24 mV during the first wet period. During the subsequent wet periods, it rapidly decreased when re-wetting started, stayed relatively stable at 0 mV thereafter. With each dry phase, the redox potential in bog increased (from 250 to 500 mV). The fluctuations between wet and dry periods at -20 cm depth were very small in the fen grassland: the redox potential at -20 cm decreased gradually from incubation start (190 mV) until the end of the third wet period (-230 mV). Conditions at -20 cm depth were favourable for methanogenesis during the second and third wet phase. In the third dry period, the redox potential increased again to a maximum of 0 mV and continuously decreased in the subsequent wet phase (to -155 mV).

3.3. CO_2 exchange

Due to vegetation development the first wet phase in both experiments is not fully comparable to later cycles. R_{eco} reacted immediately to dry and wet phases reaching a new plateau at the day of water table shift. GPP was unrelated to water table changes but was affected by vegetation growth (see below). NEE response was dominated by R_{eco} except for the first wet-dry phase. The amplitude of the plateau shifts tended to increase over the nine (short cycles) or four (long cycles) wet-dry cycles due to increasing R_{eco} in the dry phases. This indicates a legacy effect of previous wet-dry cycles by mobilization of easily oxidizable carbon.

In long cycles and in the first half of short cycles, NEE of the bog grassland remained more negative than those of the fen grassland because the higher GPP was only compensated to 59 % on average by higher R_{eco}.

Short cycles

Daily R_{eco} remained low as expected during wet phases. In fen grassland it remained at ~ 3 g C m^{-2} d^{-1} while it was significantly higher and showed an increasing tendency in the bog grassland (4.9 to 7.4 g C m^{-2} d^{-1}). During dry phases, R_{eco} was significantly higher than in wet phases but not different between bog (8.4 to 12.9 g C m^{-2} d^{-1}) and fen (5.3 to 12.1 g C m^{-2} d^{-1}) grassland. R_{eco} in dry phases showed an increasing tendency over the incubation period. Ecosystem respiration increased abruptly at the change from wet to dry phases (Fig. 4-6 top) by 5 to 7 g C m^{-2} d^{-1}, equivalent to a duplication (bog) and more than triplication (fen) of R_{eco}.

GPP increased in the bog during the first 80 incubation days (until dry phase 4) simultaneously with growing vegetation (Fig. 4-6 centre) and slightly decreased thereafter (means ranged from -3.6 to -13.1 g C m^{-2} d^{-1} in wet phases and from -11.3 to -14.6 g C m^{-2} d^{-1} in dry phases). Daily GPP continuously increased in the fen grassland during the first 80 days (Fig. 4-6 centre, increase until dry phase 4) and remained relatively stable thereafter. In the fen grassland, mean daily GPP ranged from -3.2 to -11.5 g C m^{-2} d^{-1} in wet phases and from -5.8 to -12.1 g C m^{-2} d^{-1} in dry phases. There were no differences in daily GPP between dry and wet phases in both grasslands. In agreement with its higher vegetation biomass, the bog grassland had a tendency of higher GPP than the fen grassland.

Daily NEE remained a net CO_2 sink in bog grassland except for the first wet cycle (low GPP due to recovering vegetation after cut) and the last two dry phases (when R_{eco} was highest). In the bog, daily NEE ranged from 1.3 to -7.4 g C m^{-2} d^{-1} in wet phases and from 0.7 to -5.2 g C m^{-2} d^{-1} in dry phases. On average, daily NEE in bog was 3 g C m^{-2} d^{-1} more positive and significantly higher in dry than in wet phases, mainly as a consequence of higher R_{eco}. In general, NEE in bog was higher during dry phases compared to fen, while there was no difference during wet phases.

Daily NEE in fen grassland developed from near zero or a small net CO_2 sink in the first wet cycles to a significant sink in later wet phases (-6.2 g C m^{-2} d^{-1} at incubation end), which were contrasted by small net CO_2 sources in the later dry phases. In the fen, daily NEE ranged from -0.3 to -8.9 g C m^{-2} d^{-1} in wet phases and from 1.4 to -3.0 g C m^{-2} d^{-1} in dry phases. On average, daily NEE in fen was 5 g C m^{-2} d^{-1} more positive and significantly higher in dry than in wet phases, mainly as a consequence of higher R_{eco}.

Long cycles

Daily R_{eco} was low in both grasslands at incubation start (Fig. 4-7 top; 2.5 g C m^{-2} d^{-1} in bog and 1.9 g C m^{-2} d^{-1} in fen). In subsequent wet phases, daily R_{eco} stayed low in fen grassland (~ 3 g C m^{-2} d^{-1}) while it clearly increased in the bog grassland (maximum of 8 g C m^{-2} d^{-1}). Daily R_{eco} was significantly higher during dry periods and increased from one dry period to the next in bog and fen grassland (Fig. 4-7). In dry phases, the bog grassland had about 3 g C m^{-2} d^{-1} higher respiration rates (range from 13.2 to 17.4 g C m^{-2} d^{-1}) than the fen (range from 9.9 to 14.2 g C m^{-2} d^{-1}). This agrees with higher GPP (see below) and higher brown vegetation biomass in the bog grassland. On average, daily R_{eco} was 9 g C m^{-2} d^{-1} higher in dry than in wet phases, this was equivalent to a respiration increase by factor three.

Daily GPP was lowest in both grasslands at incubation start as the vegetation was still growing. Later, daily GPP stayed at the same level of ~-7 g C m^{-2} d^{-1} in the fen grassland (Fig. 4-7) independent of the water level position. In contrast, GPP in bog grassland was about twice as high as in fen grassland with values between -11.9 and -17.2 g C m^{-2} d^{-1} independent of the water level (wet phase 1 was not considered here as vegetation was still in growth; see Fig. 4-7: high variability in GPP data in wet1). This agrees with the much higher accumulation of brown and dead biomass in the bog vegetation.

Daily NEE remained a net sink in wet phases during the entire incubation and was significantly higher in bog grassland (range of -5.2 to -9.7 g C m^{-2} d^{-1}) compared to the fen grassland (range of -3 to -5.4 C m^{-2} d^{-1}). Daily NEE was strongly influenced by increased respiration in dry phases. Under dry conditions, the fen grassland was a CO_2 source during the entire incubation period and its source strength increased from one dry period to the next (range from 1.9 to 7.5 g C m^{-2} d^{-1}). The bog grassland was a CO_2 sink during the first two dry phases (-1.4 to -4.4 g C m^{-2} d^{-1}) but then turned into a CO_2 source (with maximum emissions of 5.0 g C m^{-2} d^{-1} at incubation end). On average, daily NEE was 8 to 9 g C m^{-2} d^{-1} more positive in dry than in wet phases due to higher R_{eco}.

Comparison between short and long cycles

In fen grassland, daily R_{eco} was in the same range in short and in long cycles during wet and dry phases. In bog grassland, however, R_{eco} in dry phases was higher in the long than in short cycles while the wet phases were comparable. The changes from wet to dry conditions were comparable and resulted in a duplication of R_{eco} in bog in short cycles and a triplication in the other treatments (fen in short cycles, bog and fen in long cycles).

In general, the bog grassland was significantly (p<0.05) more productive than the fen grassland – this was supported by GPP and biomass results. Wet and dry phases did not alter the capacity to fix CO_2 both in bog and fen grassland. The bog grassland was significantly (p < 0.05) more productive when the water table changed in long cycles while the fen grassland was more productive in short water table cycles.

Daily NEE in wet phases was a consistent net CO_2 sink in short and long cycles with higher net CO_2 uptake in the bog grassland in the long cycles. The CO_2 sink strength increased at incubation start and was slowly reduced in the course of incubation.

During dry phases, the CO_2 sink strength was significantly lower or mesocosms turned to a CO_2 source due to higher ecosystem respiration. During dry phases, the fen grassland was a CO_2 source in the long cycles regime, in short cycles it was a small sink at the start but turned to a small source in the course of the incubation.

The change from wet to dry conditions resulted in a more pronounced reduction of net CO_2 uptake in long cycles (by 8 to 9 g C m^{-2} d^{-1}) than in short cycles (by 5 g C m^{-2} d^{-1}). In consequence, the grassland mesocosms turned to a net CO_2 source in the first (fen) and third (bog) long cycle, and the sixth (fen) to eighth (bog) short cycle.

3.4. CH$_4$ and N$_2$O emissions

Short cycles

Methane emissions were very low in wet and dry phases (Fig. 4-8) and were not significantly different between bog and fen grassland. Phase means ranged from -0.01 to 0.14 mg C m^{-2} h^{-1}. Individual methane emissions above 0.2 mg C m^{-2} h^{-1} were observed in six out of nine wet-dry cycles at the transition from wet to dry phases (data not shown) but returned to background levels during the first week of the dry phase.

N_2O emissions were close to zero in the fen grassland irrespective of the water table position (Fig. 4-10). In bog grassland, small amounts of N_2O were emitted during the first wet-dry phase (phase means of 1.1 (wet1) and 0.5 (dry1) mg N m^{-2} h^{-1}) and were close to zero during the rest of the incubation.

Long cycles

Methane emissions were very low during the first two wet-dry phases in bog and fen grassland (Fig. 4-9) and slightly increased in the third wet-dry phase (means of 0.3 mg C m^{-2} h^{-1} (bog) and 0.6 mg C m^{-2} h^{-1} (fen) in wet phase 3). At incubation end, methane emissions decreased to the initial range in fen while they were on average ~ 0.6 mg C m^{-2} h^{-1} in bog. In general, CH_4 emissions were not different between bog and fen grassland. Individual observations reached occasionally 1 to 4 mg C m^{-2} h^{-1} in fen grassland but never exceeded 1.5 mg C m^{-2} h^{-1} in bog grassland.

N_2O emissions were in general very low (Fig. 4-11). They were highest in bog grassland mesocosms in the first wet phase (mean of 0.4 mg N m^{-2} h^{-1}) and remained thereafter in the range of 0.1 to 0.3 mg N m^{-2} h^{-1} irrespective of the water table position. In fen grassland, N_2O was emitted in the range from 0.01 to 0.06 in both wet and dry phases without any visible trend.

3.5. GHG balance in CO₂ equivalents

The first wet-dry phase was not considered as the vegetation was still growing and, therefore, the GHG balance of wet-dry phase 1 was not comparable with subsequent wet-dry phases. The GHG balance was dominated by net CO_2 uptake as CH_4 and N_2O emissions were small throughout the incubation.

In short cycles, both grasslands were clear net GHG sinks during wet phases (mean of wet phases -19.9 ± 4.8 g CO_2-equ. m^{-2} d^{-1} in bog and -23.1 ± 7.4 g CO_2-equ. m^{-2} d^{-1} in fen; n=8). During dry phases, the bog was a clear GHG sink at incubation start (-18.4 g CO_2-equ. m^{-2} d^{-1} in the 2nd dry phase) and turned to a small GHG source at the end (2.9 g CO_2-equ. m^{-2} d^{-1} in the 8th dry phase) (mean of all dry phases -7.7 ± 7.5 g CO_2-equ. m^{-2} d^{-1}). The fen switched from a GHG sink to a small GHG source at incubation end (mean of dry phases -1.7 ± 5.5 g CO_2-equ. m^{-2} d^{-1}). The mean difference between wet and subsequent dry phase in short cycles was 12.2 ± 6.7 g CO_2-equ. m^{-2} d^{-1} (bog) and 21.5 ± 9.3 g CO_2-equ. m^{-2} d^{-1} (fen)(Fig. 4-12).

In long cycles, both grasslands were a considerable to moderate GHG sink during wet phases (mean of wet phases -27.1 ± 8.2 g CO_2-equ. m^{-2} d^{-1} in bog and -15.7 ± 4.8 g CO_2-equ. m^{-2} d^{-1} in fen; n=3) and turned to a moderate to large GHG source during dry phases (mean of dry phases 10.2 ± 11.8 g CO_2-equ. m^{-2} d^{-1} in bog and 21.3 ± 6.3 g CO_2-equ. m^{-2} d^{-1} in fen). The mean difference between wet and subsequent dry phase was much higher in long cycles (37.3 ± 5.6 g CO_2-equ. m^{-2} d^{-1} in bog and 37.0 ± 7.1 g CO_2-equ. m^{-2} d^{-1} in fen; see Fig. 4-12) than in short cycles.

4. Discussion

4.1. Fast response of peat grasslands to water table fluctuations

Vegetation response

We worked with grass species not adapted to permanently flooded conditions. Nevertheless, the vegetation coped remarkably well with the strong water stress induced by extreme wet-dry cycles and extended phases of flooding (i.e. water level at +5 cm for 42 days (=long cycles)) in our experiments. In the bog grassland, the productivity was generally higher and the vegetation coped better with longer wet phases in the long cycles regime – the vegetation reacted with higher biomass production, a partial die-off and subsequent accumulation of brown leaves and dead matter (77% of total biomass at incubation end) but no decline in green biomass. In contrast, the vegetation in the fen grassland mesocosms reacted with slow growth but lower mortality (56% dead biomass at incubation end in long cycles regime). The fen grassland was more productive when wet phases were short.

However, in an earlier experiment (Hahn-Schöfl et al. 2014) under conditions of a gradually raised water table and subsequent flooding for 3 months, the vegetation of the same fen grassland reacted similarly to the bog vegetation in the present experiment: The „grasses" (fen) had a high total biomass of 2.0 ± 0.5 kg dw m^{-2}) but with a high fraction of dead biomass (26% green, 58% brown, 16% other dead matter). Obviously, the vegetation can react in both patterns on the same site under different circumstances. The vegetation response pattern seems to be flexible and situation-specific rather than species-specific.

In both types of grassland, the died-off plant matter, which accumulated throughout the incubation, provided readily degradable and energy-rich substrates for microbial decomposition processes

under intermittent aerobic conditions.

Response of photosynthesis, respiration, CH_4 and N_2O fluxes to a dynamic water table

The capacity to fix CO_2 by photosynthesis (GPP) was not clearly affected by the dynamic change in water table in both grasslands, neither in the days after abrupt water table change nor gradually during the periods of stable water table. This is in agreement with (Leiber-Sauheitl et al. 2014) and (Lindroth et al. 2007) who showed that GPP was not affected by water level but by radiation.

Respiration reacted within days to the abrupt water table change and was two to three times higher under dry conditions. (Leiber-Sauheitl et al. 2014) found that R_{eco} fluxes were strongly negatively correlated with the water level which agrees with our findings. However, the increase in respiration in our experiment was even higher than those measured by (Estop-Aragonés and Blodau 2012) – there peat respiration of fen peat cores under experimental drought increased by a factor between 1.4 and 2.1 higher.

A similarly fast R_{eco} reaction within days was observed in a mesocosm study by (Hahn-Schöfl et al. 2014). We are not aware of any field observations immediately following strong water table fluctuations. The immediate R_{eco} response to water table change is so far unaccounted for in standard gap-filling procedures of CO_2 flux measurements (Reichstein et al. 2005; Moffat et al. 2007) for gap-filling for eddy covariance net carbon fluxes and for interpolation of manual in-situ measurements to annual CO_2 fluxes (Leiber-Sauheitl et al. 2014) but may have a significant effect on the annual CO_2 balance in peatlands.

(Estop-Aragonés and Blodau 2012) showed that aerobic CO_2 production rates decreased with time after drying presumably due to substrate limitation. Therefore, it needs to be assessed if large initial respiration pulses after a change from anaerobic to aerobic conditions will persist over longer periods.

Net ecosystem exchange (NEE) was driven by the variation in ecosystem respiration. We argue that this is fully attributed to water table driven variation in heterotrophic soil respiration (R_h) because our data showed that GPP was unaffected by water-table and the ratio of autotrophic respiration (R_a) to GPP is reported to be relatively stable – with values between 0.44 and 0.53 independent of ecosystem type (Schulze et al. 2009). Applying the R_a:GPP ratio of the literature to our data would, however, partly produce negative R_h, which is biologically impossible. Using $R_h > 0$ as constraint, we can derive a maximum possible R_a:GPP ratio for the mesocosms. For the long cycles, the maximum possible R_a:GPP ratio was 0.43 (bog) and 0.36 (fen). For the short cycles, the maximum possible R_a:GPP ratio for the bog grassland was 0.44 but only 0.23 for the fen grassland. R_a:GPP ratio for the bog grassland is close to the literature values while the fen grassland showed a lower ratio.

In dry phases, mean R_h fluxes were raised by ~ 9 g C m^{-2} d^{-1} compared to wet phases in long cycles (bog and fen) and by 4.2 g C m^{-2} d^{-1} (bog) to 6.6 g C m^{-2} d^{-1} (fen) in short cycles. The R_h increases fully match the NEE differences, providing independent evidence that water table only affects heterotrophic respiration (R_h). In wet phases, R_h:R_{eco} was 0.2 or lower, while in dry phases, R_h:R_{eco} ranged between 0.5 and 0.8. Given the consistent and reproducible response of R_h to water table, we suggest that the water table dependent R_h:R_{eco} ratio can significantly improve gap-filling and interpolation of CO_2 measurements to calculate annual carbon balances in peatlands with dynamic water table.

CH_4 flux rates were low despite the large amount of dead biomass and warm conditions. With

regard to N_2O emissions, no response to change in water table position was found.

Response of net GHG balance to simulated rewetting

A dynamic change in the water table from wet to dry conditions resulted in a reduction of net GHG uptake by 12.2 in bog and 21.5 g CO_2-equ. m^{-2} d^{-1} in fen when wet phases were relatively short (7 days in short cycles) – and both grasslands turned from moderate GHG sinks to small GHG sources at incubation end. With extended phases of flooding (42 days in long cycles), the shift of net GHG fluxes was much stronger (reduction by 37 g CO_2-equ. m^{-2} d^{-1}) – and both grasslands oscillated between strong net GHG sink and source mode.

In a previous experiment we tested a slow, stepwise rewetting. In contrast to the dynamic water table regime of this experiment, both R_{eco} and GPP were reduced with raising water table. One cm water table raise increased the net GHG uptake by 0.8 g CO_2-equ. m^{-2} d^{-1} (Hahn-Schöfl et al. 2014) which is in a similar range as our long cycle regime (increase by 0.7 g CO_2-equ. m^{-2} d^{-1} per cm water table raise). The rewetting under short cycles resulted in much lower increase of net GHG uptake (0.2 g CO_2-equ. m^{-2} d^{-1} in bog and 0.4 g CO_2-equ. m^{-2} d^{-1} in fen). Long-term flooding for three months, however, imposed a shock on the vegetation which reacted with reduced GPP, increased R_{eco} and CH_4 emissions. Long-term flooding increased GHG emissions by 27 g CO_2-equ. m^{-2} d^{-1} (in "grasses" = fen grassland, (Hahn-Schöfl et al. 2014) bringing net GHG emissions back to those observed at -30 cm water level.

4.2. The legacy of flooded periods

Is the response fully reversible when the water table switches back to the original position, and repeatable? Is there a memory effect of previous flooding or drainage events?

The redox potential response to water table switches was fully reversible and repeatable (see Fig. 4-4 and Fig. 4-5). The temporal patterns and the magnitude of redox shifts were well reproduced in the nine (short) or four (long) wet-dry cycles so that there was no indication of legacy effects or pool depletion of redox substances. The oxidative status of the peat soils was recovered within one week of dry conditions – this process was very fast and reproducible.

Similarly, there was no indication of legacy effects regarding CH_4 fluxes. The production of CH_4 is strongly connected to anaerobic conditions in the peat – these were not reached during the 7 wet days in the short cycles regime but during 10 to 20 days of flooding in long cycles. Nevertheless, CH_4 emissions remained low despite the large amount of readily degradable organic matter. CH_4 production can be suppressed even at low concentrations of alternative electron acceptors such as iron and sulphate (Limpens et al. 2008) or methanogens need longer periods for activation. One week of drainage hence can effectively avoid CH_4 emissions in a fully reproducible manner.

Under wet conditions, both grasslands acted as consistent net CO_2 sinks. The change in water table from wet to dry conditions led to an explicit reduction of the net CO_2 uptake due to increased heterotrophic ecosystem respiration. This reduction in net CO_2 uptake was ~1.7 times higher when wet phases were long. We cannot rule out whether the longer phases had a stronger stimulating effect or whether the shorter phases were not yet in equilibrium. Both grasslands turned from CO_2 sink to net CO_2 source in the course of incubation – this shift to CO_2 source took place earlier in the fen (sixth (fen) to eighth (bog) cycle in the short cycles regime; first (fen) and third (bog) cycle in the long cycles regime). Obviously, the repetition of wet-dry cycles stimulated CO_2 sources.

Respiration rates (R_{eco}) and net GHG emissions increased from one dry phase to the next (App-Fig. 4-1). We assume that this could be a substrate mobilization effect. This effect is known for DOC release in the water table fluctuation zone, and could also be due to the decomposition of the dead biomass which accumulated in the course of the experiment and was decomposed under aerobic conditions. The stimulation by past wet-dry cycles, however, is small compared to the immediate effects of switching from wet to dry conditions so that for CO_2, we only found a small legacy effect of past flooding.

4.3. Alternating water tables as low-GHG management strategies

How long do interim dry periods need to be to effectively reduce CH_4 emissions?

Lowering the water table leads to a renewal of the electron acceptor capacity in peat soils because aeration causes a re-oxidation of reduced compounds (e.g. sulfides, ferric iron, nitrate) which constrain methanogenesis (Knorr and Blodau 2009; Knorr et al. 2009). When rewetted, these electron acceptors in the peat are consumed and methanogenic conditions establish.

In our experiment, the redox potential reacted within the first week after water table switches. Conditions favourable for methanogenesis (redox potential < -150 mV) in the topsoil were only just reached after 10 to 20 days of wet conditions (see Fig. 4-5 for long cycles regime) and never occurred during the short cycles regime. Consequently, CH_4 flux rates were low despite the large amount of dead biomass and warm conditions. This shows that the risk for high CH_4 emissions during intermittent flooding is low, when enough redox equivalents are present in the top soil. One week of dry conditions fully recovered the oxidative status in the peat soils – this process was very fast and very reproducible (Fig. 4-4 and Fig. 4-5). We suggest that one week of low water table could work as a general rule of thumb for CH_4 avoidance.

The regeneration of the electron acceptor pool under experimental drought and subsequent inhibited methanogenesis after rewetting was confirmed in peat mesocosms (Knorr and Blodau 2009; Estop-Aragonés and Blodau 2012) and in the field (Knorr et al. 2009). The suppressive effect on methanogenesis after drought lasted 1 to 4 weeks after rewetting of a fen site in Southern Germany (Knorr et al. 2009). In peat mesocosms, methanogenesis was temporarily suppressed for 20 to 50 days after rewetting (Knorr and Blodau 2009). Elevated methane concentrations occur only after complete depletion of electron acceptors, although methanogenic activity recovers locally quickly from aeration and, consequently, more frequent droughts are suggested as means to prevent the establishment of methanogenic conditions for longer periods of time (Knorr and Blodau 2009).

Under long-term flooding, conditions in the peat become favourable for methanogenesis resulting in increasing CH_4 emissions (estimated maximum 16.1 mg C m^{-2} h^{-1} for the fen grassland (Hahn-Schöfl et al. 2014).

Do wet-dry cycles foster N_2O emissions?

Unexpectedly, we detected no risk of high N_2O emissions – neither when the water table changed dynamically nor when it was raised in steps (Hahn-Schöfl et al. 2014). This findings contrast with N_2O peaks in rewetting events in mineral soils and groundwater-dependent N_2O peaks in agricultural organic soils (Flessa et al. 1998). We assume that the peat soils were not yet dry enough after 1 to 2 weeks at a low water table (-45 cm) to produce N_2O instead of N_2 by denitrification. Both grassland sites have been used for agriculture for a long time and are in highly fertile

conditions. The low N_2O emissions may be due to substrate limitation caused by vegetation growth. Mean values of 1.1 NH_4-N mg l^{-1} (maximum 4.9 NH_4-N mg l^{-1}) in bog and of 0.4 NH_4-N mg l^{-1} (maximum 1.5 NH_4-N mg l^{-1}) in fen were indeed low. Ammonium rather than nitrate was the dominant mineral nitrogen form in the soils and the aerobic process of nitrification is inhibited in wet conditions. Low N_2O fluxes were also observed in field measurements on the same sites (Drösler et al. 2011).

Alternating water table as low-GHG management strategy in peat grasslands

Alternating flooding and drainage could be used to achieve low GHG emissions in peat grasslands. Some thoughts should be given to the length of the alternating wet-dry phases with respect to site-specific risks of N_2O and the adaptiveness of vegetation to wet conditions as each water table has its drawbacks.

Under permanent waterlogged conditions, conditions in become favourable for methanogenesis and there is a risk of high CH_4 emissions when readily degradable organic matter is present (Hahn-Schöfl et al. 2011). Intermittent dry periods, however, will restore the oxidative status in the peat soil and prevent high CH_4 emissions. But intermittent dry phases should be kept as short as possible to keep CO_2 release from aerobic respiration low as respiration was shown to be 2 to 3-fold higher under drained conditions. One week of dry conditions is considered as long enough to balance between CH_4 avoidance and increased CO_2 release.

The water table should be kept at a level which allows the vegetation not only to survive but to thrive – this would lead to higher net CO_2 uptake. When dying-off, the vegetation provides readily degradable organic matter for microbial decomposition which results in a risk for high CO_2 and CH_4 emissions (Hahn-Schöfl et al. 2011; Hahn-Schöfl et al. 2014). In our experiment, the change from wet to dry conditions led to additional GHG emissions of 12 to 21 g CO_2-equ. m^{-2} d^{-1} when wet phases were relatively short (short cycles) and 37 g CO_2-equ. m^{-2} d^{-1} when wet phases were long (long cycles) and a large amount of dead organic matter accumulated in the flooded periods. But permanent flooding (+5 cm) also reduced the GHG sink strength and – as the flooding lasted for more than six weeks – turned the fen grassland into a GHG source (Hahn-Schöfl et al. 2014).

Our incubation experiment showed that even if the peatland is flooded for a few weeks in spring or summer, mean CH_4 emissions were 25 times lower than the still low values observed after 3 months of flooding (Hahn-Schöfl et al. 2014) and much below the high reported literature values from eutrophic shallow lakes (Hahn-Schöfl et al. 2011).

5. Conclusions

We conducted mesocosm experiments with highly productive grasslands on contrasting peat soils simulating extreme wet-dry cycles. We tested the adaptive capacity of the vegetation to flooding stress, the short-term response times of CO_2, CH_4 and N_2O to alternating water tables and the memory effect of previous stress. Surprisingly, GPP remained relatively unaffected by strong water table oscillations and phases of flooding. Obviously, even grass species considered unsuitable for wet conditions have effective adaptation mechanisms as long as wetness stress does not persist for more than a few weeks.

Peat grasslands were a GHG sink under wet conditions (+5 cm). Draining (-45 cm) strongly reduced the GHG sink strength and turned the grasslands into a GHG source, driven by heterotrophic soil respiration and peat decomposition.

The observed short-term responses of GHG fluxes to water table changes agree with annual mean patterns (Couwenberg et al. 2008; Drösler et al. 2011). Heterotrophic soil respiration switched in less than a few days from a considerable CO_2 source in drained soil to near-zero CO_2 fluxes during flooding and vice versa. The slow response of redox potentials delays CH_4 emissions by weeks. Drainage and rewetting responses were fully reproducible over several wet-dry cycles so that one week of dry conditions is long enough to reset the soil conditions with minimal memory effects of previous water table conditions.

Recommendations for low-GHG peatland management

- In situations where drainage is practiced, avoid deeply drained conditions to avoid CO_2 loss by heterotrophic respiration, which immediately occurs when the soil is drained. Every wet day saves soil carbon, in particular during the vegetation period when biological activity is high.

- In situations where rewetting has led to extended flooding during the vegetation period with a risk of high CH_4 emissions, allow intermittent dry periods of one week to keep CH_4 emissions low. The oxidative status in the peat soil can be restored rapidly with a low water table which prevents high CH_4 emissions for weeks.

- Keep the vegetation vital, which results in higher net CO_2 uptake, and avoid the accumulation of fresh organic matter e.g. from dying-off vegetation, which bears the risk of higher CO_2 and CH_4 release under both aerobic and anaerobic conditions.

- Check soil properties for risks of high N_2O emissions which may be important due to the high global warming potential. Alternating wet-dry phases did not foster N_2O emissions in our experiments.

Acknowledgements

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Tables and Figures

Tab. 4-1: Characterization of the sampling sites in the Ahlen-Falkenberger Moor and Freisinger Moos: dominant vegetation, management and soil characteristics[*]

	Bog grassland	**Fen grassland**
Name of site in other literature[**]	Intensively managed grassland (TG1-A1; Ahlen-Falkenberger Moor)	Intensively managed grassland (TG5-F8, TG5-F9; Freisinger Moos)
Dominant vegetation	mainly *Anthoxanthum odoratum* and *Lolium perenne* with few *Taraxacum officinale*, *Cardamine pratensis* and some mosses	mainly *Festuca pratensis*, *Poa trivialis*, *Alopecurus pratensis* and *Dactylis glomerata*
Management	4-5 cuts per year, fertilization[***]	Middle intensity management: 2-3 cuts per year, low water table, fertilization[##]
	C export: no data available	C export: 470 (2007) and 192 (2008) g C m^{-2} yr^{-1}
	C import (manure): 226 (2008) and 206 (2009) g C m^{-2} yr^{-1}	C import: 135 (2007 and 2008) g C m^{-2} yr^{-1}
	mineral fertilization: 11.8 (2008) and 12.1 (2009) g N m^{-2} yr^{-1}	
Mean water table at the site[**]	< -60 cm	< -60 cm
Soil type	Ombric Fibric Histosol (Drainic)[###]	Sapric Histosol
Bulk density [g cm^{-3}][*]	0.17 ± 0.03^a	0.43 ± 0.03^b
Ash content [%][*+]	6.5 ± 1.4^a	49.4 ± 4.7^b
Carbon density [kg C m^{-3}][#*]	86.2 ± 15.6^a	208.6 ± 12.7^b
Pore volume [%][*]	83.8 ± 8.1^a	77.1 ± 1.2^a
pH[*]	3.8 ± 0.4^a	6.1 ± 0.2^{ab}

[*] soil characteristics determined from mesocosms at incubation end (mean $\pm$ SD, n = 6; different letters indicate significant differences, p<0.05, Wilcoxon test)

[**] (Drösler et al. 2011)

[***] information from (Beetz et al. 2013)

[#] belowground carbon estimated based on bulk density (Warren et al. 2012)

[##] personnal communication with Mathias Drösler

[###] information from (Frank et al. 2014) using WRB classification (WRB IUSS Working Group 2006)

[+] determined by loss on ignition at 550°C

Fig. 4-1: Biogeochemical processes in dry and wet peat mesocosms as represented by the two water table levels

	Dry	**Wet**
Water table	-45 cm	+5 cm
Redox potential	Aerobic	Anaerobic
Soil organic matter decomposition	Oxidation	Fermentation
N_2O processes	Nitrification (& denitrification)	Denitrification
CH_4 processes	Methanotrophy	Methanogenesis
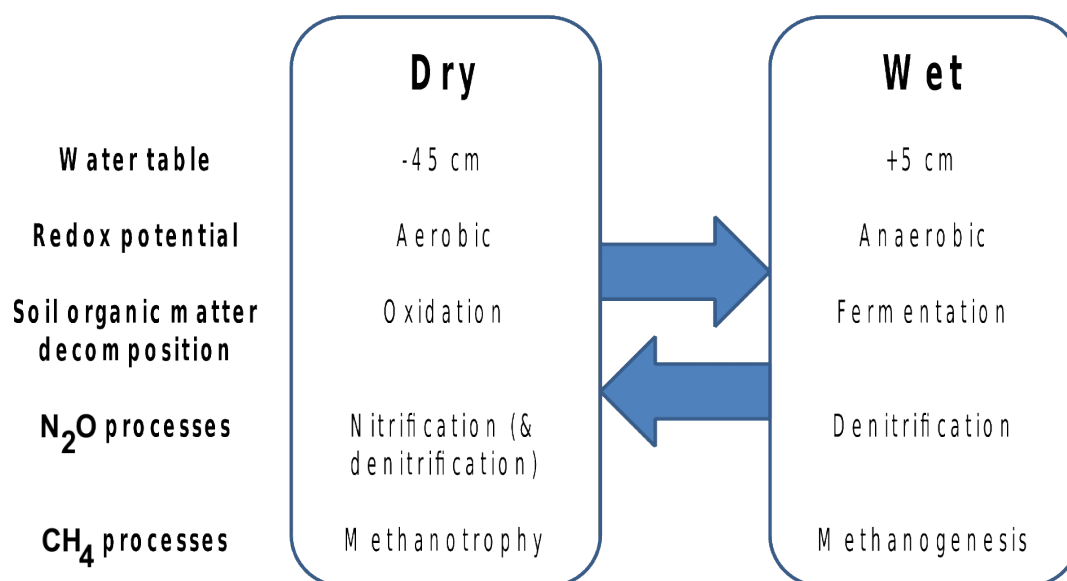
Fig. 4-2: Set-up of mesocosm and attached measurement chamber for gas exchange measurements:

a) PVC tube containing undisturbed peat core with vegetation (mesocosm), b) insulation and c) cooling system, d) redox probes with e) Ag/AgCl reference electrode, and f) soil temperature probes, g) water supply with sensor-controlled pump for water table manipulation, h) inundation tank as basin for supernatant water during flooding and as attachment for i) measurement chamber.

The transparent / opaque measurement chamber was equipped with j) two vents, k) a radiation-protected temperature sensor, l) a PAR sensor, and m) cooling packs for temperature control. Gas sampling was done via n) two ports (flow-through to a CO_2 infra-red gas analyser) or via o) a septum (manual sampling for CH_4 and N_2O analysis).
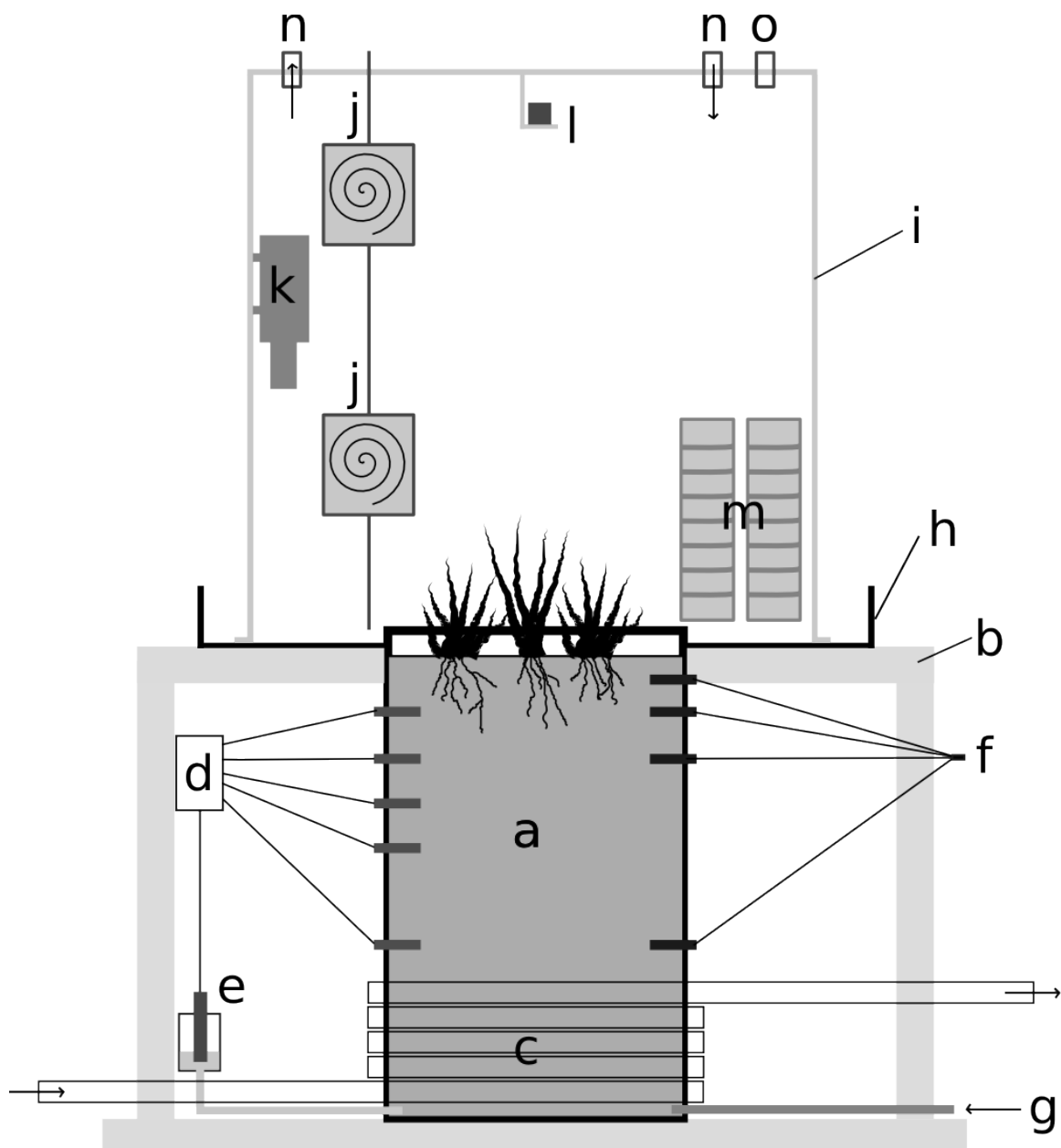
Fig. 4-3: Mean biomass in bog and fen grassland mesocosms at incubation end (separated in fraction green leaves, brown leaves, algae present in the inundation tank and other dead matter (such as dead roots and shoots, etc.); n=3). The water table changed in short (left) and long cycles (right).
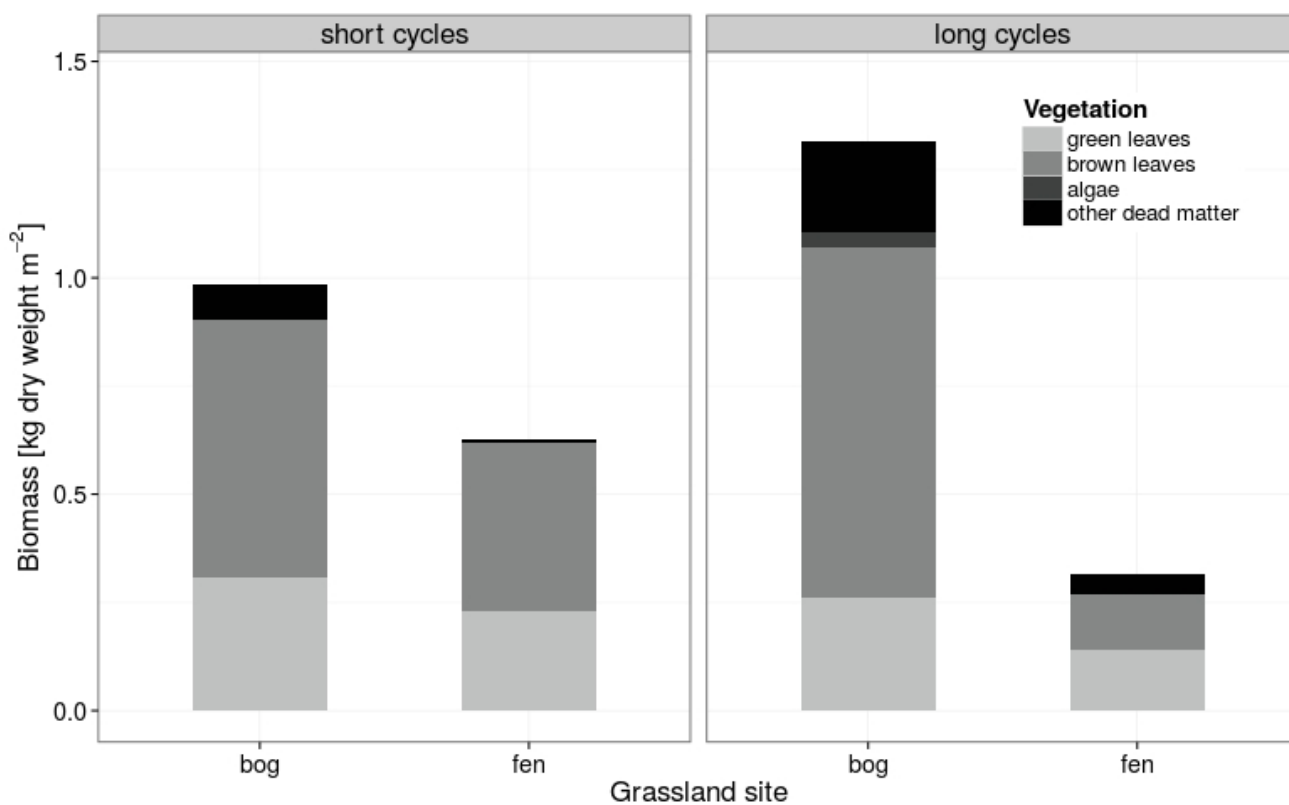
Fig. 4-4: Redox potential over the course of the experiment with changing water table in short cycles in bog (top) and fen (bottom) grasslands measured in -5, -10 and -20 cm depth (daily mean of 3 replicates, n=864). The dotted line indicates the threshold for methanogenesis.
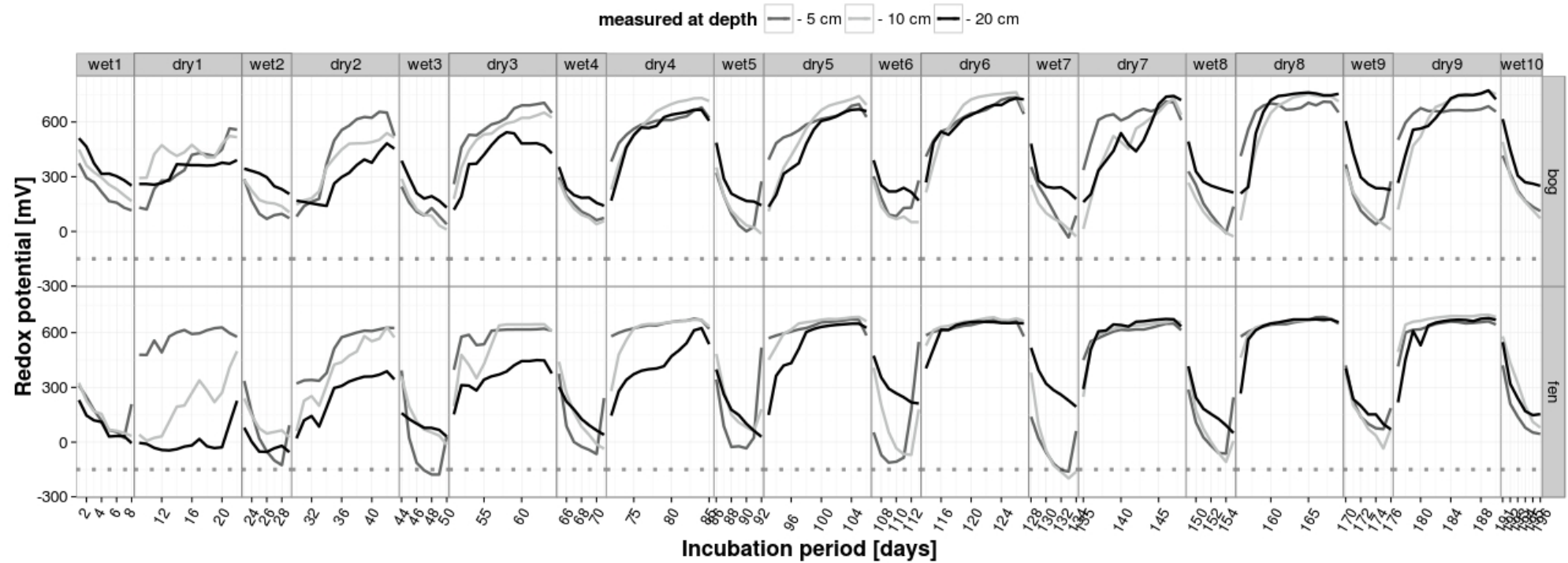
Fig. 4-5: Redox potential over the course of the experiment with changing water table in long cycles in bog (top) and fen (bottom) grasslands measured in -5, -10 and -20 cm depth (daily mean of 3 replicates, n=864). The dotted line indicates the threshold for methanogenesis.
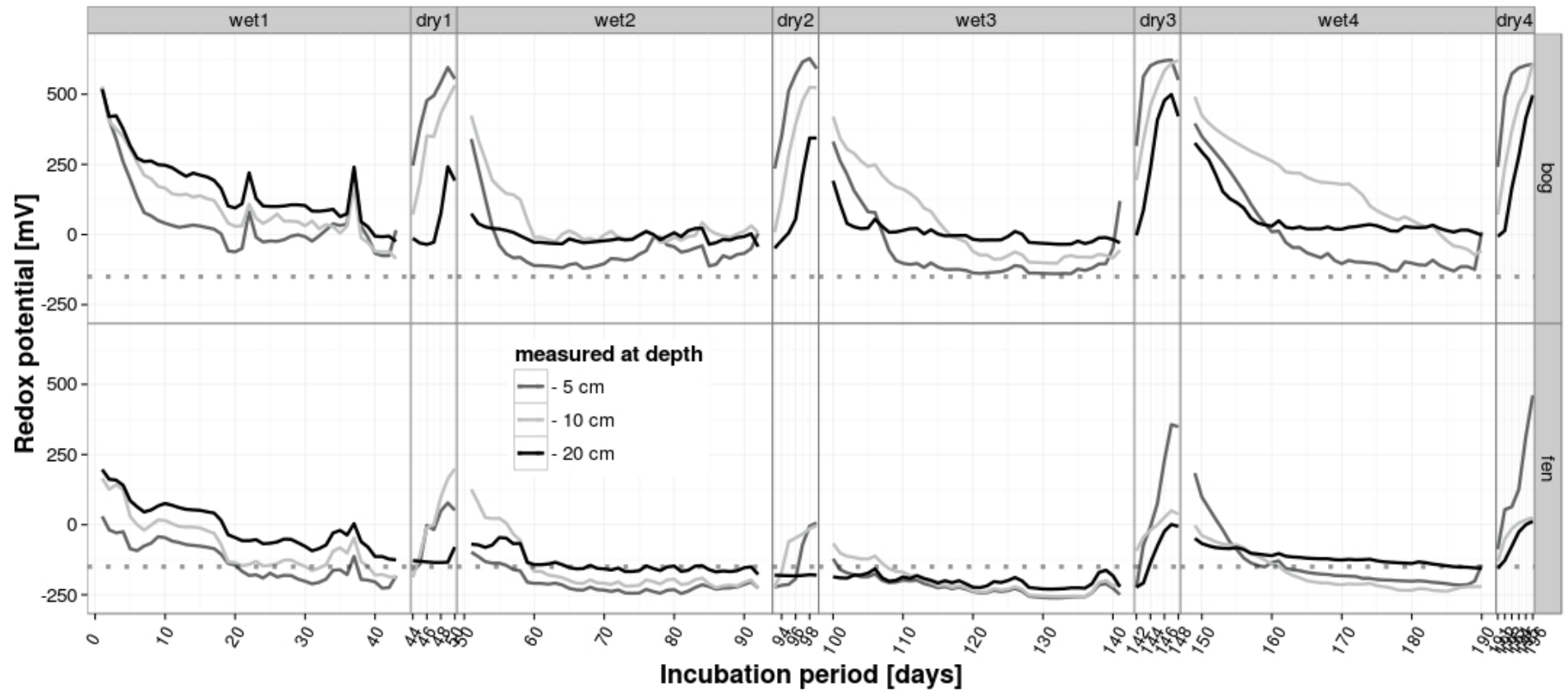
Fig. 4-6: Daily R_{eco} (top), GPP (centre) and NEE (bottom) in bog (black) and fen (grey) grassland mesocosms at dynamic water table in short cycles (modelling is based on fitting measurements to functions of (Lloyd & Taylor, 1994) and (Michaelis & Menten, 1913); crossbar shows mean ± standard deviation, n= 1 to 4)
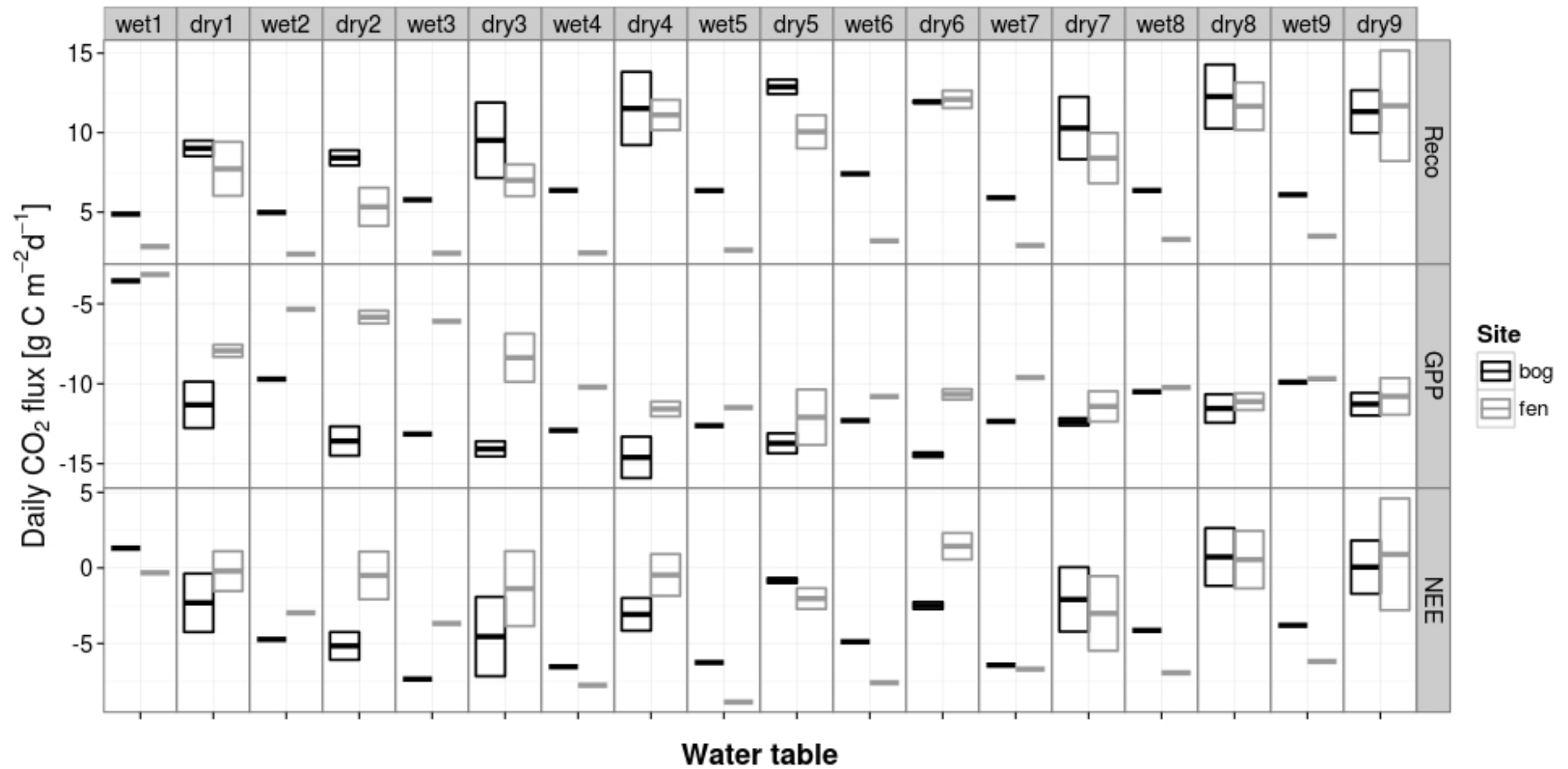
Fig. 4-7: Daily R_{eco} (top), GPP (centre) and NEE (bottom) in bog (black) and fen (grey) grassland mesocosms at dynamic water table in long cycles (modelling is based on fitting measurements to functions of (Lloyd & Taylor, 1994) and (Michaelis & Menten, 1913); crossbar shows mean ± standard deviation, n= 1 to 7)
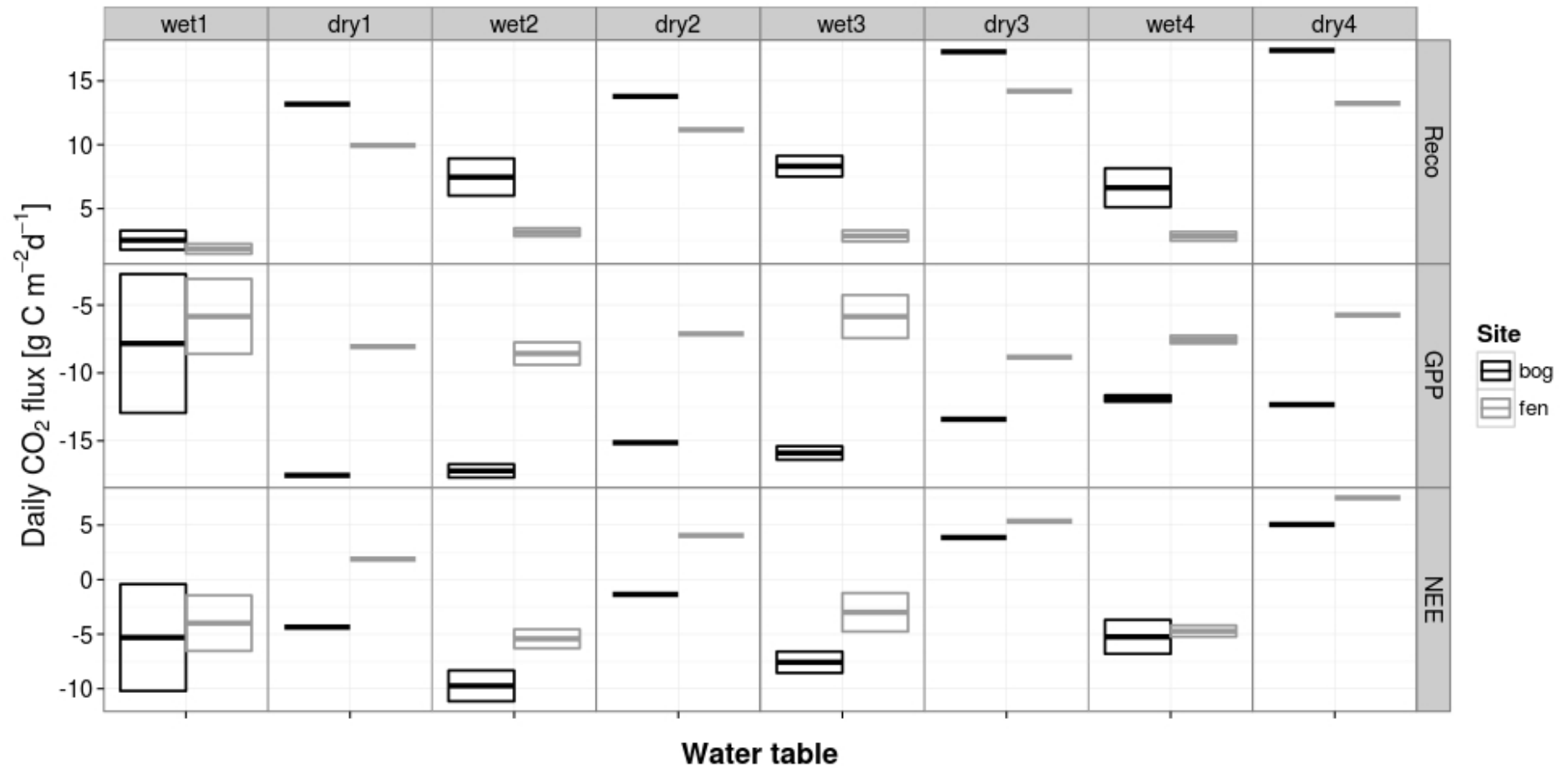
Fig. 4-8: Mean CH$_4$ flux in bog (black) and fen (grey) grassland mesocosms at dynamic water table in short cycles (mean ± sd, n=6 to 18).
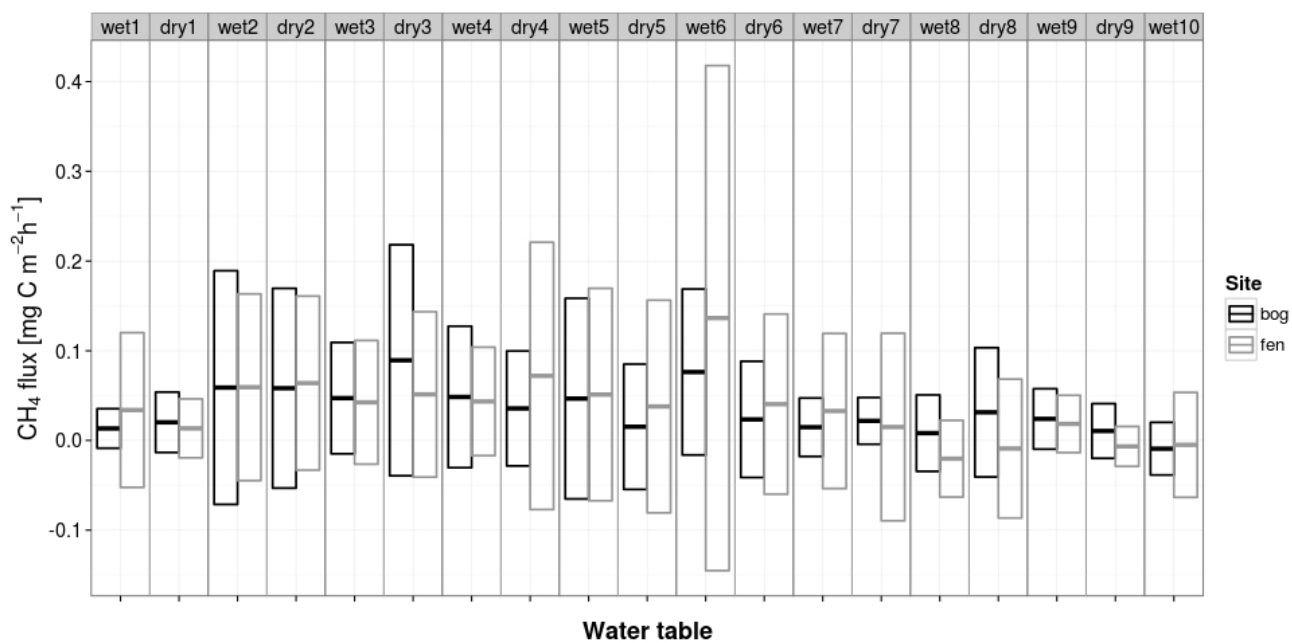
Fig. 4-9: Mean CH$_4$ flux in bog (black) and fen (grey) grassland mesocosms at dynamic water table in long cycles (mean ± sd, n=7 to 48).
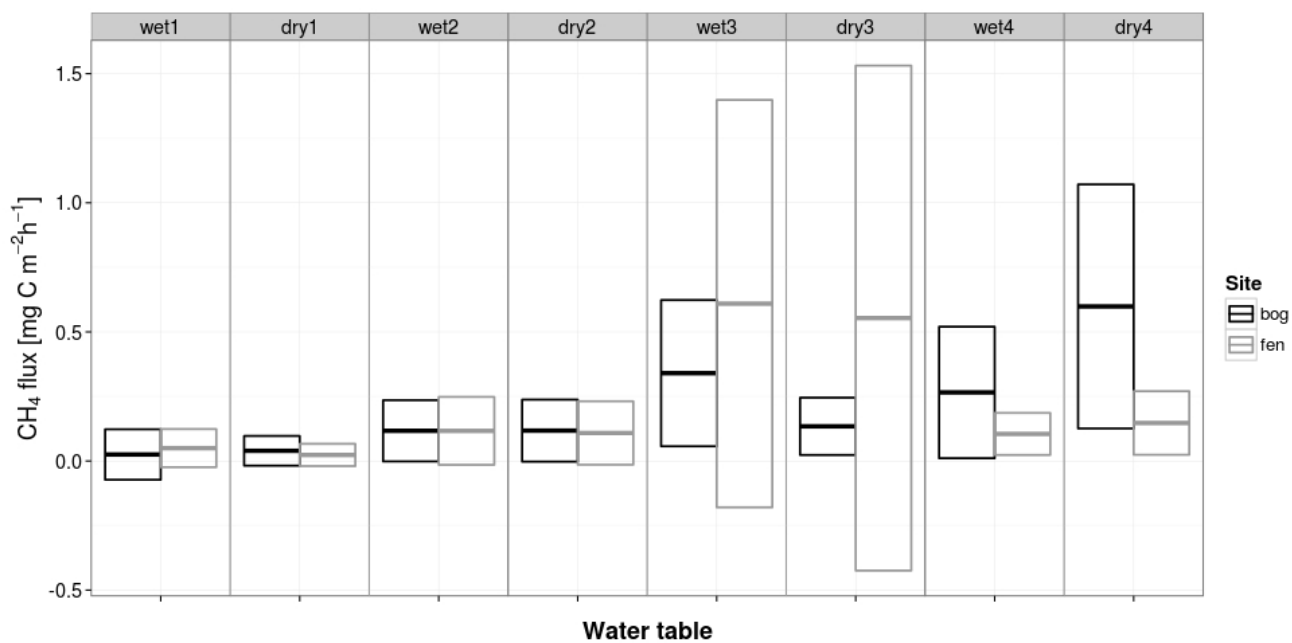
Fig. 4-10: Mean N_2O flux in bog (black) and fen (grey) grassland mesocosms at dynamic water table in short cycles (mean ± sd, n=6 to 18).
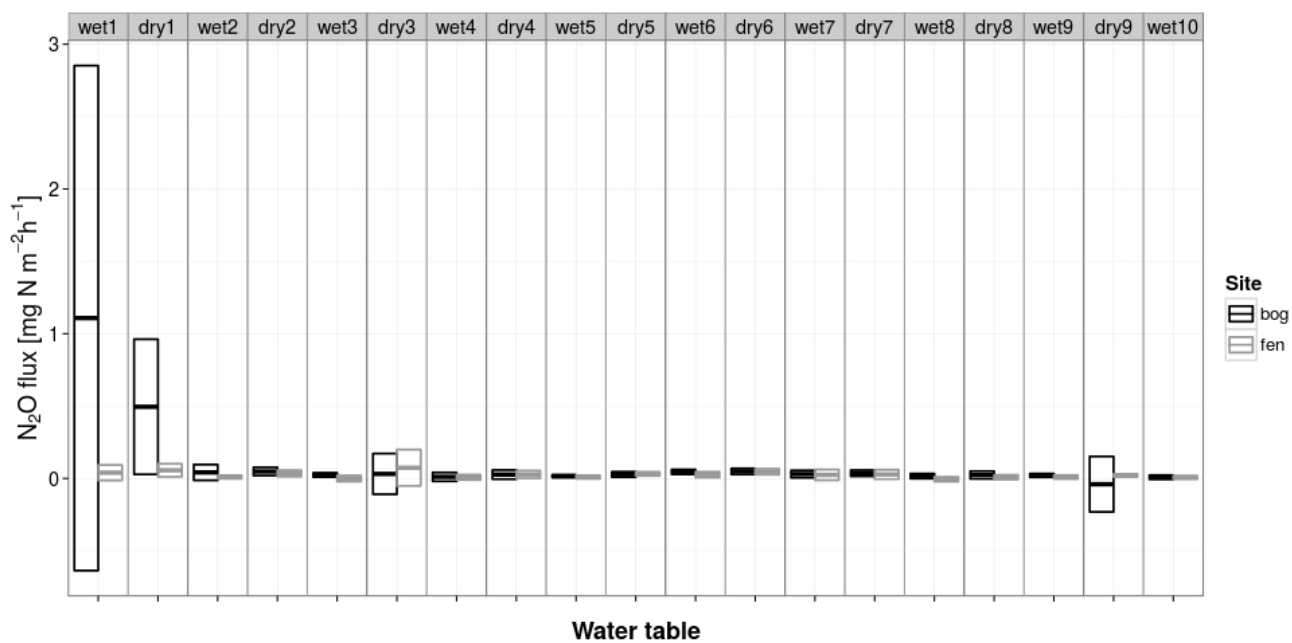
Fig. 4-11: Mean N_2O flux in bog (black) and fen (grey) grassland mesocosms at dynamic water
table in long cycles (mean ± sd, n=7 to 48).
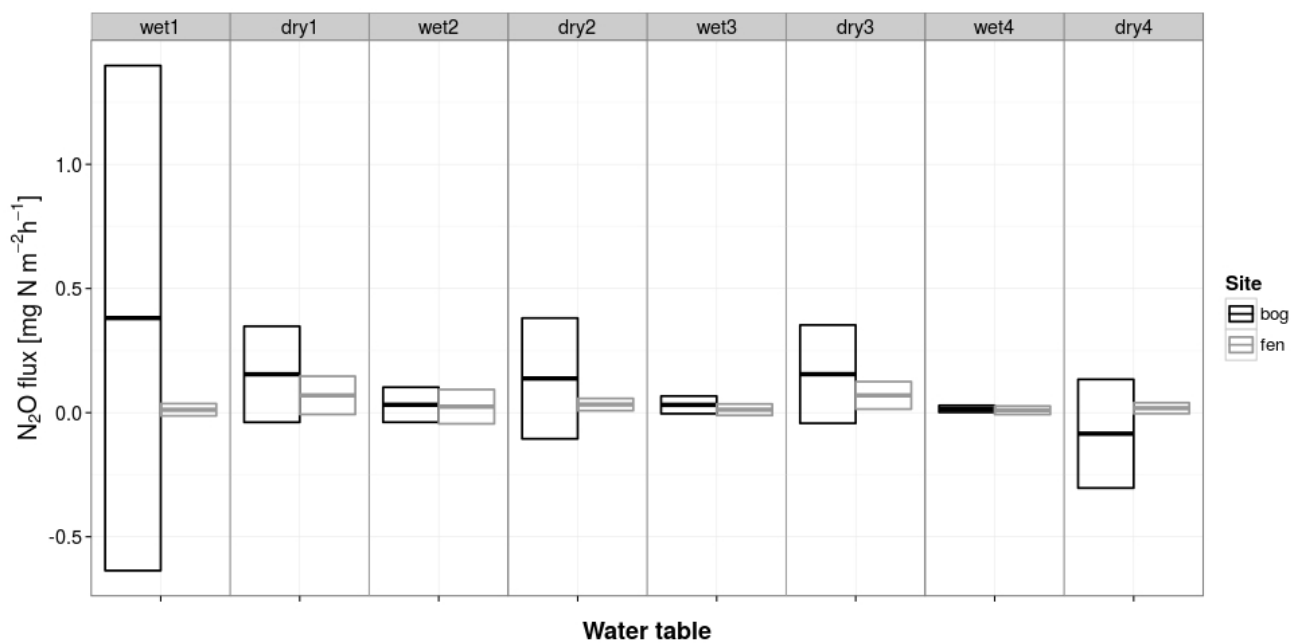
Fig. 4-12: Shift in GHG balance from wet to subsequent dry phase in bog (left) and fen (right) grassland at dynamic water table in short cycles (top) and long cycles (bottom). The first wet-dry phase was excluded due to differences in vegetation development.
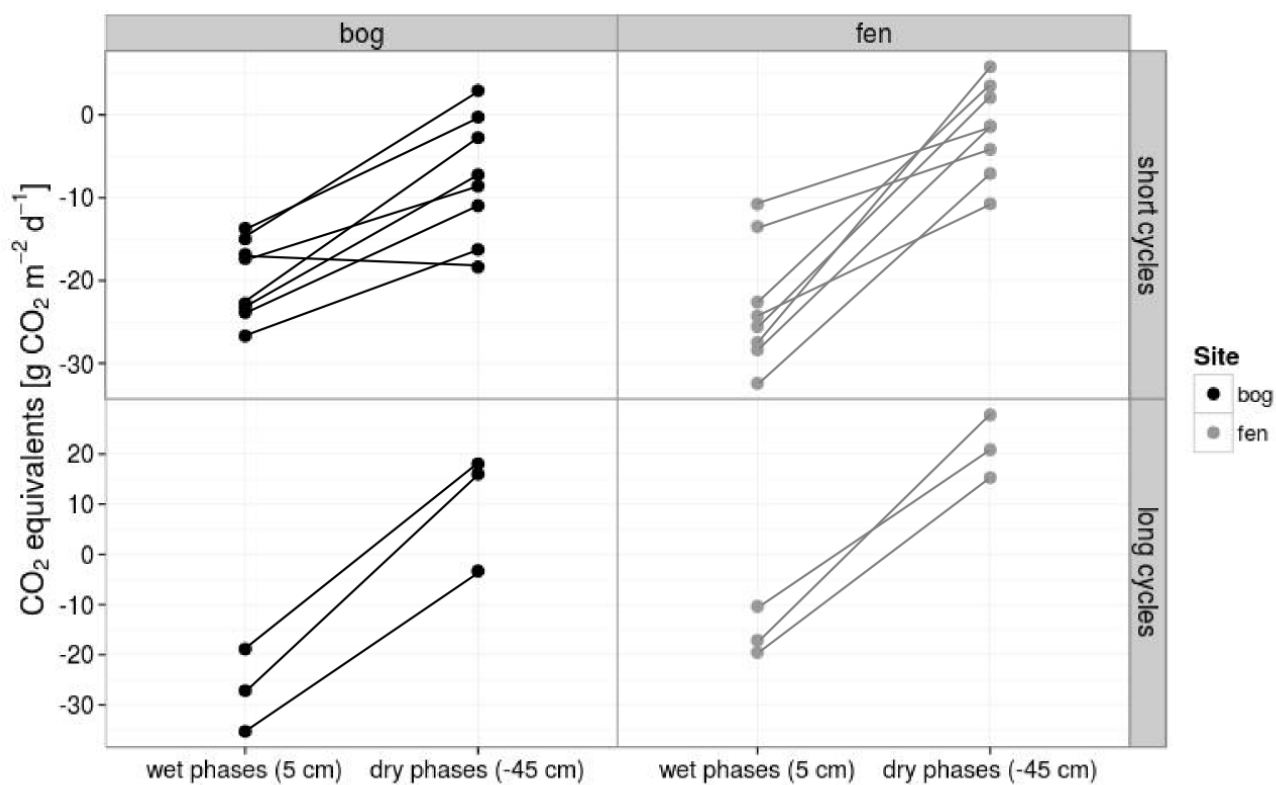
Appendix

App-Tab. 4-1: Biomass in bog and fen grassland in individual mesocosms at incubation end separated in the four fractions as presented in Fig. 4-3 (green leaves, brown leaves, algae present in the inundation tank and other dead matter) for both water table regimes (short and long cycles)

dynamic water table change in	Biomass [kg dry weight m^{-2}]			
	short cycles		long cycles	
	bog	fen	bog	fen
green leaves	0.35	0.22	0.12	0.10
	0.40	0.17	0.37	0.09
	0.16	0.29	0.29	0.23
brown leaves	0.60	0.27	0.50	0.08
	0.71	0.26	0.74	0.16
	0.48	0.64	1.19	0.14
algae	0	0	0.07	0
	0	0	0.02	0
	0	0	0.01	0
other dead matter	0.06	0	0.21	0.06
	0.03	0.02	0.15	0.08
	0.15	0	0.27	0

App-Fig. 4-1: Difference between wet and subsequent dry phases in CO_2 equivalents at dynamic water table shifts in short (left) and long (right) cycles of bog (black) and fen (grey) grassland mesocosms. The first wet-dry phase was excluded to to differences in vegetation development.
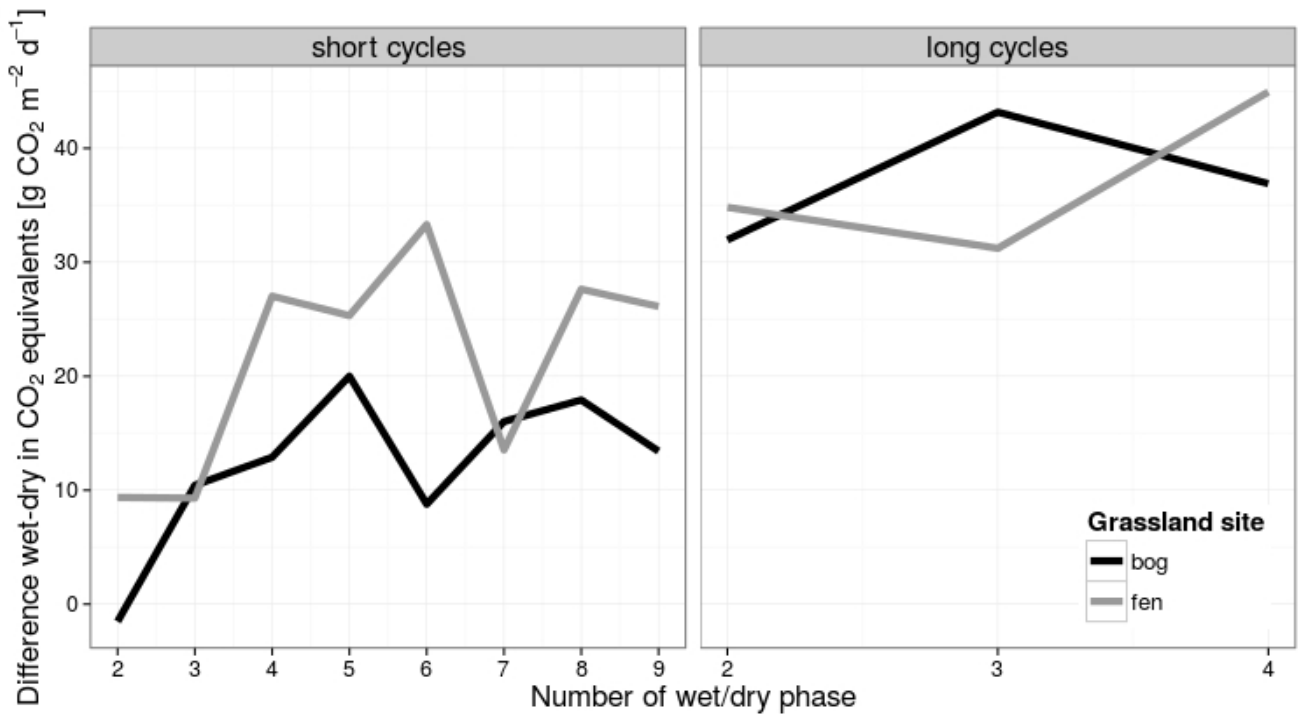
Chapter 5: Comprehensive discussion and conclusions

The first part of this chapter comprises a summary of the most important results from the incubation experiments (summary of Chapter 2, 3 and 4) and is structured based on the research questions of the three publications complemented with information in relation to our own expectations and knowledge from the literature.

In the second part, the implications for GHG mitigation by rewetting measures are given based on the presented results.

In the last part, we give general recommendations for practical rewetting.

5.1 Summary of results

5.1.1. The effect of the organic substrate for CO_2 and CH_4 emissions

Research questions:

What are the possible sources of the high CO_2 and CH_4 emissions on-site after rewetting? How do organic substrates from different depths or including/exluding fresh plant litter contribute to anaerobic GHG production? We hypothesize that the fresh plant litter can account for a large proportion of the increased CH_4 and CO_2 emissions.

- The hypothesis was confirmed by our incubations. The presence of fresh organic matter determines anaerobic GHG production – and not the quality of the bulk peat substrate itself.

- The newly-formed organic sediment layer has an extremely high potential for CH_4 production. The vegetation growing at the site was very productive and produced a large carbon pool before its dying-off. The main part thereof was presumably transferred to the organic sediment layer. The release of CH_4 could stay high – at least as long as eutrophic and inundated conditions last.

- Pure peat without any fresh plant-derived material seems to be relatively inert. Significant methane emissions cannot be expected from pure peat layers under permanently inundated conditions in the field as long as readily degradable substances are lacking.

- CO_2 and CH_4 production may occur to some extent when some labile organic matter is available, e.g from rhizodeposition or fresh litter from plant roots. CH_4 production will start after an extended lag-phase depending on the availability of alternative electron acceptors after rewetting. This available carbon pool is more limited than in the newly formed sediment layer.

- The risk of high CO_2 and CH_4 emissions after restoration is limited to waterlogged / flooded conditions and the simultaneous presence of readily degradable and energy-rich substrates for microbial decomposition processes (i.e. eutrophic peat, fresh plant litter, or newly formed organic sediments, e.g. from plants that are not adapted to flooding).

When do conditions favourable for methanogenesis occur?

- Incubation experiment performed immediately after flooding: Methanogenesis started after the complete depletion of sulfate after a 182-day lag-phase and took place only in the upper peat layer.

- Incubation after 2.5 years of flooding: The substrates for this incubation were under anaerobic conditions in the field for 2.5 years and conditions favourable for methanogenesis were established very quickly.

5.1.2. The effect of the water table on GHG fluxes: stepwise rewetting and prolonged flooding

Research questions:

How does the vegetation react to raising water level and extended flooding (water-intolerant grasses versus water-tolerant sedges)? How does the contribution of autotrophic and heterotrophic respiration change with water table?

- Under gradual rewetting (from -30 cm to 0 cm) the vegetation reacted with reduced vitality. Flooding – raising the water table from 0 cm to +5 cm – imposed a shock on the vegetation. Sedges generally had a lower productivity but recovered after several weeks of water stress while grasses partially died-off. Permanent flooding led to increased availability of readily degradable matter from recently died-off plants.

- Auto- and heterotrophic respiration were gradually reduced in both grasses and sedges which was to be expected.

Are there water table thresholds for drastic changes in GHG fluxes? At which water table position are net GHG emissions minimal? How are GHG fluxes affected by extended flooding?

- We present data on the functional role of the water table position on GHG exchange under controlled environmental conditions – which are still scarce in the literature. We are the first to use peat mesocosms with grassland vegetation typical for German fen management.

- The most favourable water table positions for minimal GHG fluxes range from -10 cm to 0 cm. This finding confirms recommendations for an optimum water table in the literature (e.g by (Drösler et al. 2008) or (Jungkunst et al. 2008)) and is based on the balance of all three GHGs (CO_2, CH_4 and N_2O).

- Stepwise raising the water table from -30 cm up to 0 cm reduced gross primary production (GPP) and ecosystem respiration (R_{eco}) leading to an increased net CO_2 uptake while CH_4 and N_2O emissions were still low. Gradual rewetting increased the net GHG uptake by 0.6 (segdes) to 0.8 (grasses) g CO_2-equivalents m^{-2} d^{-1} per cm water table raise.

- The most drastic change in GHG balance occurred with flooding which caused a significant reduction of GPP and simultaneous increase in R_{eco} and CH_4 emissions due to increased substrate availability. The flooding event caused immediate extra GHG emissions of 27 g CO_2- equivalents m^{-2} d^{-1} in grasses and 22 g CO_2-equivalents m^{-2} d^{-1} in sedges.

Raising the water table above the peat surface (flooding) has nearly cancelled the positive climatic effect in grasses compared to the driest phase (water table of -30 cm) because the lower net CO_2 uptake was more than compensated by CH_4 emissions in terms of CO_2-equivalents. In segdes, CH_4 never risked to compensate the net CO_2 uptake – the positive climatic effect was halved after flooding.

- This results confirmed the argument that the positive climate impact of rewetting may be considerably reduced when the soil is completely waterlogged due to increased CH_4 emissions. We showed that a water table above the peat surface (flooding) bore the greatest risk – not only because of increasing CH_4 emissions (as expected) but also because of increased CO_2 loss from respiration.

What is the effect of aerenchymous plants? Do sedges boost CH_4 emissions under wet conditions due to plant mediated CH_4 transport?

- Sedges did not boost CH_4 emissions under wet conditions.

- These aerenchymous plants allowed the transport of oxygen into deeper soil horizons and stabilized the redox potential. Redox conditions favourable for CH_4 production occurred ~30 days later, CH_4 production was lower and CH_4 never risked to compensate the net CO_2 uptake in the sedges mesocosms.

5.1.3. The effect of the water table on GHG fluxes: alternating wet-dry conditions

Research questions:

How do grassland vegetation, photosynthesis, respiration, CH_4 and N_2O fluxes react to a dynamic change in the water table from wet to dry conditions and vice versa? How do wet respectively dry conditions affect the net GHG balance?

- The grassland vegetation which has low flooding tolerance adapted well to wetness stress. The bog grassland showed higher biomass production and partially died-off leading to dead organic matter accumulation. The fen grassland exhibited slower growth but lower mortality.

- The capacity to fix CO_2 by photosynthesis (GPP) was unaffected by the dynamic change in water table in both grasslands. This is in agreement with the literature where it has been shown that GPP is rather affected by radiation and not by water level (Lindroth et al. 2007; Leiber-Sauheitl et al. 2014).

- Respiration was two to three times higher under dry conditions and reacted fast to abrupt water table changes. The considerable increase in peat mineralization under drainage was expected.

The reaction of R_{eco} to the strong water table fluctuations took place within days in our incubation experiment and has – to our knowledge – not been studied in such temporal resolution in the field.

This immediate R_{eco} response to water table change may have a significant effect on the annual CO_2 balance in peatlands and should be taken into account in gap-filling and interpolation procedures.

- Net ecosystem exchange (NEE) was driven by the water table driven variation in heterotrophic soil respiration.

- CH_4 flux rates were low despite the large amount of dead biomass and warm conditions. We had expected that the re-established water saturated conditions would favour methanogenesis much more strongly. N_2O emissions showed no response to changes in water table position.

- With regard to GHG balance, both grasslands acted as GHG sink under wet conditions (+5 cm). Lowering the water table (to -45 cm) turned the grasslands into a GHG source. Intermittent drainage reduced the GHG sink strength (by 12.2 in bog and 21.5 g CO_2-equ. m^{-2} d^{-1} in fen when wet phases were relatively short). This reduction in GHG sink strength with draining was higher when wet phases were long (by 37 g CO_2-equ. m^{-2} d^{-1} in both grasslands) as more readily degradable organic matter was available for aerobic respiration processes.

Is the response fully reversible when water table switches back to the original position, and repeatable? Is there a memory effect of previous flooding or drainage events?

- The response of the redox potential to water table switches was fully reversible and repeatable.

- CH_4 fluxes showed no indication of legacy effects.

- A small legacy effect of past flooding was found for CO_2. The dynamic water table change stimulated CO_2 sources. Respiration rates and net GHG emissions increased from one dry phase to the next which suggests a substrate mobilization effect. However, this stimulation by past wet-dry cycles is small compared to response to the change from wet to dry conditions.

What length of interim dry periods is needed to effectively reduce CH_4 emissions?

- Intermittent flooding as low-CH_4-emission-strategy – as done in paddy rice fields – has proven to be successfully applied in peatlands.

- Intermittent drainage of peat grasslands led to a renewal of the electron acceptor capacity. The oxidative status of the peat soils was recovered within one week of dry conditions.

- Wet conditions had to occur for up to 20 days until conditions in the topsoil of the peat were favourable for methanogenesis.

Do wet-dry cycles foster N_2O emissions?

- Alternating wet-dry conditions did not increase the risk of high N_2O emissions in the peat grasslands investigated. This finding is in contrast to our expectations and to the literature

where a fluctuating water table is generally considered to increase N_2O emissions. The dominant mineral nitrogen form in these organic soils was ammonium with low concentrations – this suggests that the determinant factor for the low N_2O emission potential was substrate availability.

Can alternating water tables work as low-GHG management strategies in peat grasslands?

- With regard to low CH_4 emissions: yes. Intermittent dry periods of one week will prevent high CH_4 emissions as they restore the oxidative status in the peat.

- Lowering the water table bears the risk for increased CO_2 emissions through heterotrophic respiration which was shown to be 2 to 3-fold higher under drained conditions. Therefore, intermittent dry phases should be kept as short as possible. This risk is higher with higher availability of readily degradable organic matter from recently died-off vegetation.

- In order to balance between CH_4 avoidance and increased CO_2 release, an intermittent period of one week under dry conditions is long enough to reset the soil conditions with minimal memory effects of previous water table conditions.

5.2. Implications for GHG mitigation by rewetting

The incubation experiments of this PhD thesis aimed to investigate some of the processes considered most important and selected factors that determine GHG fluxes – that means we investigated a few aspects of the whole complex picture. We manipulated key factors controlling GHG fluxes under controlled environmental conditions – a direct comparison of our results with results from field measurements should, therefore, be handled with caution. Furthermore, the experiments were performed with mesocosms from grassland sites – which represent the most wide-spread land-use on organic soils in Germany – but the resulting implications may not necessarily be applied to other peatland sites with different properties or differing land-use. Therefore, the recommendations given below should be seen within the limits set by laboratory experiments and do not claim to reflect all the complex processes involved in GHG production and emission from peatlands.

Peatland management aiming to reduce GHG emissions should consider the following recommendations derived from our findings. The recommendations are given in italic type, the text below presents further explanations and information derived from our experiments.

Avoid deeply drained conditions because of high CO_2 losses.

- When the peat is drained, CO_2 release by heterotrophic respiration increases immediately and considerably. CO_2 loss under drained conditions was two to three fold compared to wet conditions.

- Every wet day saves soil carbon, in particular during the vegetation period when biological activity is high. Therefore, intermittent dry phases – aiming to avoid high CH_4 emissions – should be kept as short as possible.

- This confirms in general our expectations and general knowledge in the literature and

emphasizes the importance of carbon loss at a low water table.

Conditions favourable for methanogenesis only occur after a lag-phase. A short intermittent dry period prevents high CH$_4$ production.

- Mitigation strategies for rice paddies can also be applied in peatlands. This has not been investigated so far.

- After the water table has been raised to re-create water saturated conditons, it takes weeks to establish conditions favourable for methanogenesis. This lag-phase depends on how fast alternative electron acceptors are depleted and cannot be generalized as it strongly depends on on-site conditions. Already a short period under dry conditions rapidly restores the oxidative status in the peat soil and re-creates the lag-phase. One week of dry conditions prevents high CH$_4$ emissions for weeks.

Aerenchymous plants retard methanogenesis by stabilizing the redox potential.

- Based on our findings, we could not confirm an increase of CH$_4$ release via plant mediated transport in aerenchymous plants.

- Aerenchymous plants stabilized the redox potential by allowing O$_2$ transport into deeper peat horizons and, consequently, retarded the onset of CH$_4$ production and lowered CH$_4$ emissions.

- There is not necessarily an increase in CH$_4$ emissions when wetness-adapted sedges replace a non-adapted grassland vegetation after rewetting. This finding is in contrast to what we would expect based on the information given in the literature on plants with aerenchymous tissue.

A water table slightly below the surface minimizes GHG emissions.

- Ideally, the water table is kept slightly below the soil surface (at -10 cm to 0 cm depth), which allows grassland vegetation to grow well and simultaneously limits heterotrophic respiration. In the shallow aerobic layer near the peat surface CH$_4$ oxidation may take place. This confirms recommendations of an optimum water table position given in the literature so far.

- Flooding, however, imposes a shock on vegetation, even on wetness-adapted sedges. Lowered GPP during a transition phase or higher mortality reduces net CO$_2$ uptake. Flooding extended over several weeks also increases CH$_4$ emissions.

There was no risk of high N$_2$O emissions in our experiments.

- Alternating wet-dry phases did not foster N$_2$O emissions in our experiments in contrast to our expectations.

- N$_2$O may be important in agriculturally used peatlands due to fertilization. On our sites, low mineral nitrogen and very low nitrate concentrations were present. The results may not

necessarily be generalized. Therefore, we recommend to check soil properties for risks of high N_2O emissions.

Rewetting measures should aim to support plant vitality and to avoid partial or complete dying-off of the vegetation.

- In general, climate change mitigation aims to preserve respectively to re-establish peat formation (i.e. preserving the carbon reservoir). However, the living above-ground vegetation plays an essential role in GHG production as it provides readily degradable organic matter as substrates for microbial decomposition processes – while the old peat substrate is of minor relevance.

- Abruptly raising the water table will naturally affect plant vitality. When rewetting produces permanently inundated conditions on eutrophic fen grasslands, plant species not adapted to this wet conditions presumably will die-off provoking increasing GHG emissions by providing the substrates.

- Rewetting should, therefore, be accompanied by support for a vegetation transition towards wetness-adapted species as mal-adaptation leads to reduced GPP and provides substrate for CH_4 and CO_2 production from died-off plant parts.

- Gross primary production (i.e. the capacity to fix CO_2) is an essential part of the GHG balance. Investigating net GHG emissions without considering the uptake of CO_2 via plants is incomplete and unsuitable for conclusions on the whole GHG balance of a peatland site.

5.3. Recommendations for practical rewetting

- Rewetting aiming to low-GHG-emissions should at best re-establish near-natural conditions with respect to the water table – i.e. a water table slightly below the peat surface – and a vegetation adapted to this water saturated conditions.

- Avoid permanent or extended phases of flooding as this severely effects vegetation vitality and produces GHG emissions comparable to grasslands drained to -30 cm depth. This transitional phase should be overcome as quickly as possible. Allow a vegetation transition towards wetness-adapted species.

- In situations where rewetting has led to extended flooding during the vegetation period with a risk of high CH_4 emissions, allow intermittent dry periods of one week to keep CH_4 emissions low.

- Check mineral nitrogen concentrations in the peat to identify potential risks of high N_2O emissions.

5.4. Bibliography

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Glossary

acrotelm	zone above the mean water table within a peat profile with aerobic conditions
aerenchymous plants	plant species possessing tissues (e.g. in their stems, leaves, rhizomes) which enable internal air circulation. These plants allow the exchange of gases between the rhizosphere and the atmosphere and are also called „shunt species". They provide a short-cut (shunt) for gas transport which is of particular importance with respect to CH_4 emissions.
autotrophic respiration	is the production and of CO_2 by autotrophic organisms (e.g. plants and algae; being able to fix carbon by photosynthesis)
bog	is a peatland receiving its water mostly by precipitation and which is, consequently, generally nutrient-poor and acidic (ombrotrophic)
bulk density	is peat mass per unit volume (given in g m^{-3}) and inversely related to the porosity. The bulk density of peat varies depending on its botanical composition and degree of peat decomposition.
carbon sequestration	long-term storage of CO_2, e.g. by peat formation
catotelm	zone below the mean water table with anaerobic conditions
CH_4	methane. This non-toxic, but extremely flammable gas is naturally produced by microbial processes (see methanogenesis). Methane is a major greenhouse gas with a global warming potential 25 times higher than carbon dioxide over a 100-year period.
climate impact	Greenhouse gases emitted into the atmosphere absorb infrared radiation radiated from the Earth`s surface and re-radiate this energy causing an increase in global temperature („greenhouse effect"). The GWP methodology is used to assess and compare the climate impact of different peatlands.
CO_2	carbon dioxide; is a naturally-occurring chemical compound and part of the carbon cycle (carbon fixation via photosynthesis, carbon dioxide release by respiration). Carbon dioxide is an important greenhouse gas and the increase of carbon dioxide concentration in the atmosphere has led to global warming.
CO_2 equivalent	indicates the radiative forcing of a greenhouse gas emission rate over a defined timescale (100 years) relative to carbon dioxide. It is calculated based on the gas flux rate and the GWP of the gas.

denitrification	is the reduction of nitrate or nitrite to molecular nitrogen by heterotrophic facultative anaerobic bacteria. N_2O is produced within this process as intermediate product.
DOC	dissolved organic carbon, i.e. organic carbon which remains in solution after filtration (typically with 0.45 µm filter)
drainage	is the direct human-induced lowering of the soil water table
ecosystem respiration	see under R_{eco}
fen	is a peatland receiving its water by rainfall and from surface water, having a higher nutrient level and lower acidity (minerotrophic)
flooding	raising the water table above the surface
gas chromatography	analytical method to separate und qualitatively and quantitatively analyse the compounds in a sample. In this PhD, this method was used to determine gas concentrations in air samples.
GHG	greenhouse gases. The abbreviation stands for the three key greenhouse gases carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O).
GHG balance	is the sum of the three key GHGs (CO_2, CH_4 and N_2O) in terms of CO_2 equivalents
GHG flux	rate of gas flow emitted from a defined area and over a certain amount of time. All GHG fluxes in this PhD thesis are considered relative to the compartment „atmosphere", i.e. fluxes from the soil to the atmosphere are positive – increasing the atmospheric concentration – and fluxes from the atmosphere into the soil/peat are negative – decreasing the atmospheric concentration.
GPP	gross primary production – uptake and fixation of CO_2 by photosynthesis in plants
GWP	global warming potential, a measure of the radiative forcing of a gas relative to CO_2. The GWP is calculated over a specific time interval, e.g. 20, 100 or 500 years. The GWP methodology within the *Kyoto Protocol* uses the 100-year horizon.
heterotrophic respiration	is the production of CO_2 by heterotrophic organisms (e.g. animals, fungi, heterotrophic bacteria; which do not have the ability to fix carbon)
IPCC	the *Intergovernmental Panel on Climate Change*, a scientific intergovernmental body under the auspices of the United Nations which produces reports supporting the UNFCCC

linear mixed effects model	is a statistical model containing fixed and random effects and modelling both effects as having a linear form. Fixed effects are identical for all groups in a population while random effects are allowed to differ from group to group.

Mixed effects models are used to describe relationships between a response variable and some covariates in data that are grouped according to one ore more classification factors (e.g. repeated measures data, etc.).

In a linear mixed effects model, the response variable is contributed to by additive fixed and random effects as well as an error term:

$$y_{ij} = \beta_1 x_{1ij} + \beta_2 x_{2ij} \ldots \beta_n x_{nij} + b_{i1} z_{1ij} + b_{i2} z_{2ij} \ldots b_{in} z_{nij} + \varepsilon_{ij}$$

where

y_{ij} is the value of the response variable for a particular ij case,

$\beta_1 \ldots \beta_n$ are the fixed effect coefficients (like regression coefficients) which are identical for all groups,

$x_{1ij} \ldots x_{nij}$ are the fixed effect variables (predictors) for observation j in group i (the first regressor is usually for the constant, $x_{1ij} = 1$).

$b_{i1} \ldots b_{in}$ are the random effect coefficients for group i, assumed to be mulivariately normally distributed and vary by group.

$z_{1ij} \ldots z_{nij}$ are the random effect variables (predictors), and

ε_{ij} is the error for case j in group i. The errors for group i are assumed to be mulivariately normally distributed.

LULUCF	land use, land-use change and forestry (according to EU decision 529/2013/EU)
mesocosm	peat columns including vegetation cut out from selected peatland sites used for incubation experiments in the climate chamber. The mesocosms were incubated under environmental conditions similar to field conditions and subjected to water table manipulation (see Chapter 3 and 4 of this PhD thesis).
methane oxidation	is the utilization of methane by microorganisms (methanotrophs) for their metabolism; is taking place in the aerobic zone in the peat profile
methanogenesis	is the production of methane during the (anaerobic) decomposition of organic matter by microorganisms. Methane production only occurs in anaerobic environments.
methanogens	strictly anaerobic microorganisms of the group *Archaea* producing methane
mineralization	see peat oxidation

N$_2$O   nitrous oxide. Naturally, this colourless, non-toxic gas is produced in the soil during microbial processes (see nitrification and denitrification). Nitrous oxide is a major greenhouse gas and has – considered over a 100-year period – a global warming potential 298 times higher than carbon dioxide.

NEE   net ecosystem exchange of of CO_2 – that it is the balance between gross primary production and ecosystem respiration

nitrification   is the microbial oxidation of ammonia to nitrite and into nitrate where N$_2$O may be produced as a side product. It is a strict aerobic process.

organic sediment   is a deposit of organic material that originates from recently died-off plants and water plants and sand deposited at the bottom of the shallow lake which formed after rewetting. This term is used in the context of Publication I (see Chapter 2 of this PhD thesis).

organic soils   are characterized by their (high) organic matter content and a minimum depth of the organic layer. The existing classification systems have different criteria for organic soils.

PAR   photosynthetically active radiation – those part of the (solar) radiation that is used for photosynthesis by photosynthetic organisms (the wavelength from 400 to 700 nm). PAR is quantified as µmol photons $m^{-2} s^{-1}$.

peat   is a „soft, porous or compressed, sedentary deposit of which a substantial portion is partly decomposed plant material with high water content in the natural state".

peat compaction   volume reduction of peat in the aerated zone above the water table. It results from the pressure applied on the peat surface by heavy equipment. Peat compaction lead to an increase in peat bulk density.

peat consolidation   the compression of saturated peat below the water table owing to loss of buoyancy of the top peat, increasing strain on the peat below. Consolidation increases the peat bulk density of the peat.

peat oxidation   decomposition of peat in the aerated zone above the water table (minerlization). Peat oxidation is caused by the breakdown of organic matter and results in carbon loss through the release of gaseous CO_2 to the atmosphere. The bulk density of the peat is not affected by peat oxidation.

peat shrinkage   volume reduction of peat in the aerated zone above the water table. It occurs through contraction of organic fibres when drying. Shrinkage also leads to an increase in the bulk density of the peat.

peatland   is an area with a naturally accumulated peat layer at the surface

photoacoustic infra-red gas analysis	analytical method to determine the concentration of a gas. The gas to be measured is irradiated by light of a pre-selected wavelength. The gas molecules absorb some of the light energy and convert it into an acoustic signal which is detected by a microphone.
plant mediated gas transport	gas transport via the tissue of aerenchymous plants
R_{eco}	ecosystem respiration – which is the sum of autotrophic and heterotrophic respiration in a specific ecosystem
REDD+	*Reducing Emissions from Deforestation and Forest Degradation* – a mechanism by the UNFCCC for climate mitigation
redox potential	may be used to qualitatively estimate a soil state. As biogeochemical processes in water-saturated soils take place within a defined range of redox potential values, e.g. CH_4 production, we use the redox potential to identify situations where conditions are favourable for CH_4 production (see Chapter 3 and 4 of this PhD thesis).
rewetting	is the deliberate action of raising the water table on drained soils to re-establish water saturated conditions, partially or totally reversing drainage
subsidence	lowering of the surface caused by peat oxidation and physical volume reduction of the peat
UNFCCC	the *United Nations Framework Convention on Climate Change* – the main international treaty on climate change
water table	is the surface of a body of underground water below which the soil or rocks are permanently saturated with water. The water table separates the groundwater zone (zone of saturation) that lies below it from the zone of aeration that lies above it. The water table fluctuates both with the seasons and from year to year because it is affected by climatic variations and by the amount of precipitation used by vegetation (http://www.merriam-webster.com/dictionary).
wetland	is a land with soil inundated or saturated by water. A peatland falls under the definition wetland. A Wetland represents an IPCC land-use category.

List of Figures

21 In order to be in line with the numbering of the figures in the already published Publication I the numbering
    deviates slightly from those in other chapters – leaving out the chapter number in the first place.

List of Tables

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22 In order to be in line with the numbering of the tables in the already published Publication I the numbering
    deviates slightly from those in other chapters.

Curriculum vitae

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01/2007 – 03/2015   **Doktorarbeit**, Max Planck Institut für Biogeochemie, Jena (DL), Abteilung Biogeochemische Prozesse, zum Thema „Water table and organic substrate as triggers of greenhouse gas emissions from rewetted peatlands"

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06/2000 – 04/2006   **Fachreferentin**, Umweltbundesamt Wien (AT), Abteilung Chemikalien - Fachbereich Ökotoxikologische Bewertung von Chemikalien

03/1997 – 05/1999   **Diplomarbeit**, Universität Wien (AT), zum Thema „Spurengas-Emissionen aus Buchenwald-Ökosystemen im Wienerwald"

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10/1992 – 06/1999   **Diplomstudium**, Universität Wien (AT), Studienrichtung Biologie, Studienzweig Ökologie

06/1992   **Matura**, Höhere Lehranstalt für wirtschaftliche Berufe, Zwettl (AT)