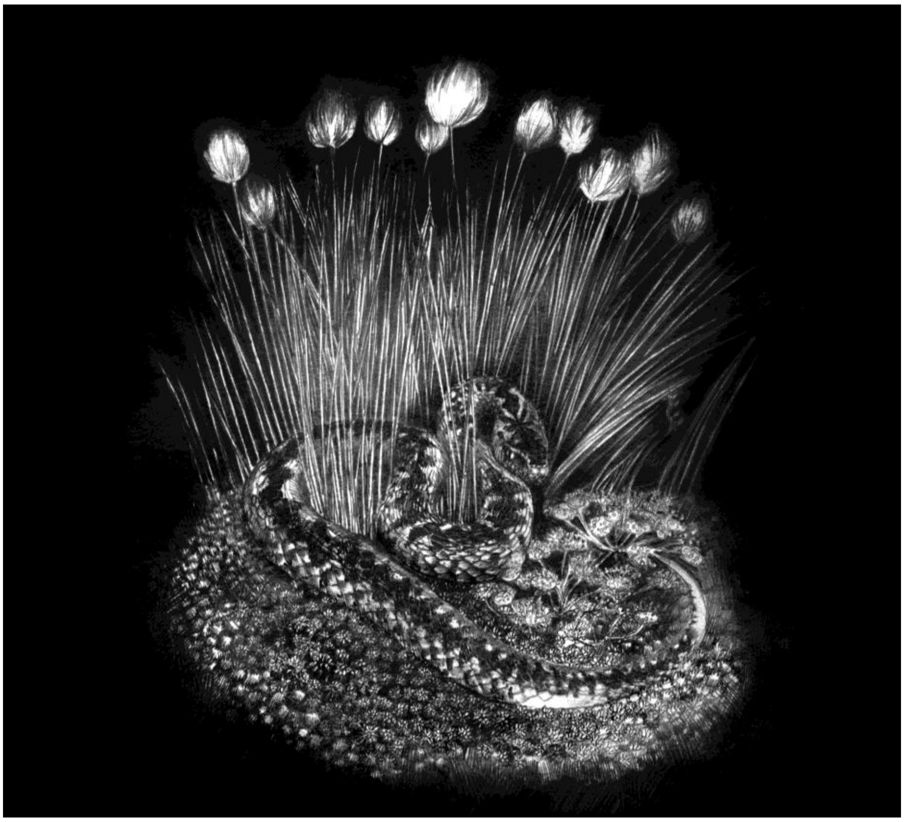
Sphagnum in a changing world – from the landscape to the isotope scale



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Sebastian Roman Schmidt
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It had something to do with the rain (The Weakerthans)

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Abstract

Peatlands play an important role in the global carbon cycle. Despite covering only 3% of the World's land area, they store up to 460 Gt carbon, representing up to one-third of the global soil carbon pool and almost the same amount of carbon that is stored in the terrestrial biosphere. Peatlands are an important long-term carbon sink because they sequester and store atmospheric carbon for thousands of years. It is assumed that future climate change might alter the floristic composition of peatlands and concomitantly their potential to accumulate carbon. An essential element for the development of raised bogs and carbon sequestration in peatlands are peatmosses of the genus *Sphagnum*. Peatlands' carbon sequestration is highly dependent on the productivity of *Sphagnum* mosses, which in turn depends on environmental conditions and particularly on peatlands' moisture conditions.

The objective of this study was to estimate the effects of global change on ombrotrophic bogs in the metropolitan region of Hamburg (MRH) in general and the performance of *Sphagnum* mosses in particular. Beside the overall threat to peatlands caused by intensive land use, multiple interacting processes between soil, water, vegetation and the atmosphere complicate evaluating the impact of projected climate change scenarios on peatlands and their possible feedback to climate. Therefore, I combined various field analyzes and measurements in relation to given environmental conditions and laboratory experiments under controlled conditions, considering different processes at different temporal and spatial scales. In a first step, I provide an overview of peatlands development and their actual distribution for the MRH on a regional scale (**chapter 1**). Secondly, I identified two bogs (Hartshoper Moor and Schweimker Moor) – reflecting the climatic gradient within the MRH – and conducted a manipulative field experiment whereby I reduced precipitation by 25% with rainout shelters and imitated nitrogen deposition by fertilization (equal to 30 kg N ha^{-1} a^{-1}). The experiment ran at two peatlands in the MRH from 2010 to 2012. On the plant community scale, I observed the vegetation cover and possible shifts of the floristic composition over three years. On the plant species scale, I analyzed the biomass production and litter decomposition of single *Sphagnum* and vascular plant species that were dominant at the study sites (**chapter 2**). Furthermore, I investigated carbon gas fluxes on the plant community scale, albeit only for five days in 2011. I analyzed the uptake of CO_2 as net ecosystem exchange (NEE), the sum of gross primary productivity (GPP) and ecosystem respiration (R_{eco}), as well as emissions of CH_4 (**chapter 3**).

To obtain insights into underlaying mechanisms influencing the productivity and the carbon cycling of single *Sphagnum* species, I conducted laboratory experiments under controlled conditions. I analyzed the photosynthetic and respiratory characteristics of a single species (*S. cuspidatum*) to determine the potential productivity under varying moisture conditions including the potential to recover after a prolonged drought in spring 2011 (**chapter 4**). Besides examining the photosynthetic capacity of *S. cuspidatum*, I also investigated the discrimination of carbon stable isotopes during photosynthesis of *S. cuspidatum* and *S. papillosum*, depending on their water content. I used the Cavity Ring-Down Spectroscopy technique to measure carbon stable isotopes during gas exchange of the mosses. I combined the results obtained in the laboratory experiments with observations in the field to retrace the growing conditions at the study sites, and - including a literature review – I estimated the potential of *Sphagnum* to recycle substrate-derived CO_2 and reduce CH_4 emissions in peatlands (**chapter 5**). I used the combined information of field and laboratory experiments to estimate the impact of global change on *Sphagnum* and peatlands in the MRH, as well as their possible feedback to the climate system. Finally, I evaluated the implications for nature conservation regarding the protection of (semi-)natural and the restoration of degraded and excavated bogs, highlighting future challenges induced by global change (**chapter 6**).

I found evidence that drier conditions might lead to changes in the vegetation composition, stimulating the growth of vascular plants at the expense of peatmosses (**chapter 2**). Vegetation responded to nitrogen addition in multiple ways, but none of the observed implications was positive with respect to *Sphagnum* performance and carbon sequestration. Fertilization directly affected *Sphagnum* through productivity being slightly lowered, presumably due to toxic reactions of N surplus. Indirectly, *Sphagnum* was affected by mortality caused by the infection with its parasite fungus *Lyophyllum palustre* or by stimulated growth of *E. vaginatum* and consequently an increased negative effect of shading. The presence of vascular plants such as *Eriophorum* might facilitate the recolonization of peatmosses in degraded peatlands, although the risk that stimulated growth might overrule positive effects on *Sphagnum* growth (e.g. by stimulating greenhouse gas emissions or shading) should be taken into account (**chapters 2, 3 & 6**).

Nevertheless, if competition with vascular plants is not a threat for *Sphagnum*, I showed that varying hydrological conditions in two experimental years – with a prolonged drought period in spring 2011 – only had small effects on its productivity suggesting certain resilience to the desiccation of both – hollow and hummock – *Sphagnum* species. *Sphagnum* was able to adapt to varying moisture conditions during the growing season and regarding their microhabitats (**chapters 2, 4 & 5**). At low water levels and concomitant low capitulum water contents, mosses grew in a dense carpet to enhance their water holding capacity. By contrast, at high water levels, the mosses reduced their growth density, presumably to avoid diffusion resistance caused by a thick water film. Nevertheless, mosses reached their highest productivity at intermediate water levels, but next to hydrological conditions, the morphological plasticity itself had a strong impact on productivity (**chapter 4**). *Sphagnum cuspidatum* was able to withstand severe desiccation, even if recovery was slow. My study indicates that *Sphagnum* mosses are able to adapt to changing hydrological conditions and resist single extreme weather events. However, if the capitulum water content is below or above the specific optimum for photosynthesis, carbon accumulation might be significantly reduced. Based on these results, carbon sequestration in peatlands might be altered substantially as a consequence of changing hydrological conditions due to future climate change. Carbon stable isotope analyses during moss photosynthesis and $\delta^{13}C$ values of

Sphagnum biomass obtained in the field, revealed that isotope discrimination differed between species (*S. cuspidatum* and *S. papillosum*) and microhabitats (hummock and hollow); moreover, it was strongly correlated with capitulum water content (**chapter 5**). Both, species-specific variation as well as differences between microhabitats could be attributed to adaptations to prevailing moisture conditions in the field. Nevertheless, I demonstrated that varying moisture conditions alone cannot explain the isotopic signature of *Sphagnum*; instead the use of different CO_2 sources by *Sphagnum* strongly contributes to $\delta^{13}C$ values. I developed two empirical models relating the carbon isotope composition of the *Sphagnum* biomass to the water content during the growing season and the carbon isotope composition of the source CO_2. Applying these models to published $\delta^{13}C$ values, I showed that up to 30% of *Sphagnums* assimilated carbon was recycled from substrate-derived CO_2.

The study site was a weak sink of carbon when the water level was high, impeding heterotrophic peat respiration, and the temperature was low, impeding the production and emission of CH_4 (**chapter 3**). In turn, when the water table was low, CO_2 was released, and after rewetting CH_4 emission was enhanced, at least in combination with high temperatures in summer. Thus, I suggest that projected climate changes with warmer and drier summers might have a negative impact on carbon sequestration in temperate peatlands, especially in the case of prolonged drought events with rewetting processes following in summer months. Furthermore, decomposition rates of vascular plant litter were higher than those of *Sphagnum* litter (**chapter 2**). Thus, replacing the living *Sphagnum* layer and its recalcitrant tissue will presumably lead to a decrease in carbon sequestration in dry peatlands, even if an enhanced productivity of vascular plant biomass might partly compensate the carbon loss. My results confirmed the earlier findings that the litter of hummock species is more resistant to decay compared to hollow species. The observed good performance of transplanted *S. papillosum* into the relatively wet carpet of *S. cuspidatum* underpins the suggestion to (re-)introduce target species to degraded peatlands to enhance restoration measures and the function of peatlands to sequester carbon (**chapter 2 & 6**). However, for the protection of the last remaining (semi-)natural *Sphagnum*-bogs and for the restoration of degraded and excavated bogs, it is necessary to adjust management to local circumstances. Finally, long-term monitoring of existing restoration measures should include preceding climate change observations to evaluate recent restoration success and future climate change projections should be integrated when planning restoration measures to assess the (local and regional) success of *Sphagnum* development in the future (**chapter 6**).

Zusammenfassung

Moore spielen eine wichtige Rolle im globalen Kohlenstoffkreislauf. Obwohl Moore weltweit nur 3% der Landoberfläche bedecken, speichern sie bis zu 460 Gt Kohlenstoff, dies entspricht etwa einem Drittel der in Böden gespeicherten globalen Kohlenstoffvorräte und etwa derselben Menge Kohlenstoff der in der terrestrischen Biomasse gespeichert ist. Moore sind bedeutende langfristige Kohlenstoffsenken, weil sie atmosphärischen Kohlenstoff für tausende Jahre festlegen und speichern.

Der zukünftige Klimawandel könnte die pflanzliche Artenzusammensetzung von Mooren und damit ihr Potential, Kohlenstoff anzureichern, verändern. Ein wesentlicher Faktor für die Entwicklung von Hochmooren und Kohlenstofffestlegung in Mooren sind Torfmoose der Gattung *Sphagnum*. Die Kohlenstofffestlegung der Moore hängt stark von der Produktivität der *Sphagnum*-Moose ab, diese wiederum ist durch Umweltbedingungen und besonders durch den Wassergehalt in Mooren bedingt.

Das Ziel dieser Studie war, die grundlegenden Effekte des globalen Wandels auf ombrotrophe Hochmoore in der Metropolregion Hamburg sowie auf die Entwicklung von *Sphagnum*-Moosen zu untersuchen. Neben der allgemeinen Gefährdung von Mooren durch intensive Landnutzung erschweren die unterschiedlichen interagierenden Prozesse zwischen Boden, Wasser, Vegetation und der Atmosphäre die Untersuchung des Einflusses projizierter Klimawandelszenarien auf Moore und ihre mögliche Rückkopplung auf das Klima. Daher habe ich verschiedene Feldstudien und Messkampagnen in Verbindung mit den herrschenden Umweltbedingungen und Laborexperimenten unter kontrollierten Bedingungen kombiniert und dabei verschiedene Prozesse auf unterschiedlichen zeitlichen und räumlichen Ebenen betrachtet.

Auf der regionalen Ebene gebe ich zunächst einen Überblick über die Entwicklung und derzeitige Verbreitung von Mooren in der MRH (**Kapitel 1**). Danach konzentrierte ich mich auf zwei Hochmoore (Hartshoper Moor und Schweimker Moor), die einen klimatischen Gradienten in der MRH abbilden. In diesen Mooren habe ich ein manipulatives vollfaktorielles Feldexperiment durchgeführt, in dem ich Niederschlag experimentell durch Niederschlagsreduktionsgestelle (um 25%) reduziert und die Stickstoffverfügbarkeit durch Düngung (30 kg N ha^{-1} a^{-1}) erhöhte habe.

Das Experiment lief in beiden Moren von 2010 bis 2012. Über diese drei Jahre habe ich auf Pflanzengemeinschaftsebene die Deckung der Vegetation auf mögliche Veränderungen in der Artenzusammensetzung untersucht. Auf Artebene habe ich Biomasseproduktion und Streuzersetzung einzelner dominanter *Sphagnum*- und Gefäßpflanzenarten analysiert (**Kapitel 2**).

Auf Ebene von Pflanzengemeinschaften habe ich außerdem an einzelnen Tagen im Jahr 2011 Kohlenstoffflüsse mit sogenannten Hauben-Messungen untersucht. Ich habe die Aufnahme von CO_2 als Netto-Ökosystem-Austausch (NEE), die Ergebnisse von Bruttoprimärproduktivität (GPP) und Ökosystemrespiration (R_{eco}) sowie CH_4-Emissionen analysiert (**Kapitel 3**).

Um Einblicke in grundlegende Mechanismen zu bekommen, die Produktivität und CO_2-Austausch einzelner *Sphagnum*-Arten beeinflussen, habe ich Laborexperimente unter kontrollierten Bedingungen durchgeführt. Ich habe photosynthetische und respiratorische Eigenschaften einer Art (*Sphagnum cuspidatum*) analysiert, um die potentielle Produktivität unter verschiedenen hydrologischen Bedingungen inklusive dem Regenerierungspotential nach einer langen Trockenphase im Frühjahr 2011 zu ermitteln (**Kapitel 4**). Neben der Untersuchung der Photosynthesekapazität von *S. cuspidatum* habe ich auch die Diskriminierung von stabilen Kohlenstoffisotopen während der Photosynthese von *S. cuspidatum* und *S. papillosum* in Abhängigkeit ihres Wassergehaltes untersucht. Ich habe die Cavity Ring-Down Spektroskopie Technik angewandt, um stabile Kohlenstoffisotope direkt während des CO_2-Austausches zu messen. Die erhaltenen Ergebnisse habe ich mit im Feld erhobenen Daten kombiniert um die Wachstumsbedingungen für die Moose während der Vegetationsperiode nachzuvollziehen. Darüber hinaus habe ich in einem Literaturreview über publizierte Signaturen von stabilen Kohlenstoffisotopen von *Sphagnum*-Biomasse, die Fähigkeit von *Sphagnum* im Torf produziertes CO_2 und CH_4 wiederzuverwerten, analysiert (**Kapitel 5**).

Des Weiteren habe ich die Ergebnisse aus Feld- und Laborexperimenten dazu genutzt, den Einfluss des globalen Wandels auf *Sphagnum* und Moore in der MRH sowie mögliche Rückkopplung auf das Klima abzuschätzen. Abschließend habe ich die Bedeutung möglicher – durch den Klimawandel bedingter – Veränderungen für den Naturschutz herausgearbeitet um zukünftig naturnahe Moor zu schützen und eine erfolgreiche Renaturierung degenerierter und abgetorfter Moore zu erreichen (**Kapitel 6**).

Meine Ergebnisse deuten darauf hin, dass trockenere Bedingungen zu Veränderungen in der Vegetationszusammensetzung führen könnten indem Gefäßpflanzen auf Kosten von *Sphagnum* profitieren (**Kapitel 2**). Die Vegetation hat unterschiedlich auf die Düngung von Stickstoff reagiert, aber keine dieser Reaktionen war positiv im Hinblick auf *Sphagnum*-Wachstum oder Kohlenstofffestlegung. Die Produktivität der Torfmoose ging durch Stickstoffdüngung leicht zurück, möglicherweise als Folge von toxischen Reaktionen auf das Überangebot an Stickstoff. Darüber hinaus führte eine erhöhte Stickstoffverfügbarkeit zu einer Infektion mit dem parasitischen Pilz *Lyophyllum palustre* sowie zu einer höheren Produktivität von *Eriophorum vaginatum*; beides wirkte sich negativ auf das Wachstum der Torfmoose aus. Das Vorkommen von Gefäßpflanzen kann zwar eine Wiederansiedlung von *Sphagnum* degradierten Mooren begünstigen. Mögliche Gefahren jedoch, die durch stimuliertes Wachstum von Gefäßpflanzen hervorgehen könnten (z.B. erhöhte Treibhausgasemission oder Beschattung) und so positiven Effekten auf die Entwicklung von Torfmoosen entgegenwirken, dürfen nicht außer Acht gelassen werden (**Kapitel 2.3 & 6**).

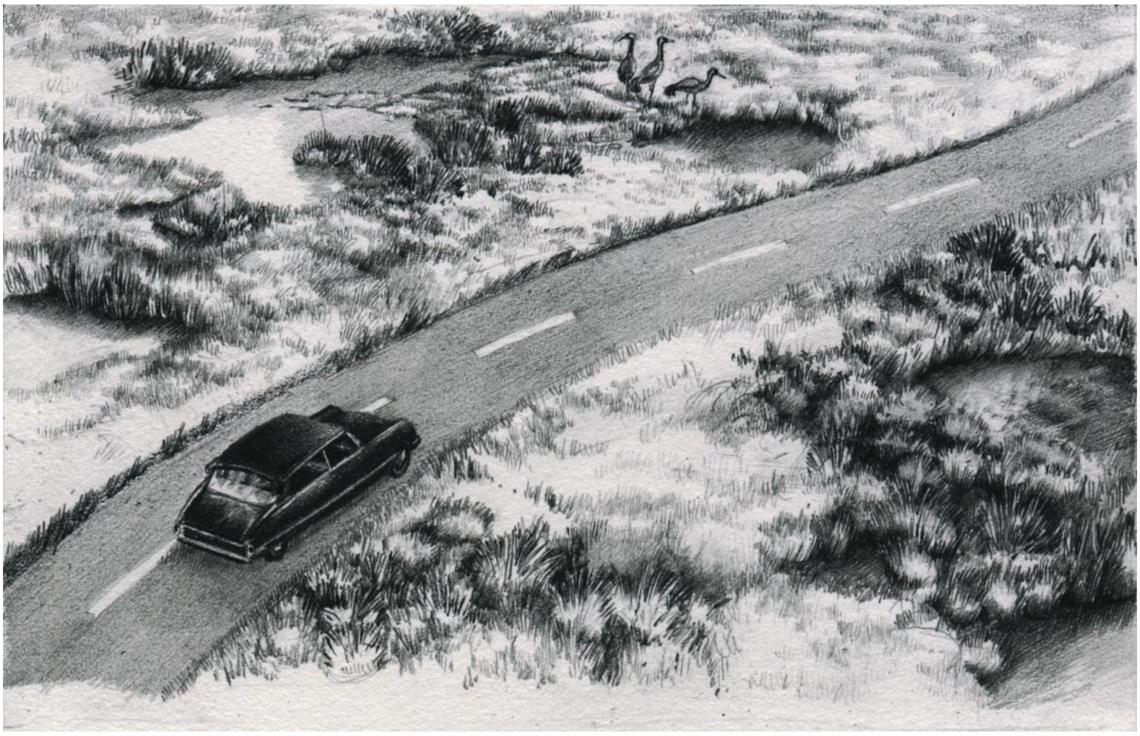
So lange Konkurrenz mit Gefäßpflanzen jedoch keine Bedrohung für *Sphagnum* darstellt, habe ich gezeigt, dass variierende hydrologische Bedingungen in zwei Untersuchungsjahren – einschließlich einer längeren Trockenperiode im Frühjahr 2011 – nur geringe Auswirkungen auf die Produktivität von Torfmoosen hatte und *Sphagnum* sich resilient gegen Austrocknung gezeigt hat. Ferner waren Torfmoose fähig, sich je nach Witterungsverhältnissen bzw. ihrer Lage zum Wasserspiegel den Begebenheiten anzupassen (**Kapitel 2,4 & 5**). Bei niedrigen Wasserständen und gleichzeitig niedrigen Wassergehalten ihrer Capitula wuchsen die Moose in relativ hoher Dichte zusammen, um das Wasser besser halten zu können. Im Gegensatz dazu wuchsen sie bei hoher Wasserverfügbarkeit relativ locker zusammen, möglicherweise um so den Diffusionswiderstand durch einen zu dicken Wasserfilm zu verringern.

Insgesamt haben die Torfmoose bei moderaten Feuchtebedingungen ihre höchsten Produktivitätsraten erzielt; dabei hatten sowohl die hydrologischen Bedingungen selbst, aber auch die dadurch beeinflussten morphologischen Anpassungen einen großen Anteil (**Kapitel 4**). Es hat sich gezeigt, dass *S. cuspidatum* großer Austrocknung standhalten kann, auch wenn die Regenerierung relativ langsam verlief. Meine Untersuchungen haben gezeigt, dass *Sphagnum* in der Lage ist sich an variierende hydrologische Bedingungen anzupassen und einzelne extreme Ereignisse, wie etwa eine längere Trockenphase, zu überstehen. Allerdings geht die Photosyntheseleistung bei nicht optimaler Wasserversorgung zurück. Daher kann sich die Kohlenstofffestlegung in Mooren maßgeblich durch den Klimawandel und damit einhergehende Änderung der Moorhydrologie verändern.

Die gleichzeitige Untersuchung von stabilen Kohlenstoffisotopen während der Photosynthese und der Isotopensignatur ($\delta^{13}C$) der *Sphagnum* Biomasse hat gezeigt, dass die Diskriminierung stabiler Isotope ($\Delta^{13}C$) sowohl zwischen den Arten (*S. cuspidatum* und *S. papillosum*) als auch zwischen ihrer Herkunft verschiedener Mikrohabitate (Bult und Schlenke) variiert; weiterhin war die Diskriminierung stark abhängig vom Wassergehalt der Torfmoosköpfchen (**Kapitel 5**). Die beobachtete Variation zwischen Arten und Mikrohabitaten könnte auf Adaptionen hinsichtlich unterschiedlicher Wasserverfügbarkeit im Moor zurückzuführen sein. Es hat sich allerdings gezeigt, dass unterschiedliche Wasserverfügbarkeit allein nicht die $\delta^{13}C$ Werten von *Sphagnum* erklären kann; vielmehr trägt die Nutzung unterschiedlicher CO_2-Quellen durch die Torfmoose stark zu ihrer Isotopensignatur bei. Ich habe daher zwei empirische Modelle entwickelt, die $\delta^{13}C$ Werte von *Sphagnum* Biomasse sowohl mit dem Wassergehalt als auch mit $\delta^{13}C$ Werten möglicher CO_2-Quellen in Relation zueinander setzt. Bei Anwendung dieser Modelle lässt sich errechnen, dass bis zu 30% des assimilierten Kohlenstoffes von Torfmoosen aus heterotropher Atmung aus dem Torf, bzw. der Oxidation von Methan stammen.

Treibhausgasemissionen im Hartshoper Moor waren starken jahreszeitlichen Schwankungen unterworfen. Bei hohen Wasserständen, die heterotrophe Atmung hemmend, sowie gleichzeitig niedrigen Temperaturen, die Produktion und Emission von CH_4 hemmend, fungierte das Moor als Kohlenstoffsenke (**Kapitel 3**). Im Gegensatz dazu hat es sich bei niedrigen Wasserständen in eine CO_2-Quelle verwandelt und nach Wiederanstieg des Wasserstandes und gleichzeitig hohen Temperaturen wurde verstärkt CH_4 emittiert. Es deutet also darauf hin, dass der projizierte Klimawandel mit trockeneren und wärmeren Sommern einen negativen Effekt auf die Treibhausgasemission aus temperaten Mooren haben könnte, insbesondere bei längeren Trockenperioden und anschließend feuchteren Bedingungen im Sommer. Darüber hinaus war die Zersetzungsrate der Streu von Gefäßpflanzen höher als die von Torfmoosen (**Kapitel 2**). Eine Verdrängung von Torfmoosen und ihrer schwer zersetzbaren Biomasse durch Gefäßpflanzen könnte daher die Kohlenstoffspeicherung in Mooren negativ beeinflussen, auch wenn höhere Produktionsraten der Gefäßpflanzen die negative Bilanz teilweise wieder ausgleichen. Weiterhin bestärken meine Ergebnisse frühere Beobachtungen, dass die Streu von Bultarten zersetzungsresistenter ist als die von Schlenkenarten. Das beobachtete gute Wachstum von verpflanztem *Sphagnum papillosum* in eine nasse Umgebung inmitten der Schlenkenart *S. cuspidatum* unterstreichen somit die Idee, bestimmte Zielarten in degradierte Moore einzubringen um die Möglichkeit einer erfolgreichen Renaturierung zu erhöhen und gleichzeitig die Funktion von Mooren als Kohlenstoffsenke wiederherzustellen

(**Kapitel 2 & 6**). Für den Schutz der letzten verbliebenen naturnahen *Sphagnum*-Moore sowie die Renaturierung degradierter oder abgetorfter Standorte ist es wichtig, lokale Besonderheiten und Voraussetzungen in Managementpläne einzubeziehen. Es sollte weiterhin ein Langzeitmonitoring bisheriger Renaturierungsmaßnahmen durchgeführt werden, welches sowohl (beobachtete) vergangene als auch (projizierte) zukünftige klimatische Veränderung einbezieht, um die Erfolgsaussichten der Entwicklung von *Sphagnum* auf lokaler und regionaler Ebene abzuschätzen (**Kapitel 6**).



1 Introduction

1.1 Peatlands: a short characterization

Peatlands are characterized by the accumulation of organic matter, peat. The definition of peat depends on the proportion of organic matter, with a minimum content of 30% the most commonly encountered value within international literature (Joosten & Clarke 2002). However, the proportion of soil organic matter exceeds 80% in many peatlands (Rydin & Jeglum 2006). In Germany, as well as many other countries, an ecosystem is defined as peatland if the peat layer at the surface is deeper than 30 cm (Joosten & Clarke 2002, Ad-hoc-Arbeitsgruppe-Boden 2005). Peat mainly consists of dead plant material and is the result of impeded and incomplete decomposition. The formation of peat normally occurs under water-saturated conditions, causing anoxic conditions. The development of peatlands is therefore the result of a water surplus in the landscape. Put briefly, peat formation and peatland development can be distinguished according to three different processes: (1) the terrestrialization of shallow lakes or slow-flowing rivers; (2) the paludification of originally dry mineral soils as a consequence of groundwater level rise or pedogenic processes; and (3) primary peat formation directly on wet mineral soils (Rydin & Jeglum 2006).

The origin and quality of the water are important criteria in terms of characterizing peatlands. The most common and widespread differentiation made is between rain-fed, ombrotrophic bogs (Hochmoor) and minerotrophic fens (Niedermoor) that are influenced by groundwater (Du Rietz 1954). Based on trophic characteristics and pH-values, a differentiation between oligotrophic bogs, eutrophic (rich) fens and mesotrophic, poor fens (Zwischenmoor) after Weber (1907) is broadly applied. The intermediate trophic state might also be a (temporal) transition stage (Übergangsmoor) in peatland development when ombrotrophication, the raising of the peat surface and the uncoupling of the mineral soil water, takes place (Aletsee 1967, Rydin & Jeglum 2006).

Peat is accumulated in many ecosystems, mostly in fens and bogs, but also in marshes, forested swamps or mangroves (Bouillon *et al.* 2008, Dommain *et al.* 2011). Whereas the latter two are mostly found in warmer climates, bogs and fens are more abundant in colder climates of the subarctic, the boreal and the temperate zone of the northern hemisphere (Lappalainen 1996). Northern peatlands cover less than 3% of world´s land surface, but they store between 270 and 460 Gt carbon as peat (Gorham 1991, Turunen *et al.* 2002). This amount of sequestered carbon is around 15 – 30% of the world´s soil organic carbon pool, and almost similar to all terrestrial biomass (Joosten & Couwenberg 2008, Limpens *et al.* 2008a). The annual carbon sequestration in northern peatlands is estimated to be up to 70 Mt (Clymo *et al.* 1998).

An essential element for the development of raised bogs and carbon sequestration in peatlands are peatmosses of the genus *Sphagnum.* On the one hand, *Sphagnum* mosses act as ecological engineers, creating an acidic, nutrient poor, cold and anoxic environment (van Breemen 1995). On the other hand, decomposition of *Sphagnum* material is relatively slow, owing the recalcitrance of its litter (Johnson & Damman 1991). Thus, the interaction of anoxic conditions and slow-decaying litter leads to the accumulation of organic material, peat, and consequently to the pronounced capacity of bogs to sequester carbon. Based upon the assumption that *Sphagnum* covers half of the northern peatland areas and stores up to 150 Gt of carbon, it has been suggested that peatmosses store more carbon than any other plant genus in the world (Clymo & Hayward 1982, Rydin & Jeglum 2006).

1.2 Global change – a general overview

Emissions of greenhouse gases (GHGs) such as carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) has increased strongly in recent centuries, far exceeding pre-industrial values. Changes in atmospheric GHG concentrations are the main drivers for climate change in the recent past, and probably also in the future (Solomon *et al.* 2007). Changes of the climate system have been observed since observations of the climate began, with further changes expected based on these observations and future emission scenarios. Global warming is unequivocal and was on average 0.13 °C per decade on land surface between 1956 and 2005. Consistent with warming, there has also been an increase in ice and snow melting and concomitantly a rising sea level. In the case of precipitation, changes have been observed with large regional differences, but areas affected by drought are presumed to have increased globally. Furthermore, extreme weather events such as heavy precipitation and heat waves have increased in the recent past (Solomon *et al.* 2007). Most GHG emissions are expected to continuously increase, at least in the near future. Thus, the atmospheric CO_2 is expected to double the current 380 ppm by 2100 (Meehl *et al.* 2007). Similar to changes observed in the past, projections for future climate change vary on a temporal and spatial scale. In Europe, temperature is projected to increase between 2.0 °C and 5.0 °C by 2100, with continental areas more affected than those under maritime influence. Regarding the precipitation regime, projections for the future are less uniform. Whereas south Europe might receive more than 30% less annual precipitation, northern Europe might receive up to 20% more over the year. In Central Europe, precipitation changes are projected to be small regarding the entire year, but with increasing amounts in winter months and decreasing precipitation during the summer. The risk of prolonged drought events in summer is likely to increase in both southern and central Europe (Christensen *et al.* 2007).

Beside GHG emissions and climatic changes, biotic exchange, increasing land-use activity and atmospheric nitrogen deposition are considered important components of future global environmental changes (Vitousek 1994, Sala *et al.* 2000). Land-use changes may affect biodiversity due to the conversion of natural and diverse ecosystems to agricultural land. Furthermore, land-use changes have a major impact on GHG emissions, either from the conversion of natural ecosystems by the drainage of peatlands, deforestation, or agricultural use, especially via fertilization, animal grazing and the cultivation of rice (Leifeld 2013).

Beside the above-mentioned emission of N_2O, nitrogen emissions and consequent nitrogen deposition in the form of NH_3 and NO_x increased by a multiple compared to pre-industrial values, especially in North America, Europe and Asia (Galloway 1995). Global atmospheric emissions of NO_x and NH_3 are further expected to double from the 1990s to 2050 (Galloway *et al.* 2004). High nitrogen loads are considered a current and increasing threat for the structure and functioning of many ecosystems, reflecting one of the most important factors causing a decrease in plant diversity (Sala *et al.* 2000, Bobbink *et al.* 2010, Phoenix *et al.* 2012).

1.3 Peatlands and global change – multiple interactions

While peatlands and their function to sequester carbon are dependent on climatic conditions, they may also affect the global climate themselves. Whereas growing peatlands sequester large amounts of carbon, every year approximately 3 Gt C is released by degenerated peatlands (excavation, drainage, cultivation, etc.) or fire (Joosten & Couwenberg 2008). Thus, peatlands have been carbon sinks for thousands of years but due to land use and environmental changes, they have converted to sources for CO_2 emissions today. The main reason for the decline in peatland area and the most obvious threat for peatlands in future is the intense anthropogenic use, by either drainage for agricultural use or mining for horticulture or fuel. Additionally, long-term environmental changes are assumed to intensify the pressure on these sensitive ecosystems (Dise 2009). Beside the release of carbon due to the loss of peatland ecosystems through degeneration and land-use, changes in vegetation composition are the most important factor affecting the carbon cycle. During the Holocene, peatlands were continuously subjected to changing climatic conditions, with remarkable shifts in vegetation composition (Chambers *et al.* 1997, Barber *et al.* 1998). Whereas peatlands previously had a net cooling effect on climate (Frolking & Roulet 2007), for future estimations the balance between carbon sequestration and the release of greenhouse gases (CO_2, N_2O and CH_4) is unclear. On the one hand, a long-term shift in vegetation composition might result in shifts in litter quality and enhanced decomposition (Cornelissen *et al.* 2007). On the other hand, an increase of productivity might override the effect of increasing decay (Charman *et al.* 2013).

Due to multiple interactions between climate, nutrient availability and land use on the one hand and peatlands on the other, it is difficult to make reliable and precise predictions concerning the effect of global change on peatlands and their function to sequester carbon, as well as their possible feedback on the climate system via greenhouse gas emissions (Heijmans *et al.* 2008, Limpens *et al.* 2008a).

The combination of (projected) increased temperatures, reduced summer precipitation and increased evapotranspiration determines the hydrology of peatlands and causes decreasing water tables. In drained peatlands, caused by climate change or land-use activities, oxygen penetration in the peat above the water table is increased and heterotrophic respiration mineralises peat organic matter. This leads to a release of CO_2 and other greenhouse gases such as N_2O (Waddington *et al.* 2001, Alm *et al.* 2007, Strack *et al.* 2009). Furthermore, increasing temperatures are assumed to stimulate decomposition and carbon release in peatlands, especially in synergy with decreasing peat moisture (Hogg *et al.* 1992, Ise *et al.* 2008, Dorrepaal *et al.* 2009).

By contrast, CH_4 is produced in the anoxic part of the peat layer. The produced CH_4 is either released to the atmosphere – directly or via aerenchyma of vascular plants – or is oxidized by methanotrophic bacteria (Sundh *et al.* 1994, Kutzbach *et al.* 2004). Beside high water levels, higher temperatures lead to an increase of CH_4 production in the peat (Bergman *et al.* 1998, van Hulzen *et al.* 1999, Estop-Aragones & Blodau 2012). In particular, permafrost melt is assumed to increase CH_4 emissions from high-latitudinal peatlands (Christensen *et al.* 2004). Furthermore, enhanced CH_4 release frequently occurs in rewetted restoration sites due to the high availability of easily degradable organic matter in the upper soil layer, although it has been assumed that the medium-term impact of CH_4 on climate decreases with time in rewetted peatlands (Joosten 2006, Höper *et al.* 2008, Trepel 2008).

The vegetation cover plays a crucial role in the carbon cycle of peatlands, with many changes in peatland´s carbon dynamics resulting from changes in vegetation composition (Heijmans *et al.* 2008). The quality and chemical composition of organic matter determines the decomposition of plant material and the production of CH_4. The formation of both CO_2 and CH_4 are assumed to be higher for vascular plant litter compared to *Sphagnum*-dominated peat, due to the lower degradability of the moss tissue and root exudates produced by vascular plants (Bergman *et al.* 2000, Scheffer *et al.* 2001, Reiche *et al.* 2010). In the case of CH_4, not only the production, but also the consumption and transport are strongly species-specific (Strom *et al.* 2005, Koelbener *et al.* 2010). On the one hand, roots of vascular plants may transport oxygen into the rhizosphere, which can be used to oxidize CH_4. On the other hand, CH_4 can be emitted by upward transport through the aerenchymatous pathway into the atmosphere (Laanbroek 2009, Moore *et al.* 2011). Even if some plants, e.g. cushion plants, are known to oxidise large amounts of soil CH_4, it is assumed that vascular plants emit more CH_4 than a living *Sphagnum* layer (Nykanen *et al.* 1998, Fritz *et al.* 2011). Low CH_4 emission in *Sphagnum*-dominated peatlands might also result from the documented symbiosis of the mosses with methanotrophic bacteria and the “recycling” of produced CH_4 (Raghoebarsing *et al.* 2005, Kip *et al.* 2010, Larmola *et al.* 2010).

Thus far, I have documented some aspects of climatic parameters and land use on greenhouse gas emissions in peatlands, as well as the possible contribution of peatlands to climate change. Furthermore, I have underpinned the impact of the vegetation and different plant functional types (vascular plants vs. peatmosses). However, the other way round, how does climate change influence the vegetation of peatlands? Climate is the key factor for peatland development. In particular, *Sphagnum*-dominated raised bogs are strongly dependent on water surplus, occurring when precipitation exceeds evapotranspiration, with minimum annual precipitation of 500 - 600 mm (Gignac & Vitt 1990, Gajewski *et al.* 2001). As *Sphagnum*-bog distribution is dependent on a positive water balance, minimum and maximum temperatures for *Sphagnum* occurrence are difficult to define and strongly coupled with the mean annual precipitation. The abundance of *Sphagnum* is highest in regions with mean annual temperatures between -2° and 6°C, but the mean annual temperature can be up to 10° C in regions with high annual precipitation (Gignac *et al.* 2000, Gajewski *et al.* 2001).

It is generally assumed that increased temperatures stimulate the growth and productivity of *Sphagnum* (Moore 1989, Sonesson *et al.* 2002, Gunnarsson 2005). Nevertheless, the response of the mosses is species-specific and may strongly differ on spatial scales (Robroek *et al.* 2007b, Breeuwer *et al.* 2008). Particularly in high-latitude peatlands, lengthening of the growing season might enhance *Sphagnum* productivity, as long as higher radiation and a possibly greater risk of photoinhibition do not negatively affect the mosses (Loisel *et al.* 2012, Genet *et al.* 2013). Furthermore, warming might negatively affect productivity by altering the structure and concomitantly moisture-holding and transporting capacity of *Sphagnum* mosses (Dorrepaal *et al.* 2004). Whereas increasing temperature might positively affect *Sphagnum* productivity in high-latitudinal peatlands, in warmer regions enhanced temperatures might negatively affect the water balance by increasing evapotranspiration or decreasing water tables (Gunnarsson *et al.* 2004, Charman *et al.* 2008).

The synergetic effect of increasing temperatures, decreasing summer precipitation and elevated evapotranspiration is likely to alter the hydrology in peatlands and moisture conditions for *Sphagnum* growth, leading to reduced moss photosynthesis and productivity (Lafleur *et al.* 2003, McNeil & Waddington 2003). Furthermore, repeated desiccation and prolonged drought leads to decreasing productivity and enhances the risk of severe damages and mortality of peatmosses (Schipperges & Rydin 1998, Bragazza 2008, Robroek *et al.* 2009a). Contrarily, the growth and productivity of vascular plant species in northern peatlands is assumed to increase with elevated temperatures and drier conditions, and the moss-dominated ombrotrophic bogs might turn into an ecosystem dominated by graminoids, shrubs and trees (Laine *et al.* 1995, Breeuwer *et al.* 2009, Heijmans *et al.* 2013).

Under water-saturated conditions, CO_2 is often the limiting factor for *Sphagnum* photosynthesis and productivity, leading to the assumption that elevated CO_2 concentrations might stimulate growth of the mosses (Silvola 1990). However, experimentally increased CO_2 concentrations have had an ambiguous effect on *Sphagnum* growth in previous studies, with decreasing productivity under warmer conditions (Berendse *et al.* 2001, Heijmans *et al.* 2002a, Heijmans *et al.* 2002b). By contrast, vascular plants might profit from elevated CO_2 concentrations, at least for a short time, as long as other nutrients such as nitrogen or phosphorus do not become limiting (Moore 2002, Fenner *et al.* 2007).

Increasing nitrogen deposition is a current threat for many ecosystems (Bobbink & Hettelingh 2011). Ombrotrophic bogs are nutrient-poor ecosystems, often dominated by *Sphagnum* mosses that are well adapted to these conditions. High nitrogen loads might impede *Sphagnum* growth directly due to ammonium toxicity or increasing vulnerability to the infection by parasites (Baxter *et al.* 1992, Limpens *et al.* 2003b). Furthermore, enhanced N-supply might exceed the capacity of *Sphagnum* to absorb the nutrient with the consequence of nutrient leaching into the rhizosphere and increasing nutrient availability for vascular plants (Lamers *et al.* 2000, Limpens *et al.* 2011). As long as no other nutrient becomes the limiting factor for vascular plants, nitrogen addition promotes the growth of vascular plants, with shifts in vegetation composition expected or already observed (Tomassen *et al.* 2004, Fritz *et al.* 2012).

1.4 Peatlands in the metropolitan region of Hamburg (MRH)

The initiation of peatland formation in Northern Germany and the MRH started after the last glaciation, around 11 000 years BP, and the formation of ombrotrophic raised bogs initiated during the Atlantikum (7500 – 4500 BP) (Overbeck 1975, Couwenberg *et al.* 2001). The genesis of peatlands was partly interrupted or started delayed, caused by transgression phases of the North Sea and climate fluctuations during the Holocene (Gerdes *et al.* 2003, Behre 2004). Depending on geomorphological and climatic characteristics, various peatland types developed during the Holocene. Whereas rain-fed bogs are the dominant peatland type in the lowlands of north-west Germany (Lower-Saxony), paludification mires, percolation mires and terrestrialisation mires are the most abundant peatland types in north-east Germany (Mecklenburg- Western Pomerania) (Joosten & Succow 2001, Zauft *et al.* 2010). Schleswig-Holstein is characterized by marshes, Saale glaciation moraine (Geest) and Weichsel glaciation moraine and covered by a mosaic of various mire types in a relatively small area (Drews *et al.* 2000, Schrautzer 2004). Peatlands in Mecklenburg-Western Pomerania are almost exclusively fens and fens are also more abundant than raised bogs in Schleswig-Holstein. In the lowlands of Lower-Saxony, the dominant peatland type is ombrotrophic bogs (LLUR 2012). The most important and largest bogs in Germany are located in western Lower-Saxony; for example, the “Bourtanger Moor” in the German-Dutch borderland and the bog complex in the lowlands of the rivers Leda and Hunte near Oldenburg. However, raised bogs were also a typical component of the landscape within the MRH, with regional characteristics depending on geomorphological constraints and their varying genesis (Schneekloth 1970-1983, Overbeck 1975) (Fig 1.1).

Coastal peatlands developed during regression phases. They developed in depressions behind a natural levee and were influenced by occasional inundation events. Today, they are mostly located under the sea level or are covered by clay and salt marsh vegetation (Dierssen & Dierssen 2001, Behre 2004). The last remaining bog in the marshlands of Schleswig-Holstein is the “Weißes Moor”, north-west of Heide. A special floristic feature of this bog is the occurrence of *Rubus chamaemorus* L. at its southerly limits of distribution (Müller 1965). The “Ahlenmoor” near Cuxhaven also developed in the transition zone of marsh and the sandy Geest. It was subjected to several marine advances during the Holocene and currently contains one of the last (semi-)natural bog remnants of Northern Germany (Müller 1973, Behre 1976). Within the Geest in Schleswig-Holstein, the “Himmelmoor” is located in the catchment of the rivers Pinnau and Bilsbek, within a depression mainly filled by fluvial sands (Grube *et al.* 2010).

The largest peatlands in the region develop in the catchments of rivers whose flow and level are influenced by tides. A mosaic of various wetlands and mire complexes (fens and raised bogs) developed in the lowlands of the rivers Eider, Treene and Sorge (Schleswig-Holstein), caused by marine and river inundations and terrestrialisation of shallow lakes (Drews *et al.* 2000).

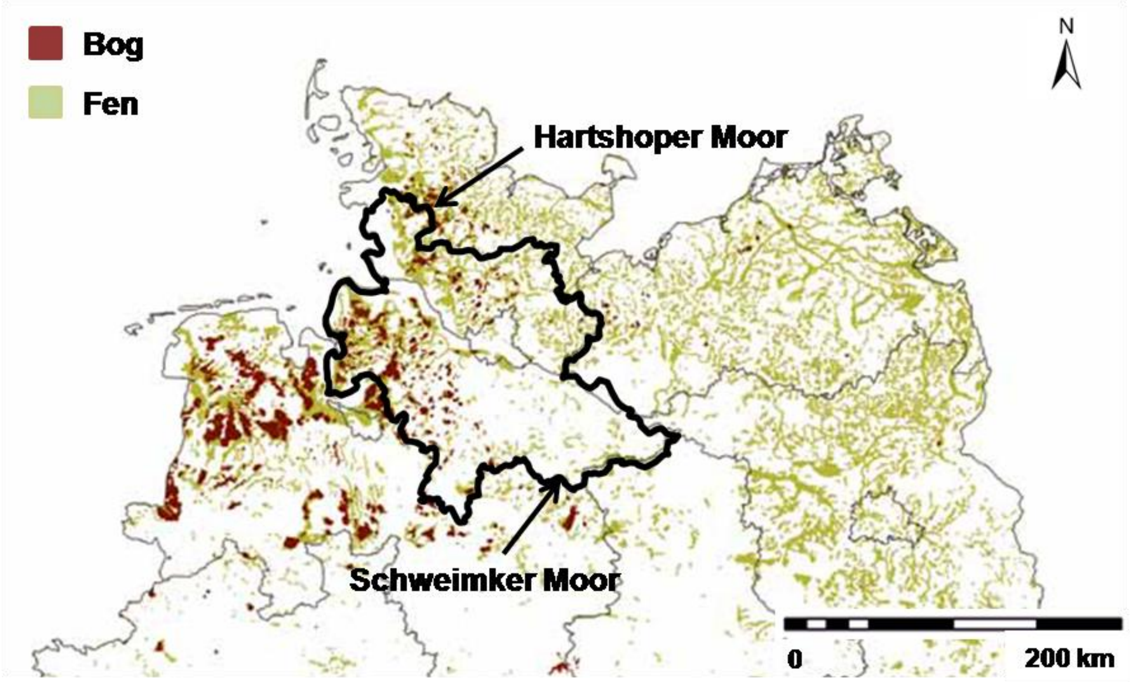


Fig 1.1 Distribution of peatlands in Northern Germany and the Metropolitan region of Hamburg (black frame) and position of the study sites Hartshoper Moor and Schweimker Moor (based on geological mapping 1:200 000, BGR 2011. Modified after M. Sommer (ZALF), in NABU (2012)).

The most expanded peatlands of the MRH developed in the so-called "Weser-Elbe-Triangle" between Bremen, Hamburg and Cuxhaven; for example, the "Teufelsmoor" in the glacial valley of the rivers Hamme and Wümme (Grosse Brauckmann 1969, Overbeck 1975).

Before urbanization, large mire complexes developed in the area of Hamburg, mostly in the transition zone of the marshes of the rivers Elbe and Alster and the sandy Geest (e.g. the mire-belt in the "Altes Land"), as well as in consequence of the terrestrialisation of glacial lakes (e.g. "Großes Moor im Duvenstedter Brook") (Engelschall 2010).

The landscape of the "Lüneburger Heath nature reserve" is characterized by poor sandy Podzols and plenty of small peatlands developed in depressions without discharge in the past. However, due to geomorphological and climatic constraints such as increasing continentality (i.e. warmer and drier summers), large peatlands are scarce in this region. One example is the "Pietzmoor" near Schneverdingen (Overbeck 1975, Pott 1999). Furthermore, some peatlands developed in the lowlands of the rivers Aller, Meiße and Ise, i.e. the raised bogs of "Ostenholzer Moor" and "Großes Moor bei Gifhorn", the latter of which is the southeasternmost raised bog of the North German plain. In the south-eastern part of the MRH, the "Wendland", only a few small peatlands developed in a small depression in the moraine landscape. These peatlands – such as the small raised bog “Maujahn” – are characterized by sparse tree cover (*Pinus sylvestris* L.) and the occurrence of *Ledum palustre* L., already indicating the influence of a continental-boreal climate (Müller 1965, Pott 1999).

A similar geomorphological and floristic pattern can be observed in the hilly moraine landscape of eastern Schleswig Holstein, where small peatlands and bogs developed in many kettle-holes after glaciation, i.e. the “Salemer Moor” and the “Schwarzsee” near Mölln (Lötschert 1964, Rickert 2001, Lindner-Effland 2002, Rickert 2005). An example of a larger kettle-hole mire is the raised bog “Dosenmoor’” near Neumünster, which developed by terrestrialization of a shallow glacial lake (Wagner 1994) .

1.5 Two representative peatlands in the MRH

For my study, I have chosen two raised bogs to represent the climatic gradient (see chapter 1.6) within the metropolitan region of Hamburg. I conducted a manipulative field experiment in these peatlands (see chapter 2), with various samplings (e.g. *Sphagnum* sampling for laboratory experiments, see chapter 4 & 5) and measurements (e.g. gas flux measurements, see chapter 3) additionally carried out.

Hartshoper Moor

The raised bog Hartshoper Moor is located within the Eider-Treene-Sorge-lowlands in Schleswig-Holstein. After deglaciation, the region was influenced by frequent inundations of the rivers Eider, Treene and Sorge, as well as the nearby North Sea, and characterized by shallow lakes and depressions without discharge. In this environment, an extensive mosaic of different wetland and peatland types has developed during the last 12 000 years (Drews *et al.* 2000). This development was interrupted several times by transgressions and regression processes and thus the formation of the raised bog Hartshoper Moor initiated between 3000 and 4000 BP after the terrestrialization of water-filled depressions and shallow lakes (Nissen & Röhr 2011). Since the 16th century, drainage and channelization have heavily influenced the water balance of the region, with agriculture and concomitantly the drainage of peatlands intensified during the 20th century (Drews *et al.* 2000).

Whereas the entire extent of the wetland complex within the Eider-Treene-Sorge lowlands involved several thousand hectares, the Hartshoper Moor had a size of approx. 550 ha (Jacobsen 1997). At the margin, manual peat extraction activities were carried out at the small scale for hundreds of years and not before the 1950s the raised bog was intensively drained and used as pasture. The land was divided into numerous parcels with a diverse use intensity and drainage history (Kolb[1], personal communication). In total, only ca. 100 ha were not cultivated, but also influenced by drainage of surrounding areas. Nowadays, major parts of the peatland are abandoned, with restoration and different rewetting measures having been applied by the foundation “Stiftung Naturschutz Schleswig-Holstein” since 2007, in

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[1] Thomas Kolb, mayor of Sophienhamm and member of „Runder Tisch Hartshoper Moor“

collaboration with local actors ("Runder Tisch Hartshoper Moor"). The rewetted area of the Hartshoper Moor has a size of around 250 ha and is implemented as a NATURA 2000-area, as well as being protected under the FFH-directive (MLUR 2012, Hansen 2013). The vegetation all over the peatland is heterogeneous, yet relatively homogenous within the different parcels, depending on the former use, the period after abandonment and the success of the applied restoration measures. Whereas a dense *Sphagnum* carpet partly developed in old manual peat-cutting areas, a birch-forest established on drier spots. The former pasture land is dominated by *Juncus effusus* L. in wide areas, although various sedges and sporadically peatmosses occur at older uncultivated locations. Furthermore, *Molinia caerulea* (L.) Moench and the shrub *Myrica gale* L. are frequent all over the peatland (Jacobsen 1997 and own observations).

In the 1980s, one parcel of 7 ha was abandoned and different rewetting measures were initiated by "Unabhängiges Kuratorium Landschaft Schleswig-Holstein e.V." (Brehm[2], personal communication). Ditches were refilled and the discharge was restricted with a plastic sheet. The vegetation within this parcel is heterogeneous, with relatively dry areas are mainly dominated by *Molinia caerulea*, while other relatively wet patches are characterized by a microtopography typical for raised bogs with hummocks dominated by *S. magellanicum* and *S. capillifolium* and hollows dominated by *S. cuspidatum* and *S. fallax*. Other peatmosses found in this parcel are *S. rubellum*, *S. compactum*, *S. palustre*, *S. papillosum*, *S. angustifolium* and *S. fimbriatum* (the list is not exhaustive). Furthermore, different patches of wet heath vegetation, dominated by *Erica tetralix* L. and *Empetrum nigrum* L. and accompanied by *Vaccinium oxycoccus* L. and *Andromeda polifolia* L., can be found. The frequent occurrence of *Narthecium ossifragum* (L.) Huds. is striking. Invading birches are removed regularly. Moreover, an area of 20 m x 50 m was digged in the 1980s, for experimental reasons, and the upper 30 cm of the soil was removed (Brehm, personal communication). In this experimental area, spontaneous succession was allowed to develop. After around 30 years, a relatively homogenous carpet of *Sphagnum cuspidatum*[3], accompanied by *S. fallax* was established. Within the carpet, several small hummocks, mainly formed by *S. papillosum*, have developed. The dominant vascular plant is *Eriophorum angustifolium* Honck., growing loosely within the carpet. Furthermore, single tussocks of *E. vaginatum* L. and *Molinia caerulea* can be found, as well as single patches dominated by *Rhynchospora alba* (L.) Vahl. On disturbed spots, *Drosera intermedia* Hayne and *D. rotundifolia* L. frequently occur. The field experiment was set up in this experimental area.

Schweimker Moor

Schweimker Moor is located in the "Lüneburger Heide nature reserve" and is one of the southeasternmost bogs of the North German Plain. The peatland complex is situated in a depression at the foot of three hills: Rasberge, Teichberg and Schweimker Holz (Müller *et al.*

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[2] Kuno Brehm, founder of "Unabhängiges Kuratorium Landschaft Schleswig-Holstein e.V."

[3] Nomenclature of *Sphagnum* species according to Michaelis (2011)

1985). In the slightly inclining depression, paludification initiated after deglaciation and the formation of a raised bog started in the Subatlantic around 2000 - 3000 BC, with relatively cool and moist climatic conditions (Selle 1936, B. Urban, unpublished data). The nature-sanctuary called “Schweimker Moor and Lüderbruch” is located in the counties of Gifhorn and Uelzen and the total extent is around 834 ha. The protected area is characterized by different wetland types, with the center consisting of a raised bog (about 260 ha) and a fen-belt (about 150 ha) (Driesner 1997). Apart from small excavations by hand at the margin, the bog was unaffected until the 1960s. Between 1964 and 1987, the center was drained and excavated industrially. Since 1989, the area has been protected and since 1991 has been subjected to various restoration measures, with the excavation field leveled out and ditches refilled step-by-step. Additionally, establishing birches and pines have been regularly removed since rewetting (Driesner 1997, Hansen 2009). The field experiment was set up at the northern edge of the former exploitation field.

Today’s vegetation still reflects the ancient structure of the field. The wettest parts, mainly old ditches, are dominated by a *Sphagnum cuspidatum* carpet with loosely growing *Eriophorum angustifolium*. Next to the wet ditches, *Eriophorum vaginatum* colonizes wide areas of the peatland. In these areas, mainly *S. cuspidatum*, but also *S. fallax* and *S. fimbriatum*, are often co-occurring with the cotton grass. Other, drier parts of the excavated surface are characterized by wet heath and dominated by *Erica tetralix* and *Calluna vulgaris* (L.) Hull. Furthermore, *Molinia caerulea* has become the dominant species in some areas. On disturbed spots, *Drosera rotundifolia* might become relatively abundant. *Betula pubescens* Ehrh. and *Pinus sylvestris* can be found all over the peatland and the occurrence and age of the trees mainly depends on the frequency of removal. Even more than twenty years after rewetting, some isolated bare-peat batches can be observed. Beside the central excavation field, the peatland complex is characterized by a large number of pools created by former hand-digging activities. Locally and on a small scale, Driesner (1997) observed typical bog vegetation in these parts, with the hummock-forming peatmosses *S. magellanicum*, *S. rubellum* and *S. papillosum* and vascular plant species such as *Vaccinium oxycoccus* and *Erica tetralix*. In wetter parts, typical hollow species such *S. cuspidatum*, *S. fallax*, *S. denticulatum* and *S. flexuosum* were found, accompanied by *Rhynchspora alba* and *Eriophorum angustifolium*. Occasionally, the following peatmosses were observed: *S. subsecundum*, *S. palustre*, *S. pulchrum* and *S. squarrosum*.

1.6 Some aspects of global change in the MRH

The climate of the metropolitan region of Hamburg is dominated by maritime influences, with mild winters, cool summers and stable precipitation throughout the year. With increasing distance to the North Sea, the average annual precipitation decreases and the annual amplitude of temperature increases. The annual average temperature in the North-West of the region (Cuxhaven) was 9.2°C during the period 1971-2000, and 8.9°C in the South-East (Lüchow). The annual precipitation during the same period was 834 mm in Cuxhaven and only

523 in Lüchow (Rosenhagen *et al.* 2011). Long-term average precipitation at "Hartshoper Moor" is 818 mm and 670 mm at "Schweimker Moor". Annual average temperature is similar at both sites with 8.6°C, yet is characterized by a lower annual amplitude (15.6 K) at the maritime site compared to 16.8 K at the rather continental site (Table 1.1).

Changing Climate has been directly observed in the MRH during the last 120 years. Schlünzen *et al.* (2010) analysed the data of 45 climate stations to retrace changes in temperature and precipitation within the region. Between 1891 and 2007, mean annual temperature increased by around 0.07 K per decade, with this effect even more pronounced for shorter periods, i.e. 0.6 K between 1978 and 2007. Annual precipitation increased by around 8 mm per decade during the period from 1891 to 2007, with this increase more pronounced in June and the winter months, while a decreasing trend was observed for April and July.

Table 1.1 Mean annual temperature and precipitation at Hartshoper Moor (H) and at Schweimker Moor (S) for the reference period 1971 – 2000. Data were obtained from the nearest weather stations of Germany's National Meteorological Service (DWD).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
Temp. [°C]													
H	1.1	1.3	3.8	7.0	11.7	14.7	16.7	16.6	13.1	9.2	5.0	2.4	8.6
S	0.5	1.0	4.0	7.7	12.7	15.4	17.3	16.9	13.1	8.8	4.3	1.8	8.6
Prec. [mm]													
H	69	42	57	45	50	78	76	71	82	86	83	79	818
S	61	43	54	45	49	69	64	61	53	52	54	65	670

Climate projections are dependent on temporal and spatial scales and vary among different emission scenarios. Based on the IPCC emission scenarios A2, A1B and B1 and the regional climate models REMO (Jacob & Podzun 1997) and CLM (Rockel *et al.* 2008), climate changes were simulated for different future periods (Jacob *et al.* 2008, Rechid *et al.* 2013). Over all scenarios and models, an increase in temperature is predicted for the metropolitan region, being more pronounced at the end of the 21st century, with 1.9-3.3K, compared to the middle of the century (0.9-2.0 K). The increased temperature is expected to be highest for winter months. Furthermore, increasing temperatures are expected to be more pronounced in the south-east of the MRH.

The simulations of future precipitation pattern are ambiguous on both a seasonal and a long-term scale. Whereas most simulations show increasing precipitation for all seasons until 2050, the total annual amount of precipitation is expected to increase for the period 2071-2100, although summer precipitation might decrease by up to around 20%. Additionally, the projection of longer periods in summer without precipitation and concomitant higher maximum temperatures might enhance the risk of prolonged drought events. To illustrate the climatic conditions during the study period 2010-2012, monthly deviations of temperature and precipitation compared to the reference period 1971-2000 were calculated (Fig 1.2). The study period was characterized by relatively warm and dry spring months and relatively moist and cool summer months. The projected reduced precipitation and prolonged droughts in summer were not observed in the study period, but especially the exceptional dry and warm spring 2011 might provide valuable advice for future climate change scenarios. For further details of the climatic conditions at the study sites, see chapter 2.3.

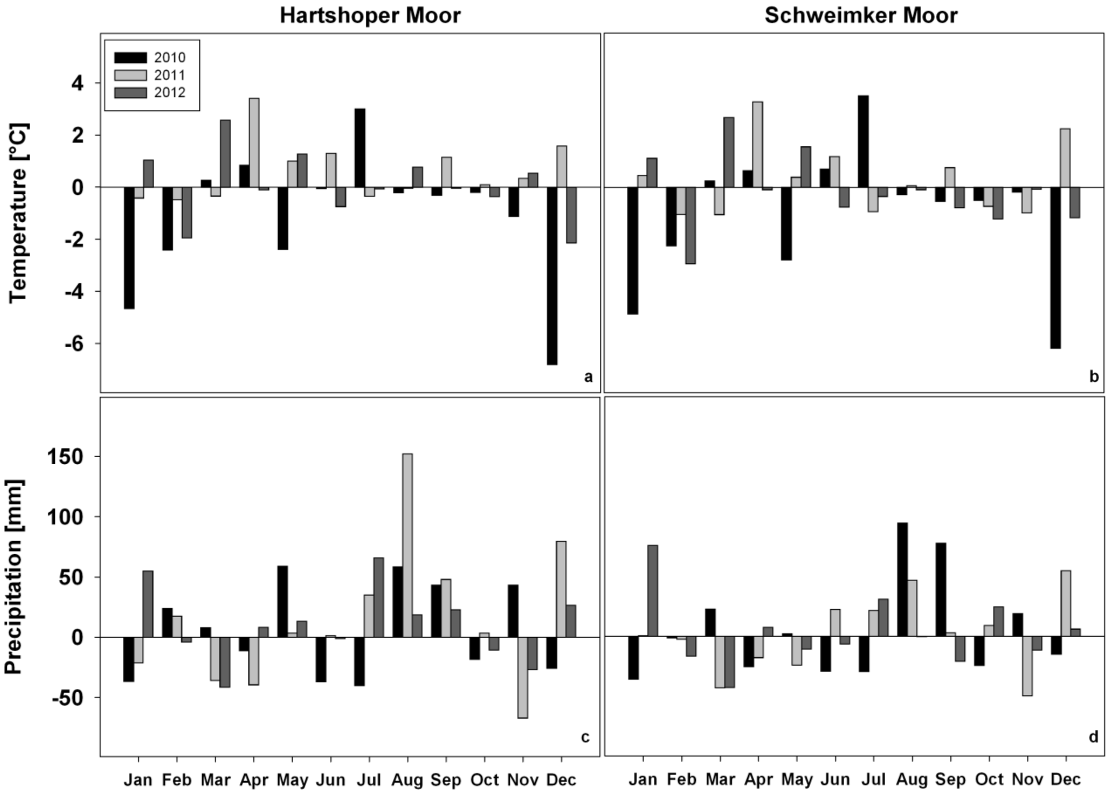


Fig 1.2 Deviation of mean monthly temperature and precipitation during the study period 2010 – 2012 at Hartshoper Moor (a, c) and Schweimker Moor (b, d) from long term means of the reference period 1971 – 2000. Data for the reference period were obtained from the nearest weather stations of Germany's National Meteorological Service (DWD). For further details see chapter 2.

Nitrogen deposition at Hartshoper Moor was 25 kg ha^{-1} a^{-1} and at Schweimker Moor was 18 kg ha^{-1} a^{-1} in 2007 (Builtjes *et al.* 2011). Although, NO_x and NH_3 emissions in central Europe and Germany have been decreasing since the 1990s (Wright *et al.* 2001, Wochele *et al.* 2010), many areas and ecosystems are still subject to critical N loads. For the near future, only marginal improvements are predicted, and thus a continuous threat particularly for nutrient-poor ecosystems is expected (Hettelingh *et al.* 2008, Bobbink & Hettelingh 2011).

1.7 Impact of global change on peatlands in the MRH

Drainage, peat excavation and agricultural land-use have resulted in the almost complete disappearance of the original mire areas of the MRH. Furthermore, increasing atmospheric nitrogen deposition is a serious threat for the nutrient-poor ecosystems. Whereas around 9% of the federal states Schleswig-Holstein and Lower Saxony (incl. Bremen and Hamburg) were previously covered with peatlands, today growing bogs with a living *Sphagnum* moss layer only cover around 2600 ha in Lower Saxony and around 540 ha in Schleswig-Holstein (Table 1.2). Somewhat larger areas are covered with degenerated bog stages (i.e. relatively dry sites with *Molinia caerulea* or *Betula pubescens*) and former – and now rewetted – manual peat-cutting areas. Nevertheless, a substantial proportion of the original peatland area has been irreversibly destroyed by drainage or ongoing peat mineralization (LANU-SH 2002, NLWKN 2006, LLUR 2012). Some small peatlands may still show typical bog vegetation, but hydrologically unaffected peatlands are no longer existent in northern Germany (Ellenberg 1996). Furthermore, most of the 35 occurring peatmoss species are endangered and the most important peat-forming species of northern Germany during the Holocene – *Sphagnum imbricatum* – is extinct (Dierssen 1996).

Table 1.2 Total cover of all peatland types and separately of raised bogs and their actual use and state in the federal states of Schleswig-Holstein and Niedersachsen (modified after LANU-SH 2002, NLWKN 2006 and LLUR 2012). The indications in percentage refer to the total cover of peatlands and to the cover of raised bog, respectively. Data were not available for all categories listed, therefore the sum of cover-percentages does not necessarily reach 100%. Data are based on latest mapping calculations; deviations from older publications are possible and may indicate the irreversible disappearance of peatlands (and peatland soils) due to land-use activities.

	Schleswig-Holstein		**Lower-Saxony**	
	ha	%	ha	%
Peatlands	**145.000**		**419.000**	
drained and abandoned	20.500	14.1	60.700	14.5
agricultural use	107.000	73.7	279.000	66.6
forest on drained peatlands			34.000	8.1
peat excavation	60	0.04	26.000	6.2
Raised bogs	**30.000**		**234.800**	
(semi-) natural	540	1.8	2.600	1.1
degenerated (heath, purple moor grass, etc.)	5.780	19.1	27.300	11.6
degenerated (forest)	4.000	13.2	21.000	8.9
heavily disturbed	20.000	65.7	184.000	78.3

On the one hand, industrial peat excavation is still proceeding, with the longest-running permissions ending in 2040. On the other hand, the ecological importance of peatlands is recognized by the political authorities. Beside other federal states, Lower Saxony and Schleswig-Holstein have formulated regional programs to protect peatlands and to restore and rewet cut-over bogs (LANU-SH 2002, NLWKN 2006, LLUR 2012). Along with their function of storing and retaining great quantities of water, and their contribution to conservation of biodiversity, current and future restoration measures also focus on their potential to store and sequester carbon and fix nutrients such as nitrogen and phosphorus (LLUR 2012).

The most important threat for peatlands in the MRH in the past was intensive land-use. Studies on possible future climate change impacts on raised bogs and *Sphagnum* performance in the region as well as the possible feedback of peatlands on climate change scenarios are scarce. Beside the conservation of the last remaining (semi-) natural remnants of bogs, nature conservancy will face the challenge of how to (re-)establish typical peatland vegetation, as well as peatland´s function to sequester carbon in the future and stop carbon storage degradation under changing and presumably more difficult climatic conditions and ongoing high nutrient availability.

1.8 Objectives of the thesis

Studies dealing with the impact of global change on peatland vegetation and the feedback to climate change are often based on local or regional scale investigations, with specific spatial features impeding the transfer of findings to other regions. Conversely, large-scale or global models are difficult to break down to the regional scale. The overall aim of my study was to elucidate possible effects of projected regional climate change on the vegetation and function of characteristic peatlands of the MRH. Therefore, I carried out various analyses on the plant community scale in two different *Sphagnum*-dominated bogs, observing possible shifts of the floristic composition and analyzing the productivity of the vegetation. Furthermore, I investigated physiological and morphological behaviors and adaptations on the scale of specific organisms – mosses of the genus *Sphagnum* – in response to varying moisture conditions. Finally, on the smallest scale, I focused on carbon stable isotope characteristics in peatmosses, because the isotopic composition of plants permits drawing conclusions concerning environmental growing conditions. Beside the regional consideration of global change impacts on *Sphagnum*-bogs, I also integrated field observations with laboratory experiments and a literature review to underpin the multiple and crucial role of *Sphagnum* mosses in the global carbon cycle.

Chapter two is based on a field experiment that I carried out in two peatlands located along a climatic gradient in the MRH. I experimentally reduced precipitation and enhanced nitrogen available for the plants. I particularly focused on the possible contrasting effects of the applied treatments on vascular plants and *Sphagnu*m mosses. The experiment was conducted over three years to analyze (1) the productivity of the vegetation and (2) shifts in the vegetation cover and the floristic composition of the peatlands. Furthermore, I also analyzed (3) the litter decomposition of different species to evaluate carbon sequestration. To detect possible synergetic effects of reduced precipitation and enhanced nutrient supply, the experiment was carried out in a full-factorial design. Finally, both peatlands should be compared to reveal the influence of the current different climatic condition of both sites and possible pre-adaptations of the vegetation to differing moisture conditions.

Chapter three presents the result of flux measurements of CO_2 and CH_4 at Hartshoper Moor. Measurements were carried out five times in 2011 and were related to varying climate conditions during the year. The measurements were embedded into the field experiment to determine (1) the impact of nitrogen supply and reduced precipitation on CO_2 exchange and CH_4 emissions. Furthermore, I used climatic and hydrological data to estimate the environmental conditions under which the study site might function as a potential sink for CO_2 (2). Finally, gas fluxes were related to the biomass of vascular plants and the cover of *Sphagnum* to elucidate the influence of the vegetation on carbon gas fluxes (3).

Chapter four focuses on the species-specific responses of the peatmoss *Sphagnum cuspidatum* to an extreme drought event in spring 2011, as well as varying moisture conditions later in the year. I determined (1) the growth performance of *S. cuspidatum* during the growing season in the field in relation to varying moisture conditions. Beside the field analyses, a laboratory experiment using infrared gas analyzer (IRGA) technology was carried out to determine (2) its capacity to recover after desiccation and (3) the dependence of capitulum water content on the photosynthetic performance. Finally, I combined the information obtained in the field and from CO_2 exchange measurements to estimate the net carbon uptake of the mosses over the growing season (4).

Chapter five deals with carbon stable isotope discrimination during photosynthesis of *Sphagnum* mosses. I used the Cavity Ring-Down Spectroscopy (CRDS) technology to determine (1) species-specific characteristics of two different *Sphagnum* mosses and (2) the role of moisture conditions on the isotopic composition of moss tissue. Beside moisture conditions, the use of different carbon sources (atmospheric CO_2 vs. substrate-derived CO_2) also determines the carbon isotopic composition of peatmosses. Thus, I developed empirical models to disentangle the different factors influencing the isotope composition of the biomass (3) and calculated the isotopic composition of the source CO_2 used by the mosses in the field (4). In a literature review, I applied the models to published $\delta^{13}C$ values to estimate the capacity of *Sphagnum* to recycle carbon (5).

2 The impact of nitrogen fertilization and reduced precipitation on vegetation composition, plant biomass production and litter decomposition

2.1 Introduction

Peatlands accumulate high amounts of atmospheric carbon and therefore play a key role in the global carbon cycle (Gorham 1991). They are an important long-term carbon sink because they sequester and store atmospheric carbon for thousands of years (Charman *et al.* 2013). The ability of peatlands to sequester carbon strongly depends on climatic and hydrological conditions, given that the productivity of the vegetation and formation of new peat biomass on the one hand and carbon losses of decaying plant material on the other are driven by temperature, radiation, humidity and water table depth, determining anoxic conditions (Belyea & Malmer 2004, Limpens *et al.* 2008a, Loisel *et al.* 2012). Furthermore, hydrochemical conditions have a significant influence on the vegetation as well as carbon fluxes, especially in ombrotrophic peatlands. The wet and nutrient poor environment of the rain-fed ecosystem allows only well adapted vascular plant and moss species to exist (Malmer *et al.* 1994, Hajkova *et al.* 2011). *Sphagnum* covers around half of the northern peatlands, and thus the genus plays a crucial role in the carbon and nutrient cycle in peatlands (Clymo & Hayward 1982, Rydin & Jeglum 2006). Due to the ability of a living *Sphagnum* layer to intercept water and nutrients before percolating to the rhizosphere and being available for vascular plants, as well as the high cation exchange capacity of the peatmosses, they are able to create their own acidic and nutrient poor habitat, which is unfavorable for many vascular plants (Brehm 1968, Woodin & Lee 1987, van Breemen 1995). Beside anoxic conditions hampering the decomposition of plant litter, another important characteristic of *Sphagnum* for carbon sequestration is its slow decay due to the recalcitrance of its litter, containing resistant phenolic compounds (Johnson & Damman 1991, Limpens & Berendse 2003a).

The ecosystem peatland is a fragile interaction between vegetation, water and the atmosphere and changes of the environmental conditions might alter species composition as well as their function to sequester carbon. Thus, due to land use (i.e. draining or excavating) and environmental changes, many peatlands have converted to carbon sources at present (Moore 2002, Limpens *et al.* 2008a).

Increasing atmospheric nitrogen deposition is considered a major threat for *Sphagnum*-dominated peatlands, reducing carbon sequestration (Bobbink & Hettelingh 2011, Limpens *et* *al.* 2011, Bragazza *et al.* 2012). The impact of high nitrogen loads is manifold and peatmosses might be affected directly or indirectly.

In contrast to many vascular plants for which N is the limiting nutrient, high N doses do not dilute in the moss tissue by stimulated growth. Instead, N accumulates in the moss biomass (Aerts *et al.* 1992, Lamers *et al.* 2000). Whereas N concentrations of c. 0.5% are reported in unpolluted parts of the world, in Central Europe or in fertilization experiments concentrations can be up to 1.5%, a level at which saturation occurs (Bragazza *et al.* 2005, Wiedermann *et al.* 2009a, Schmidt *et al.* 2010, Fritz *et al.* 2012). If N is not the limiting nutrient, it is mainly stored in soluble amino acids to prevent ammonium toxicity (Baxter *et al.* 1992, Limpens & Berendse 2003b, Wiedermann *et al.* 2009b). Consequently, metabolic stress inhibits *Sphagnum* growth and productivity. Granath *et al.* (2009) reported the best photosynthetic performance at N concentrations between 1.0 and 1.5%. It is questionable whether adding limiting nutrients alleviates the negative effect. On the one hand, adding phosphorus might enhance growth and dilute excess nitrogen in the moss tissue, but on the other hand typical stress indicators such as elevated amino acid concentration are still present (Fritz *et al.* 2012).

In addition to impeded growth, *Sphagnum* is no longer able to intercept the nutrient in its dense carpet at high N deposition levels. Critical N loads for ombrotrophic bogs can be separated into three steps: at low deposition rates (< 10 kg ha^{-1} a^{-1}), *Sphagnum* growth is stimulated by additional N and the *Sphagnum* layer immobilizes N completely; at intermediate rates between 10 and 20 kg ha^{-1} a^{-1}, *Sphagnum* still accumulates nitrogen, although in metabolically cost-intensive free amino acids; and at high deposition levels (> 20 kg ha^{-1} a^{-1}), the 'natural filter' of peatmosses fails and N concentrations in the rhizosphere increase (Malmer *et al.* 1994, Lamers *et al.* 2000, Tomassen *et al.* 2003, Bobbink & Hettelingh 2011). At intermediate levels, a shift of the floristic composition within the genus *Sphagnum* might occur, favoring nitrophilous species such as *S. fallax* (Lütt 1992, Limpens *et al.* 2003c). At high N deposition levels, N is not immobilized by the peatmosses and a substantial shift from a living peatmoss layer towards the dominance of vascular plants is expected (Heijmans *et al.* 2002c, Tomassen *et al.* 2004, Wiedermann *et al.* 2007). At last, high N loads might enhance the risk of *Sphagnum* being infected by pest such as fungal parasites or epiphytic algae (Limpens *et al.* 2003b).

Shifts in the vegetation of peatlands are expected to have major impacts on carbon sequestration. Whereas total biomass production is expected to be only slightly affected by enhanced N supply, litter decomposition and ecosystem respiration are expected to increase significantly (Juutinen *et al.* 2010). Litter quality plays a key role for decomposition rates in peatlands (Lang *et al.* 2009). *Sphagnum* litter is recalcitrant to decay, and thus faster decaying vascular plant litter would enhance the release of carbon (Johnson & Damman 1991, Dorrepaal *et al.* 2005, Bragazza *et al.* 2006). Furthermore, the chemistry of the *Sphagnum* litter itself, characterized by higher N concentrations, might lead directly to higher decomposition rates or indirectly by releasing more N during decomposition, which increases N availability in the rhizosphere (Aerts *et al.* 2001, Breeuwer 2008). Increasing N availability in the peat not only stimulates vascular plant growth but also the microbial activity (Bragazza *et al.* 2012).

Beside nutrient dynamics, hydrology determines the floristic composition and carbon sequestration in peatlands. *Sphagnum* mosses are well adapted to wet and anoxic conditions (van Breemen 1995). *Sphagnum*-dominated bogs have a typical microtopography, so-called hummocks and hollows, with a typical zonation of different species with distance to the water-table (Andrus *et al.* 1983, Rydin 1993, Robroek *et al.* 2007a). Hummock species are characterized by a high water holding capacity and an efficient capillary water transport to avoid desiccation, as well as being able to grow high above the water table (Clymo & Hayward 1982). In contrast, the morphological features of hollow species (i.e. thinner branch leaves, lower growth densities and photosynthetic cell arrangement) lead to lower resistance to CO_2 uptake and higher productivity (Rice & Schuepp 1995, Gunnarsson 2005), and further see chapter four.

Sphagnum photosynthesis is highly dependent on the capitulum moisture content (Titus *et al.* 1983, Silvola & Aaltonen 1984). Beside morphological characteristics, capitulum water content also depends on the distance to the water table, the capacity of capillary transport of the mosses to the capitulum and hysteresis effects (Hayward & Clymo 1982, Kellner & Halldin 2002). Furthermore, precipitation directly affects moisture conditions within the living *Sphagnum* layer and has a strong impact on *Sphagnum* photosynthesis and CO_2 exchange (Robroek *et al.* 2009a, Strack & Price 2009). Prolonged drought might cause severe desiccation of peatmosses and hamper the potential recovery or lead to the enhanced mortality of peatmosses (Gerdol *et al.* 1996, Bragazza 2008).

Whereas an intact *Sphagnum* layer might be resilient to single drought events, long-term changes in hydrology might substantially alter the floristic composition of peatlands (Rydin & Barber 2001). On the one hand, a shift within the genus *Sphagnum* might occur, favoring hummock species over hollow species (Robroek *et al.* 2007b, Robroek *et al.* 2009a). Furthermore, drier conditions might favor vascular plants species over bryophytes, possibly leading to a shift within the vascular plant cover, from graminoid species to the dominance of ericoid and tree species (Laine *et al.* 1995, Weltzin *et al.* 2003, Breeuwer *et al.* 2009). As mentioned above, the shift in the vegetation is expected to have negative effects on carbon sequestration due to replacing recalcitrant *Sphagnum* litter by faster decomposing vascular plant litter (Dorrepaal *et al.* 2005). Additionally, reduced moisture and lower water tables can directly increase carbon release rates by stimulating aerobic decomposition in peatlands (Alm *et al.* 1999, Strack *et al.* 2009).

The interacting effects of decreasing water and increasing nitrogen availability are obvious: besides higher mineralization rates under dry conditions, the immobilization of nutrients by *Sphagnum* is reduced due to lower N uptake rates, as well as lower photosynthetic rates and growth (Aerts *et al.* 2001, Aldous 2002b, Gerdol *et al.* 2007). A multitude of studies have been carried out in recent decades to elucidate the role of increasing nitrogen deposition and climatic factors on peatland vegetation and carbon sequestration (for review see Limpens *et* *al.* 2011). Nevertheless, field studies investigating the combined effect of drought and increasing nitrogen availability on peatland vegetation remain scarce (Tomassen *et al.* 2004).

To elucidate possible interacting effects of reduced (summer) precipitation and enhanced nitrogen availability, we conducted a fertilization experiment and simultaneously reduced incoming precipitation. We analyzed the growth performance of peatmosses to estimate their ability to withstand unfavorable conditions as well as the biomass production of mosses and vascular plants, in order to reveal possible competitive shifts between both functional types. Besides the analyses of species composition and biomass production, we also carried out a litter decomposition experiment to evaluate the impact on carbon sequestration in peatlands.

2.2 Material & Methods

Study site

The field experiment was carried out in two peatlands in Northern Germany: Hartshoper Moor 54°17’N, 9°26’E) and Schweimker Moor (52°47’N, 10°37’E). Both peatlands were used and drained in the past; Hartshoper Moor mainly for grazing, while peat was excavated at Schweimker Moor. At both sites, restoration measures started in the 1980s, with the peatlands rewetted and ditches refilled. At Hartshoper Moor, the experiment was set up in an area where the top layer (30 cm) was removed and a *Sphagnum* layer dominated by *S. cuspidatum* – with disjunct occurrence of *S. fallax*, *S. fimbriatum* and *S. papillosum* – established. Within the moss layer, *Eriophorum angustifolium* is abundant, while *Molinia caerulea* and *Eriophorum vaginatum* are also relatively frequent. At Schweimker Moor, wide areas are dominated by tussocks of *Eriophorum vaginatum*. *S. cuspidatum* is the dominant peatmoss, both between and within the tussocks. At both sites, invading birches were regularly removed during recent decades. Nitrogen deposition at Hartshoper Moor was 25 kg ha^{-1} a^{-1} and 18 kg ha^{-1} a^{-1} at Schweimker Moor in 2007 (Builtjes *et al.* 2011).

Field Experiment

In spring 2010, the experimental sites were equipped with wooden boardwalks. Afterwards, 20 plots with apparently homogeneous microtopography and vegetation were selected in each peatland. The field experiment was performed over three years from 2010 to 2012. The experimental design was full factorial with nitrogen addition, reduced precipitation and the combination of both. Each treatment ran with five replicates, while five control plots were also installed. We randomly assigned the treatments to the twenty plots. Nitrogen addition was planned at 35 kg ha^{-1} a^{-1}; however, due to periodically high water tables and the risk of uncontrolled discharge of the added nitrogen, some fertilization events had to be cancelled. In 2011, only 20 kg ha^{-1} a^{-1} was given, compared to 30 kg ha^{-1} a^{-1} in both other years. Nitrogen was added as ammonium nitrate (NH_4NO_3, 50:50) four and six times, respectively, from May to September, yielding 5 kg ha^{-1} a^{-1} per fertilization. The fertilizer was dissolved in 4 L distilled water. The unfertilized plots were watered with the same amount of pure water. In order to reduce precipitation on the experimental plot, we used rainout-shelters modified after (Yahdjian & Sala 2002). The shelters measured 3 m x 3 m and were covered to 25% with UV-light transmissible greenhouse film. Assuming that the rainout-shelters reduced not only the input of precipitation but also the amount of wet nitrogen deposition, we compensated nitrogen input under the shelters. To minimize possible side-effects, the size of the experimental plots was 2 m x 2 m, with each plot separated by a minimum 3 m buffer zone.

Meteorological and hydrological measurements

Meteorological data was monitored with automatic weather stations. At Hartshoper Moor, the weather station was equipped with a data logger (CR 1000, Campbell Scientific, North Logan, USA), a sensor for photosynthetic active radiation PAR (SKP 215, Skye Instruments, Llandrindod Wells, UK), a precipitation gauge (ARG 100, Campbell Scientific, North Logan, USA) and soil temperature sensors (107-L, Campbell Scientific, North Logan, USA). Measurements were recorded every 10 seconds and stored as means of 30 min. Additionally, temperature (EBI 20-T, Ebro, Ingolstadt, Germany) and the water table (Mini-Diver, Schlumberger Water Services, Delft, Netherlands) were logged independently every 30 min. Similar instrumentation was used at Schweimker Moor, although the CR 800 data logger (Campbell Scientific, North Logan, USA) was used and a PAR-sensor was not installed.

To monitor the effect of the rainout-shelters, air and soil temperature were measured on plots with and without shelters. Air temperature was measured at a height of 50 cm above the ground and soil temperature at a depth of 10 cm below the ground. Automatic weather stations were installed at the end of 2010. Therefore, meteorological parameters for 2010 are given for the nearest weather station (DWD, Germany´s Meteorological Weather Service), which was approx. 6 km away in the case of Hartshoper Moor (Station Hohn-Airport) and approx. 40 km in the case of Schweimker Moor (Station Faßberg).

Field samplings and chemical analyses

The impact of experimental treatments on the performance of peatmosses was monitored at Hartshoper Moor for *S. cuspidatum* growing in hollows. Furthermore, three cylinders (15 cm in diameter and 15 cm in depth) of *S. papillosum* originated from Esterweger Dose (53°7’N, 7°37’E) were transplanted into hollows of each plot. These transplanted mosses were used for further analyses. At Schweimker Moor, *S. cuspidatum* growing in wet hollows and within drier tussocks of *Eriophorum vaginatum* was monitored. In the following, comparisons between those four groups are referred to as factor species/habitat. In terms of vascular plants, most analyses concentrated on dominant cottongrasses *E. angustifolium* (Hartshoper Moor) and *E. vaginatum* (Schweimker Moor).

Sphagnum cores (53 mm in diameter and 50 mm in depth) were collected from each plot at the end of October in each year. At Hartshoper Moor, *S. cuspidatum* was additionally sampled sporadically several times during all years, and a total of 13 times. Water table depth was measured manually at each position subsequent to samplings. Samples were carefully transferred to the laboratory, where the samples were separated into the top 1 cm (capitula), the subcapitulum (1-2 cm) and the stem (2-5 cm). The fresh weight (fw) for each section was determined, with the dry weight (dw) calculated after drying for 48 h at 60°C. Additionally, the bulk density (g/cm^3) was calculated for each fraction. The water content of peatmosses is expressed as the ratio of fresh and dry biomass (fw/dw).

To monitor the length increment of *Sphagnum*, in 2010 a modified cranked wire method was applied (Clymo 1970). We inserted a brush (10 cm long and 2 cm in diameter) attached to a metal wire (30 cm long) upside down into the moss carpet. The wire was used as a reference point and the length increment of mosses was calculated as the decreasing length of the wire above the moss carpet. However, unfortunately this modified cranked wire method did not provide reliable results. Thus, another method to monitor length increment was applied in 2011 and 2012. At the end of April, we marked the mosses with white thread directly below their capitulum. Three individuals of each species/habitat were equipped with the thread in each plot. At the end of October, the marked mosses were harvested and length increment determined, based upon the distance between capitulum and thread.

The biomass production of peatmosses was calculated as a function of length increment (between the thread and capitulum) and bulk density (Clymo 1970). Due to their specific differences in length increment, the stem section and subcapitulum section were used for bulk density calculations in the respective cases of *S. cuspidatum* and *S. papillosum*. While the capitulum is generally not used for mass-growth calculations, differences in capitulum growth densities between different treatments should be included into the calculations of the productivity (Pakarinen 1978, Gunnarsson & Rydin 2000). Thus, productivity P was calculated as

$$P = L \times D + \Delta M_c, \tag{2-1}$$

with L being the length increment, D being the shoot density and ΔM_c representing the difference between treatments and the control in terms of capitulum dry mass. In our experiment, no differences between capitulum dry mass were observed, although the formation of new stems and new capitula was observed in 2011 after mosses experienced severe desiccation during a drought period in spring. In this case, capitulum dry mass was included in calculations of productivity.

Every year in early September, species composition was determined using a point-intercept sampling (Jonasson 1988). This method allowed additionally determining the annual aboveground biomass by clipping and weighting biomass after finishing the experiment and retrospectively calculating the biomass within the experimental plots (Shaver *et al.* 2001, Robroek *et al.* 2010). Within each experimental plot, a subplot of 60 cm x 60 cm was defined randomly at one corner. In each subplot, a narrow pin was passed through a perforated plate and lowered within the vegetation at evenly distributed points (64 points at Hartshoper Moor and 36 at Schweimker Moor). The number of hits was counted for each species and correlated to dry biomass harvested in early September 2012. Cover of the moss layer was calculated by the number of hits at the surface divided by the total number of pins.

Measurements of decomposition rates were conducted for two *Sphagnum* species (*S. cuspidatum* and *S. papillosum*) and two *Eriophorum* species (*E. angustifolium* and *E. vaginatum*) using minicontainers (Eisenbeis *et al.* 1999). The polyethylene minicontainers had a volume of around 1.5 cm^3 and are closed at the ends with plastic gauze discs (mesh size of 500 µm). Plant material was collected in May 2010 from their typical microhabitats at Hartshoper Moor. For *Sphagnum*, the upper part of the shoots (2-7 cm), from greenish to light brown and with a fresh and coherent structure, was used as litter. For *Eriophorum*, standing dead leaf material was used. All samples were air-dried at room temperature and sub-samples were oven-dried (48 h at 60°C) to calculate the oven-dry weight of the air-dried samples. Air-dried plant material was filled into the containers; 150 mg for *Sphagnum* and 200 mg for *Eriophorum* (± 10 mg each). Minicontainers were buried c. 10 cm below the surface in early July. The containers were collected after 4, 10, and 16 months. Fine roots grown in the container were removed and the remaining litter was weighted to determine mass loss. In total, 240 containers were buried (4 species x 3 harvests x 20 plots). The experiment was only carried out in the Hartshoper Moor. Mass loss analyses resulted in lower values for samples harvested after 10 months compared to those harvested after four months, probably due to the insufficient removal of external plant material; therefore, data was not included into analyses.

The nitrogen and carbon content of dry and homogenized biomass of the two cottongrasses and the four moss species/habitats and of *Sphagnum* litter was measured with an element analyzer (EA3000, EuroVector, Milan, Italy). Porewater of the *Sphagnum* layer (uppermost 100 mm) was collected by connecting syringes (50 ml) to soil moisture samplers (10 cm Rhizon SMS; Eijkelkamp Agrisearch Equipment, Giesbeek, the Netherlands). Porewater samples were stored at -18 °C until further analysis. Ammonium was measured colourimetrically and nitrate was measured with liquid chromatography technique (1200 Series HPLS System, Agilent Technologies, Santa Clara, USA).

Data analyses

The relationship between water table and *Sphagnum* capitulum water content, as well as possible effects of rainout shelters on the water content was analyzed for all *Sphagnum* species/habitats in October 2011 and October 2012. Due to the expected correlation between water table and water content, we carried out an ANCOVA with water table as a co-variable and the fixed factors reduced precipitation, species/habitat and time. Water content was additionally determined for *S. cuspidatum* at Hartshoper Moor for a total of 13 samplings during the three growing seasons, analyzed as described above without factor species/habitat. Changes of vascular plant biomass and *Sphagnum* cover over time were analyzed separately for both peatlands using repeated measures ANOVA with nitrogen addition and reduced precipitation (in the following, also referred to as “nitrogen” and “precipitation” for simplicity) as fixed factors. In order to analyze *Sphagnum* growth characteristics (productivity, length increment and shoot density), a one-way ANOVA was initially carried out to reveal differences between the peatlands. Subsequently, a four-way ANOVA was carried out with the fixed factors nitrogen, precipitation, time and species/habitat. The same procedure was applied for nitrogen content, separately for peatmosses and for both cottongrass species. The litter experiment was only conducted at Hartshoper Moor, and thus the factor of peatland was not included in the analyses. Mass loss was compared for all four species, using four-way ANOVA as described above. Litter chemistry was only determined for both *Sphagnum* species, whereby we carried out two independent two-way ANOVAs, one with the factors nitrogen and precipitation and subsequently one with the factors species and time, because initial litter chemistry (before experimental treatments were conducted) was included into analyses. Porewater chemistry was only measured at Hartshoper Moor and analyzed using three-way ANOVA with the fixed factors nitrogen, precipitation and time. For more detailed information, analyses were separated into samples taken before and after fertilization. Subsequent to all ANOVA analyses, Tukey’s post hoc tests were carried out, while Levene’s test was applied to ensure homoscedascity. Due to its vulnerability to missing values, repeated measures ANOVAs were only applied for analyses with an equal number of samples. To calculate vascular plant biomass retrospectively, a linear regression was conducted with the factors of the number of hits in 2012 and harvested biomass in 2012. The parameters obtained were used to calculate the biomass in 2010 and 2011, with the normality of residuals ensured. All analyses were carried out using the software STATISTICA 9.0 (StatSoft, Tulsa, OK).

2.3 Results

Climatic conditions

Annual precipitation at Hartshoper Moor ranged between 886 mm in 2010 and 995 mm in 2011 (Fig 2.1). The mean annual temperature was lowest in 2010 at 7.4 °C and highest in 2011 at 9.2 °C. At Schweimker Moor, annual precipitation ranged from 691 mm in 2011 to 725 mm in 2010. The coolest year was 2010, with a mean temperature of 7.6 °C, while the warmest year was 2011, with a mean temperature of 8.9 °C. In 2010, both sites were characterized by relatively dry months in June and July, with mean precipitation of less than 40 mm, and relatively wet months in August and September, with mean precipitation of 127 mm at Hartshoper Moor and 143 mm at Schweimker Moor. 2011 was characterized by a severe drought in spring, with a mean monthly precipitation of less than 25 mm at both sites between March and May. Spring was also relatively dry in 2012, with a mean monthly precipitation of less than 40 mm. In 2011 and 2012, the summer period from July to September was relatively wet at Hartshoper Moor, with a mean precipitation of 155 mm in 2011 and 112 mm in 2012. During the same period, mean monthly precipitation at Schweimker Moor was 83 mm in 2011 and 62 mm in 2012. The water table at Hartshoper Moor was at the surface of the moss layer during the winter months, and decreased in spring and early summer of 2010 and 2011 to around -20 cm and only to around -12 cm in early summer of 2012. The water table rose in July of every year and was mostly near the surface in late summer and autumn. At Schweimker Moor, water table fluctuations were more pronounced, with maximum values of 25 cm below the surface between June and August. The water table rose with the beginning of the wetter period in late summer, and hollows were water saturated between October and March. Depending on the exact size and position, the water table was between 35 cm and 55 cm below tussocks of *Eriophorum vaginatum* in summer and between 10 cm and 30 cm below the tussocks in winter.

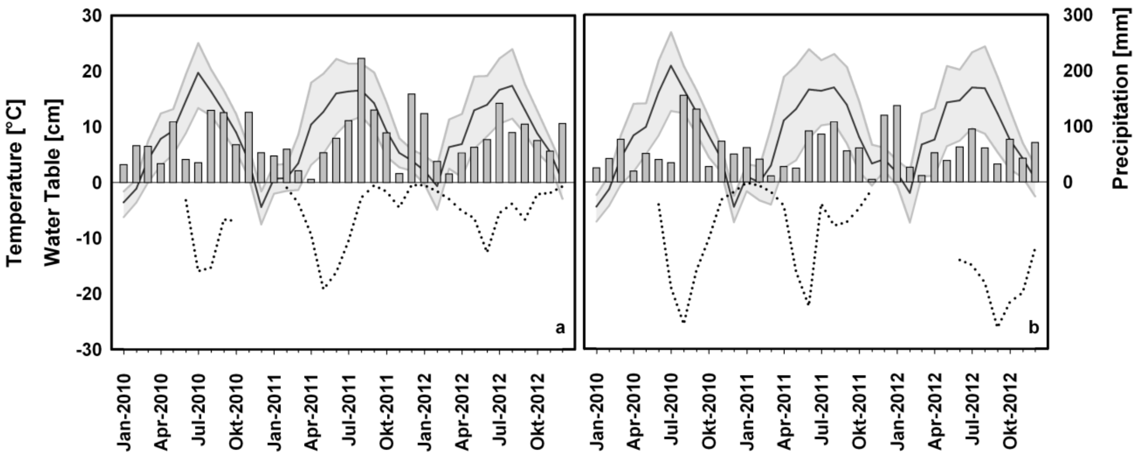


Fig 2.1 Climatic and hydrological conditions at Hartshoper Moor (a) and Schweimker Moor (b) in the years 2010 – 2012. Data for 2010 were obtained from nearby weather stations (see material & methods). The dasehd line shows the mean monthly water table below the moss surface, data is not complete due to logistical problems. The solid line shows mean monthly air temperature and the grey shade represents the amplitude of mean monthly minimum and maximum temperature. The bars show the mean monthly preciptation.

Furthermore, we compared monthly and daily temperature means as well as minimum and maximum values of one plot each with and without rainout shelters. None of the temperature parameters significantly differed between the treatments.

Porewater nitrogen concentration

NH_4NO_3 concentration of porewater samples taken immediately before nitrogen fertilization differed between fertilized and non-fertilized plots (F = 16.1, $p < 0.001$) and varied significantly during the season 2011 (F = 18.1, $p < 0.001$). The difference between fertilized and non-fertilized plots was highest in June with 41.0 µmol l^{-1} (SD 23.1) in control plots and 88.7 µmol l^{-1} (SD 51.8) in fertilized plots. No differences were found at the end of the season in September, with concentrations of around 6 µmol l^{-1} in all treatments. Nitrogen addition remarkably enhanced NH_4NO_3 porewater concentrations immediately after fertilization compared to plots without N addition (F = 22.6, $p < 0.001$). The effect was highest in May with a concentration of 268.8 µmol l^{-1} (SD 188.4) and lowest in July with a concentration of 128.4 µmol l^{-1} (SD 111.7) (F = 4.5, $p < 0.05$). Moreover, control plots showed slightly increased nitrogen porewater concentrations after fertilization in May and June, compared to samples taken before fertilization at the same plots (Fig 2.2).

The porewater nitrate concentration was less than 1 µmol l^{-1} before adding nitrogen, with only fertilized plots in May and June showing significant increased concentrations, with 20.0 µmol l^{-1} (SD 5.9) and 22.7 µmol l^{-1} (SD 8.3), resulting in a significant interaction between nitrogen*time (F = 6.7, p < 0.001). NO_3^- concentrations were significantly enhanced immediately after N addition in fertilized plots (F = 13.6, p < 0.01) being highest in May with 117.6 µmol l^{-1} (SD 41.5) and lowest in July with 55.9 µmol l^{-1} (SD 25.9). In May, unfertilized plots showed remarkably elevated NO_3^- concentration with 44.6 µmol l^{-1} (SD 38.0) directly after fertilizing surrounding plots (Fig 2.2b).

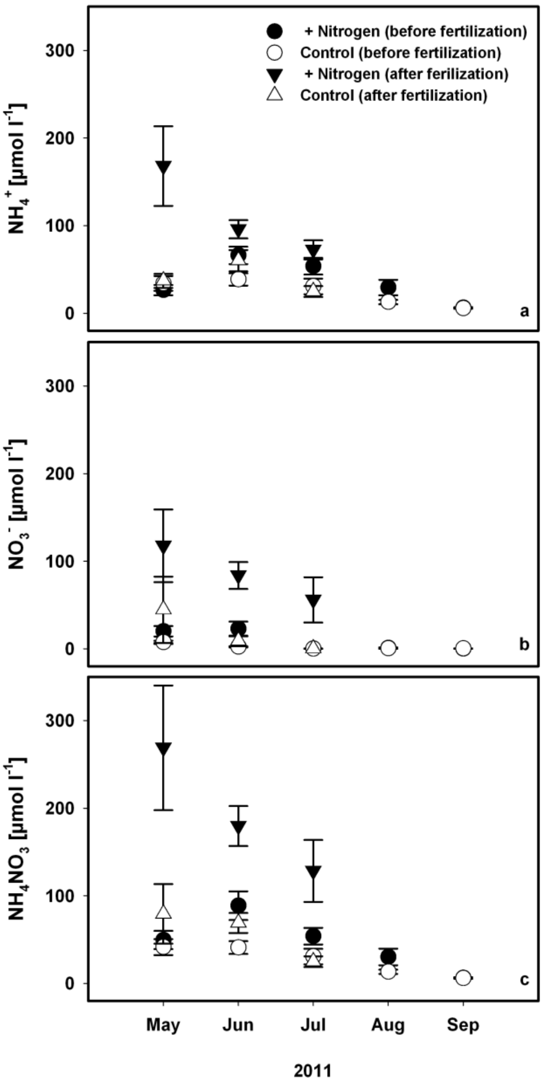


Fig 2.2 Porewater nitrogen concentration presented as NH_4^+ (a), NO_3^- (b), and NH_4NO_3 (c). Circles represent samplings prior to fertilization events and triangles represent samplings immediately after fertilization. Filled symbols represent plots with nitrogen fertilization and open symbols represent plots without fertilization. Given are means (± SE, n = 8 - 10). Please note that in August for NO_3^- and in September for all N forms no differences were found between fertilized and non-fertilized plots and only values for control plots are presented.

Ammonium porewater concentration (sampled prior to fertilization) was enhanced in fertilized plots ($F = 7.6$, $p < 0.01$) and varied significantly during the season ($F = 14.3$, $p < 0.001$). The interaction between nitrogen*time was marginally significant ($F = 2.2$, $p < 0.1$). The difference between fertilized and non-fertilized plots was most pronounced in June, with NH_4^+ concentrations of 38.0 µmol l^{-1} (SD 7.0) in unfertilized plots and 66.1 µmol l^{-1} (SD 9.9) in fertilized plots. In September, no differences were observed between treatments, with NH_4^+ concentrations of less than 10 µmol l^{-1} in all plots (Fig 2.2a). After fertilization, NH_4^+ concentration was significantly higher in fertilized plots than control plots ($F = 23.4$, $p < 0.001$) and higher in May, with 168.0 µmol l^{-1} (SD 45.4), than June and July, with 96.0 µmol l^{-1} (SD 10.4) and 72.5 µmol l^{-1} (SD 10.9), respectively ($F = 4.5$, $p < 0.05$). In June, unfertilized plots showed relatively high NH_4^+ concentrations of 60.0 µmol l^{-1} (SD 12.2). Reduced precipitation showed no clear pattern in terms of nitrogen porewater concentration, and single significant interactions with the nitrogen treatment and time are not presented here.

Sphagnum water content

Sphagnum water content was highly correlated with the water table for samples from both peatlands analyzed in October 2011 and October 2012 ($r^2 = 0.72$, $p < 0.001$), as well as for *S. cuspidatum* analyzed 13 times at Hartshoper Moor ($r^2 = 0.83$, $p < 0.001$).

Besides the effect of the water table, the first analysis revealed significant differences between species/habitat and time, as well as an interactive effect of both (Table 2.1). Water content (fw/dw) was lowest for *S. cuspidatum* growing in cottongrass tussocks, with 8.3 (SD 2.7) in 2011 and 7.7 (SD 1.3) in 2012, and highest for *S. papillosum* from hollows at Hartshoper Moor, with 34.9 (SD 3.9) in 2011 and 38.5 (SD 4.2) in 2012 (Fig 2.3).

Table 2.1 Results of ANCOVA for differences of *Sphagnum* capitulum water content between the precipitation treatment, sampling date, and species/habitat and their interactive effects. Water table was used as co-variable. All species/habitats were analysed in October 2011 and October 2012. *S. cuspidatum* at Hartshoper Moor was analysed 13 times during the experimental period 2010 – 2012. nd = not determined; ns = not significant; (*) = p < 0.1; * = p < 0.05; ** = p < 0.01; *** = p < 0.001.

	All species/habitats			*S. cuspidatum* (Hartshoper Moor)		
	df	F	p	df	F	p
Water table	1	18.4	***	1	52.2	***
(1) Precipitation	1	4.0	*	1	6.1	*
(2) Time	1	5.3	*	12	22.2	***
(3) Species/habitat	3	45.5	***		nd	
(1)*(2)	1	0.0	ns	12	1.37	ns
(1)*(3)	3	1.5	ns		nd	
(2)*(3)	3	6.0	**		nd	
(1)*(2)*(3)	3	0.2	ns		nd	

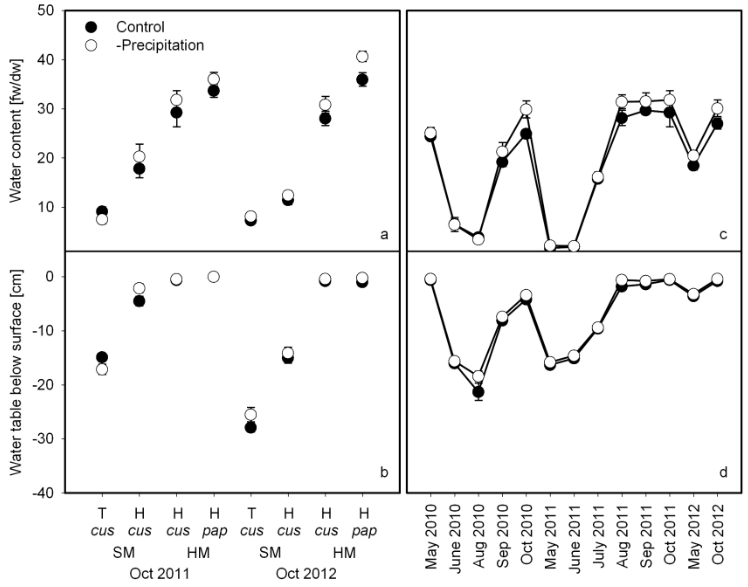


Fig 2.3 Mean water content of, and mean water table beneath *S. cuspidatum* (*cus*) and *S. papillosum* (*pap*) growing in hollows (H) or within cottongrass tussocks (T) (± SE). Mosses originated from Schweimker Moor (SM) and Hartshoper Moor (HM) (a, b) and *S. cuspidatum* from Hartshoper Moor (c, d). Each data point represents 16 – 20 replicates.

At Hartshoper Moor, lowest water contents for *S. cuspidatum* were observed during the prolonged drought in spring 2011, while highest values were found in later summer and autumn (Fig 2.3). Moreover, reduced precipitation had a significant effect on capitulum water content, leading to slightly higher values if precipitation was reduced (Table 2.1). The mean water content for all mosses sampled in October 2011 and October 2012 was 21.1 (SD 11.6) in control plots and 23.6 (SD 13.0) in plots with reduced precipitation. At Hartshoper Moor, the mean water content of 13 samplings of *S. cuspidatum* was 17.5 (SD 10.9) in control plots and 18.8 (SD 12.2) in plots with rainout shelters.

Sphagnum growth and productivity

Sphagnum biomass production strongly differed between different species/habitats (Table 2.2), being the highest for *S. cuspidatum* in hollows, with 255 g m^{-2} (SD 107), and the lowest for *S. cuspidatum* growing on tussocks of cottongrass, with 135 g m^{-2} (SD 85), both at Schweimker Moor (Fig 2.4a). With 210 g m^{-2} (SD 108), biomass production was higher in 2011 than 2012, with 178 g m^{-2} (SD 87). The interactive effect between species/habitat and time was mainly due to the high production rates of *S. cuspidatum* growing in hollows at Schweimker Moor in 2011, recorded at 319 g m^{-2} (SD 117).

The reduction of precipitation had no effect on *Sphagnum* biomass production. Nitrogen fertilization led to decreased biomass production, albeit only in 2011. In 2011, biomass production on fertilized plots was reduced, with 185 g m^{-2} (SD 88) compared to the control plots with 234 g m^{-2} (SD 122).

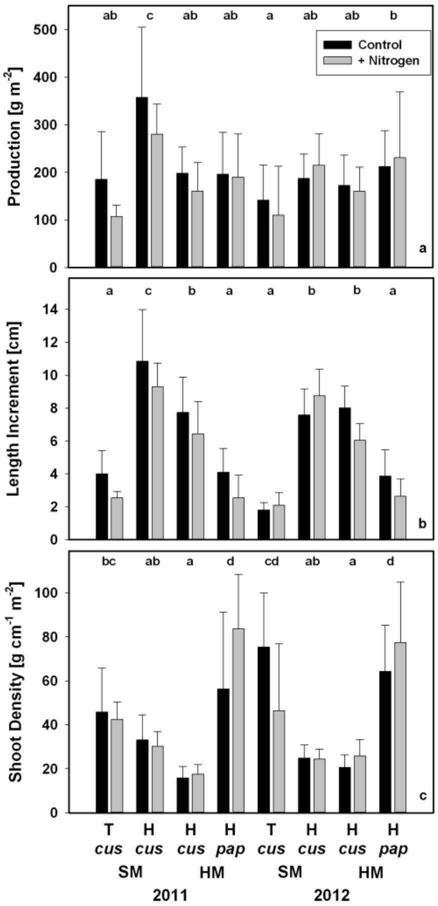


Fig 2.4 Growth performance of peatmosses in 2011 and 2012 affected by nitrogen addition (n = 8 - 10). Production (a), length increment (b), and shoot density – presented as means (± SD) – of *S. cuspidatum* (*cus*) and S. papillosum (pap) growing in hollows (H) or within cottongrass tussocks (T). Mosses originated from Schweimker Moor (SM) and Hartshoper Moor (HM). Different letters indicate significant differences between species/ habitats ($p < 0.05$, Tukey´s HSD test). For further statistics see Table 2.2.

In 2012, biomass production was 178 g m^{-2} (SD 103) on fertilized plots, similar to the 179 g m^{-2} (SD 69) on control plots.

Length increment showed a similar pattern to biomass production (Fig 2.4b). It was significantly higher for *S. cuspidatum* growing in hollows with 9.0 cm (SD 2.3) at Schweimker Moor and 7.1 cm (SD 1.8) at Hartshoper Moor. The *S. papillosum* increment was 3.3 cm (SD 1.5), while *S. cuspidatum* growing in cottongrass tussocks gained only 2.6 cm (SD 1.2). Length increment was generally higher in 2011, with 6.0 cm (SD 3.4), than 2012, with 5.1 cm (SD 2.9). Maximum growth was observed in 2011 at Schweimker Moor for mosses growing in hollows with 10.1 cm (SD 2.5), which explains the interactive effect of species/habitat and time (Table 2.2). Nitrogen fertilization significantly reduced length increment (Table 2.2), although analyzing the interaction of nitrogen and time revealed that length increment was only higher on control plots in 2011, with 6.7 cm (SD 3.5), compared to control plots in 2012 and fertilized plots in both years, ranging between 4.9 cm (SD 3.0) and 5.4 cm (SD 2.9).

Shoot density was highest for *S. papillosum* with 70 g cm^{-1} m^{-2} (SD 28), followed by *S. cuspidatum* growing on cottongrass tussocks with 53 g cm^{-1} m^{-2} (SD 26) (Fig 2.4c). *S. cuspidatum* growing in hollows had the lowest shoot density with 21 g cm^{-1} m^{-2} (SD 7) at Hartshoper Moor and 28 g cm^{-1} m^{-2} (SD 8) at Schweimker Moor. Nitrogen fertilization only affected *S. papillosum*, leading to an increase from 61 (SD 28) to 81 g cm^{-1} m^{-2} (SD 25), whereas conversely *S. cuspidatum* growing on cottongrass tussocks showed a decrease from 62 (SD 27) to 45 g cm^{-1} m^{-2} (SD 23) (Table 2.2). Differences between both peatlands were neither observed for biomass production nor length increment or shoot density (Table 2.2).

Table 2.2 Results of one-way ANOVAs for differences of *Sphagnum* biomass production, length increment and shoot density between peatmosses originated from different peatlands and results of four-way ANOVAs for differences between experimental treatments, species/ habitats and time and their interactive effects. ns = not significant; (*) = p < 0.1; * = p < 0.05; ** = p < 0.01; *** = p < 0.001.

		Production [g m^{-2}]		Length Increment [cm]		Shoot density [g m^{-2} cm^{-1}]	
	df	F	p	F	p	F	p
Peatland	1	0.6	ns	1.4	ns	1.1	ns
(1)Nitrogen	1	3.3	(*)	13.3	***	0.1	ns
(2)Precipitation	1	0.1	ns	0.0	ns	1.3	ns
(3)Species/Habitat	3	13.2	***	135.7	***	47.2	***
(4)Year	1	3.8	(*)	10.2	**	1.9	ns
(1)*(2)	1	0.1	ns	0.0	ns	0.0	ns
(1)*(3)	3	0.4	ns	1.7	ns	4.4	***
(2)*(3)	3	0.6	ns	1.2	ns	1.7	ns
(1)*(4)	1	3.3	(*)	3.7	(*)	1.6	ns
(2)*(4)	1	0.4	ns	0.2	ns	0.7	ns
(3)*(4)	3	4.9	**	3.1	*	2.3	(*)
(1)*(2)*(3)	3	0.4	ns	0.0	ns	0.1	ns
(1)*(2)*(4)	1	1.3	ns	0.4	ns	0.0	ns
(1)*(3)*(4)	3	0.4	ns	2.1	ns	1.1	ns
(2)*(3)*(4)	3	0.6	ns	1.1	ns	0.4	ns
(1)*(2)*(3)*(4)	3	1.9	ns	1.0	ns	0.7	ns

Sphagnum cover and vascular plant biomass

At Hartshoper Moor, *Sphagnum* cover was negatively affected by nitrogen fertilization and time, while also the interaction nitrogen*time was significant (Table 2.3). The cover decreased from almost 100% in all plots in 2010 to 81% (SD 17) in 2011 and 76 % (SD 12) in 2012 in fertilized plots and to 96% (SD 9) in 2011 and 85% (SD 18) in 2012 in non-fertilized plots. Vascular plant cover, expressed as standing biomass, was not affected by fertilization. Instead, the interaction between reduced precipitation and time was significant (Table 2.3). Whereas no differences were observed between the treatments in 2010 and 2011, only the standing biomass in control plots decreased in 2012 compared to the two other years.

Table 2.3 Results of RM-ANOVAs for differences of vascular plant biomass and *Sphagnum* cover as dependent on experimental treatments and time and their interactive effects. ns = not significant; (*) = p < 0.1; * = p < 0.05; ** = p < 0.01; *** = p < 0.001.

		Biomass [g m^{-2}]		***Sphagnum* Cover [%]**	
	df	F	p	F	p
Hartshoper Moor					
(1) Nitrogen	1	0.0	ns	4.3	**(*)**
(2) Precipitation	1	0.3	ns	2.3	ns
(1)*(2)	1	1.3	ns	0.4	ns
Time	2	0.8	ns	19.1	***
Time*(1)	2	1.2	ns	3.7	*
Time*(2)	2	4.4	*	1.7	ns
Time*(1)*(2)	2	0.2	ns	2.6	**(*)**
Schweimker Moor					
(1) Nitrogen	1	4.6	*	2.1	ns
(2) Precipitation	1	16.3	**	11.7	**
(1)*(2)	1	0.0	ns	0.1	ns
Time	2	5.6	**	5.8	**
Time*(1)	2	1.5	ns	0.6	ns
Time*(2)	2	0.2	ns	0.9	ns
Time*(1)*(2)	2	1.2	ns	0.1	ns

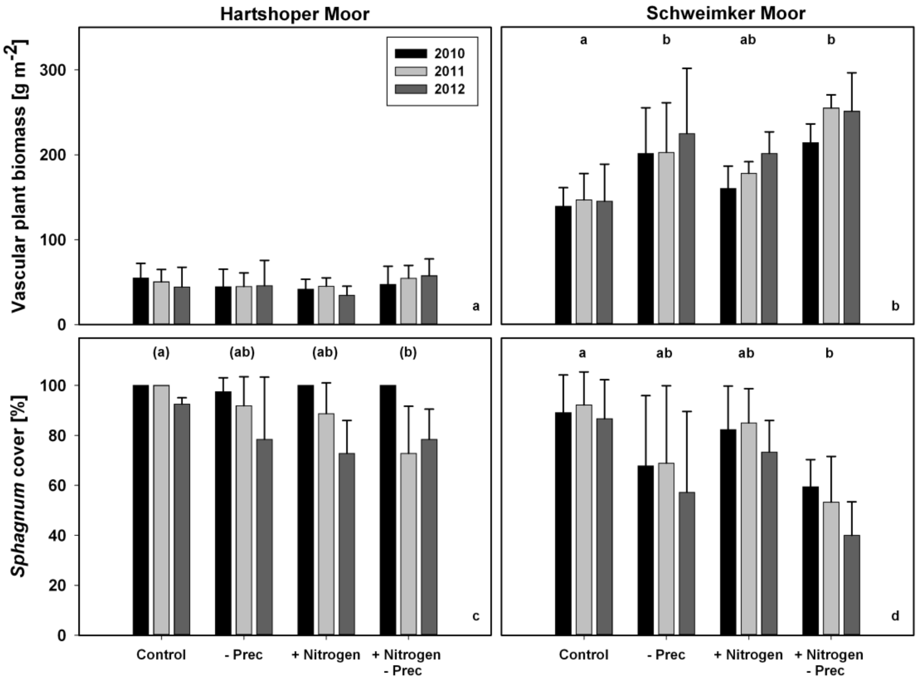


Fig 2.5 Vascular plant biomass and *Sphagnum* cover in the course of the experiment (2010-2012). Presented are means (± SD, n = 5) for each experimental treatment for the standing living biomass [g m^{-2}] of vascular plants at Hartshoper Moor (a) and at Schweimker Moor (b) and the cover [%] of peatmosses of both peatlands (c, d). The treatment reduced precipitation is abbreviated as -Prec. Different letters indicate differences between experimental treatments (p < 0.05; Tukey´s HSD test).

At Schweimker Moor, *Sphagnum* cover significantly decreased from year-to-year on plots with reduced precipitation (Table 2.3). Cover was highest in control plots, with around 90% in all years. In plots with N fertilization, *Sphagnum* cover decreased from 82% (SD 17) after one year to 73% (SD 13) after three years of the experiment. Reduced precipitation led to a cover of 68% (SD 28) in 2010 and 57% (SD 32) in 2012. The cover on plots with combined N fertilization and reduced precipitation decreased to 60% (SD 11) after one year and further decreased to 40% (SD 13) after three years in 2012. Nevertheless, nitrogen fertilization was not observed to have a significant effect on *Sphagnum* cover (Table 2.3).

Vascular plant cover was reversely affected by the experimental treatments, being highest after three years on plots with reduced precipitation and N addition and lowest on control plots without differing with time (Fig. 2.5). In the case of vascular plant biomass, alongside reduced precipitation and time, N fertilization also had a significant effect (Table 2.3).

Table 2.4 Nitrogen concentration of peatmosses (means ± SD) dependent on their origin analyzed using one-way ANOVA and dependent on experimental treatments (nitrogen and precipitation), species/habitat and time using four-way ANOVA. Different letters indicate differences within subjects (p < 0.05, Tukey´s HSD test). ** = p < 0.01; *** = p < 0.001. Only significant interactions between subjects are presented.

	N [%]	n	df	F	p
Peatland			**1**	**70.8**	***
Hartshoper Moor	1.60 (±0.34)	101			
Schweimker Moor	1.17 (±0.40)	107			
Nitrogen			**1**	**175.7**	***
Control	1.18 (±0.38)	104			
Addition	1.57 (±0.39)	104			
Precipitation			**1**	**20.2**	***
Control	1.30 (±0.44)	105			
Reduction	1.46 (±0.41)	103			
Species/Habitat			**3**	**81.8**	***
Hartshoper Moor					
S. cus (hollow)	1.59 (±0.34)^a	54			
S. pap (hollow)	1.61 (±0.36)^a	47			
Schweimker Moor					
S. cus (hollow)	1.28 (±0.53)^b	54			
S. cus (tussock)	1.05 (±0.33)^c	53			
Year			**2**	**37.2**	***
2010	1.46 (±0.38)^a	75			
2011	1.51 (±0.43)^a	58			
2012	1.20 (±0.42)^b	75			
Interactions					
Nitrogen*Species			**3**	**5.1**	**
Species*Year			**6**	**12.4**	***

N concentration

Nitrogen concentration in vascular plant biomass differed between *E. angustifolium* from Hartshoper Moor and *E. vaginatum* from Schweimker Moor (F = 70.8, $p < 0.001$) and was also affected by N fertilization (F = 175.7, $p < 0.001$). N concentration was highest in fertilized plots at Hartshoper Moor with 1.21% (SD 0.08), and lowest in unfertilized plots at Schweimker Moor with 1.08% (SD 0.09). N concentration in peatmosses also differed between the two peatlands, being higher at Hartshoper Moor than Schweimker Moor (Table 2.4). Furthermore, nitrogen addition as well as reduced precipitation led to significantly increased N concentrations (Table 2.4). Whereas no differences were found between *S. papillosum* and *S. cuspidatum* at Hartshoper Moor, N concentration at Schweimker Moor was higher for mosses growing in hollows than for those growing in cottongrass tussocks (Table 2.4).

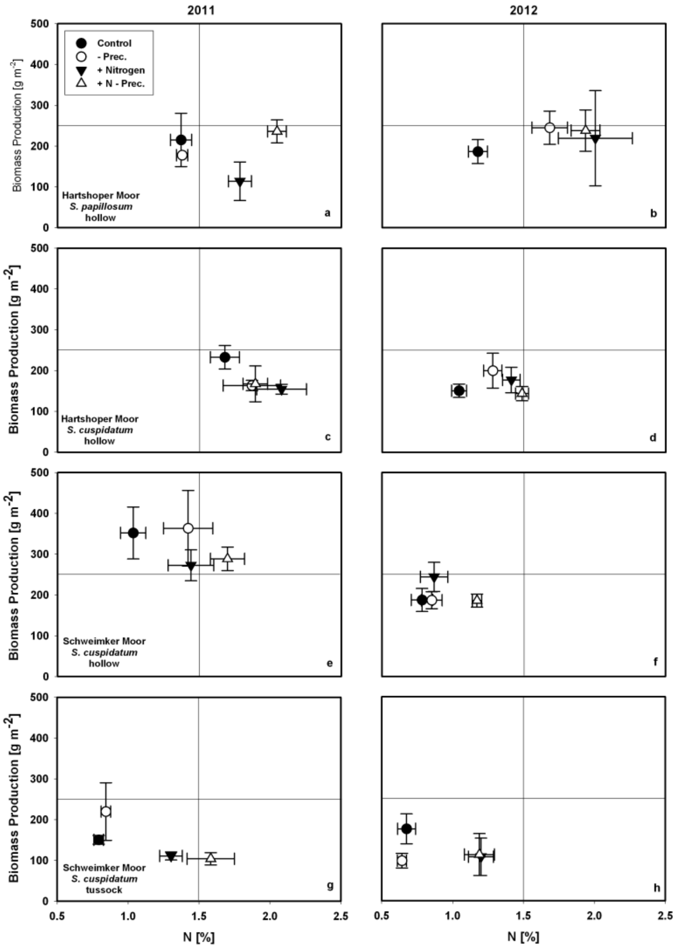


Fig 2.6 Biomass production of peatmosses in relation to N concentration and dependent on experimental treatment. Given are means (± SE, n = 4 – 5) for each treatment: nitrogen fertilization (filled triangles), reduced precipitation (open circles), combination of both treatments (open triangles), and control (filled circles) for *S. papillosum* (a, b) and *S. cuspidatum* (c, d) from Hartshoper Moor and *S. cuspidatum* from Schweimker Moor, either from hollow (e, f) or from cottongrass tussocks (g, h), sampled 2011 (a, c, e, g) and 2012 (b, d, f, h).

Nitrogen concentration was significantly lower in 2012 than in both previous years (Table 2.4). The significant interaction between nitrogen*species was caused by a higher increase of N concentration in *S. papillosum* (+ 0.52%) and *S. cuspidatum* growing in tussocks (+ 0.50%) than in *S. cuspidatum* growing in hollows at Hartshoper Moor (+ 0.22%) and Schweimker Moor (+ 0.31%) (Fig 2.6). A reduction of N concentration in 2012 was – in contrast to all other samples – not observed for *S. papillosum*, which explained the significant interaction between species and time (Table 2.4).

A relationship between N content and biomass production was only observed in 2011 (Fig 2.6), with production rates decreasing with increasing nitrogen concentrations. In 2012, when overall reduced N concentrations in *Sphagnum* biomass were recorded, this pattern was not observed.

Table 2.5 Results of ANOVAs for litter chemistry and mass loss. Litter chemistry was analyzed by two independent two-way ANOVAs, first with the factors nitrogen and precipitation and subsequently with the factors species and time (the factor time includes initial litter chemistry, prior to experimental application). Mass loss was analysed using four-way ANOVA including all four factors and their interactive effects. nd = not determined; ns = not significant; (*) = p < 0.1; * = p < 0.05; ** = p < 0.01; *** = p < 0.001.

	N [%]			C/N [%]			Mass Loss [%]		
	df	F	p	df	F	p	df	F	p
(1)Nitrogen	1	1.1	ns	1	1.1	ns	1	2.6	ns
(2)Precipitation	1	0.0	ns	1	0.0	ns	1	0.7	ns
(3)Species	1	46.8	***	1	32.1	***	3	61.5	***
(4)Time	2	51.5	***	2	42.7	***	1	35.7	***
(1)*(2)	1	0.3	ns	1	0.2	ns	1	2.0	ns
(3)*(4)	2	2.7	(*)	2	4.5	*	3	5.0	**
(1)*(3)		nd			nd		3	1.1	ns
(2)*(3)		nd			nd		3	0.4	ns
(1)*(4)		nd			nd		1	6.1	*
(2)*(4)		nd			nd		1	2.5	ns

Table 2.6 Litter chemistry of *Sphagnum* prior to the decomposition experiment and after four, respectively 16 months buried at Hartshoper Moor. Different letters indicate differences between species and time (p < 0.05, Tukey´s HSD test).

	S. papillosum			*S. cuspidatum*		
	Initial	4 months	16 months	Initial	4 months	16 months
N [%]	1.07 (±0.10)^{a}	0.76 (±0.11)^{c}	0.80 (±0.09)^{bc}	0.93 (±0.06)^{ab}	0.64 (±0.10)^{d}	0.58 (±0.04)^{d}
C/N	43.7 (±5.1)^{a}	63.6 (±8.2)^{b}	61.1 (±7.0)^{b}	48.5 (±3.0)^{a}	73.7 (±9.5)^{c}	79.7 (±5.5)^{c}

Litter decomposition

Mass loss differed between the different species and was dependent on the duration for which the litter was buried (Table 2.5). Moreover, a significant interaction between species*time was observed. Litter decomposition of *Sphagnum* mosses did not significantly differ after 4 and 16 months, respectively. Mass loss of *S. papillosum* increased from 22% to 24% and loss of *S. cuspidatum* increased from 28% to 31%. By contrast, mass loss of *E. angustifolium* increased from 18% in 2010 to 30% in 2011. Decomposition of *E. vaginatum* was already high after four months, with 36%, and increased to 41% after 16 months.

Nitrogen fertilization had no clear effect on litter decomposition in the first four months, although it led to increased decomposition rates for all species after two seasons (Fig. 2.7). Nitrogen concentration and the C/N ratio of *Sphagnum* litter differed significantly between the two species (Table 2.6). At the beginning of the experiment, litter quality was nearly identical, with slightly higher N concentrations and concomitantly slightly lower C/N ratios for *S. papillosum* (Table 2.6). Nitrogen content of buried litter decreased more in *S. cuspidatum* after four months, which led to higher C/N ratios of decomposing litter of this species. A further change in N content and C/N ratio (after 16 months) was not observed.

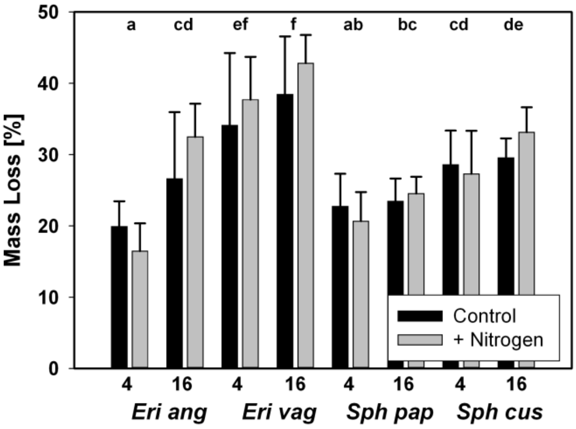


Fig 2.7 Litter decomposition at Hartshoper Moor dependent on nitrogen fertilization after 4 and after 16 months. Given are means (± SD) of mass loss [%] of the two cottongrass species *E. angustifolium* (*Eri ang*) and *E. vaginatum* (*Eri vag*) and the two peatmosses *S. papillosum* (*Sph pap*) and *S. cuspidatum* (*Sph cus*). Different letters indicate differences between species and the time litter was buried ($p < 0.05$, Tukey´s HSD test), for further statistics see Table 2.5.

2.4 Discussion

General comments

The fact that the rainout shelters showed no effect on the analyzed parameters in many cases – especially on the water content characteristics of *Sphagnum* – raises the question whether the object of reducing precipitation by 25% was successful. The design of the roofs with strips of plastic to reduce the precipitation might have led to an unequal distribution of passing water. Peatland vegetation is strongly dependent on the distance to the water table. Thus, it is questionable whether the interception of a small amount of precipitation had any impact on the water table. Beside the water table, peatland vegetation responds independently to precipitation events, although only if water table is relatively low and precipitation is intercepted (e.g. by *Sphagnum*) before percolating through the moss layer. During many periods of the experiment, we observed either relatively wet conditions with high water tables or relatively dry conditions with long periods without any precipitation, or little enough that all species suffered severely by desiccation. Some findings are somewhat strange, i.e. that the rainout shelters led to a slight increase in peatmosses water content. This could be explained by side effects of the roofs, such as increasing humidity and decreasing evapotranspiration, parameters that were not measured in the field. Another explanation could be that the random distribution of the experimental treatments in the field led to an agglomeration of control treatments at relatively dry spots, given that a smooth slope within both experimental fields was observed.

Inorganic nitrogen in form of NH_4^+ and NO_3^- varied during 2011 in control plots. Whereas nitrogen concentration was very low in late summer, relatively high ammonium concentrations and slightly enhanced nitrate concentrations were observed in control plots in spring and early summer. This might be explained by agricultural fertilization in the surrounding landscape (Lütt 1992) or reduced uptake by peatmosses caused by their inactivity during the extreme dry spring, resulting in an enhanced accumulation in the soil pore water. Nitrogen addition led to a substantial short-term increase of porewater nitrogen concentration, and was more pronounced under wet conditions. *Sphagnum* generally has higher uptake rates under wet conditions, which could explain higher N concentrations in the porewater during dry periods (Woodin & Lee 1987). Nevertheless, the observed decrease of N concentration in porewater with increasing water table in fertilized plots might also be caused by enhanced dilution of the added nitrogen. In some cases, nitrogen concentration was slightly enhanced in control plots and plots with reduced precipitation directly after fertilization, indicating an uncontrolled dilution of small proportion of fertilizer into the control plots and/or a fertilizing effect of compensation nitrogen addition under the rainout shelters. Thus, it is unclear whether the fertilized plots effectively received the experimentally required nitrogen load. Due to the specific N uptake rates of *Sphagnum*, it is likely that the added N led to a strong surplus for only a short time after fertilization, whereas most of the time N concentrations in the porewater were lower – especially for nitrate – than considered optimal for *Sphagnum* (Rudolph & Voigt 1986, Jauhiainen *et al.* 1998).

The uncertainties surrounding the success of the experimental applications should be taken into account when discussing possible ecological impacts of reduced precipitation and nitrogen addition.

Sphagnum water content

Capitulum water content is a key driver for *Sphagnum* photosynthesis and accordingly for biomass production and carbon sequestration (Titus *et al.* 1983, Silvola 1990). Despite single water content analyses, only providing a snap-shot of the entire growing season, some differences between species and habitats became obvious. As expected, capitulum water content largely reflects the position of the mosses in relation to the water table. Highest water contents for *S. papillosum* as well as relatively moderate values for *S. cuspidatum* growing far from the water table between cottongrasses can be explained by their denser growth and hence a higher water holding capacity compared to *S. cuspidatum* growing in hollows (Titus & Wagner 1984, Strack & Price 2009). The wide range of different water contents in *S. cuspidatum* from 13 samplings in Hartshoper Moor cannot be entirely explained by the distance to the water table. Extreme low water contents in spring might be explained by the extreme drought prior to sampling, rather than only by the water table, which was even lower the year before. Even small rain events can prevent mosses from desiccation and lead to higher water contents and higher productivity during dry periods (Robroek *et al.* 2009a, Strack & Price 2009). The positive effect of the rain-out shelters on capitulum water content was surprising. While no interaction with time was observed, it is obvious that differences were most pronounced at high water tables. Excess water might hamper CO_2 diffusion to the chloroplasts of the mosses, leading to lower productivity rates (Silvola 1990), although the rainout shelters had no effect on productivity and water content differences were ecologically rather small, and thus possible reasons for the observed effect cannot be discussed here.

Sphagnum growth and productivity

As expected, the high variability of water content among species/habitats was also reflected in *Sphagnum* biomass production, leading to lowest productivity rates with greatest distance to the water table (Weltzin *et al.* 2001). Large interannual variation of productivity rates for mosses growing in hollows is dedicated to varying growth conditions between wet and dry years (Lütt 1992, Gunnarsson 2005). Therefore, higher rates observed for 2011 than 2012 – particularly for hollow mosses from Schweimker Moor – seem somewhat surprising given that mosses seriously suffered from the severe drought in spring 2011. Mosses damaged by desiccation recovered after rewetting, and favorable temperature and moisture conditions in summer and autumn 2011 led to high productivity rates, which seem to compensate the deficiency of the unproductive spring months (see chapter 4). It is assumed that fluctuating and decreasing water tables might favor typical hummock and lawn species such as

S. papillosum and *S. magellanicum* over hollow species such as *S. cuspidatum* (Breeuwer *et al.* 2009). In our study, S. *cuspidatum* and *S. papillosum* growing in the same environment – with fluctuating and low summer water tables – had almost identical productivity rates. Whereas biomass production was lower than reported for *S. cuspidatum* – apart from hollow samplings at Schweimker Moor in 2011 – production was in the range reported before for *S. papillosum* (Gaudig 2001, Gunnarsson 2005), which might indicate that low summer water tables affected especially *S. papillosum* only marginally. Nevertheless, it might also be explained by neglecting possible high productive periods between autumn and spring in our analyses, given that *Sphagnum* production was calculated for the period from the end of April until the end of October (Asada & Warner 2003).

Whereas differences of productivity were relatively moderate between species and habitats, they were – as expected – more pronounced for length increment and shoot density (Hajek 2009). Both parameters underpin the adaptation of growth characteristics of peatmosses to their habitat. *S. cuspidatum* from hollows invests more in length increment to keep pace with the water table. Conversely, *S. cuspidatum* growing remote from the water table mainly invests in shoot density to enhance the water holding capacity. In natural bog ecosystems, this normally leads to a typical zonation of different species with looser growing species close to water table and thick mosses with a denser growth at drier hummocks (Andrus *et al.* 1983, Rydin 1993). In restored and rewetted bogs, fast colonizing species such as *S. cuspidatum* dominate the moss layer and typical species-specific zonal variation is not developed (Smolders *et al.* 2003). Morphological adaptation to varying moisture conditions, represented by the dense growth of *S. cuspidatum* within cottongrass tussocks, was observed before for peatmosses (Grosvernier *et al.* 1997) (see also chapter 4) and might be enhanced when growing in monoculture and lacking in competition. *Sphagnum papillosum* naturally occurs in wet lawns as well as drier hummocks (Laine *et al.* 2009), and was transplanted from relatively dry conditions, which might explain the denser growth compared to *S. cuspidatum*.

A large number of studies have been carried out in recent decades to elucidate the impact of increasing nitrogen deposition on peatland vegetation, and particularly *Sphagnum* mosses. Increased nitrogen deposition might affect *Sphagnum* directly; for instance, altering the productivity, or indirectly by altered competitive relations (Lamers *et al.* 2000, Limpens *et al.* 2003a). It is generally assumed that N fertilization has a negative effect on *Sphagnum* productivity (Gunnarsson & Rydin 2000), although species specific differences and interactions of nitrogen availability with other environmental factors draw an inconsistent picture (Limpens *et al.* 2011, Granath *et al.* 2012). The inconsistence mentioned often derived by comparing different studies with varying environmental conditions. Our results reflect the heterogeneous response of N addition on peatmosses with varying effects on productivity between both species and years with different climatic conditions.

It is assumed that high N uptake leads to nitrogen saturation in peatmosses, which increases metabolic stress (Rudolph & Voigt 1986, Baxter *et al.* 1992, Arroniz-Crespo *et al.* 2008), and particularly if phosphorus becomes the limiting nutrient (Bragazza *et al.* 2004, Fritz *et al.* 2012).

Unfortunately, phosphorus was not determined in this study, although the negative effect of high N concentrations on productivity of *S. cuspidatum* only occurred in 2011, accompanied by high capitulum N concentrations. In 2012, N concentrations were significantly lower and a decreasing productivity was not observed. While our experimental approach does not allow for the calculation of a threshold of N concentration for *Sphagnum* productivity, our results support suggested values of 1.2% - 1.5% (Lamers *et al.* 2000, van der Heijden *et al.* 2000, Bragazza *et al.* 2004). The probable threshold of N concentration and a supposed critical N : P ratio in *Sphagnum* tissue might explain contrasting effects of N addition observed especially in fast growing plants from wet habitats such as *S. fallax* or *S. cuspidatum* (Lütke Twenhöven 1992, Gunnarsson & Rydin 2000, Granath *et al.* 2012). Baxter *et al.* (1992) observed that *S. cuspidatum* from sites with higher N loads could profit from added ammonium, while it was toxic for mosses originated from sites with lower loads. This could explain why *S. papillosum* was not negatively affected by N fertilization, because the transplanted mosses originated from an area where N loads are substantially higher (approx. 35 kg ha^{-1} a^{-1}), than at the study site (Builtjes *et al.* 2011). Previous studies have reported that decreasing biomass production is often expressed in reduced length increment (Gunnarsson & Rydin 2000, Bragazza *et al.* 2004), which was indeed confirmed in our study. Contrarily, N addition might enhance the shoot density, cancelling out the effect of reduced length increment on biomass production, given that it occurred for *S. papillosum* and was also observed earlier for *S. magellanicum* (Heijmans *et al.* 2002a). Whereas the effect of experimental treatments on *Sphagnum* growth performance do not permit drawing definite conclusions, the effect of N supply on *Sphagnum* cover and vascular plant biomass appears more clear.

Sphagnum cover and vascular plant biomass

Above-ground biomass of *E. angustifolium* was not affected by fertilization. The added nutrient was accumulated only in the porewater for a short time, and only at low water tables. We suggest that most of the added nitrogen at Hartshoper Moor was directly absorbed by the *Sphagnum* layer (Woodin & Lee 1987) or quickly diluted and therefore unavailable in high doses for the vascular plants. Another possible explanation is that N was not the limiting nutrient, which is indicated by – even slightly – higher N concentrations in the biomass from fertilized plots (Heijmans *et al.* 2002a). The successive decrease of *Sphagnum* cover in fertilized plots occurred independently from vascular plant growth and was caused by the invasion of the fungus *Lyophyllum palustre*. At the beginning of the experiment, the infection of *S. cuspidatum* by the parasite was only observed on a small area relatively far away from the experimental plots. The implications caused by infection of *S. cuspidatum* by *L. palustre* were similar as described by Limpens *et al.* (2003b), although the infection almost always resulted in necrosis in our case. Transplanted *S. papillosum* seemed not to be infected by the fungus, due to either the species' lower susceptibility or the overall small coverage of the transplants.

At Schweimker Moor, a direct relationship between the increase in vascular plant biomass (almost exclusively *E. vaginatum*) and the decrease in *Sphagnum* cover is obvious. *E. vaginatum* tussocks might favor the colonization and establishment of peatmosses in mined peatlands (Tuittila *et al.* 2000), but generally a high cover of the dense growing species hampers *Sphagnum* growth by shading or covering the mosses with litter (Malmer *et al.* 1994). By contrast, *Sphagnum* produces unfavorable wet, acid and nutrient poor conditions for vascular plants (van Breemen 1995), while concomitantly a decrease in *Sphagnum* cover enhances growing conditions for vascular plants. As *Sphagnum* productivity was only slightly reduced by N addition and not by reduced precipitation, the reason for the observed changes in *Sphagnum* cover and biomass production of *E. vaginatum* caused by both experimental applications must be due to a stimulation of cottongrass growth. The response of *E. vaginatum* to N addition is presumably coupled to phosphorous availability (Tomassen *et al.* 2004); however, due to only slightly increased N concentration of *E. vaginatum* in fertilized plots, we suppose that the added nitrogen diluted in the plant tissue by stimulated growth (Shaver *et al.* 1986, Leith *et al.* 1999).

The impact of reduced precipitation on *E. vaginatum* is difficult to explain. It is assumed that they are able to grow at a wide range of moisture conditions and since the water table constantly does not decrease more than 30 – 40 cm below the surface – which was not the case in our study – changes in biomass production are reported to be low (Wein 1973, Lavoie *et al.* 2005, Bragazza 2006, Breeuwer *et al.* 2009). The water table was not affected by the rainout shelters, although the positive effect of reduced precipitation on biomass production indicates that cottongrass tussocks are able to create their own microhydrological conditions. Indeed, the underlying mechanism for the observed pattern remains unclear.

Litter decomposition

Litter decomposition in peatlands strongly depends on water conditions, species specific features such as initial litter quality, as well as the time at which the litter was buried (Clymo 1965, Hajek 2009). Compared to other studies, decomposition rates of *Sphagnum* litter were relatively high, especially given that our experiment was carried out in a relatively wet environment, yet were still in the reported range of 5 – 25% after one or two years (Scheffer *et al.* 2001, Dorrepaal *et al.* 2005, Bragazza *et al.* 2006, Breeuwer 2008, Hajek 2009, Lang *et al.* 2009, Bragazza *et al.* 2012). Mass loss of *Eriophorum vaginatum* was comparable to other studies (Breeuwer 2008, Bragazza *et al.* 2012), but higher than reported by (Aerts *et al.* 2006). Mass loss of *E. angustifolium* was low after one year (Limpens & Berendse 2003a), but equaled an amount of ca. 30% after two years reported before (Trinder *et al.* 2008).

Differences in mass loss were expected between growth forms, being higher for graminoids than mosses (Scheffer *et al.* 2001, Dorrepaal *et al.* 2005). The predicted pattern was observed for *E. vaginatum*, although the mass loss of *E. angustifolium* was surprisingly lower than for *Sphagnum* species after one year. Given that we did not determine the initial litter quality of cottongrass species and that decomposition studies dealing with *E. angustifolium* are scarce, we assume that litter quality was the reason for the slow decomposition of this species, as it might have relatively high concentrations of resistant phenolic compounds (Dorrepaal *et al.* 2005, Breeuwer 2008). Differences between both *Sphagnum* species underpin earlier findings that hummock Sphagna are intrinsically more decay-resistant than hollow species, even with a comparable C/N ratio of initial litter (Johnson & Damman 1991, Hajek 2009). The observation that *Sphagnum* litter, in contrast to *Eriophorum* litter, showed no further mass loss after one season is often attributed to initial leaching of water soluble compounds and a remaining highly refractory fraction (Clymo 1965, Scheffer *et al.* 2001, Hajek 2009) .

It is generally assumed that an increase of N availability leads to higher decomposition rates in peatlands, caused by either a simultaneously increasing N content of plant material or increasing microbial activity (Bragazza *et al.* 2007). Decreasing N contents and increasing C/N ratios of *Sphagnum* litter over time reflect an indication of net N mineralization, which is typical for *Sphagnum* layers. Generally, the inhibition of microbial decomposition might be caused by – among other factors – the acidic environment, the recalcitrant cell wall material of peatmosses and the efficient absorption of nutrients from percolating water by *Sphagnum* (Woodin & Lee 1987, Verhoeven *et al.* 1990, Scheffer *et al.* 2001). Nevertheless, in contrast to the observed effect of slightly increasing mass loss by N addition in the second year, N release was not enhanced by fertilization. The expectation that increasing N availability might enhance microbial activity and concomitantly N immobilization (Bragazza *et al.* 2007) was not met and N mineralization is presumably overruled by other factors such as initial litter quality (Breeuwer 2008). In our study, plant litter was not subjected to N fertilization prior to burial, and thus, assuming that enhanced N deposition will alter initial litter N concentration, an increasing N release is also expected (Breeuwer 2008).

2.5 Conclusion

The experimental design hardly allows drawing conclusions in terms of how reduced precipitation might affect peatland vegetation and carbon sequestration. Nevertheless, we gained an indication that drier conditions might lead to changes in the vegetation composition, stimulating the growth of vascular plants at the expense of peatmosses (Malmer *et al.* 1994, Laine *et al.* 1995). While peatlands are responding in multiple ways to nitrogen addition, none of the observed implications were positive with respect to *Sphagnum* performance and carbon sequestration. Fertilization directly affected *Sphagnum* through slightly lowered productivity, presumably due to toxic reactions of N surplus (Rudolph & Voigt 1986, Lamers *et al.* 2000). Moreover, *Sphagnum* was indirectly affected by mortality caused by the infection with its parasite fungus *Lyophyllum palustre* (Limpens *et al.* 2003b) or by stimulated growth of *E. vaginatum* and consequently an increased negative effect of shading (Malmer *et al.* 1994). Furthermore, it is likely that increasing N deposition will alter litter quality, directly leading to higher N contents in the biomass, which presumably enhances N mineralization and concomitantly increasing N availability in the rhizosphere of vascular plants (Verhoeven *et al.* 1990, Breeuwer 2008). Replacing the living *Sphagnum* layer and its recalcitrant tissue by vascular plants and the higher decomposability of its litter will presumably lead to a decrease in carbon sequestration in dry peatlands (Dorrepaal *et al.* 2005, Malmer *et al.* 2005), even if an enhanced productivity of vascular plant biomass might partly compensate the carbon loss

(Charman *et al.* 2013). Nevertheless, if competition with vascular plants is not a threat for *Sphagnum*, we show that varying hydrological conditions in two experimental years – with a prolonged drought period in spring 2011 – only had small effects on its productivity, suggesting certain resilience to desiccation of both – hollow and hummock – *Sphagnum* species. Furthermore, the predicted shift in dominant *Sphagnum* species from hollow to hummock vegetation with decreasing water table might generally support the resilience of the genus to prolonged drought events and decreasing water availability (Robroek *et al.* 2007a, Breeuwer *et al.* 2009), while the slower decomposition rates of these species might compensate possible negative effects on carbon sequestration with increasing aerobic conditions (Belyea 1996). The good performance of transplanted *S. papillosum* into the relatively wet carpet of *S. cuspidatum* underpins the suggestion of (re-)introducing this species to degraded peatlands in order to enhance restoration measures and the function of peatlands to sequester carbon (Smolders *et al.* 2003). The presence of vascular plants such as *E. vaginatum* might facilitate the recolonization of peatmosses in degraded peatlands, although it is necessary to consider the risk that stimulated growth might overrule positive effects on *Sphagnum* growth and its potential to enhance methane emissions from peatlands (Greenup *et al.* 2000, Lavoie *et al.* 2005). Hence, if global change leads to changing vegetation replacing *Sphagnum* by vascular plants such as *E. vaginatum*, carbon sequestration is likely to be negatively influenced by climate change and negative effects of high N inputs might be more pronounced under desiccated conditions (Tomassen *et al.* 2004, Breeuwer 2008).

3 Effects of prolonged drought and subsequent rewetting on CO_2 and CH_4 fluxes

3.1 Introduction

Northern peatlands store up to 15 – 30% of the world's soil organic carbon pool, which is almost the same amount stored in the terrestrial biomass (Gorham 1991, Turunen *et al.* 2002). However, despite covering only 3% of the global land surface, peatlands play a crucial role in global carbon cycling (Limpens *et al.* 2008a). Carbon in peatlands is stored as incompletely decomposed plant material and accumulated over thousands of years during the Holocene (Tuittila *et al.* 2012). Carbon cycling and the balance between accumulating and releasing carbon are strongly dependent on climatic conditions.

Peatlands generally developed in areas with a positive water balance, with higher rates of precipitation than evapotranspiration, favoring water-saturated conditions, which in turn result in the incomplete decomposition of plant remains and the formation of peat. The interaction between oxic and anoxic conditions is the main factor effecting carbon storage and release in peatlands. Thus, temperature and precipitation, controlling the water budget, are important variables determining peatland development (Gajewski *et al.* 2001). On the one hand, CO_2 production in peat soils is lower under anoxic conditions due to hampered heterotrophic respiration and peat decomposition. On the other hand, high water tables commonly lead to higher CH_4 emission rates due to the necessity of anaerobic conditions for methanogenesis (Alm *et al.* 1999, Lafleur 2009). Methane production and methane oxidation occur close to the water table at the aerobic-anaerobic boundary, and thus water table position often determines CH_4 emissions (Moore & Roulet 1993, Sundh *et al.* 1994, Kettunen *et al.* 1999). Beside lowering the water table and deepening the oxic zone in the peat, increasing temperatures stimulate the production of CH_4 in the saturated peat layer and the oxidation of CH_4 in the oxic layer (Basiliko *et al.* 2004). However, it has been shown that CH_4 emission increases at high temperatures, because production of CH_4 is more strongly enhanced than its consumption (van Winden *et al.* 2012). A similar counteracting effect of increasing temperatures controls the balance between biomass production and decomposition in peatlands, with both processes assumed to increase with rising temperatures (Heijmans *et al.* 2008, Charman *et al.* 2013).

Another key driver for carbon dynamics in peatlands is the vegetation. Drier conditions resulting from increasing temperatures and decreasing precipitation in summer are assumed to have far-reaching effects on the vegetation in mid-latitudinal peatlands (Weltzin *et al.* 2003, Heijmans *et al.* 2013). While warmer and drier conditions in summer may enhance primary productivity for *Sphagnum* mosses as well as vascular plants, overall it is expected that the stimulation of vascular plant growth will lead to a suppression of the *Sphagnum* moss cover (Breeuwer *et al.* 2009). The expected shift from a functioning moss layer towards the dominance of graminoids, shrubs and trees will presumably alter the litter quality, leading to enhanced decomposition in the absence of recalcitrant *Sphagnum* litter (Scheffer *et al.* 2001, Breeuwer 2008). By contrast, higher productivity compensate for the enhanced decomposition rates still leading to carbon accumulation in peatlands. Furthermore, the vegetation is important in methane dynamics, with vascular plants providing easily degradable substrates to methanogens via root exudation or root litter production (Whalen 2005). Furthermore, they may favor the emission of CH_4 by the transport via their aerenchyma from the anoxic peat layer to the atmosphere bypassing the aerobic zone of potential oxidation (Schütz *et al.* 1991, Kutzbach *et al.* 2004). Conversely, they can also stimulate methane oxidization by transport and release of O_2 to water-saturated and anoxic peat layers. However, it has been shown that CH_4 emissions are higher when vascular plants are present, compared to peatlands dominated by *Sphagnum*, because methanotrophic bacteria are often associated with peatmosses (Frenzel & Rudolph 1998, Raghoebarsing *et al.* 2005, Kip *et al.* 2010).

Furthermore, nutrient availability influences carbon dynamics in peatlands. Increasing nitrogen deposition is assumed to promote microbial decomposition, e.g. by amelioration of litter quality or stimulating microbial activity (Bragazza *et al.* 2006, Bragazza *et al.* 2012). Moreover, nitrogen in the form of ammonium and nitrate can inhibit methane oxidation and methanogenesis, respectively (Bedard & Knowles 1989, Conrad 1996), and has been observed to have an impact on vascular plant cover, promoting methane emission from peatlands (Granberg *et al.* 2001).

Prolonged drought events and concomitant irrigations on peat physical properties and changing porewater chemistry (Deppe *et al.* 2010, Estop-Aragones & Blodau 2012) as well as desiccation-induced impairment of plant metabolism (Schipperges & Rydin 1998, Robroek *et al.* 2009a) might have a peculiar impact on gas fluxes. Hence, we carried out CO_2 and CH_4 flux measurements in a restored bog in 2011 – characterized by an exceptional dry spring and a following relatively wet summer – to evaluate the response of greenhouse gas (GHG) fluxes to extreme drought events. These measurements were embedded to a manipulative field experiment where nitrogen was added and precipitation was reduced to elucidate the possible interacting effects of drought and nutrient supply (see chapter two).

3.2 Material & Methods

Study site

The field experiment was carried out at Hartshoper Moor in Northern Germany (54°17’N, 9°26’E). The experiment was set up in an area where the top layer (30 cm) was removed in the 1980s and a *Sphagnum* layer dominated by *S. cuspidatum* – with disjunct occurrence of *S. fallax*, *S. fimbriatum* and *S. papillosum* – has been established. *Eriophorum angustifolium* is abundant within the moss layer and *Molinia caerulea* and *Eriophorum vaginatum* are relatively frequent.

The experimental design was full factorial with nitrogen addition (20 kg ha^{-1} a^{-1} in 2011), reduced precipitation (- 25%) and the combination of both. In total, 20 plots with a size of 4 m² were installed; each treatment ran with five replicates and five control plots were additionally installed (for further details, see chapter 2.2).

Meteorological and hydrological measurements

Meteorological data was monitored with an automatic weather station. The weather station was equipped with a data logger (CR 1000, Campbell Scientific, North Logan, USA), a sensor for photosynthetic active radiation PAR (SKP 215, Skye Instruments, Llandrindod Wells, UK), a precipitation gauge (ARG 100, Campbell Scientific, North Logan, USA) and soil temperature sensors (107-L, Campbell Scientific, North Logan, USA). Measurements were recorded every 10 seconds and stored as 30 min means. Additionally, temperature 1 m above the surface (EBI 20-T, Ebro, Ingolstadt, Germany) and the water table (Mini-Diver, Schlumberger Water Services, Delft, Netherlands) were logged independently every 30 min.

Chamber measurements

Plastic collars (60 cm x 60 cm) were permanently installed at each of the 20 plots, by inserting them approximately 50 cm deep into the peat soil to assure that they also reached under the water table during dry periods. The positions of the collars were chosen to represent the typical vegetation composition of the whole plot. These collars were used for CO_2 flux measurements, as well as for CH_4 flux measurements. Collars were equipped with a groove around the top, filled with water during measurement to avoid gas exchange. Gas flux measurements were performed five times in 2011 (Fig 3.1).

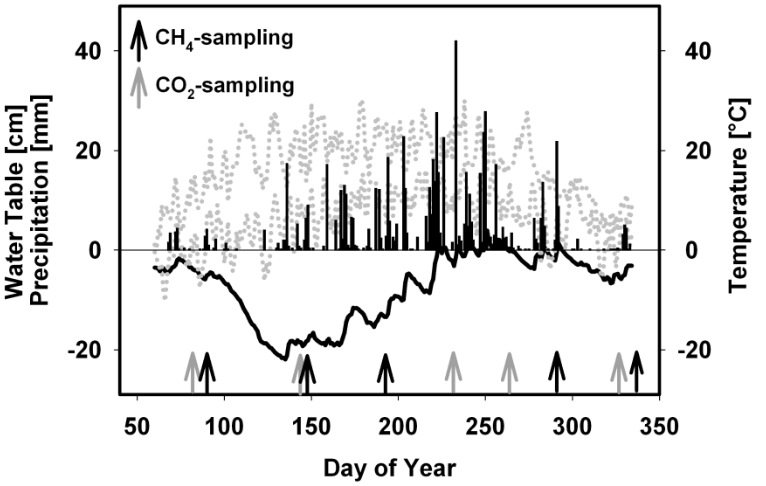


Fig 3.1 Meteorological and hydrological conditions at Hartshoper Moor in 2011 and days of gas flux measurements. The dotted grey lines represent daily minimum and maximum temperatures, respectively. The black line shows mean daily water table position in relation to the vegetation surface and the black bars show the daily precipitation.

CO_2 flux measurements

To measure CO_2 fluxes, a closed, transparent, climate-controlled chamber system with an infrared gas analyzer (IRGA, LI-840, LI-COR inc., Lincoln, USA) was used as described by Schneider *et al.* (2012). Additionally, the chamber was equipped with a PAR-sensor inside the chamber. Measurements were conducted for three minutes with recording CO_2, water vapor, PAR and temperature every second. First, net ecosystem exchange (NEE) was measured at ambient light conditions. Subsequently, the transparent chamber was shaded in two intensities with black gauze in order to increase the number of measurements and gain a wide spectrum of different light conditions for modeling (Burrows *et al.* 2005, Elsgaard *et al.* 2012). After the first measurement with the transparent chamber, a second measurement was performed while shading the chamber with one layer of gauze (approx. 50% original PAR) and a third with two layers (approx. 30% of original PAR). Subsequently, the chamber was darkened in a fourth measurement with an opaque cover (PAR = 0) to estimate ecosystem respiration (R_{eco}). Between each measurement, the chamber was removed and ventilated to obtain ambient CO_2 concentrations within the camber. Measurements were generally conducted between 10:00 am and 02:00 pm when PAR reached the maximum and the measuring order of the plots was randomized.

CH_4 flux measurements

Measurements were conducted with closed aluminium chambers (60 cm x 60 cm x 32 cm). They were equipped with a fan, a pressure vent, a thermometer for chamber air temperature and a sampling port. Two circular openings (4 cm diameter) at the front site were open while setting the chamber on the collar and closed afterwards to reduce initial pressure shocks. Six samples were taken of the chamber headspace with 60 ml plastic syringes connected to the sampling port via three-way stopcocks, within the closing time of 20 minutes. Sampling started directly after closing, and the remaining five samples followed in intervals of four minutes. Gas samples were subsequently analyzed in the lab using a GC equipped with a flame ionization detector (HP 5890 Packard Series II, Wilmington, USA). Syringes were connected to the column via a sample loop. Analyses were conducted within four days after sampling, with each sample analyzed twice. Two standard gases were used for calibration (1.7 ppm and 200 ppm CH_4), being injected three times before and after samples of three plots. CH_4 concentrations of the samples were calculated based on the means of the two calibration events being closest before and after the measurement of the samples.

CO_2 and CH_4 flux calculation

Fluxes of CO_2 and CH_4 were calculated from concentration changes over time. According to the micrometeorological sign convention, negative flux values represent a net loss of CO_2 from the atmosphere to the vegetation (CO_2 uptake through photosynthesis), and positive values represent emissions of CO_2 through both autotrophic and heterotrophic respiration (Lund *et al.* 2009). The same applies for CH_4 fluxes.

Flux calculation of each single CO_2 chamber measurement was conducted with an updated version of the MATLAB® routine of Kutzbach et al. (2007) using linear and non-linear regression. Given that no linear increase or decrease of GHGs within the chamber headspace can be expected (Kutzbach *et al.* 2007) an exponential fitting was normally used to determine initial concentration changes. The first and last 10 seconds of the 180 data points of each measurement were discarded, and the flux rate was calculated at t = 10 s from the remaining 160 data points, with water vapor dilution correction of CO_2 concentrations. Each single flux curve was reviewed for abnormalities such as abrupt changes in slope due to e.g. changes in PAR derived from cloud movements. If possible, the flux was recalculated by using only a part of the 160 s interval with constant conditions (minimum 40 s). Second, the dataset was checked by plotting the standard deviation of the residuals against the flux magnitudes to see how the point cloud was distributed. Flux calculations with outlying standard deviations of the residuals were checked again for mistakes, e.g. in data preparation, and were discarded from the dataset if the mistake could not be eliminated. Standard deviations of the residuals of 98% of the data were lower than 0.55 ppm and had a mean of 0.42 ± 0.06 ppm, which is remarkably low as the noise of the IRGA is specified to be <1 ppm. Finally, it was screened whether the non-linear fitted curves were concordant with the theoretical model of Kutzbach et al. (2007). If CO_2 flux curvatures showed an upward concavity, the slope of the linear regression was used instead for estimating the flux, as executed by Schneider *et al.* (2012). It was shown that a linear flux calculation achieves more robust flux estimates for this type of flux curves (Schäfer 2012).

Net ecosystem exchange (NEE), ecosystem respiration (Reco) and gross primary production (GPP) fluxes were calculated for five sampling days in 2011. GPP fluxes were calculated as the difference of the measured NEE and Reco fluxes. In a first step, we used the data for Reco and GPP (at ambient light, $GPP_{ambient}$) for simple comparisons between the experimental treatments, as well as between the different sampling dates.

Furthermore, to model light-dependent GPP for the entire day, a rectangular hyperbolic light response curve (Schäfer 2012) was fitted to the GPP data using the nonlinear least square (nls) function provided by the software R (R Development Core Team 2012) (Fig 3.2):

$$GPP = (a * b * PAR) / (a + b * PAR) \tag{3-1}$$

To evaluate the appropriateness of the hyperbolic model compared to a linear regression model, Akaike information criterion (AIC) for both models was compared. Additionally, it was ensured that standard error of the obtained parameter a – indicating the light saturation point (P_{max}) – did not exceed the obtained magnitude of P_{max}.

Due to the strongly clustered distribution of temperature values, caused by the small number of sampling days and the relatively short period of measurements during the day, a model including the temperature dependence of CO_2 fluxes was lacking. Thus, NEE was calculated as the sum of modelled half-hourly GPP (based on half-hourly PAR values measured in the field) and the means of measured Reco fluxes for each day, showing negative values for a net CO_2 uptake and positive values for a net CO_2 emission.

Flux calculation of each CH_4 chamber measurement was conducted with an updated version of the MATLAB® routine of Forbrich et al. (2010) using linear and non-linear regression. Each single flux curve was reviewed for abnormalities such as abrupt changes in slope; for instance, due to ebullition. As only six concentration measurements were available for flux calculation, the application of the non-linear regression model was checked by the Akaike information criterion with small sample correction (AICc), as proposed by Forbrich et al. (2010). The derived CH_4 fluxes were used for simple comparison between experimental treatments and sampling dates. To estimate CH_4 fluxes for each day, we used all flux data and corresponding air temperature (T) values to calculate the following hyperbolic model:

$$CH_4 = (a + T) / (1 + b + T) \qquad (3\text{-}2)$$

Again, the AIC was used to ensure the advantage of this model compared to a linear regression model and other hyperbolic models that were preselected based on the shape of the scatter plot. Subsequently, daily CH_4 fluxes for each sampling were calculated based on half-hourly temperature values. The small number of sampling days (n = 5) did not allow including the factor water table to calculate daily CH_4 fluxes.

To assess the GHG-potential of CH_4 emissions and approximately estimate whether the study site serves as a carbon source or as a sink, calculated CH_4 fluxes were converted to CO_2 equivalents using the factor 25 (Solomon *et al.* 2007).

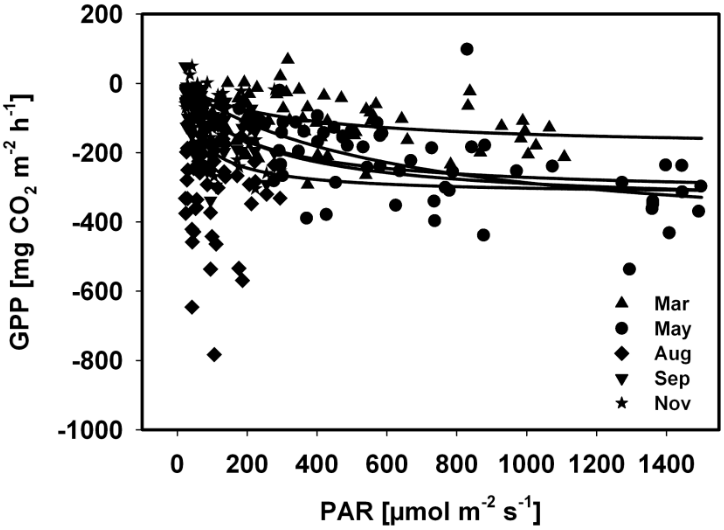


Fig 3.2 Light-dependent gross primary productivity (GPP) and corresponding light response curves for each sampling date. For calculation of the light response curves, a hyperbolic model was fitted to the measured data for each day (see equation 3-1).

Vascular plant biomass and *Sphagnum* cover

Species composition was determined using a point-intercept sampling (Jonasson, 1988). Within each collar used for gas flux measurements, a narrow pin was passed through a perforated plate and lowered within the vegetation at 64 evenly distributed points. The number of hits was counted in 2011 and 2012 for each species. Cover of the moss layer was calculated by the number of hits at the surface divided by the total number of pins. Biomass of all plots was harvested at the beginning of September 2012. This method allowed determining the annual aboveground biomass by clipping and weighting biomass after finishing the experiment in 2012 and calculating the biomass retrospectively for 2011 (Robroek *et al.*, 2010; Shaver *et al.*, 2001).

Statistics

To examine the impact of the experimental treatments on vascular plant biomass and *Sphagnum* cover, we carried out two-way ANOVAs with the fixed factors “reduced precipitation” and “nitrogen fertilization”, ensuring the homogeneity of variances and normality of the data. In the case of GHG fluxes, our data did not meet the assumptions of homogeneity and normality, even after Box-Cox-transformation. Thus, we carried out Mann-Whitney U-Tests to analyze the effect of the experimental treatments on GHG fluxes. Neither the precipitation treatment (CH_4: $p = 0.51$, R_{eco}: $p = 0.21$, GPP: $p = 0.36$) nor the nitrogen treatment (CH_4: $p = 0.53$, R_{eco}: $p = 0.67$, GPP: $p = 0.69$) had a significant effect on greenhouse gas fluxes. Therefore, the data were pooled for further analyses. In order to reveal seasonal differences, we compared gas fluxes between the different sampling dates using the non-parametric Kruskal-Wallis test. To identify differences between the sampling dates, we computed post-hoc comparisons of mean ranks of all pairs of groups. Furthermore, linear regression models were calculated to determine the influence of temperature and water level on greenhouse gas fluxes. First, we used daily mean soil temperature and water level values, as well as mean CH_4 flux, R_{eco} and GPP values for each sampling date ($n = 5$). For a more detailed analysis, we additionally carried out linear regression models with the exact air temperature for each gas flux sample (CH_4 flux: $n = 79$, R_{eco} and GPP: $n = 99$). In the case of GPP, the value obtained during ambient light measurements ($GPP_{ambient}$) was used for all statistical analyzes. The GPP values obtained by manually altering light conditions were excluded and only used for modeling daily CO_2 fluxes.

The normality of residuals was ensured for all regression analyses. All statistical analyses were carried out using the software STATISTICA 9.0 (StatSoft, Tulsa, OK).

3.3 Results

Aboveground vascular plant biomass (mainly *Eriophorum angustifolium*) was 47.3 g (SD 17.3) dry weight per m^{-2} dry, with no significant differences observed between the experimental treatments (see also chapter 2.3). Mean *Sphagnum* cover was 88.4% (SD 15.4). Here, nitrogen fertilization ($F = 7.15$; $p < 0.05$) and reduced precipitation ($F = 4.51$; $p = 0.05$) had a significant effect, prompting a decrease from around 95% cover in control plots to 81% and 82%, respectively.

2011 was characterized by an exceptional dry spring, with less than 25 mm mean monthly precipitation between March and May, and a relatively wet summer, with 155 mm mean monthly precipitation between July and September. The water table was at the surface in early spring, fell down during April and reached -20 cm in May. From July onwards, the water table rose again and was at the surface again in August (Fig 3.1). Furthermore, the mean annual temperature was 8.9 °C and thus slightly higher than during the reference period of 1971 – 2000, although mean monthly temperature from April to June was between 1 to 3 °C higher than in the reference period (Fig 3.1). For a more detailed description of meteorological data and vegetation data, see chapter 2.

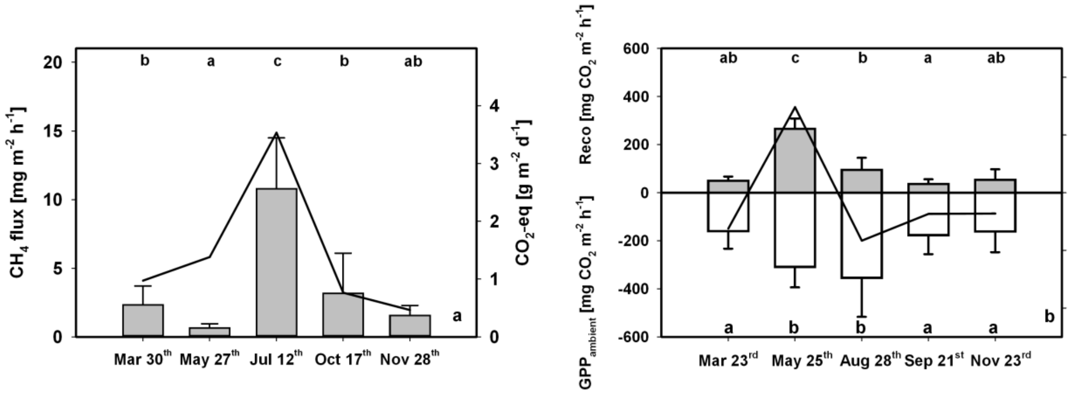


Fig 3.3 Daily gas flux measurements. (a) Bars show CH_4 fluxes for each sampling date (means ± SD, n = 4) and the black line represents the calculated daily greenhouse gas potential of the emitted methane in CO_2 equivalents. (b) Grey bars show measured ecosystem respiration (R_{eco}) and white bars show the corresponding gross primary productivity ($GPP_{ambient}$) measured at ambient light conditions (means ± SD, n = 4 – 5). The black line represents the calculated net ecosystem exchange (NEE). Different letters indicate significant differences ($p < 0.05$) between sampling dates.

CH_4 fluxes differed significantly between the sampling dates (H = 56.89; $p < 0.001$; Fig 3.3a), with highest fluxes observed in July with 10.77 mg CH_4 m^{-2} h^{-1} (SD 3.71) and lowest values in May with 0.64 mg CH_4 m^{-2} h^{-1} (SD 0.31). Ecosystem respiration R_{eco} also showed a significant seasonal variation (H = 62.24; $p < 0.001$; Fig 3.3b), with highest R_{eco} rates measured in May with 265.87 mg CO_2 m^{-2} h^{-1} (SD 42.53) and lowest rates in September with 36.73 mg CO_2 m^{-2} h^{-1} (SD 19.25). GPP measured at ambient light intensities was significantly higher in May and in August than the other months (H = 42.05; $p < 0.001$), ranging from -159.23 mg CO_2 m^{-2} h^{-1} (SD 73.84) in March to -353.21 mg CO_2 m^{-2} h^{-1} in August (SD 162.61)(Fig 3.3b).

Calculating integrated daily values including the temperature dependence of CH_4 fluxes and the light dependence of GPP, the study site served as a weak carbon sink in March and November, with an uptake of around 0.25 g m^{-2} d^{-1} CO_2-equivalents. By contrast, in May the study site released 4.4 and in summer (July/August) around 1.8 g m^{-2} d^{-1} CO_2-equivalents. Whereas CO_2 amounted for nearly 70% of the total emissions in May, CH_4 was the main source of released carbon in summer (Fig 3.3).

Linear regression analyses (Fig 3.4) revealed that the CH_4 flux was dependent on neither the water table ($r^2 = 0.04$; $p = 0.74$) nor the daily mean soil temperature ($r^2 = 0.59$; $p = 0.13$). On the other hand, ecosystem respiration was dependent on the water level ($r^2 = 0.91$; $p < 0.05$). The linear relation between daily soil temperature and R_{eco} was not significant ($r^2 = 0.06$; $p = 0.70$). Similar to CH_4, GPP was dependent on neither water table ($r^2 = 0.19$; $p = 0.47$) nor soil temperature ($r^2 = 0.57$; $p = 0.14$). However, a closer look revealed weak yet significant correlations between the CH_4 fluxes ($r^2 = 0.54$; $p < 0.001$), R_{eco} ($r^2 = 0.20$; $p < 0.001$) and GPP ($r^2 = 0.21$; $p < 0.001$), with the exact corresponding air temperature during the measurement (Fig 3.5).

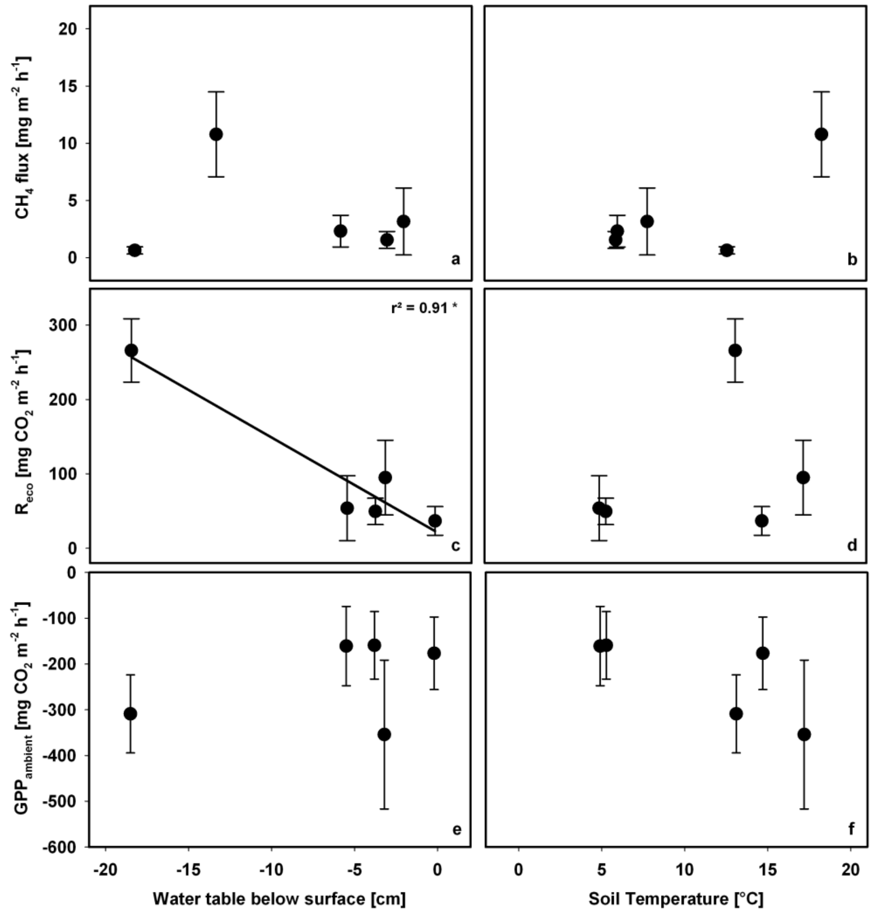


Fig 3.4 CH_4 fluxes (a, b), R_{eco} (c, d) and $GPP_{ambient}$ (e, f) in relation to water table and soil temperature, presented as daily means. Linear regressions are presented in case of significance ($p < 0.05$). * = $p < 0.05$. For further details, e.g. sampling sizes, see Fig 3.3.

The partly high variation of CH_4 fluxes between the sampling plots could be explained by neither the vascular plant biomass at the end of the vegetation period ($F = 0.01$; $p = 0.91$) nor the cover of *Sphagnum* mosses ($F = 0.24$; $p = 0.63$). The relationship between the vascular plant biomass and CO_2 fluxes was weak, but R_{eco} significantly increased with increasing plant biomass ($r^2 = 0.25$; $F = 5.87$; $p < 0.05$). In the case of *Sphagnum* cover, no relationship was observed ($F = 0.49$; $p = 0.49$). Moreover, no relationship was observed between either GPP and vascular plant biomass ($F = 0.61$; $p = 0.44$) or between GPP and *Sphagnum* cover ($F = 0.82$; $p = 0.38$).

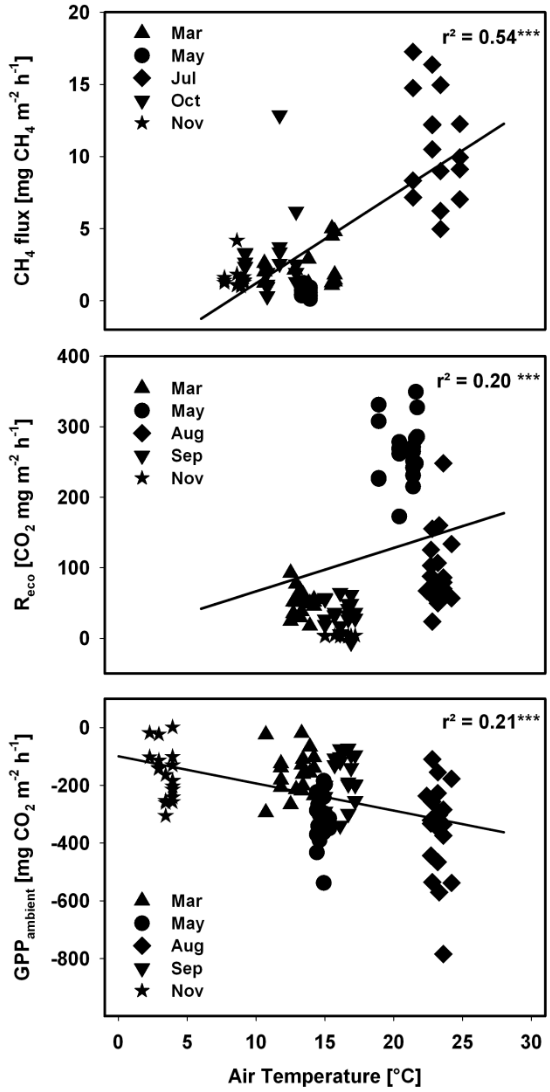


Fig 3.5 CH$_4$ fluxes (a), R$_{eco}$ (b) and GPP$_{ambient}$ (c) in relation to air temperature for each single measurement (CH$_4$: n = 79, CO$_2$: n = 99). Linear regressions are presented. *** = $p < 0.001$.

3.4 Discussion

The limited dataset does not allow modeling GHG fluxes for the entire year of 2011 and thus care must be taken when drawing conclusions from only five days of measurement. Our sampling design does not provide sufficient information to disentangle the multiple interacting effects of climatic and hydrological parameters such as temperature and water level on greenhouse gas emissions. Furthermore, the experimental treatments “reduced precipitation” and “nitrogen fertilization” should not be discussed here, given that the lack of significant results regarding GHG fluxes might be the result of overall problems concerning the performance of the field experiment (see chapter 2.4). However, it is remarkable that the *Sphagnum* cover had no effect on GHG fluxes, even if the cover – and concomitantly biomass for carbon assimilation – decreased in plots with N fertilization and reduced precipitation. We suggest that a decline of *Sphagnum* of 10 – 15% might only have small effects on overall GHG fluxes, which were presumably overruled by other factors such as temperature and water table. Nonetheless, with the aforementioned uncertainties in mind, our data highlights some interesting insights into the influence of water level and temperature on CH_4 and CO_2 fluxes.

Photosynthesis as well as autotrophic and heterotrophic respiration is dependent on temperature, expecting higher CO_2 uptake and emissions rates with increasing temperature. Thus, it has been suggested that increased primary production might compensate carbon losses by enhanced decomposition caused by increasing temperatures (Heijmans *et al.* 2008, Charman *et al.* 2013). Our results underpin that temperature has no or only a weak effect on CO_2 fluxes as long as peat is water saturated, as our results only show a net CO_2 release in May (with a water table of -18.5 cm). In all other months with nearly identical water tables – ranging between -5.0 and -0.2 cm – CO_2 was accumulated with similar rates, independent from temperature. Only in August were GPP and R_{eco} slightly enhanced, presumably caused by peak vascular plant biomass and leaf area. Particularly in March, (the end of) September and November, it is likely that CO_2 exchange was mainly driven by *Sphagnum*, with vascular plants either not yet fully developed or already senescent, respectively. GPP was surprisingly high in May, because *Sphagnum* mosses appeared severely stressed by desiccation without showing photosynthesis or respiration (Schipperges & Rydin 1998, see also chapter 4), indicating that vascular plants exclusively contributed to CO_2 uptake here. In contrast, high R_{eco} rates are caused by autotrophic respiration of vascular plants and heterotrophic respiration of the peat (Riutta *et al.* 2007). The fact that R_{eco} rates were much higher in May than August indicates that heterotrophic respiration rather than (aboveground) autotrophic respiration was the main driver of CO_2 emission, caused by decreasing moisture and decreasing anoxic conditions resulting from the prolonged drought in spring (Lafleur 2009, Lund *et al.* 2012). Although no relationship between the vegetation cover – neither aboveground vascular plant biomass nor the cover of *Sphagnum* mosses – and GPP was observed, increasing R_{eco} rates with increasing vascular plant biomass indicates that litter quality and the amount of substrate available for decomposition contributes significantly to the total carbon release of peatlands, especially if vascular plants benefit at the expense of *Sphagnum* of warmer and drier conditions (Breeuwer 2008, Heijmans *et al.* 2008). Furthermore, we suggest that R_{eco} was almost exclusively driven by autotrophic respiration of *Sphagnum* in May, September and November, due to high water tables and the fact that measured R_{eco} rates are in the range of observed dark respiration rates of *Sphagnum* capitula (see chapter 4.3).

Overall, CH_4 emissions were in the range of ombrotrophic bogs as previously reported (Whalen 2005, Saarnio *et al.* 2009, and references therein), being in the lower range in May and the upper range in July. It has generally been stated that both temperature and water level have a large impact on methane emission, depending on production and consumption rates (van Winden *et al.* 2012). It has been assumed that CH_4 production as well as CH_4 oxidation increase with increasing temperatures and rising water levels (Frenzel & Karofeld 2000, Kip *et al.* 2010). In our study, methane emissions appeared to be strongly dependent on temperature, whereas the water table had no effect on CH_4 fluxes. Unfortunately, our sampling was carried out at either high temperatures (July) or high water tables (all other months); therefore, we are unable to disentangle the interacting effect of both factors. However, in accordance with earlier findings, our results suggest that as long as the temperature does not exceed 15 °C, almost all produced CH_4 is oxidized and consumed. Evidence suggests that the balance between methanogenic and methanotrophic activity is relatively stable up to a certain temperature threshold between 15 and 20 °C, especially if *Sphagnum* and their associated methanotrophs are involved (Larmola *et al.* 2010, van Winden *et al.* 2012).

Although temperature obviously overruled possible effects of the water level on CH_4 fluxes, some other potential factors controlling CH_4 fluxes should be briefly discussed. In May, the water table was the lowest observed during the season, and concomitantly CH_4 fluxes were almost zero. The strong decline in CH_4 emission in May supports earlier findings that the methanogenic activity is negatively affected if the water table decreases below 15 – 20 cm (Moore & Roulet 1993, Shannon & White 1994). Beside the methanogenic inactivity in the oxic layer, the methanotrophic activity might be enhanced in a deeper aerated peat layer (Sundh *et al.* 1994), and methane might be oxidized before entering the rhizosphere of vascular plants being transported to the atmosphere via their aerenchyma (Fritz *et al.* 2011). Furthermore, the low availability of easily degradable substrate such as root exudates in the saturated layer and the recalcitrance of peat in deeper layers decrease CH_4 production when the water table is low (Yavitt & Lang 1990, Whalen 2005).

Low CH_4 emissions are expected during and directly after prolonged drought, due to low production rates resulting from the oxygen-induced impairment of methanogens and/or a suppression of methanogenesis due to the enhanced availability of alternative electron acceptors such as sulfate and ferric iron (Knorr *et al.* 2009, Estop-Aragones *et al.* 2013). The sampling in July was carried out approximately one month after the prolonged drought in spring. The effect of delayed recovery of methane production and emission after drought appears to be relatively small compared to other studies (Kettunen *et al.* 1999, Knorr *et al.* 2008), indicating that the drought was not sufficiently severe and long to impede the recovery of methane production or show the high resilience of methanogens to temporarily oxic conditions (Oquist & Sundh 1998, Deppe *et al.* 2010). Furthermore, drought events strongly reduce the CH_4 oxidation potential, and even if the methanotrophic activity generally recovers after water level rise (Larmola *et al.* 2010), it is likely that CH_4 oxidation in July had not yet entirely recovered, leading to (in combination with higher temperatures) the relatively strong release of CH_4. Beside the effect of temperature and the possible disequilibrium between methanogenic and methanotrophic activity after drought, the enhanced availability of easily degradable substrate accumulated in the rewetted rhizosphere of vascular plants might have had an impact on the high emission rates observed in July.

It is generally assumed that plant-associated CH_4 oxidation is lacking in *Eriophorum* species, and in contrast, they are known to efficiently transport CH_4 to the atmosphere via their aerenchyma (Schimel 1995, Frenzel & Rudolph 1998). However, the lacking relationship between standing vascular plant biomass and CH_4 emission in our study might indicate that pathways other than plant aerenchyma were responsible for gas transport. Additionally, *Eriophorum angustifolium* was relatively sparsely growing at our study site, and therefore differences in gas fluxes between plots could hardly result from differences in the living biomass.

In conclusion, the study site is assumed to be a weak sink of carbon when water level is high, impeding heterotrophic peat respiration, and when temperature is low, impeding the production and the emission of CH_4. In turn, CO_2 is released when water table is low, and CH_4 emission is enhanced after rewetting, at least in combination with high temperatures in summer. Thus, we suggest that projected climate changes with warmer and drier summers might have a negative impact on carbon sequestration in temperate peatlands, especially in the case of prolonged drought events with rewetting processes following in summer months.

4 Can *Sphagnum* keep pace with hydrological changes?

4.1 Introduction

Peatlands play an important role in the global carbon cycle. They cover only 3% of the World's land area but store up to one third of the global soil carbon pool, nearly the same amount of carbon that is stored in the terrestrial biosphere (Bridgham *et al.* 2006). Peatlands are an important long-term carbon sink because they sequester and store atmospheric carbon for thousands of years (Charman *et al.* 2013). Carbon sequestration depends on the productivity of the vegetation and the formation of new peat biomass and on decay losses as CO_2, CH_4 or dissolved organic carbon (Belyea & Malmer 2004, Malmer *et al.* 2005). Both, production and decomposition are strongly dependent on climatic and hydrological conditions such as temperature, radiation, humidity and water table depth (Limpens *et al.* 2008a, Strack *et al.* 2009, Loisel *et al.* 2012).

Northern peatlands formed after Holocene deglaciation. They were permanently affected by varying climatic conditions and causing themselves a feedback to climatic changes (Frolking & Roulet 2007, Charman *et al.* 2013). Hence, the vegetation structure of peatlands as well as their function to store carbon varied strongly during the Holocene. A key genus for carbon sequestration is *Sphagnum*, since peatmosses cover half of the northern peatland areas and store more carbon than any other plant genus in the world (Clymo & Hayward 1982).

The formation of *Sphagnum* dominated bogs in the northern hemisphere started roughly 3000 – 6000 years BP during a relatively wet and cool period (Rydin & Jeglum 2006). Once established *Sphagnum* works as an ecological engineer creating its own acidic, cool and anoxic ecosystem, conditions which are unfavourable for many other plants (van Breemen 1995). Although the initiation of raised *Sphagnum* bogs is linked to a cooler climate, historically, the lowest peat accumulation rates were found during relatively cool periods, e.g. during the Little Ice Age (Mauquoy *et al.* 2002).

Reconstruction of climatic conditions and carbon sequestration in the past are considered a useful tool to predict future changes (Gorham *et al.* 2012). Nevertheless, the impact of a future climate change on peatlands and their function to sequester carbon is not yet clear. Uncertainties originate from the dependence of climate model projections on their spatial and temporal scale and possible contrasting responses to different climatic parameters (Adkinson *et al.* 2011).

Whereas high-latitudinal peatlands may benefit from increasing temperatures and higher mean precipitation predicted for these regions, temperate peatlands in Central Europe may suffer from decreasing summer precipitation (Belyea & Malmer 2004, Christensen *et al.* 2007). Increasing temperatures enhance the primary productivity in peatlands, either directly or indirectly (Adkinson *et al.* 2011, Loisel *et al.* 2012), while microbial activity and concomitantly litter decomposition is expected to increase (Dorrepaal *et al.* 2009). An increase of productivity may override the effect of increasing decay on carbon sequestration (Charman *et al.* 2013).

According to future climate scenarios for Central Europe, the combination of increased temperatures, reduced summer precipitation and increased evapotranspiration will alter the hydrology of peatlands dramatically and will cause decreasing water tables (Moore 2002). Consequently, *Sphagnum* photosynthesis and productivity decreases with enhanced aerobic decomposition in the unsaturated peat layer (Gunnarsson *et al.* 2002, McNeil & Waddington 2003). Species composition may be affected by climate change, within the genus *Sphagnum* as well as between peatmosses and invading vascular plants (Weltzin *et al.* 2003, Malmer *et al.* 2005, Breeuwer *et al.* 2009). Additionally, reduced precipitation may directly hamper growth and net CO_2 assimilation of peatmosses and consequently the accumulation of carbon (Robroek *et al.* 2009a). Contrarily, even small rain events may have a positive effect on capitulum water content and hence on carbon uptake (Strack & Price 2009).

To avoid water loss and subsequent desiccation, peatmosses have an effective system to lift water by capillary transport and to store water in dead hyaline cells (Hayward & Clymo 1982) and different *Sphagnum* species occupy specific niches along a hummock-hollow gradient and may avoid desiccation (Andrus *et al.* 1983). The water holding capacity of species growing on dry hummocks is higher due to their specific morphology avoiding desiccation. In contrast, hollow species are reported to be either more vulnerable to climatic drought - because of the lack of morphological adaptations -, or less vulnerable - because they grow closer to the water table. Speculations on the vulnerability of hollow populations to drought are contradictory and information on desiccation tolerance (vs. avoidance) of peatmosses is scarce (Schipperges & Rydin 1998, Hajek & Beckett 2008). However, moisture conditions strongly affect *Sphagnum* growth and carbon sequestration, and prolonged drought may lead to enhanced mortality or may reduce the potential of peatmosses to recover (Gerdol *et al.* 1996, Bragazza 2008).

Previous studies investigating the potential of peatmosses to recover after desiccation were carried out under laboratory conditions, where moss capitula were exposed to drought. In this study we investigated *in-situ* the potential of the hollow species *Sphagnum cuspidatum* to recover after desiccation and the dependence of varying moisture conditions during the growing season on photosynthesis and productivity. We determined (i) the growth performance of *S. cuspidatum* during the growing season in the field and (ii) in dependence of varying moisture conditions. We analyzed (iii) the short-term recover of the mosses exposed to the severe drought in spring and determined further (iv) the seasonal variation of CO_2 exchange. Finally, we combined the information obtained in the field and from CO_2 exchange measurements to model (v) the carbon uptake of peatmosses over the growing season depending on peatland's moisture conditions.

4.2 Material & Methods

Field site and sampling

Sampling took place on a peatland restoration site at Hartshoper Moor, Germany (54°17’N, 9°26’E). *Sphagnum cuspidatum* was sampled seven times in 2011 (see Table 4.1). At Each sampling date, 16-20 intact cores (53 mm in diameter and 50 mm in depth) were collected and used for following measurements.

To observe the growing conditions in the field an automatic weather station was installed and equipped with data logger (CR 1000, Campbell Scientific, North Logan, USA), a sensor for the photosynthetic active radiation (SKP 215, Skye Instruments, Llandrindod Wells, UK) and a precipitation gauge (ARG 100, Campbell Scientific, North Logan, USA). Measurements were recorded every 10 seconds and stored as means of 30 min. Additionally, temperature (EBI 20-T, Ebro, Ingolstadt, Germany) and the water table (Mini-Diver, Schlumberger Water Services, Delft, Netherlands) were logged independently every 30 min.

Sphagnum analysis

Water content, growth density and chlorophyll content were determined for each sampling. The water content is expressed as the ratio of fresh weight to dry weight (fw/dw) and was determined after oven-drying the mosses for 48h at 60 °C. The capitulum growth density was calculated as the dry weight per area (g m^{-2}) for the uppermost centimeter. Chlorophyll analyses were conducted with approx. 10 mg of homogenized fresh leafs. Plant material was extracted with $CaCO_3$ saturated dimethylsulphoxide for 40 min at 60 °C. Subsequently, the extraction was centrifuged (13.000 U/min for 10 min), the absorbance of the supernatant determined at wavelengths of 648 nm and 665 nm and the chlorophyll content quantified after Barnes *et al.* (1992). To determine the biomass production over the growing season, at the end of April totally 60 *Sphagnum* individuals (three at 20 different locations within the site) were equipped with white thread directly below the capitula. At the end of October, the marked mosses were harvested and the biomass production could be calculated as a function of length increment (between the thread and the capitulum) and shoot density (Clymo 1970). Moreover, we were able to retrace precisely the development of *S. cuspidatum* during the growing season 2011 because a severe drought in spring killed the capitula of the mosses. With the beginning of a wetter period in summer they built new stems with new capitula and this new developed tissue could be related to a defined time period. Carbon content of the biomass harvested in October was determined using an element analyzer (EA3000, EuroVector, Milan, Italy).

Gas exchange measurements: Experimental set up

For gas exchange measurements, only mosses sampled in May (S1), June (S2), July (S4), and September (S6) were used. Prior to the first measurements, capitula of mosses were cut and transferred carefully to a basket covered with nylon gaze keeping the moss structure as undisturbed as possible.

Measurements of CO_2 were conducted using an open gas exchange system. The mosses were placed in a glass chamber (160 cm³) that was closed air tight. Mosses were allowed to acclimatize to conditions in the chamber for at least fifteen minutes. The chamber was connected on one side to an air supply unit (ASUM-2-GC/EC, ADC, Hoddesdon, UK) providing a constant flow rate of ambient air and at the other side to an infrared gas analyzer (LCA 2 System, ADC, Hoddesdon, UK). The mean CO_2 concentration of ambient air was 400 ppm (± 10 ppm) and light intensity for net photosynthesis measurements was between 250 and 300 µmol m^{-2} s^{-1} (PAR), assuring light saturating conditions (e.g. Maseyk *et al.* 1999). The constant flow rate of air passing the chamber was 200 ml min^{-1} and to mix the air in the chamber a magnetic stirrer was used. Immediately after passing the chamber, temperature was controlled to assure a temperature of 25.2 °C (SD 1.5 °C). Before entering the analyzer, air was dried with a water trap. Simultaneously, air passed an identical chamber without mosses and CO_2 exchange was calculated as the differences between the concentrations of both chambers. Fresh weight of all samples was measured before and after each measurement to calculate the water content (WC). After the last measurement dry weight of each sample was recorded after oven-drying for 48h at 60° C.

Gas exchange: Recovery after dehydration

In May and June (S1 and S2), capitula of *S. cuspidatum* appeared to be severely damaged due to their strikingly colorless appearance. Directly after sampling, mosses were weighed to determine the fresh weight. The following day weighing was repeated to ensure the same water content as during sampling. Afterwards, photosynthetic and respiratory activity was measured as described above. After the measurement and during the next days, mosses were carefully rehydrated with rain water and were stored water saturated under ambient light and temperature conditions. Subsequently, gas exchange measurements were repeated five times in eleven days in case of S1 and four times in ten days in case of S2. To ensure identical moisture conditions near optimum capitula water content, capitula were carefully blotted using paper towels until they reached a water content of 11.5 (± 1.6) to ensure preferable moisture conditions for photosynthesis.

Gas exchange: Dependence on capitulum water content and seasonal variation

For mosses of S2, S4, and S6 gas exchange was measured with different capitula water contents. Whereas samples of S2 were rewetted for ten days before water dependent measurements were carried out (see section on recovery), mosses of S4 and S6 were measured the day after harvesting. Prior to the first measurement, mosses were saturated with deionized water by spraying the water carefully to avoid free water not adhering to the capitula. Afterwards, the capitula were carefully blotted using paper towels for the next measurement with a lower water content. This procedure was repeated until a decrease in net photosynthesis was observed. This was the case after four to seven measurements for each single sample. Dark respiration of each sample was measured at one water content as respiration is assumed not to be water dependent (Dilks & Proctor 1979).

To model the relationship between capitulum water content (WC) and net photosynthesis (NP), we calculated different nonlinear regression models using the nonlinear least square (nls) function provided by the software R (R Development Core Team 2012). A preselection of appropriate models was carried out based on the shape of the scatter plot of all NP values versus capitulum water content. Afterwards, these models were compared using the Akaike information criterion (AIC). The function which best predicted the relationship between capitulum water content and net photosynthesis was the asymmetric hump-shaped curve of the Weibull model:

$$NP = (a / b) * (WC / b)^{a-1} * e^{(-WC / b)\,\hat{}\,c} \qquad (4\text{-}1)$$

Modeled carbon balance in the course of the year

To determine seasonal distinctions of gas exchange characteristics we modeled the net carbon uptake for the entire growing season. Due to the strong correlation between water table and capitulum water content, we were able to calculate the capitulum water content for each hour. Subsequently, we used the Weibull model to calculate the net photosynthesis at the respective water content on an hourly base. We used the PAR values of the climate station in the field to calculate net primary production (NPP). For PAR = 0 µmol m^{-2} s^{-1} we used values obtained for dark respiration and for PAR values > 300 µmol m^{-2} s^{-1} we used net photosynthesis values at the respective water content. For PAR values between 0 and 300 µmol m^{-2} s^{-1} we simplified light saturation models assuming a linear increase from the dark to light saturation. In total, we calculated six different models, for S2, S4, and S6 on the dry mass basis (per g dry weight) and for each on an area basis (per m^{-2}). For the area based models, we used the respective growth density of each sampling date. Further, to check the plausibility of our findings based on gas exchange measurements, we opposed the results to the biomass data obtained in the field.

Data analysis

To analyze differences in capitulum water content, growth density and chlorophyll content between all sampling dates, one-way ANOVAs followed by Tukey’s post hoc test were performed. In case of unequal variances, Welch’s ANOVA was applied. The same procedure was carried out to compare optimum water contents (for photosynthesis), maximum photosynthesis and dark respiration rates for S2, S4, and S6. To reveal differences in net photosynthesis and dark respiration between S1 und S2 a, T-Test was carried out. To analyze the relationship between water table and capitulum water content a linear regression model was calculated where the normality of residuals was ensured. Besides non-linear regression models to describe the relationship between water content and net photosynthesis, all analyses were carried out using the software PAST (Hammer *et al.* 2001).

4.3 Results

Field conditions

The weather in 2011 was characterized by an exceptional dry spring and a relatively wet summer (Fig. 4.1). Mean monthly precipitation was around 40 mm from January to June, being lowest in April with 5.6 mm, and around 140 mm from July to October, being highest in August with 223 mm. The longest period without any precipitation was 15 days at the end of April. Water table fluctuations were about 20 cm with lowest levels during the dry spring. Single rain events in spring had no effect on the water table, only some consecutive days with rain fall in the middle of June caused an increasing water table. From August to October, hollows were permanently water saturated. The mean monthly temperature (until October) ranged from 3.5 °C in March to around 16 °C from June to August. Photosynthetic active radiation (PAR) was highest between April and June with, on average, 9 to 10 hours daily of PAR values greater than 300 µmol m^{-2} s^{-1}. Between July and October this period decreased to 7.6 hours daily. In other months the daily photoperiod with PAR values greater 300 µmol m^{-2} s^{-1} didn’t exceed 4.6 hours daily.

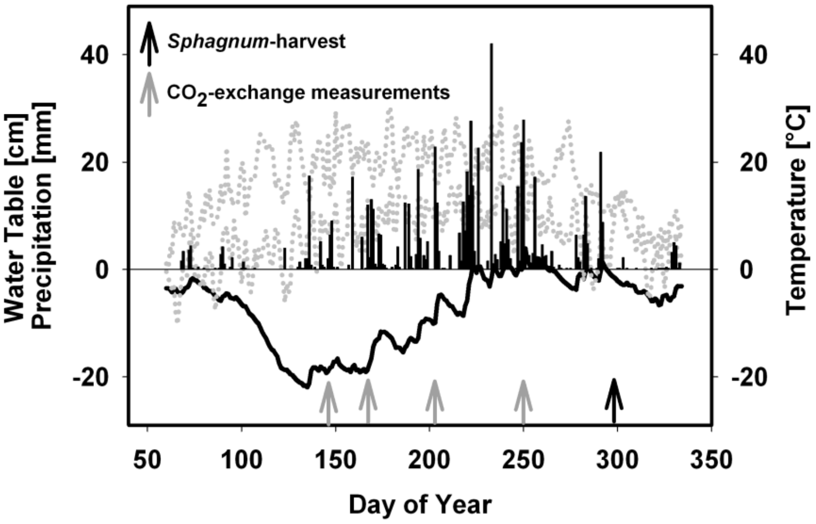


Fig 4.1 Meteorological and hydrological conditions at Hartshoper Moor of the year 2011, days of *Sphagnum* CO_2-exchange measurements and *Sphagnum* harvest for productivity determination. The dotted grey lines represent daily minimum and maximum temperatures, respectively. The black line shows mean daily water table position in relation to the vegetation surface and the black bars show the daily precipitation.

Performance of *Sphagnum* in the field

Capitulum water content of *S. cuspidatum* differed strongly between samplings (F = 427.5; $p < 0.001$) and ranged from 2.0 (fw/dw) in May and mid-June to 31.6 and 30.6 (fw/dw) in September and October (Table 4.1). The capitulum water content was strongly correlated with the measured water table ($r^2 = 0.99$, $p < 0.001$), being on average 24.4 (fw/dw) for the entire growing season. Capitulum growth density was highest in June and July and lowest from August to October (Table 4.1; F = 52.15; $p < 0.001$). Total chlorophyll content (Chl. a + Chl. b) was also variable during the growing season, being significantly lower in May and mid-June than in the other months (F = 43.82; $p < 0.001$). Considered separately, chlorophyll a and b showed the same characteristics as the total chlorophyll content and the ratio (a/b) did not differ during the year (Table 4.1). Total biomass production at the end of the growing season was 179 g m^{-2} (SD 59) with a C concentration of 45.9% (SD 1.4).

Table 4.1 Performance of *S. cuspidatum* in the field. Water content (WC), growth density and chlorophyll (Chl) content [mg g^{-1}] of *S. cuspidatum* during the growing season 2011 presented as mean (± SD; n = 16 – 20). Different letters indicate interseasonal differences (Tukey's post-hoc test; $p < 0.05$). ns = non significant; (*) = $p < 0.1$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. nd = not determined.

	S1	S2	S3	S4	S5	S6	S7	F	p
	May 26th	June 16th	June 30th	July 21st	August 11th	September 7th	October 25th		
WC actual	1.9 (±0.8)^{a}	2.0 (±0.7)^{a}	12.6 (±1.7)^{b}	16.0 (±2.8)^{b}	29.8 (±4.8)^{c}	31.6 (±4.3)^{c}	30.6 (±6.8)^{c}	427.5	***
Growth density	157 (±58)^{a}	219 (±45)^{b}	205 (±39)^{b}	209 (±42)^{b}	54 (±12)^{c}	77 (±22)^{c}	64 (±35)^{c}	52.2	***
Chl a	0.80 (±0.35)^{a}	0.69 (±0.17)^{a}	nd	2.42 (±1.08)^{b}	2.68 (±0.69)^{b}	2.63 (±0.68)^{b}	2.64 (±0.57)^{b}	44.5	***
Chl b	0.29 (±0.14)^{a}	0.29 (±0.06)^{a}	nd	0.97 (±0.47)^{b}	0.99 (±0.19)^{b}	1.02 (±0.23)^{b}	0.99 (±0.18)^{b}	44.7	***
Chl total	1.10 (±0.48)^{a}	0.98 (±0.21)^{a}	nd	3.38 (±1.54)^{b}	3.66 (±0.74)^{b}	3.70 (±0.91)^{b}	3.63 (±0.74)^{b}	43.8	***
Chl a/b	2.76 (±0.67)	2.47 (±0.68)	nd	2.55 (±0.20)	2.70 (±0.09)	2.63 (±0.26)	2.65 (±0.18)	1.1	ns

Recovery of Photosynthesis and Respiration after Rehydration

The day after harvesting and before rehydration, peatmosses sampled in May and mid-June showed neither photosynthesis nor dark respiration. After two days of rehydration, mosses of both samples showed photosynthetic and respiratory activity but in case of S1 with a negative net CO_2 balance until day seven after rewetting (Fig. 4.2). Afterwards, net photosynthesis increased until day nine with no further increase until day eleven. In case of S2, net photosynthesis was positive since day two after rehydration and increased slightly until day seven. Between day seven and day nine no further increase was observed. At the end of the experiment net photosynthesis was similar for both samples ($p = 0.29$). Whereas dark respiration of mosses of S2 was constant between day two and the end of the experiment, it decreased strongly for mosses of S1 between day two and day seven after rehydration. Similar to net photosynthesis, after ten, respectively eleven days, dark respiration did not differ between mosses of both sampling campaigns ($p = 0.96$) and equaled the amount of net photosynthesis.

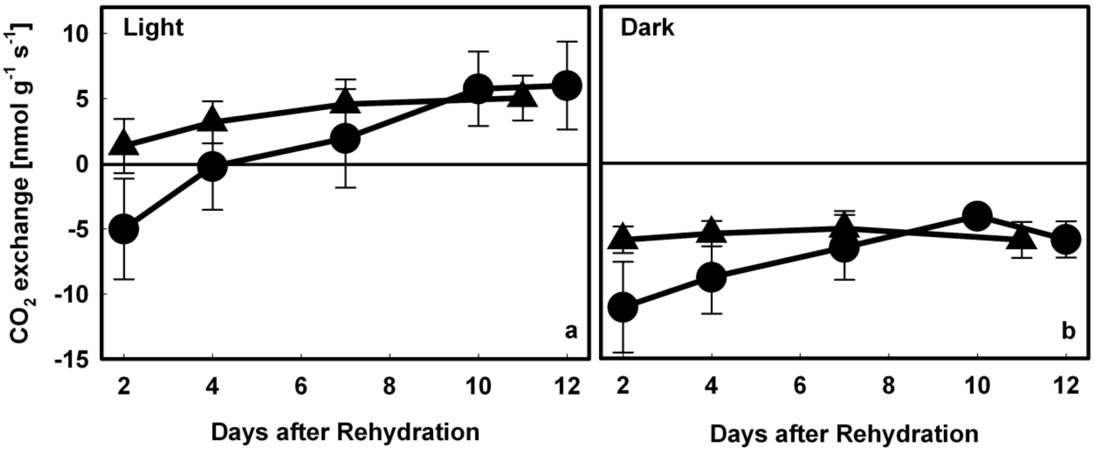


Fig 4.2 CO_2 exchange of peatmosses after rehydration. Net photosynthesis (a), measured at PAR = 300 µmol m^{-2} s^{-1}, and dark respiration (b) of *S. cuspidatum* after rehydration (n = 20; Mean ± SD). Circles represent mosses sampled in May (S1) and triangles mosses sampled in June (S2).

Gas exchange: Dependence on capitulum water content and seasonal variation

The dependence of net photosynthesis on the capitulum water content of *Sphagnum cuspidatum* followed an asymmetric optimum curve, with a sharp decrease below and a weaker decrease above the specific optimum (Fig 4.3). The optimum water content varied strongly during the season being lowest in June and highest in September (Table 4.2; F = 24.21; $p < 0.001$).

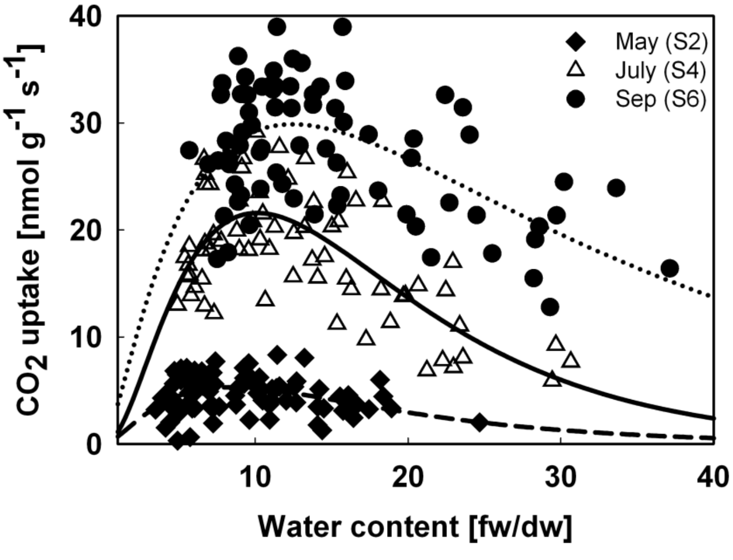


Fig 4.3 Dependence of CO_2 assimilation on capitulum water content of *S. cuspidatum*. Mosses sampled in June (S2; triangles and dashed line), in July (S4; diamonds and solid line) and in September (S6; circles and dotted line). Presented are the measured values (4-7 measurements for 16 moss samples of each sampling date) and the calculated Weibull model.

Table 4.2 Photosynthetic characteristics of *S. cuspidatum* at different times in 2011 (mean ± SD; n = 16). For each sample four to seven measurements were carried out with different water contents (WC) to determine the optimum WC at which mosses show maximum net photosynthesis (NP_{max}) rates based on their dry weight (dw), on total chlorophyll content (Chl) and on their growth density in the field. Respiration in the dark (R_d) was only measured with one WC. Different letters indicate interseasonal differences (Tukey's post-hoc test; $p < 0.05$). ns, non significant; (*) = $p < 0.1$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Nd = Not determined.

	S1 May 26th	S2 June 16th	S4 July 21st	S6 September 7th	F	p
Optimum WC [fw/dw]	Nd	7.7 (±2.1)^a	10.2 (±1.8)^b	12.3 (±1.7)^c	24.2	***
NP_{max} [nmol g^{-1}(dw) s^{-1}]	Nd	5.7 (±1.6)^a	21.8 (±4.2)^b	32.1 (±4.1)^c	231.7	***
NP_{max} [nmol mg^{-1}(Chl) s^{-1}]	Nd	6.2 (±1.9)^a	7.6 (±3.4)^{ab}	8.5 (±1.9)^b	3.2	*
NP_{max} [mg m^{-2} h^{-1}]	Nd	199 (±78)^a	706 (±112)^b	413 (±108)^c	103	***
R_d [nmol g^{-1} s^{-1}]	5.9 (±1.4)	5.9 (±1.4)	7.1 (±1.5)	5.9 (±2.0)	2.3	(*)
R_d [mg m^{-2} h^{-1}]	147 (±47)^a	206 (±57)^b	236 (±72)^b	73 (±29)^c	29.2	***

On the dry mass basis, maximum net photosynthesis at the specific optimum water content was also highly variable with lowest values in June and highest values in September (Table 4.2; F = 231.7; $p < 0.001$). If net photosynthesis was referenced to chlorophyll, the variation between lowest values in spring and highest values in late summer became much smaller (Table 4.2; F = 3.23; $p < 0.05$). Concerning the alternating growth density during the year, maximum net photosynthesis on an area basis was lowest again in June but highest in July (Table 4.2; F = 103; $p < 0.001$). On the dry mass basis, dark respiration differed only slightly during the year being marginally higher in July than in the other months (Table 4.2; F = 2.3; $p < 0.1$). Dark respiration calculated on the area basis was highest in June and July and lowest in September (Table 4.2; F = 29.18; $p < 0.01$).

Modeled carbon balance in the course of the year

CO_2 balance was rarely positive calculated for mosses sampled in June (Fig 4.4). For mosses sampled in July and in September calculated CO_2 assimilation increased between March and April and decreased sharply with the beginning of May. In the middle of June, CO_2 uptake increased strongly to highest values during the year and further decreased constantly until the end of the growing season. The area based model revealed higher maximum values for S4 samples than for S6 samples in April and July (Fig 4.4a), whereas on a dry mass basis, S6 mosses showed higher CO_2 uptake rates all year round (Fig 4.4b).

Summarizing the CO_2 exchange for the entire growing season, mosses of S2 lost CO_2 and accumulated CO_2 uptake was higher for mosses of S6 than for mosses of S4 (Table 4.3). Due to the denser growth in July than in October, the differences of accumulated CO_2 uptake were less pronounced calculated on the area basis than on the dry mass basis. Regarding the carbon balance of peatmosses, the calculated carbon sequestration in the wet period between the middle of June and the end of October was less for all modeled samplings than determined in the harvested biomass (Table 4.3). Nevertheless, considering and summing up the respective maximum accumulation rates of S4 and S6, the calculated carbon accumulation nearly equals the carbon actually accumulated in the *Sphagnum* biomass (Fig 4.4c).

Table 4.3 Extrapolated CO_2 exchange and carbon sequestration based on the seasonal differences of photosynthetic properties. The carbon balance presented, integrates continuous hourly time series of capitulum water content and photosynthetic active radiation (PAR). Water dependent photosynthesis rates were calculated using the Weibull model presented in equation (4-1). For PAR = 0 [µmol m^{-2} s^{-1}] values obtained for dark respiration and for PAR values > 300 [µmol m^{-2} s^{-1}] net photosynthesis values at the respective water content were used. For PAR values between 0 and 300 [µmol m^{-2} s^{-1}] a linear increase from the dark to light saturation was assumed. Furthermore, C concentration and the amount of C sequestered in biomass, based on harvest in October, are given as means (± SD, n = 16).

		S2 June 16th	S4 July 21st	S6 September 7th	S7 October 25th
CO_2 uptake [g g^{-1} dw]	March 1st –Oct. 25th	-1.95	0.69	5.33	
	June 17th – Oct. 25th	-1.11	0.50	3.35	
CO_2 uptake [g m^{-2}]	March 1st –Oct. 25th	-426	144	410	
	June 17th – Oct. 25th	-243	105	258	
C uptake [g m^{-2}]	March 1st –Oct. 25th	-116	39	112	
	June 17th – Oct. 25th	-66	29	70	
C content of biomass [%]					45.9 (±1.4)
C sequestration [g m^{-2}]	June 17th – Oct. 25th				82 (±27.1)

4.4 Discussion

Recovery of photosynthesis and respiration after rehydration

Peatmosses behaved similarly to a prolonged *in-situ* drought in the field as to experimentally induced desiccation under controlled conditions. Our results underpin the observation that within the first days after rewetting, *Sphagnum* shows no or only poor net photosynthesis (Silvola 1991, Gerdol *et al.* 1996, Schipperges & Rydin 1998, Robroek *et al.* 2009a). The reported reduction of photosynthetic rates after rewetting to about 20% of the initial values (Schipperges & Rydin 1998, Robroek *et al.* 2009a) is confirmed by our results if maximum photosynthetic rates of S1 and S2 after rewetting are compared to those sampled in the wetter period later in the year (S4 and S6). The reason for the poor recovery after rewetting is supposed to be the result of chlorophyll degradation which is known to continue at the inition of rewetting (Gerdol *et al.* 1996). The slow recovery to a positive CO_2 balance observed for mosses of S1 is related to the high initial respiration which can be explained by energy demanding repair processes of damaged tissue, and/or by leakage of cell compounds of damaged cells (Gupta 1977, Robroek *et al.* 2009a). The lack of high initial respiration rates for mosses of S2 indicates a less pronounced dehydration of the samples due to repeated small rain events before sampling. Irreversible damages as consequence of drought and heat reported for *Sphagnum* species grown on hummocks (Bragazza 2008) were not be observed for *S. cuspidatum*, even if their appearance was pale and whitish as consequence of the strong chlorophyll degradation.

Based on the short-term recovery to photosynthesize, the ability of axillary buds to grow when the apex is destroyed by drought and to build a new stem and capitulum is an effective mechanism for long-term recovery (Clymo & Hayward 1982). This lateral growth of new moss tissue was observed with beginning of the wet period in the middle of June and it was responsible for most of the net primary production in 2011.

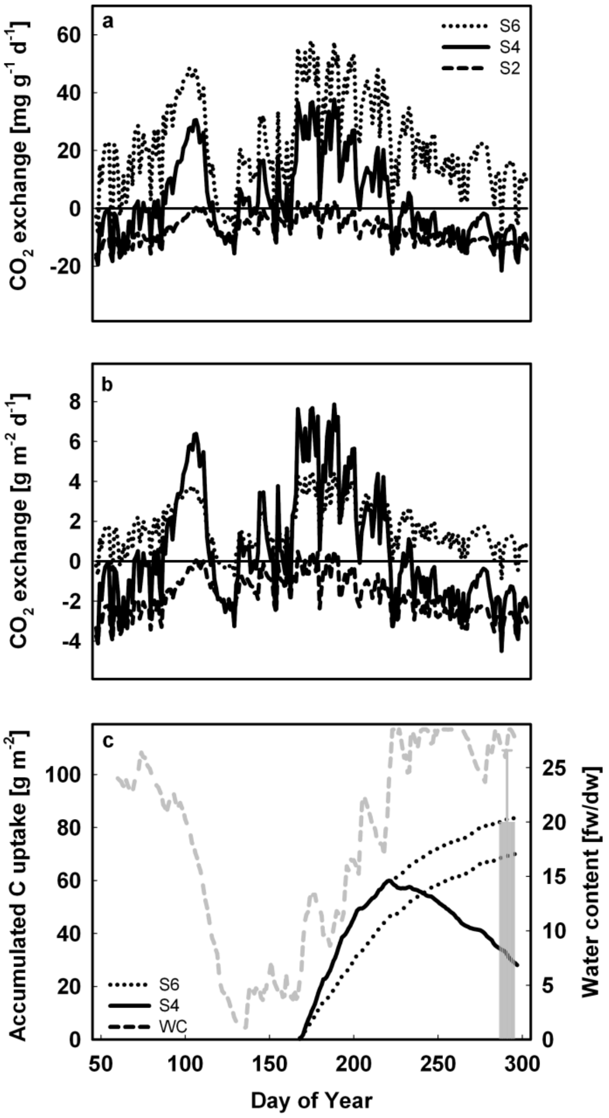


Fig 4.4 Modeled CO$_2$ exchange and carbon uptake during the growing season. Daily CO$_2$ exchange calculated for the growing season based on the dry mass (a) and on the growth density per area (b) for mosses sampled in June (S2; dashed line), in July (S4; solid line) and in September (S6; dotted line). Accumulated carbon (c) is presented from mid-June to the end of October for S4 (solid line) and S6 (dotted line), for the combination of both, and for the harvested biomass (grey bar; mean ± SD, n = 16). The dashed grey line shows the calculated water content (WC) based on water table measurements.

Gas exchange: Dependence on capitulum water content and seasonal variation

Net photosynthesis is strongly water dependent and follows a typical asymmetric optimum curve. Generally, maximum net photosynthesis and the respective optimum water content vary among species and seasons. The results obtained for *S. cuspidatum* are within the reported range and represent the lower end for mosses sampled in spring (S2) and the upper end for mosses sampled in July (S4) regarding the growth density and for mosses sampled in September (S6) regarding the dry weight (Murray *et al.* 1989, Silvola 1990, Williams & Flanagan 1996, Schipperges & Rydin 1998, van Gaalen *et al.* 2007, Robroek *et al.* 2009a). With increasing water content above the optimum, diffusion resistance to CO_2 rises and assimilation becomes CO_2-limited (Titus *et al.* 1983, Silvola 1990). Below the optimum water content, it is assumed that CO_2 is not the limiting factor for photosynthesis (Silvola 1990). Instead, assimilation rates decrease as the maximum efficiency of the photosystem II and the electron transport rate abruptly decreases (Maseyk *et al.* 1999, van Gaalen *et al.* 2007, Harris 2008). At very low water contents, hyaline cells are fully dehydrated, cell turgor declines and the mosses start losing cytoplasmic water of the photosynthetic cells (Hajek & Beckett 2008). The latter mechanism and the concomitant strong chlorophyll degradation can explain the low maximum photosynthesis rates for S2, because calculated on the basis of chlorophyll content instead of the dry mass, seasonal differences of net photosynthesis were relatively small. In contrast, to avoid diffusion resistance to CO_2 at high water contents, the loose growth density of S6 mosses might serve as an adaptation to reduce thick water films at the photosynthetic cells (Proctor *et al.* 1992, Rice & Schuepp 1995). Desiccation starts at higher water contents for mosses grown under wet conditions which explain the seasonal shift in optimum water contents (Titus *et al.* 1983, Schipperges & Rydin 1998). The denser growth under dry conditions helps to avoid light stress of inner leaves and subsurface photosynthetic layers (Zona *et al.* 2011).

Productivity of *Sphagnum* varies between species, sections of the genus and microhabitats and is highest for species of the section Cuspidata and for mosses grown in wet carpets and hollows (Gunnarsson 2005). The variation in productivity between species is attributed to their phylogeny and to their species-specific zonation along a hydrological gradient (Andrus *et al.* 1983, Rydin 1985, Gunnarsson 2005). Particularly, the dense structure of dry hummocks may enhance the water holding capacity (Hayward & Clymo 1982). Depending on varying climatic conditions, strong seasonality in productivity of peatmosses is expected (Asada & Warner 2003). Here we show, that the mosses of the same species and microhabitat are able to adapt to seasonal climatic conditions and that this morphological plasticity itself has a strong influence on productivity.

Modeled carbon balance in the course of the year

The high seasonal plasticity *S. cuspidatum* to adapt to varying and extreme hydrological conditions has a substantial impact on the carbon balance during the growing season. On the one hand, mosses harvested in late summer (S6) perform better than mosses sampled earlier in the year. The highest modeled daily accumulation rates are based on the dry mass at very high water contents as well as at very low water contents all over the year (Fig 4.4a). On the other hand, the looser growth density provides less photosynthetic tissue for carbon accumulation and hampers the ability to store external water to avoid drought stress. Consequently, the highest modeled net CO_2 uptake was calculated for S4 in early spring and in July when mosses grew in a dense carpet at intermediate moisture conditions (Fig 4.4b). Based on growth density characteristics, mosses performed best in that season, in which they were sampled. In July, with optimal moisture conditions, mosses of S4 gained more CO_2 than mosses of S6. In contrast, under water saturated conditions, the dense growth seems to be a disadvantage for photosynthesis as a net loss of CO_2 was calculated for mosses of S4. Under wet conditions only for mosses with a loose growth density (S6) the model showed a net CO_2 gain. Even if *S. cuspidatum* is typical for species in wet and submerged habitats (Laine *et al.* 2009), it shows the best photosynthetic performance at intermediate water contents of 7-12 (fw/dw) and consequently highest productivity at a water table of about 10-15 cm below the moss carpet. The limits of peatmosses' ability to keep pace with spontaneous changing moisture conditions within one season might be a tradeoff for high productivity under favorable conditions and their ability to withstand to extremes of wet and dry.

Sphagnum cuspidatum's biomass production during the growing season was slightly lower than reported by Gunnarsson (2005), most likely due to the severe drought in spring. The fact that for all models the total carbon uptake is calculated to be less than found in the harvested biomass is dedicated to the temperature dependence of CO_2 exchange. Peatmoss photosynthesis is reported to reach its optimum near 20 °C (Titus & Wagner 1984, Maseyk *et al.* 1999). Our measurements made at 25 °C may thus underestimate carbon assimilation. Dark respiration rates decrease with decreasing temperatures, leading to an additional overestimation of respiratory carbon loss in our calculations, especially for relatively cool nights in spring and autumn (Titus & Wagner 1984, Maseyk *et al.* 1999). However, mixing the maximum accumulation rates of S4 and S6 for the respective season, the calculated carbon uptake nearly equals the carbon actually accumulated in the *Sphagnum* biomass. This indicates the appropriateness of short-term CO_2 measurements to model long-term carbon accumulation if seasonal variation of morphological adaptations is included in the calculations.

4.5 Conclusion

We show high plasticity in *Sphagnum cuspidatum* and demonstrate the advantages of a denser (less desiccation) and looser growth (higher maximum photosynthesis). The mosses are able to adapt morphologically within one growing season to respond to both desiccation under dry conditions and diffusional limitation under wet conditions. Beyond adapting to a broad range of hydrological conditions, we show that *Sphagnum* is able to resist to prolonged drought, even if recovery is slow. We conclude that peatmosses may keep pace with climate change-induced warmer and drier conditions. However, even if *Sphagnum* is able to adapt spontaneously to varying environmental conditions, we show that stable and permanently moist conditions are the optimum for *Sphagnum* performance and carbon accumulation. If moisture conditions deviate from the specific optimum for *Sphagnum* mosses, the productivity of the mosses und consequently the carbon sequestration in peatlands may be reduced under changing hydrological conditions due to future climate change. Furthermore, we show, that short-term experiments on CO_2 exchange of peatmosses are a useful tool to estimate long-term carbon uptake if seasonal plasticity is integrated in the calculations.

5 Carbon stable isotopes in *Sphagnum* – dependent on water content and source CO_2

5.1 Introduction

Northern peatlands play an important role in the global carbon cycle. Despite only covering 3% of the world’s land area, they store up to one third of the global soil carbon pool and almost the same amount of carbon that is stored in the terrestrial biosphere (Bridgham *et al.* 2006). Carbon fluxes are strongly influenced by environmental conditions. In particular, the hydrology and presence or absence of anoxic conditions is a key driver for carbon storage and release in peatlands (Limpens *et al.* 2008a). A key genus for carbon sequestration is *Sphagnum*, assuming that peatmosses cover half of the northern peatland areas and store more carbon than any other plant genus in the world (Clymo & Hayward 1982).

The carbon stable isotope composition of plants is considered a useful tool in examining environmental conditions such as light, temperature and water availability and can improve our understanding in plant resource acquisition and interactions between plants and their environment (Dawson *et al.* 2002). The varying distribution of carbon stable isotopes among and within plants reveals a multitude of information about the carbon cycle and processes involved in carbon transformation (Farquhar *et al.* 1989, Hobbie & Werner 2004). The use of C isotopes of plant material as an ecological integrator is based on the correlation between environmental conditions and the biochemical fractionation of the isotopes during gas exchange, as well as the assumption that the discrimination against ^{13}C during photosynthesis is mainly driven by the carboxylating enzyme Rubisco (Dawson *et al.* 2002, Bowling *et al.* 2008), at least in the case of C_3 plants.

Carbon stable isotopes of *Sphagnum* biomass are used to determine (paleo-) hydrological conditions in peatlands (Price *et al.* 1997, Menot & Burns 2001, Loisel *et al.* 2009), to elucidate the photosynthetic performance of the mosses (Williams & Flanagan 1996, 1998) or estimate their capacity to recycle methane in symbiosis with methanotrophic bacteria (Raghoebarsing *et al.* 2005, Kip *et al.* 2010).

Discrimination against $^{13}CO_2$ during photosynthesis is generally believed to affect all *Sphagnum* mosses in the same way, and thus a narrow range of isotopic signatures is expected (Proctor *et al.* 1992). Therefore, the observable wide range of carbon isotope values for *Sphagnum* must relate to a either strong variation of discrimination with environmental parameters (temperature or moisture conditions) or species-specific features (e.g. arrangement of photosynthetic cells), or both (Rice 2000, Skrzypek *et al.* 2007, Loisel *et al.* 2009). It is assumed that Sphagna occurring on dry hummocks show more discrimination than Sphagna occurring closer to the water table, given that they are photosynthesizing at lower water content and hence lower external diffusional resistance (Price *et al.* 1997). However, for Sphagna (especially for *S. cuspidatum*) grown in wet hollows and other submerged mosses, it is known that they vary widely in their isotopic values (Proctor *et al.* 1992, Price *et al.* 1997, Menot & Burns 2001, Liebner *et al.* 2011). The combined consideration of the $\delta^{13}C$ of the product (e.g. bulk moss material) and potential carbon sources (atmospheric CO_2 vs. substrate-derived CO_2) allows understanding carbon cycling in peatlands and evaluating the role of *Sphagnum* for greenhouse gas emission and carbon sequestration (Raghoebarsing *et al.* 2005, Dorrepaal *et al.* 2009). Several recent studies have highlighted the symbiotic relationship of mosses with methane-oxidizing bacteria, showing that the methane emission potential of peatlands is heavily reduced by this biotic interaction (Raghoebarsing *et al.* 2005, Chen & Murrell 2010, Kip *et al.* 2010, Liebner *et al.* 2011).

In order to draw conclusions from $\delta^{13}C$ values in *Sphagnum* about growth conditions of the peat mosses and sources of the fixed carbon, it is crucial to elucidate the processes leading to discrimination in the moss tissue. Beside the process of discrimination, the isotopic signature of plant tissue is also dependent of the isotopic composition of the source CO_2 (Keeley & Sandquist 1992). Whereas atmospheric CO_2 has a $\delta^{13}C$ value of around -8‰, the source CO_2 for photosynthesis of Sphagna might be more depleted in ^{13}C, given that this CO_2 might be partly derived from the decomposition of organic matter or oxidation of methane.

However, the mechanisms of isotope discrimination of *Sphagnum* are not fully understood and the interpretation of isotope values often remains at least partly speculative. Within many studies, information on both peatlands moisture conditions and the potential carbon source is not available, or the interaction between both factors is not carefully considered.

We used the Cavity Ring-Down Spectroscopy (CRDS) to carry out online measurements of ^{13}C discrimination ($\Delta^{13}C$) during gas exchange in *Sphagnum cuspidatum* and *Sphagnum papillosum* (originating from either hummocks or hollows), while we experimentally altered capitulum water content and recorded net assimilation rates. We combined the information about discrimination during photosynthetic CO_2 uptake and its dependence on water content and species with $\delta^{13}C$ values of sampled moss tissue grown in the natural habitat under well documented moisture conditions. Furthermore, we calculated two different models to demonstrate the necessity of considering both, the capitulum water content and the $\delta^{13}C$ of the source CO_2 in order to correctly interpret carbon isotope values of Sphagna. Using these models, we were able to estimate the $\delta^{13}C$ of the CO_2 fixed by Sphagna, which is not measurable in the field. Finally, we applied our models to $\delta^{13}C$ values reported in previous studies to identify the carbon source for *Sphagnum* assimilation and estimate the amount of substrate-derived carbon taken up by the mosses.

5.2 Material & Methods

Study site and moss sampling

Sampling took place on a peatland restoration site at Hartshoper Moor, Germany (54°17’N, 9°26’E) in October 2011. In total, 14 cores (53 mm in diameter and 50 mm in depth) were collected: five cores each of *Sphagnum papillosum* from hollows and nearby hummocks, as well as four cores of *S. cuspidatum* from hollows.

To observe the growing conditions, we permanently logged the water table (Mini-Diver, Schlumberger Water Services, Canada) and determined the capitulum water seven times, expressed as the ratio of fresh weight to dry weight (fw/dw). Additionally, capitulum growth density was calculated as the dry weight per area (g m^{-2}).

We were able to retrace the development of *S. cuspidatum* during the growing season 2011, because a severe drought in spring killed the capitula of the mosses. They built new stems with new capitula with the beginning of a wetter period in summer. Furthermore, due to our permanent logging of the water table, frequent determination of capitulum water content and the strong correlation between both parameters, we were able to estimate the mean capitulum water content at which the mosses must have synthesized their biomass.

Experimental design

After collection, the moss samples were transported to the laboratory and stored at 21 °C and a photosynthetic photon flux density (PPFD) of around 50 µmol m^{-2} s^{-1} in the cores for one week before starting the experiment. To prevent desiccation, mosses were sprayed every day with deionized water. Prior to the first measurements, capitula of mosses were cut and carefully transferred to a basket covered with nylon gaze, ensuring that the moss structure was kept as natural as possible. The samples were subsequently saturated with deionized water by spraying the water carefully to avoid free water not adhering to the capitula. A LED panel (90 Led's with a ratio of 7 red : 1 orange : 1 blue; *Bloom*Power ufo 90, spLED GmbH, Germany) was used as light source. The mosses were subjected to a PPFD of photosynthetic active radiation (PAR, 300-700nm) of 300 µmol m^{-2} s^{-1}.

Measurements of $^{12}CO_2$ and $^{13}CO_2$ and the simultaneous calculation of $\delta^{13}CO_2$ were conducted using a flow through Cavity Ring-Down Spectrometer (CRDS, G2132-*i*, Picarro, USA) connected to an external pump. Accordingly, the mosses were placed in a glass chamber (160 cm^3) that was closed air tight and connected on one side (inflow) to a Tedlar gas bag (100 L) filled with ambient air and on the other side (outflow) to the CRDS. The mean CO_2 concentration of ambient air was 415 ppm, with an isotopic composition of -11.5‰. The constant flow rate of air passing the chamber was 34 ml min^{-1}. Measurement intervals for $\delta^{13}CO_2$ were around 2 seconds, with mosses allowed to acclimatize to conditions in the chamber for at least five minutes. Subsequently, average data of the next five minutes was recorded for further calculations when standard deviation for this period was less than 0.5 ppm for $^{12}CO_2$ and less than 0.2‰ for $\delta^{13}CO_2$. For moisture dependent measurements, different capitula water contents were attained by allowing the moss samples to dry gradually at ambient air. To ensure stable conditions, gas concentrations and stable isotopic composition in the inflowing air were measured three times per day. Furthermore, the measured $\delta^{13}CO_2$ values of the inflowing gas were used as reference values to calculate $^{12}CO_2$ and $^{13}CO_2$ gas exchange of the mosses, taken as the difference between CO_2 passing the chamber with and without mosses.

S. cuspidatum was measured at four different water contents and *S. papillosum* at seven to eight different water contents per sample. The fresh weight of all samples was measured before and after each measurement to calculate the water content (WC), expressed as the ratio of fresh weight to dry weight (fw/dw). After the last measurement in the CRDS, the dry weight of each sample was recorded after oven-drying for 48h at 60° C. Subsequently, the $\delta^{13}C$ values of organic carbon (C_{org}) were measured with an isotope-ratio mass spectrometer (Delta V, Thermo Scientific, Germany) coupled to an elemental analyzer (Flash 2000, Thermo Scientific, Germany).

Calculations

To model the relationship between capitulum water content (WC) and net photosynthesis (NP), we calculated different nonlinear regression models using the nonlinear least square (nls) function provided by the software R (R Development Core Team 2012). A preselection of appropriate models was carried out based on the shape of the scatter plot of all $\delta^{13}C$ values along the capitulum water content gradient. Subsequently, these models were compared using the Akaike information criterion (AIC). The function that best predicted the relationship between capitulum water content and net photosynthesis was the asymmetric hump-shaped curve of the Weibull model:

$$NP = (a / b) * (WC / b)^{a-1} * e^{(-WC / b) \wedge c} \tag{5-1}$$

$\delta^{13}C$ values of biomass samples are expressed relative to the VPDB (Vienna Pee Dee Belemnite) standard using the external standards IAEA C6 (-10.8‰ vs. VPDB), USGS40 (-26.39‰ vs. VPDB) and IVA soil 33802153 (-27.46‰ vs. VPDB) according to the following equation:

$$\delta^{13}C\ [‰] = (R_{sample}/R_{Standard} - 1) * 1000 \tag{5-2}$$

where R represents the ratio of heavy and light isotopes in the sample and the VPDB standard, respectively.

Online ^{13}C discrimination (Δ) during photosynthesis was calculated, as previously described (Evans *et al.* 1986), as

$$\Delta = [\xi * (\delta o - \delta_e)] / [1000 + \delta_o - \xi * (\delta o - \delta_e)], \tag{5-3}$$

where $\xi = c_o/(c_e - c_o)$, with c_e and c_o being the CO_2 concentration and δ_e and δ_o representing the isotopic composition of the air entering and leaving the chamber, respectively. To predict the $\delta^{13}C$ of *Sphagnum* biomass, obtained values for online discrimination were used by rearranging the following equation:

$$\Delta = [(\delta_s - \delta_p) / (1000 + \delta_s)] * 1000, \tag{5-4}$$

where δ_s and δ_p are the isotopic composition of the source CO_2 and the plant, respectively. Furthermore, we calculated linear regression models for Δ dependent on the water content (WC):

$$\Delta = a * WC + b, \quad (5\text{-}5)$$

with parameters a for the regression slope and b for the y-axis intercept (see Table 5.1 for obtained values for the different species and microhabitats).

To predict (i) the capitulum water content (WC) based on the $\delta^{13}C$ of the source air and the $\delta^{13}C$ of the biomass and (ii) the $\delta^{13}C$ of the source air (δ_s) based on the WC and the $\delta^{13}C$ of the biomass, we simplified and rearranged equation (5-4) and substituted Δ as presented in equation (5-5) by a * WC + b obtaining

$$WC = (\delta_p + b - \delta_s) / -a \text{ (model A)}, \quad (5\text{-}6)$$

and

$$\delta_s = \delta_p + b + WC * a \text{ (model B)} \quad (5\text{-}7)$$

with δ_s and δ_p being the isotopic composition of the source air and the plant biomass, respectively. Model A was calculated with two different values for the source CO_2: -8‰ representing atmospheric CO_2 and -16‰ assuming an influence of substrate-derived carbon, already depleted in $\delta^{13}C$. Model B was calculated with two different water contents: assuming an optimal water content of 10 (fw/dw) and with a water content of 30 (fw/dw) reflecting wet and almost saturated conditions.

To predict the proportion (p) of recycled CO_2 as carbon source for *Sphagnum* assimilation, we applied a mixing model described by the following equation:

$$\delta_s = p * \delta_{ryc} + (1 - p) * \delta_{atm}, \quad (5\text{-}8)$$

with $\delta^{13}C$ values for recycled carbon (δ_{ryc}) of -27‰ (assuming decaying biomass) for the sections Acutifolia and Sphagnum and -56‰ (assuming methane oxidation) for the section Cuspidata, respectively (Keeley & Sandquist 1992, Raghoebarsing *et al.* 2005). The $\delta^{13}C$ of the atmosphere (δ_{atm}) was assumed to be -8 ‰.

Evaluation of *Sphagnum* $\delta^{13}C$ data

The water content and source CO_2 models (model A and B) were evaluated with published $\delta^{13}C$ values of *Sphagnum* capitula. Only $\delta^{13}C$ values were used if means were reported or could be calculated by the data presented. Studies only giving a range with extreme values as well as values obtained from greenhouse experiments were excluded. In the cases whereby discrimination values were given, $\delta^{13}C$ values of the biomass were calculated if the applied calculation was described in the study. We only considered the three most studied sections of the genus: Acutifolia and Sphagnum, representing moist to dry habitats, as well as Cuspidata, representing wet or submerged habitats.

Data analyses

Regression models shown in Fig 5.2 were obtained by including all data points per species and microhabitat. To statistically analyze differences for net assimilation rates and online $\delta^{13}C$ discrimination between the species and microhabitats, all models were additionally calculated for each field sample (n = 5 for *S. papillosum* and n = 4 for *S. cuspidatum*). Values for maximum assimilation rates and optimum water content obtained by the Weibull model as well as parameters for the linear discrimination model, values for biomass $\delta^{13}C$ and growth density were analyzed using one-way ANOVA, followed by Tukey's post hoc test (see Table 5.1). In case of unequal variances, Welch's ANOVA was applied. The normality of residuals was ensured for all regression models. Besides nonlinear regression models, all analyses were carried out using the software STATISTICA 9.0 (StatSoft, Tulsa, OK).

5.3 Results

Field conditions

During sampling, the water table was at the soil surface in hollows and at a depth of -25 cm on hummocks. Water table fluctuations in 2011 were around 20 cm, with lowest levels during the exceptional dry months of March to June (mean monthly precipitation of around 40 mm). From June to October (mean monthly precipitation of around 140 mm), hollows were permanently water saturated.

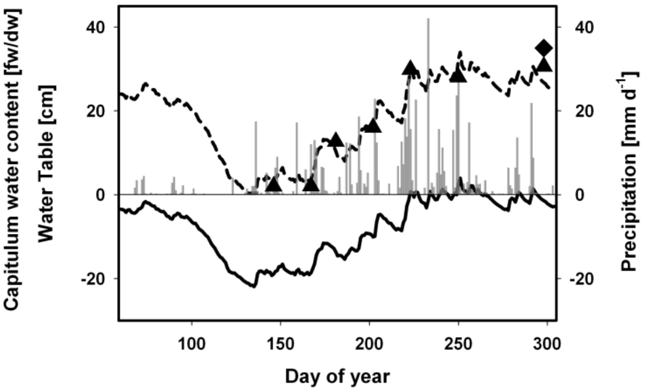


Fig 5.1 Hydrological conditions at Hartshoper Moor during the growing season 2011. The solid line shows the water table logged in 30 min intervals. The triangles show the capitulum water content of *S. cuspidatum* at seven sampling dates (n = 16). With a linear regression model (r^2 = 0.98), the capitulum water content was calculated for the whole year (dashed line). The diamond shows a single sampling date (n = 16) for water content of *S. papillosum* growing in a wet hollow. The grey bars show the daily precipitation.

Capitulum water content of *S. cuspidatum* ranged from 2.0 (fw/dw) in June to 30.6 (fw/dw) in October. The capitulum water content was strongly correlated with the measured water table ($r^2 = 0.98$, $p < 0.001$), and thus capitulum water contents could be estimated for the entire growing season based on measured water tables being 22.8 (fw/dw) on average (Fig. 5.1). Carbon stable isotope values of the biomass were significantly lower in hummock samples than in *Sphagnum* (both species) from hollows (Table 5.1). Capitulum growth density was highest in hummocks and similar for both species from hollows (Table 5.1).

Table 5.1 Isotopic and ecophysiological characteristics of *S. papillosum* and *S. cuspidatum*. Values are given as the mean with the standard deviation in parentheses. F and p values according to ANOVA. Different letters indicate different groups following Tukey's post hoc test. Slope (a) and y-axis intercept (b) correspond to the linear model of δ^{13}C discrimination in relation to water content, equation (5-5), which is graphically displayed in Fig 5.2b.

			S. papillosum		*S. cuspidatum*
	F	p	Hummock (n=5)	Hollow (n=5)	Hollow (n=4)
Biomass δ^{13}C [‰]	21.9	**	-27.5 (±0.6)^{a}	-24.8 (±1.1)^{b}	-24.0 (±0.3)^{b}
Optimum water content [fw/dw]	3.5	(*)	10.3 (±0.7)^{a}	12.5 (±1.0)^{b}	10.7 (±2.2)^{a}
Max. assimilation rate [nmol g^{-1}s^{-1}]	4.6	*	19.9 (±5.9)^{a}	28.3 (±3.9)^{b}	30.1 (±6.6)^{b}
Δ^{13}C at optimum water content [‰]	6.3	*	20.6 (±0.4)^{a}	20.8 (±0.4)^{a}	18.8 (±1.6)^{b}
Capitulum growth density [g m^{-2}]	10.1	**	102.4 (±23.6)^{a}	58.2 (±10.6)^{b}	65.7(±9.1)^{b}
Parameters for linear Discrimination model					
slope (a)	7.1	*	-0.59 (±0.11)^{a}	-0.39 (±0.07)^{b}	-0.32 (±0.15)^{b}
y-axis intercept (b) at WC = 1 (max. Δ^{13}C)	5.4	*	26.13 (±2.86)^{a}	25.27 (±2.49)^{a}	21.22 (±1.38)^{b}

Gas exchange and isotope discrimination

The dependence of net assimilation rates on the capitulum water content of *Sphagnum* followed an asymmetric optimum curve, with a sharp decrease below and a slight decrease above the specific water content optimum (Fig 5.2a). Assimilation rates were highest for *S. cuspidatum* and lowest for *S. papillosum* originating from hummocks (Table 5.1). The optimum water contents slightly differed, being lowest for hummock samples and highest for *S. papillosum* originating from hollows (Table 5.1).

The relationship between capitulum water content and carbon stable isotope discrimination was linear (Fig 5.2b). Discrimination was highest at very low water contents, with values between 21.2‰ for *S. cuspidatum* and 25.3‰ and 26.1‰ for *S. papillosum* from hollows and hummocks, respectively (Table 5.1, Fig 5.2).

At high water contents of 40 (fw/dw), when mosses were saturated, Δ^{13}C decreased to 3.2‰ for hummocks species and hollow species to values between 8.8‰ for *S. cuspidatum* and 10.1 ‰ for *S. papillosum*, respectively (Fig 5.2).

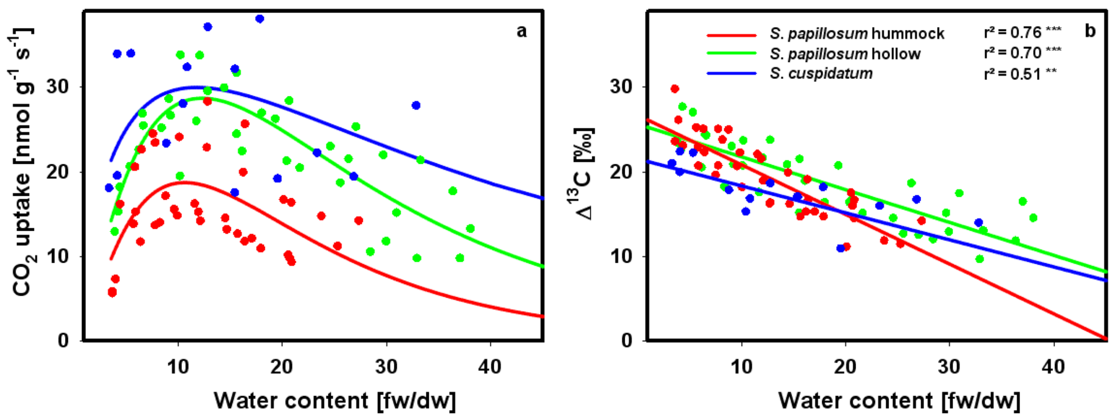


Fig 5.2 Dependence of (a) CO$_2$ assimilation and (b) photosynthetic discrimination (Δ) against ^{13}C on capitulum water content. Presented are the measured values (dots) as well as the calculated regression models (lines). The Weibull model calculated for carbon assimilation rates was used to estimate maximum assimilation rates and to identify the corresponding optimum water content for photosynthesis. The parameters obtained for the linear model for discrimination during carbon uptake were further used to predict the carbon isotopic composition of *Sphagnum* biomass, the water content of *Sphagnum* capitula and the δ^{13}C isotopic composition of the carbon source (see Fig 5.3). The parameters of the linear model of δ^{13}C discrimination in relation to water content, equation (5-5), are presented for each species in Table 5.1.

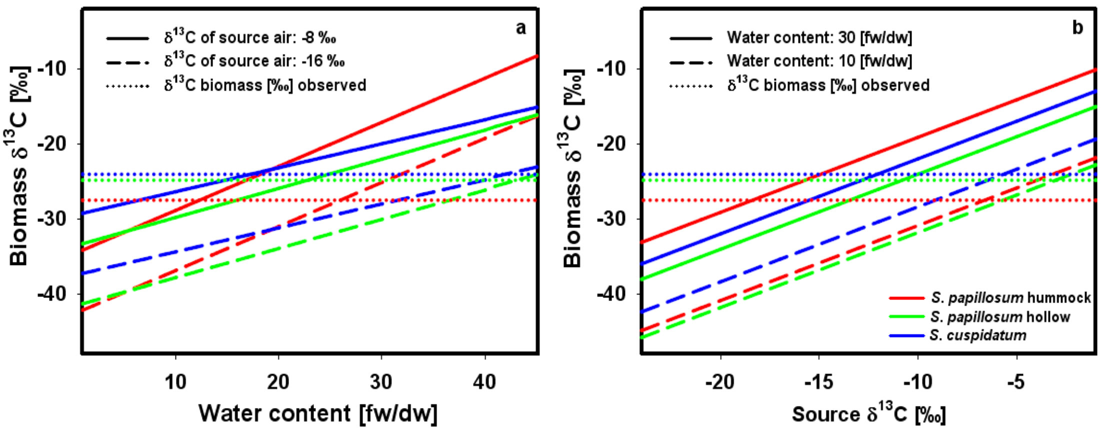


Fig 5.3 Relationship of water content, source δ^{13}C and δ^{13}C of the biomass. (a) Predicted biomass δ^{13}C dependent on capitulum water content for two different source δ^{13}C values (-8‰ and -16‰) calculated with model A. (b) Predicted biomass δ^{13}C dependent on source δ^{13}C for two different water contents (10 and 30) calculated with model B. The dotted lines show the δ^{13}C values of the combusted biomass of *S. cuspidatum* and *S. papillosum* originating from either hollows or hummocks (see Table 5.1). The intersections of the dotted lines with the solid and the dashed lines determine the water content and δ^{13}C of the source air, respectively. For linear regression models, parameters shown in Table 5.1 were used and applied to equations (5-6) and (5-7).

Modeling of *Sphagnum* water content and $\delta^{13}C$ of fixed CO_2

According to model A (Fig 5.3a), the range of predicted isotopic composition of the biomass varied from less than -40‰ to up to -10‰ for water contents between 1 and 40 (fw/dw), depending on the species and $\delta^{13}C$ of source CO_2. Running model A with the measured $\delta^{13}C$ values of the biomass, we calculated that the water content during carbon assimilation must have been 12.0 and 22.5 (fw/dw) for *S. papillosum* from hummocks and hollows, respectively, provided that the $\delta^{13}C$ of the source CO_2 is -8‰. Running model A with a $\delta^{13}C$ of -16‰ for source CO_2, the calculated water content increases to 15.2 (fw/dw) for hummocks and 43.0 (fw/dw) for hollows. For *S. cuspidatum*, the model revealed water contents of 17.3 (fw/dw), assuming $\delta^{13}C$ of -8‰, and 42.4 (fw/dw), assuming $\delta^{13}C$ of -16‰ for source CO_2, respectively. Running model B with a water content of 10 (fw/dw), the $\delta^{13}C$ of the source was estimated to be higher (less negative) than -8‰ for all samples (Fig 5.3b). For water contents of 30 (fw/dw), reflecting wet and almost saturated conditions, the predicted $\delta^{13}C$ of the source was between -11‰ and -12‰ in the case of all samples from hollows and -18.5‰ in the case of *S. papillosum* from hummocks.

In order to cross-check our models, we compared the results for *S. cuspidatum* with water content values directly measured in the field. The measured water content of 22.8 (fw/dw) was not reproduced if the source $\delta^{13}C$ was assumed to be -8‰, which would result in a water content of 17.3 (fw/dw). By contrast, with the known water content, we were able to precisely estimate the $\delta^{13}C$ of the source CO_2, which must have been on average -9.9‰ during the growing season.

Evaluation of published *Sphagnum* δ13C data

The review on published $\delta^{13}C$ values of *Sphagnum* biomass revealed no differences between different sections of the genus (Table 5.2). In case of the section Cuspidata, highest observed $\delta^{13}C$ values were around -23‰. According to our model A, the predicted water content was between 20.8 (fw/dw) and 58.3 (fw/dw), assuming $\delta^{13}C$ values of source CO_2 at between -8‰ and -20‰, respectively. The predicted water content decreases for the lowest reported $\delta^{13}C$ values of around -35‰, to (theoretical) values between -16.2 (fw/dw) and 21.4 (fw/dw), depending on the $\delta^{13}C$ of the source. For water contents between 10 (fw/dw) and 30 (fw/dw), model B predicts source $\delta^{13}C$ values between -4.6‰ and -10.9‰ for the highest reported $\delta^{13}C$ biomass values and between -16.4 and -22.7‰ for the lowest observed biomass values.

Applying a simple mixing model (equation 5-8), the contribution of methane as a carbon source for *Sphagnum* of the Cuspidata section might be more than 30% at water contents of permanently more than 20 (fw/dw). The contribution of methane in the case of the highest reported $\delta^{13}C$ values was negligible, even at high water contents (maximum 5%). For species of the sections Acutifolia and Sphagnum, the range of reported $\delta^{13}C$ values was much narrower (Table 5.2). Assuming a $\delta^{13}C$ of the source air of -8‰, the predicted water content was between 5.8 and 16.9 (fw/dw) (Table 5.3). It increased to values between 16.0 (fw/dw) and 27.1 (fw/dw),

Table 5.2 Overview of δ^{13}C values of *Sphagnum* biomass obtained from a literature review. Values are presented for three different sections and are given as the mean with standard deviation in parentheses. If no standard deviation is presented, it was not given in the original paper or could not be calculated from the presented data. Standard deviation of the mean of each section was calculated independently from values given in each single study. No significant differences between the sections were observed (F = 0.46; p = 0.63). Species names in parentheses were adopted from the original study; these taxa are also denominated as *Sphagnum capillifolium* by other authors.

Acutifolia			Sphagnum			Cuspidata		
Species	δ^{13}C	Study	Species	δ^{13}C	Study	Species	δ^{13}C	Study
capillifolium	-28.6	(Proctor *et al.* 1992)	*centrale*	-27.0	(Hornibrook *et al.* 2000)	*cuspidatum*	-34.7	(Proctor *et al.* 1992)
capillifolium	-26.3 (±1.0)	(Price *et al.* 1997)	*magellanicum*	-25.6 (±0.8)	(Price *et al.* 1997)	*cuspidatum*	-22.9 (±2.4)	(Menot & Burns 2001)
capillifolium	-25.1 (±0.9)	(Menot & Burns 2001)	*magellanicum*	-29.4	(Rice *et al.* 2008)	*cuspidatum*	-26.2 (±2.1)	(Price *et al.* 1997)
capillifolium	-28.6 (±0.8)	(Loisel *et al.* 2009)	*magellanicum*	-24.8 (±1.4)	(Menot & Burns 2001)	*cuspidatum*	-26.0	(Raghoebarsing *et al.* 2005)
(*tenerum*)	-26.2	(Rice *et al.* 2008)	*magellanicum*	-27.9	(Proctor *et al.* 1992)	*fallax*	-27.3 (±0.1)	*(Jassey et al. 2012)*
(*capillaceum*)	-27.6	(Hornibrook *et al.* 2000)	*magellanicum*	-27.0 (±0.7)	(Kleinebecker *et al.* 2009)	*fallax*	-30.5	(Rice *et al.* 2008)
fimbriatum	-26.9	(Hornibrook *et al.* 2000)	*magellanicum*	-26.6 (±1.1)	(Loisel *et al.* 2009)	*pulchrum*	-26.9 (±1.6)	(Loisel *et al.* 2009)
fuscum	-27.9	*(Aerts et al. 2009)*	*magellanicum*	-29.1	(Broder *et al.* 2012)	*recurvum*	-30.0	(Rice *et al.* 2008)
fuscum	-27.7 (±1.2)	(Loisel *et al.* 2009)	*magellanicum*	-31.3	(Hornibrook *et al.* 2000)	*recurvum*	-27.4	(Hornibrook *et al.* 2000)
girgensohnii	-27.7	(Rice *et al.* 2008)	*palustre*	-28.4	(Rundel *et al.* 1979)	*recurvum*	-29.5 (±0.3)	*(Toet et al. 2006)*
subnitens	-27.8	(Proctor *et al.* 1992)	*palustre*	-29.6 (±0.3)	*(Toet et al. 2006)*	*riparium*	-27.2	(Hornibrook *et al.* 2000)
subnitens	-26.3 (±0.5)	(Price *et al.* 1997)	*papillosum*	-25.8 (±0.9)	(Price *et al.* 1997)			
			papillosum	-26.7	(Proctor *et al.* 1992)			
			portoricense	-28.5	(Rice *et al.* 2008)			
Mean (SD)	-27.2 (±1.1)			-27.7 (±1.8)			-28.1 (±3.1)	

assuming a source CO_2 of -14‰, and values between 26.2 (fw/dw) and 37.3 (fw/dw), running the model with $\delta^{13}C$ of -20‰ for the CO_2 source.

According to our model B, for highest reported $\delta^{13}C$ values of -24.8‰ and -25.1‰ for both sections, the calculated $\delta^{13}C$ of the source was around -4.0‰ for water contents of 10 (fw/dw), around -10‰ for contents of 20 (fw/dw) and around -16‰ running the model with a water content of 30 (fw/dw). For lowest reported values of the section Acutifolia, the range for predicted $\delta^{13}C$ of source CO_2 was between -7.8‰ and -19.5‰ for water contents between 10 and 30 (fw/dw). In case of the section Sphagnum, $\delta^{13}C$ of source CO_2 was calculated between -10.5‰ and -22.2‰.

The mixing model predicts a contribution of substrate-derived carbon between 0% and 10% for water contents of 10 (fw/dw). For water contents of 20 (fw/dw), the calculated proportion was also around 10% for the highest observed biomass $\delta^{13}C$ values, increasing to around 30% for the lowest observed isotopic biomass values.

Table 5.3 Predicted water content and source $\delta^{13}C$ modeled on the basis of biomass $\delta^{13}C$ values obtained from the literature review. The observed ranges of $\delta^{13}C$ of three different *Sphagnum* sections are taken from Table 5.2. To estimate the water content, model A, given in equation (5-6), was calculated with three different $\delta^{13}C$ values of the source air. To estimate the $\delta^{13}C$ of the source, model B, given in equation (5-7), was fed with three different capitulum water contents. Bold numbers represent realistic values as discussed in the text. Small numbers are assumed to be unrealistic and are presented to show the significance of an appropriate model to interpret $\delta^{13}C$ values of moss biomass.

		Water content predicted [fw/dw]			**Source $\delta^{13}C$ predicted [‰]**		
		$= (\delta_p + b - \delta_a) / -a$			$= \delta_p + b + WC * a$		
	Range (max; min) of	with source $\delta^{13}C$			with water content		
Section	biomass $\delta^{13}C$ [‰]	-8‰	-14‰	-20‰	10	20	30
Acutifolia	-25.1	**16.4**	26.6	36.8	-4.3	**-10.1**	-16.0
	-28.6	**10.4**	20.6	30.8	**-7.8**	**-13.6**	-19.5
Sphagnum	-24.8	**16.9**	27.1	37.3	-4.0	**-9.8**	-15.7
	-31.3	**5.8**	**16.0**	26.2	**-10.5**	**-16.3**	-22.2
Cuspidata	-22.9	**20.8**	39.6	58.3	-4.6	**-7.7**	**-10.9**
	-34.7	-16.2	2.6	**21.4**	**-16.4**	**-19.5**	**-22.7**

5.4 Discussion

Field conditions

With $\delta^{13}C$ values of -27.48‰ for *S. papillosum* grown on hummocks and $\delta^{13}C$ values of -24.81‰ and -24.03‰ for *S. papillosum* and *S. cuspidatum* grown in wet hollows, the carbon isotopic composition of *Sphagnum* biomass falls in the expected range, underlining the relationship between *Sphagnum* $\delta^{13}C$ and their microhabitats (Proctor *et al.* 1992, Price *et al.* 1997, Rice 2000, Loisel *et al.* 2009).

The higher growth density for *Sphagnum* grown in hummocks reflects the adaptation to the drier habitat (Rydin 1985). The strong relationship between water table and capitulum water content was expected, even if precipitation might have an additional effect on the water content, especially at low water tables (Robroek *et al.* 2009a).

Gas exchange and isotope discrimination

Water dependent net photosynthesis followed a typical asymmetric optimum curve. Above the optimum and with increasing water content, diffusion resistance to CO_2 raises and assimilation becomes CO_2-limited (Titus *et al.* 1983, Silvola 1990). Concomitantly, discrimination against ^{13}C decreases with increasing diffusional limitation (Rice & Giles 1996, Williams & Flanagan 1996).

Desiccation of *Sphagnum* starts when all external water is evaporated and dehydration of the hyaline cells initiates, which is assumed to be close to the optimum water content for assimilation rates (Murray *et al.* 1989). This is supported by our results, with $\Delta^{13}C$ values of around 20‰ at their optimum water content, which is typical for C_3 plants when discrimination by Rubisco is fully expressed (Farquhar *et al.* 1989) (Table 5.1, Fig 5.2). Below the optimum water content, CO_2 is assumed not to be the limiting factor for photosynthesis (Silvola 1990). Instead, assimilation rates decrease as the maximum efficiency of the photosystem II and the electron transport rate abruptly decreases (Maseyk *et al.* 1999, van Gaalen *et al.* 2007, Harris 2008). At very low water contents, hyaline cells are fully dehydrated, cell turgor declines and the mosses start losing cytoplasmic water of the photosynthetic cells (Hajek & Beckett 2008). The further increase in discrimination against ^{13}C is explained by the decrease in photosynthetic capacity, caused by the metabolic slowdown and an increase in the conductance to CO_2 (Williams & Flanagan 1998). The lower maximum discrimination at dry conditions in *S. cuspidatum* might be due to the low water storage capacity of its relatively small hyaline cells (Hajek & Beckett 2008), with increased diffusion resistance through the external water film already starting to appear at very low water contents. By contrast, *S. papillosum* stores more water in its hyaline cells and the mosses might have relatively high water contents, while the photosynthetic cells are still exposed to the atmosphere (Proctor *et al.* 1992).

Furthermore it is assumed that discrimination tends towards 4.7‰ for aquatic plants, caused by diffusion of CO_2 through water (0.7‰), equilibrium dissolution of CO_2 into water (1.1‰) and diffusion in air through the boundary layer (2.9‰) (Henderson *et al.* 1992, Williams & Flanagan 1996). Here, we show that minimum discrimination by aquatic *Sphagnum* is likely to be around 10‰. The relatively high $\Delta^{13}C$ values at high water contents and the smoother slope of decreasing discrimination with increasing water contents observed for hollow samples can be explained by growth adaptations of peat mosses to higher water contents (Rydin 1993). To avoid diffusional limitation under wet conditions, a looser growth density and the exposition of photosynthetic cells at the leaf surface help to reduce thick water films directly at the photosynthetic cells and lower resistance to gas exchange (Proctor *et al.* 1992, Rice & Schuepp 1995). The higher growth density for Sphagna grown in hummocks leads to a higher water holding capacity to avoid drought stress, yet concomitantly enhances diffusion resistance (Hayward & Clymo 1982, Titus & Wagner 1984).

Modeling of *Sphagnum* water content and $\delta^{13}C$ of fixed CO_2

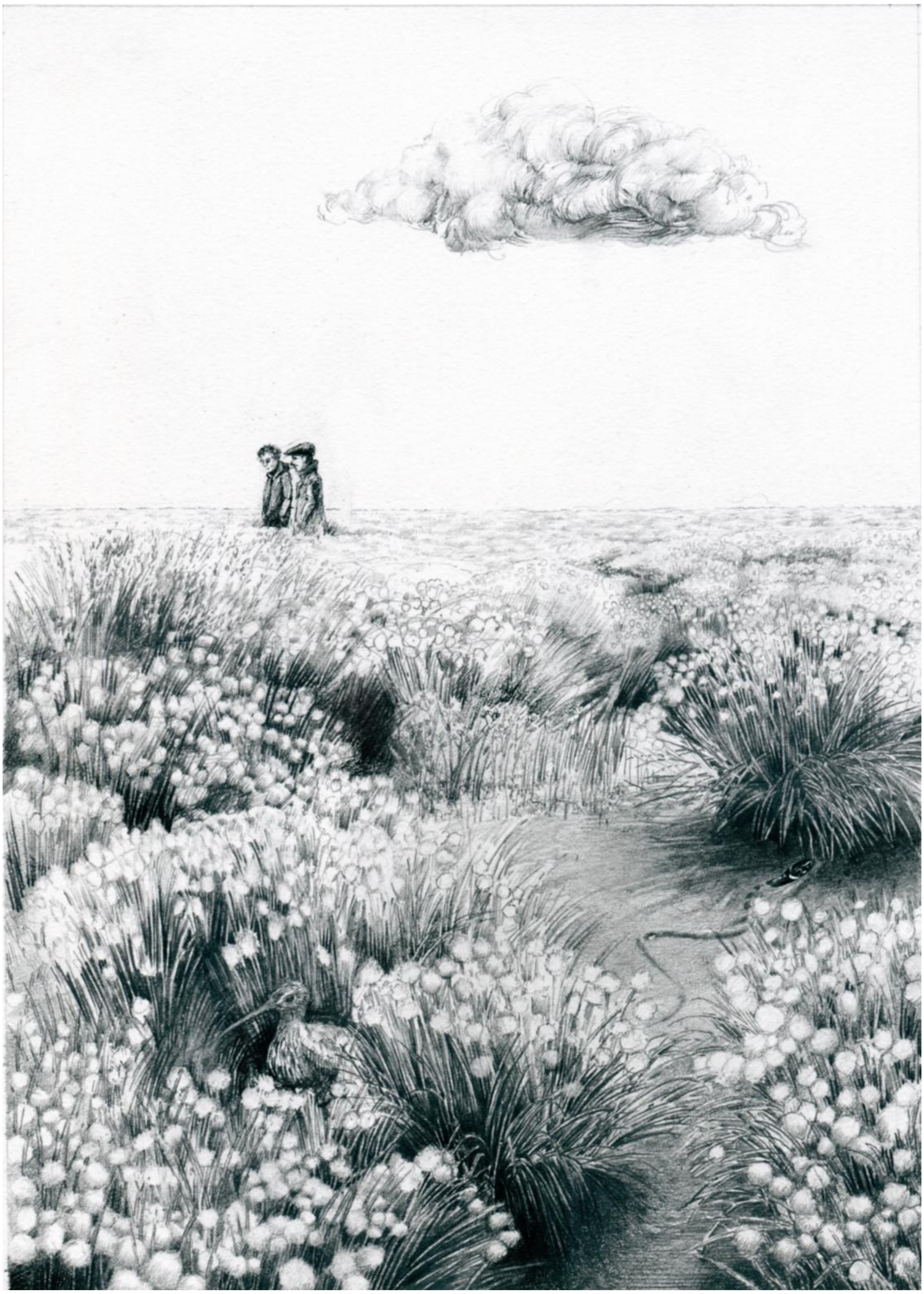
We show that the $\delta^{13}C$ signature of *Sphagnum* biomass integrates both capitulum water content and the isotopic composition of source CO_2. Consequently, the water content during the growing season can be predicted when signatures of different carbon sources are carefully considered. On the other hand, knowing the moisture content of peatlands allows identifying the $\delta^{13}C$ values of source CO_2 fixed by peatmosses, a parameter not measurable in the field. Carbon isotope discrimination varies among seasons and $\delta^{13}C$ values of moss tissue integrate environmental conditions over the period during which the biomass was synthesized (Rice 2000). Therefore, knowledge about the environmental conditions during *Sphagnum* growth is essential to draw a conclusion from $\delta^{13}C$ values of the biomass. Generally, it is difficult to determine the period during which a moss capitulum was built (Aldous 2002a). Fortunately, we were able to exactly retrace the development of *S. cuspidatum*, allowing us to estimate the moisture conditions and subsequently calculate the isotopic composition of carbon assimilated by the mosses. The isotopic composition of the source CO_2 of -9.9‰ indicates that the mosses assimilated a reasonable amount of substrate-derived carbon (Keeley & Sandquist 1992).

Evaluation of published *Sphagnum* $\delta^{13}C$ data

Surprisingly, reported $\delta^{13}C$ values of *Sphagnum* biomass did not differ between the different sections of the genus. Nevertheless, the large variance for species of the Cuspidata section, typical for wet hollows, is striking. According to our models, the highest observed $\delta^{13}C$ values of -22.9‰ for this section can be explained by relatively high water contents between 20 and 30 (fw/dw), with a corresponding isotopic composition of the source CO_2 being between -7.7‰ and -10.9‰. The lowest observed $\delta^{13}C$ values of -34.7‰ are likely due to high water contents and a carbon source strongly depleted in $\delta^{13}C$ such as methane (Proctor *et al.* 1992, Raghoebarsing *et al.* 2005, Kip *et al.* 2010). The conclusion remains speculative for intermediate $\delta^{13}C$ values of around -27‰ (typical for C3 plants), given that both the water content and carbon source might have an influence on the isotopic composition of moss tissue. In this case, assimilation of methane derived CO_2 might be overestimated, especially because diffusion and concomitantly discrimination by Rubisco is not entirely restricted, even at high water contents (Rice & Giles 1996, Williams & Flanagan 1996).

Peatmosses of the sections Acutifolia and Sphagnum occur at the top of dry hummocks, as well as in relatively wet hollows (Laine *et al.* 2009). Therefore, predicted water contents running model A with $\delta^{13}C$ values of the carbon of -8‰ seem to be in a realistic range. The influence of substrate-derived carbon might only play a distinct role in the case of lowest reported values of less than -30‰ for the section Sphagnum, because water contents of permanently more than 20 (fw/dw) are rarely observed (Wagner & Titus 1984, Robroek *et al.* 2009a, Strack & Price 2009). For the highest reported $\delta^{13}C$ values of -24.8‰ and -25.1‰ of model B, the water content must have been more than 10 (fw/dw), given that the calculated $\delta^{13}C$ of the source of -4.0‰ and -4.3‰, respectively, are unrealistic, as they are higher than the atmospheric isotopic composition. A carbon source with $\delta^{13}C$ values higher than the atmosphere, e.g. HCO_3^- derived from limestone, might be excluded in the acidic environment of peat bogs (Keeley & Sandquist 1992), despite a distinct influence of calcareous groundwater possibly occurring (Lamers *et al.* 1999). A carbon source depleted in ^{13}C might probably only has an influence on the isotopic composition of the moss biomass in the case of high water contents and low $\delta^{13}C$ values of the biomass. In respect of the relatively dry habitats, the CO_2 source might rather be the underlaying and decaying peat biomass and should therefore have a $\delta^{13}C$ value of around -27‰ (Keeley & Sandquist 1992). The calculated amount of maximum 25% recycled carbon might be due to high CO_2 production rates under aerobic conditions and a direct release of decomposed CO_2 between the hummocks (Smolders *et al.* 2001). Furthermore, the dense structure of hummocks hampers the outward diffusion of released CO_2 to the atmosphere more than looser growing lawns, which enhances the effect of a CO_2 trap of hummocks in comparison to wetter habitats (Lamers *et al.* 1999, Limpens *et al.* 2008b)

In conclusion, our results clearly underpin that substrate-derived carbon is an important source for the assimilation of *Sphagnum* under many circumstances. However, we show that the knowledge of peatland´s moisture conditions and the consideration of species-specific characteristics are crucial for a realistic estimate of the actual potential to recycle carbon in Sphagna. Furthermore, estimations of historical hydrological conditions on the base of *Sphagnum* biomass $\delta^{13}C$ values, e.g. in paleoclimatic studies, must take into account that the signature of the carbon source obviously does not equal atmosphere $\delta^{13}C$. Finally, it becomes obvious that the widespread approach to calculate carbon isotope discrimination on the base of the isotopic composition of the biomass might lead to uncertainties if it cannot be assured that the CO_2 source purely consists of well mixed air from the atmosphere.



6 Synthesis

6.1 Impact of global change on *Sphagnum* performance and productivity

Sphagnum productivity strongly depends on moisture conditions, especially on the capitulum water content, and varies between species and habitats (Robroek *et al.* 2007a). Thus, lowest biomass production in the field was observed for *S. cuspidatum* growing relatively far above the water table within tussocks of *Eriophorum vaginatum*. Mosses originating from a wetter environment only slightly differed between species. Reported higher productivity for *S. cuspidatum* compared to *S. papillosum* (Gaudig 2001, Gunnarsson 2005) was not confirmed in this study, indicating that growing conditions rather than species-specific characteristics determined *Sphagnum* productivity.

Moisture conditions strongly differed between 2011 and 2012. Regarding the Hartshoper Moor field site, 2011 was characterized by a prolonged drought in spring and a substantial lower water table compared to 2012. Hence, it was somewhat surprisingly that biomass production of *Sphagnum* mosses only slightly differed – without showing a clear trend – between the two years. Evidence suggests that the mosses recovered after the extreme drought in spring and were highly productive under favorable conditions in summer and autumn.

To elucidate the dependence of *Sphagnum* productivity on water content and particularly the impact of severe desiccation on *Sphagnum* assimilation, I carried out a laboratory experiment. I documented that the metabolism of *S. cuspidatum* slowed down in spring 2011 – showing neither photosynthesis nor respiration – when mosses were severely damaged by desiccation. However, the mosses recovered after rewetting in the laboratory, albeit recovery was slow and photosynthetic capacity not fully developed. While previous studies analyzing *Sphagnum* drought tolerance were based on experimentally induced desiccation, my results, based on desiccated mosses from the field, confirm earlier findings (Schipperges & Rydin 1998, Robroek *et al.* 2009a). In the laboratory experiment, *Sphagnum* assimilation in the observed capitula recovered in the short term to around 20% of the maximum values measured for mosses grown under favorable conditions. However, it was observed in the field that the mosses invested in the long-term in the development of a new stem and a new capitulum, presumably based on the short-term potential to repair the photosynthetic apparatus, which was apparently strongly damaged (Clymo & Hayward 1982).

Besides the potential to recover after desiccation, I also analyzed the moisture dependent CO_2 exchange of *Sphagnum* in the laboratory experiment. As reported before, net assimilation of peatmosses is reduced below and above a specific optimum capitulum water content. At low water levels, the photosynthetic capacity of peatmosses is reduced due to an overall metabolic slowdown when desiccated (Schipperges & Rydin 1998, Williams & Flanagan 1998, Hajek &

Beckett 2008). By contrast, at high water levels, assimilation becomes CO_2-limited due to excess water enhancing diffusion resistance to CO_2 (Silvola 1990). This observation is also reflected by concomitantly decreasing discrimination (Δ) against $^{13}CO_2$ with increasing water contents, assuming that discrimination by Rubisco decreases when moss photosynthesis becomes CO_2-limited (Rice & Giles 1996, Williams & Flanagan 1996). Nevertheless, analyses of Δ^{13} CO_2 during photosynthesis revealed that CO_2 diffusion is not completely restricted in peatmosses, even with high water contents. The conclusion that *Sphagnum* has an effective strategy to avoid diffusion resistance when growing close to the water is supported by the observation that, photosynthesizing with high water contents, $\Delta^{13}C$ by Rubisco declined substantially less in mosses originating from hollows compared to those growing in dry hummocks. In order to avoid diffusional limitation under wet conditions, a looser growth density and the exposition of photosynthetic cells at the leaf surface help to reduce thick water films directly at the photosynthetic cells, as well as lowering resistance to gas exchange (Proctor *et al.* 1992, Rice & Schuepp 1995).

Morphological adaptations expressed through varying growth densities were observed between species as well as within species growing in different habitats. The growth density of *S. papillosum* was generally higher than that of *S. cuspidatum*, highlighting the general adaption and occurrence of *S. papillosum* to drier habitats (Gunnarsson *et al.* 2004). Furthermore, growing in a hummock well above the water table, the capitulum growth density of *S. papillosum* was almost twice that of mosses of the same species growing close to the water table, while the shoot density (the segment up to 4 cm below the capitulum) was significantly higher for *S. cuspidatum* growing within dry *Eriophorum* tussocks compared to mosses of the same species growing in wet hollows. Interestingly, the mosses are able to adapt to varying moisture conditions within one growing season. I show that *S. cuspidatum* at Hartshoper Moor was growing in a dense carpet when the water table was low in spring 2011, whereas the species grew loosely when the water table was high later in the year. The capitulum growth density was around four times higher in dry months than in months with a high water table. Differences in growth densities alter the water holding capacity of the mosses and concomitantly the relationship between water content and carbon assimilation. Gas exchange measurements revealed that, related to their dry weight, the highest maximum net photosynthesis rates were obtained for both species when they were loosely growing. In contrast, related to their growth density and calculated per square meter, the mosses assimilated more carbon when growing in a dense carpet. Accompanied by varying growth densities, the water content identified as the optimum for photosynthesis also varies. The highest *Sphagnum* photosynthesis rates amongst both species from different habitats were observed at intermediate water contents of between 7 and 12 [fw/dw]. Roughly estimated, this water content corresponds to a water table of 10 – 15 cm below the surface, at least for *S. cuspidatum* growing in hollows. Due to their higher water holding capacity, mosses originating from relatively dry hummocks are assumed to tolerate lower water tables without showing lower water contents (Rydin 1985). However, the water content of *Sphagnum* mosses is also influenced by precipitation events, hysteresis and evaporation (Kellner & Halldin 2002, Strack & Price 2009). Thus, my observations indicate that *Sphagnum* rarely assimilates under optimum moisture conditions. I conclude that the ability to keep pace with spontaneous changing moisture conditions is limited within one season and might reflect a trade-off for being capable of high productivity under favorable conditions and able to withstand both extreme dry and extreme wet conditions.

Chamber measurements of CO_2 fluxes include the entire vegetation, which complicates determining the effect of single species effects on total gas fluxes. Nevertheless, given that vascular plants did not contribute to carbon uptake in early spring and in late autumn due to not developed or senescent leaves, it is likely that *Sphagnum* alone was responsible for the assimilation of carbon in these months (Münchberger 2013). Thus, the calculated daily carbon uptake of the mosses was 0.19 g C m^{-2} in late September and November and 0.32 g C m^{-2} in March. The calculated mean daily C uptake of *Sphagnum* in the laboratory experiment – including various growth density characteristics over the year – was 0.65 g C m^{-2}. Based on the harvested biomass, the daily carbon uptake for a 130-day period between June and October was calculated to amount 0.63 g C m^{-2}. Whereas the upscaling of punctual measurements to year-round models bears the risk of misjudging important (unknown) parameters, the evaluation of biomass harvest at the end of the year hardly allows drawing conclusions about the growing conditions during the year. However, the combination of both methods provides valuable information. First, the measurements in the laboratory should reflect growth characteristics to prevent over- or underestimations of CO_2 exchange of *Sphagnum* in the field. Second, when vascular plants are inactive, chamber measurements in the field provide reliable results of carbon uptake by *Sphagnum*, even if it was only the case in early spring and in autumn during this study. In these months, characterized by low temperatures and high water tables, carbon uptake was underestimated compared to rates calculated on the basis of harvested biomass. Thus, the results indicate that most carbon was taken up by *Sphagnum* in summer months, stimulated by high temperatures and more favorable moisture conditions. Furthermore, the contribution of *Sphagnum* to overall CO_2 uptake in summer months must have been relatively high compared to vascular plant assimilation.

The impact of nitrogen fertilization on *Sphagnum* productivity was somewhat ambiguous. Nevertheless, my results confirm earlier findings that *Sphagnum* productivity is not negatively affected by increasing N availability unless the N concentration of the biomass does exceed 1.2 – 1.5% (Lamers *et al.* 2000, van der Heijden *et al.* 2000, Bragazza *et al.* 2004). At low nitrogen loads, N fertilization is assumed to stimulate *Sphagnu*m growth until other nutrients such as phosphorus become the limiting factor and N cannot be diluted in the biomass by stimulated growth (Lamers *et al.* 2000, Fritz *et al.* 2012). Hence, N concentrates in the biomass until excess N becomes toxic for *Sphagnum* (Baxter *et al.* 1992). I demonstrate that it is not only the N surplus that determines the N availability and the uptake of *Sphagnum*, as the productivity of the mosses was not negatively affected by fertilization in 2012, in contrast to 2011. Interestingly, N fertilization provoked alterations in moss morphology in some cases, leading to a decrease in length increment. In case of *S. papillosum*, a concomitant increase in shoot density was observed, cancelling out the reduced length increment regarding the total biomass production. As shown before, the denser growth will enhance the water holding capacity of the mosses and prevent desiccation. Furthermore, the total biomass production of *S. papillosum* was not negatively affected, even when N concentrations in the biomass were relatively high. *S. papillosum* originated from an area with substantially higher atmospheric N deposition and was transplanted to the Hartshoper Moor. Thus, these mosses were presumably adapted to high N availability. This underpins earlier findings that the tolerance of *Sphagnum* to survive or even profit from relatively high N loads is enhanced when the mosses were continually exposed to elevated concentrations throughout their life (Baxter *et al.* 1992).

Besides the direct effect of moisture and nutrient availability on *Sphagnum* productivity, multiple interactions between the mosses and vascular plants also determine their performance (Malmer *et al.* 1994). Ombrotrophic bogs are generally nutrient-poor ecosystems, developed in areas with sufficient water supply. Additionally, *Sphagnum* acts as an ecological engineer, creating an acidic, nutrient poor, cold and anoxic ecosystem (van Breemen 1995) and hence generating an unfavorable environment for most vascular plants. In my field experiment, I demonstrated that enhanced nutrient availability as well as reduced precipitation might favor the growth and productivity of vascular plants, which in turn has been assumed to have a negative effect on *Sphagnum* performance. As long as the *Sphagnum* layer is able to intercept nutrients, they are not available for vascular plants. The ‘natural filter’ of peatmosses fails and N concentrations in the rhizosphere increases above a distinct threshold of N deposition, becoming available for vascular plants (Lamers *et al.* 2000, Bobbink & Hettelingh 2011). At Schweimker Moor, the N surplus presumably stimulated growth of *Eriophorum vaginatum*. Furthermore, the growth of *E. vaginatum* was increased when precipitation was reduced, indicating that drier conditions also change the competitive balance, hampering *Sphagnum* growth by shading or covering the mosses with litter (Malmer *et al.* 1994). Thus, the increase of drier conditions in peatlands (caused by increasing temperatures and/or decreasing precipitation) and ongoing high nutrient availability has been assumed to promote a shift in the vegetation towards the dominance of graminoids, shrubs and trees (Laine *et al.* 1995, Breeuwer *et al.* 2009).

To conclude, both drier conditions and high nitrogen availability are assumed to have negative effects on *Sphagnum* growth and productivity. Nevertheless, the mosses seem to tolerate wide ranges of moisture conditions as well as nitrogen depositions. Even if productivity decreases, *Sphagnum* species might adapt to moderate environmental changes and/or a shift within the species might occur. It has already been suggested that *Sphagnum* species typical for hollows lose their competitive strength under drought relative to hummock species, which are already adapted to relatively dry conditions due to their morphology and higher water-holding capacity (Breeuwer *et al.* 2008). However, extreme events such as prolonged droughts might severely affect *Sphagnum*, due to increasing risk of mortality (Bragazza 2008). Hence, my results indicate that *Sphagnum* is more susceptible to shifts in the vegetation than being directly affected by global change (except of land use), as long as other stressors such as the infection by parasites or extreme weather events are absent.

6.2 Impact of *Sphagnum* bogs on the climate system

The impact of peatlands on the climate system is primarily related to their function to sequester and store carbon. The sequestration of carbon depends on the balance between the assimilation of CO_2 by biomass production and the decomposition of the litter produced. The long-term function to store carbon is based on the accumulation of peat, comprising the incomplete decomposed plant organic matter. At present, the estimated annual carbon sequestration in northern peatlands is around 70 Mt (Clymo *et al.* 1998). Carbon sequestration over the Holocene – subjected to varying climatic conditions and hence varying sequestration rates – resulted in the accumulation of peat and a carbon storage of up to 460 Gt in northern peatlands (Gorham 1991).

Beside the effects on *Sphagnum* and vascular plant productivity discussed above, I have shown that the decomposition of plant material differed between species. On the one hand, *Sphagnum* species growing in dry hummocks showed lower decomposition rates than typical hollow species. Regarding the aforementioned possible shift in the *Sphagnum* cover favoring hummock species, the observed slower decay rates of those species might lead to higher carbon sequestration in *Sphagnum*-dominated bogs (Hajek 2009).

Nevertheless, I demonstrated in the litter experiment, as was also indicated by measured R_{eco} rates, that decay rates of vascular plant litter were higher than those of the recalcitrant tissue of *Sphagnum*. Thus, the expected shift in the vegetation cover towards the dominance of vascular plants will presumably lead to reduced carbon sequestration (Dorrepaal *et al.* 2005, Malmer *et al.* 2005), even if an enhanced productivity of vascular plant biomass might partly compensate the carbon loss (Charman *et al.* 2013). Apart from changes in litter quality, the fact that *Sphagnum* even took up carbon at low temperatures in spring and late autumn, when vascular plants were inactive, it is questionable whether climate change-induced increasing productivity of vascular plants might compensate the possible decrease of *Sphagnum* cover and its year-round carbon uptake.

Furthermore, the observed increasing mass loss of vascular plant litter as well as increasing N concentrations in plant biomass caused by N fertilization are in accordance with the assumption that high N deposition rates will promote carbon loss from peatlands due to the amelioration of litter quality and enhanced microbial activity (Verhoeven *et al.* 1990, Bragazza *et al.* 2006).

Regarding carbon gas fluxes in the Hartshoper Moor, it was observed that both CO_2 and CH_4 fluxes strongly varied during the course of the year. My results indicate that as long as the water table is high, little or no CO_2 is released from the peat. Furthermore, the measured ecosystem respiration R_{eco} was mainly caused by autotrophic rather than heterotrophic respiration. R_{eco} rates were only substantially enhanced in May 2011, when the water table was relatively low. Conversely, in spring and autumn, when vascular plants were presumably inactive, only small R_{eco} rates were detected, being approximately in the range that I measured for dark respiration rates of *Sphagnum* capitula. Temperature has generally been assumed to play a crucial role for CO_2 production and emission from peatlands (Lafleur *et al.* 2005, Dorrepaal *et al.* 2009), although my results support the assumption that in the absence of oxic conditions in the peat layer, temperature is not the limiting factor of heterotrophic soil respiration (Gazovic *et al.* 2013). However, increasing temperatures might affect the water table and reduce moisture conditions, leading to increasing aerobic conditions and concomitantly increasing soil respiration rates.

Water table and temperature are further important factors determining CH_4 fluxes in peatlands, and it is difficult to disentangle the combined effect of both factors. High temperatures and high water levels are commonly associated with high CH_4 production rates (Whalen 2005). Nevertheless, I have demonstrated that the interplay of both factors determines CH_4 emissions. I showed that as long as the temperature was relatively low, CH_4 emission rates were low without showing substantially variation and independent from the actual water table. This finding supports previous studies reporting a strong increase of CH_4 emission above around 15 °C (Bergman *et al.* 2000, van Winden *et al.* 2012). Furthermore, my results are in accordance with earlier findings that CH_4 emissions are very low at water tables below 15 – 20 cm, even at high soil temperatures (Moore & Roulet 1993, Shannon & White 1994). CH_4 emissions are the result of both methane production and oxidation. It has been shown that oxidation of CH_4 is often associated with *Sphagnum* mosses (Raghoebarsing *et al.* 2005, Larmola *et al.* 2010) and, using carbon stable isotope analyses, I demonstrated that Ch_4 was presumably consumed by *Sphagnum* through the symbioses with methanotrophic bacteria. I assume that CH_4 production and consumption was in equilibrium at low temperatures and that at temperatures above 15 °C methane retention failed because methanogenic activity exceeded the oxidation potential of methanotrophs (van Winden *et al.* 2012).

Furthermore, carbon stable isotope analyses indicated that substrate-derived carbon might be an important CO_2 source for *Sphagnum* assimilation, via either methane oxidation in wet habitats or directly derived from decaying peat biomass in dry habitats. Although carbon stable isotope analyses might be a useful tool to evaluate the potential of *Sphagnum* to recycle carbon, I demonstrated that the knowledge of peatland´s moisture conditions as well as the consideration of species-specific characteristics is crucial for a realistic estimate. In a review of published $\delta^{13}C$ values of *Sphagnum* biomass, I showed that the carbon isotopic composition varies between values of -22.9‰ and -34.7‰. Particularly in the case of mosses grown in wet habitats, low (more negative) $\delta\ ^{13}C$ values indicate the uptake of substrate-derived CO_2. By contrast, for mosses growing well above the water table, presumably the effect of drier growing conditions – and concomitantly higher discrimination against ^{13}C due to lower diffusion resistance – is primarily reflected in low $\delta^{13}C$ values in the biomass.

Global change in the form of increasing temperatures and decreasing summer water tables, in combination with high nitrogen deposition, might have far-reaching effects on carbon cycling in peatlands. Increasing temperatures might increase CH_4 and (at least under dry conditions and by stimulating low water levels) CO_2 emissions from peatlands. The effect of decreasing water tables in summer is assumed to have ambiguous effects on greenhouse gas fluxes, stimulating CO_2 and concomitantly impeding CH_4 emissions. Moreover, I showed that high nitrogen deposition might stimulate decomposition and hence carbon losses. I demonstrated that the vegetation plays a crucial role in the carbon cycle of peatlands, with evidence suggesting that a living and functioning *Sphagnum* layer is the most determining factor for the potential to sequester carbon in bogs, and thus extremely important to inhibit or decelerate carbon losses stored in underlaying peat reservoirs.

6.3 Global change and *Sphagnum*-bogs in the MRH – implication for nature conservation

In the introductory chapter, I provide an overview of the current status of peatlands and *Sphagnum*-bogs in the metropolitan region of Hamburg (MRH). It is obvious that the most important threat for peatlands in the MRH is land-use. The most widespread use of peatlands in the region is meadows and pastures and, to a lesser extent, cropland (Röder 2012). Furthermore, peat excavation still takes place in around 11% of former bog areas in Lower-Saxony (LLUR 2012) as well as to a smaller extent in Schleswig-Holstein (e.g. Himmelmoor). Despite restoration measures of peatlands in the MRH taking place since the 1980s, due their function to sequester and store carbon, environmental authorities are increasingly focusing on peatland protection and restoration in recent years. The environmental authorities of the German federal states with a significant abundance of peatlands (Schleswig-Holstein, Mecklenburg-Western Pomerania, Lower-Saxony, Brandenburg and Bavaria) have recently elaborated objectives to protect peatlands under consideration of their impact on climate change (LLUR 2012). Four major goals were identified: (1) the strict protection of the last (semi-) natural peatlands; (2) the rewetting and revitalization of peatlands (minimum 5 – 10%), including their biocoenosis and functions; (3) a sustainable use ensuring high water levels (e.g. paludiculture and *Sphagnum* farming); and (4) a substantial reduction of greenhouse gas emissions.

In the following, I briefly evaluate the challenges to accomplish the above-mentioned objectives regarding projected regional climate scenarios. Peatland development as well as restoration success depends on a multitude of interacting environmental factors. The results of my thesis deliver valuable information about the impact of global change on the development of *Sphagnum*-bogs in the MRH and their possible feedback to the climate system.

Overall, it is difficult to draw conclusions concerning how *Sphagnum* growth in certain peatlands in the region will perform in the future, and the results of my thesis do not allow explicit recommendations for peatland restoration or management. However, it is likely that the risk of prolonged drought and severe desiccation of *Sphagnum* will be higher under more continental conditions in the southeast of the MRH in future than under oceanic conditions in northwestern peatlands. During the Holocene, peatlands were continuously subjected to changing climatic conditions with remarkable shifts in vegetation composition, although stable periods lasting for centuries were also detected (Chambers *et al.* 1997, Barber *et al.* 1998).

Stable conditions are particularly reported for ombrotrophic *Sphagnum*-bogs, indicating their resilience to changing environmental conditions, even if accompanied with shifts within the genus *Sphagnum* (Rydin & Barber 2001). However, *Sphagnum*-bogs are dynamic ecosystems, and thus gradual shifts in the vegetation have been observed in recent decades, and mainly attributed to allogenic processes such as increasing temperatures, surface drying and increasing nitrogen deposition (Gunnarsson *et al.* 2002, Heijmans *et al.* 2013). Therefore, to protect the last remaining (semi-)natural bogs of the MRH, it is essential to improve or at least maintain the growing conditions for *Sphagnum*. Even if raised bogs are theoretically independent from groundwater, today they are located in a heavily disturbed landscape and at least margins of the bogs have been used in many cases. Hence, to ensure favorable and stable moisture conditions, water management for the entire catchment should be implemented because projected drier and warmer conditions in summer are likely to increase surface drying and the risk of desiccation of peatmosses. Furthermore, a buffer to agricultural land is required to prevent direct pollution with nutrients.

Apart from the protection of only small areas of (semi-)natural raised-bogs, the restoration of these unique ecosystems under changing conditions represents a future challenge and a major task for nature conservation (Rochefort & Lode 2006). In many peatlands, peat excavation will be shut down in the near future; for instance, the last permissions for peat exploitation in MRH will expire 2040 in the county of Cuxhaven. The abandonment of cut-over bogs provides the opportunity for restoration, and rewetting measures are planned for most peatlands in the region (NLWKN 2006). An essential element for the development of raised bogs and carbon sequestration in peatlands are *Sphagnum* mosses and, hence, the re-establishment of *Sphagnum* diversity is crucial (Robroek *et al.* 2009b). However, it has been observed that the water table strongly varies within re-wetted bogs and that recolonizing *Sphagnum* is vulnerable to drought, especially in dry summers (Schouwenaars & Gosen 2007). Thus, suitable locations for restoration measures must be identified, with a good prospect for relatively high and stable water levels and thus the development of *Sphagnum*-dominated vegetation, depending on the remaining peat type (Tomassen 2004).

The resilience of *Sphagnum*-bogs to climatic changes is attributed to a functional acrotelm, the uppermost layer of bog peat, characterized by high porosity and high hydraulic conductivity, both of which decrease with depth. Thus, the acrotelm is hydrological self-regulating and has the ability to retain water in drier periods (Ingram 1978, Edom 2001). Therefore, the development of a functioning acrotelm has been recognized as an important factor in determining a successful restoration and the re-establishment of *Sphagnum* diversity (Smolders *et al.* 2003).

Simple restoration measures such as the blockage of former primary drainage ditches might effectively promote the recovery of typical bog vegetation and impede the establishment of undesired vegetation (González *et al.* 2013a). Furthermore, the colonization of *Sphagnum* is often facilitated by the growth of pioneer vascular plants such as *Eriophorum vaginatum* (Tuittila *et al.* 2000, Jauhiainen *et al.* 2002), resulting in efficient carbon sinks (Kivimaki *et al.*

2008). The beneficial co-occurrence of *E. vaginatum* and *S. cuspidatum* could also be observed at the former peat extraction field at Schweimker Moor since rewetting in the 1980s, although my results indicate that decreasing precipitation and high nitrogen loads might stimulate the growth of *Eriophorum*, endangering the successful re-establishment of *Sphagnum*.

Nevertheless, after the spontaneous colonization of *Sphagnum* species such as *S. cuspidatum* and *S. fallax*, the re-establishment of a functioning acrotelm has stagnated in many cases due to the absence of *Sphagnum* species with better water holding capacities (Grosvernier *et al.* 1997, Smolders *et al.* 2003). It has been suggested that after the establishment of fast colonizing hollow species, the introduction of target species such as *S. magellanicum*, *S. papillosum*, *S. rubellum* and *S. fuscum* might enhance the successful recovery of a functioning acrotelm (Smolders *et al.* 2003, Chirino *et al.* 2006, Robroek *et al.* 2009b). My results are in accordance with earlier findings suggesting that these species are less sensitive to environmental changes and more effective in sequestering carbon (Breeuwer *et al.* 2009). Regarding projected climate change scenarios, I conclude that the future restoration success of peat bogs depends more than ever on the presence of the aforementioned target species.

The restoration of peatlands mainly aims to reestablish a unique ecosystem with its typical species' inventory as well as its functions to sequester carbon. Moreover, in both excavated peatlands and bog grasslands, *Sphagnum* farming might be a promising approach to foster carbon storage and concomitantly, creating an alternative to fossil white peat as a raw material for horticultural growing media (Gaudig *et al.* 2012).

The successful re-establishment of typical *Sphagnum*-bog vegetation requires the evaluation of a particular area regarding its catchment hydrology and water chemistry, physical and chemical peat properties, as well as the current vegetation cover (Rochefort & Price 2003, and references therein). I conclude that peatland management and restoration must be adjusted to local circumstances and climate change projections should be integrated to assess the prospect of successful *Sphagnum*-bog development. In locations where *Sphagnum* development is not promising and a future sequestration of carbon is not expected, restoration measures as well as land-use activities should focus on the carbon storage function in the underlying peat deposit, which are often already successful by maintaining high water tables.

6.4 Further research needs

A regional monitoring of realized restoration measures and the development of (semi-)natural peatlands in the last decades would be desirable to evaluate the potential to restore *Sphagnum*-bogs in the MRH. Many vegetation surveys have been carried out during recent decades in peatlands of Northern-Germany, with a large number of permanent survey plots established. However, a continuous resampling of vegetation data is lacking in many peatlands and considerations on the regional scale are scarce. It would be profitable to integrate regional climate observations (e.g. Schlünzen *et al.* 2010) and peatland vegetation dynamics to retrace changes in temperature and precipitation and possible shifts in peatland vegetation.

Furthermore, future regional climate projections (Rechid *et al.* 2013) could be used to estimate peatland development and restoration prospects of the MRH. Nevertheless, for certain estimates of regional peatland development and carbon cycling in peatlands, further research is needed on different scales.

A major effort has been made in recent decades to determine adequate restoration measures to maintain the function of peatlands to store carbon and promote their potential to sequester carbon in the future (Rochefort & Lode 2006). Nevertheless, further research for the successful (re-)establishment of *Sphagnum* is needed, regarding the requirements of either transplanted target species (Chirino *et al.* 2006, Robroek *et al.* 2009b) or the establishment from spores (Sundberg & Rydin 2002, Gahlert *et al.* 2012). In particular, the long-term monitoring of the re-introduction of target species is scarce and should be addressed in further research. Additionally, the development of new tools for an early monitoring might be helpful to improve restoration success (González *et al.* 2013b).

Carbon cycling and gas fluxes can be measured at different temporal and spatial scales. Observations vary from individual species over plant communities and ecosystems up to the global scale and carbon cycling has been observed for short snapshots (e.g. measuring photosynthesis of individual plants under certain conditions), over growing seasons or a few years (e.g. biomass production and litter decomposition), as well as up to hundreds or thousands of years (e.g. paleoclimatic studies from peat stratigraphy). Whereas long-term observations on a large spatial scale are useful to estimate the global impact of peatlands on carbon cycling, they hardly allow for disentangling underlying processes. Small scale measurements contain, however, uncertainties by scaling up. Future research in peatlands should fill this gap by combining analyses on different scales, i.e. using eddy covariance technique to survey gas fluxes on the ecosystem scale, closed chamber technique for the plant community scale and the leaf chamber technique for the species scale (Forbrich *et al.* 2011, Münchberger 2013). Furthermore, the application of carbon stable isotope analyses might be a promising tool to determine past and current growing conditions of individual plant species, as well as estimating the role of *Sphagnum* in recycling carbon and thus lowering the CO_2 and CH_4 emission of peatlands. Therefore, analyses of carbon stable isotope discrimination during photosynthesis should be amplified to other *Sphagnum* species. The obtained information could be used to either estimate the potential of single species to retain respired carbon or determine their optimum growing conditions. Moreover, the application of carbon stable isotope analyses of greenhouse gases in peatlands is scarce i.e. (e.g. Dorrepaal *et al.* 2009) and could provide valuable information concerning their production, transport pathways, consumption and emission.

Stable isotope analyses could also be applied to retrace nitrogen cycling in peatlands. The natural abundance of ^{15}N in plant biomass and peat, as well as the use of ^{15}N as a tracer, could help to retrace N fluxes in peatlands, as well as evaluating the capacity of *Sphagnum* to intercept and absorb the nutrient before percolating to the rhizosphere being available for vascular plants (for review see Robinson 2001). Furthermore, a species-specific consideration of *Sphagnum* to tolerate high N deposition might be indicated by the observation that some species occasionally grow well without showing toxic reactions under N loads above those assumed to be critical for the mosses (Lamers *et al.* 2000, Bragazza *et al.* 2004). In particular, possible interacting effects with other environmental factors such as light, temperature or moisture should be integrated in future analyses to specify the effect of high nitrogen loads on *Sphagnum* metabolism and the competitive balance between *Sphagnum* and vascular plants.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Cooperation and contributions

The thesis consists of four chapters as well as a general Introduction and a Synthesis. In the following I provide an overview of cooperation with other scientists and declare my own contributions to this thesis. I wrote the introductory chapter (chapter one) as well as the thesis synthesis (chapter six).

Further contributions:

Chapter two

The field experiment was designed in cooperation with Maren Meyer-Grünefeldt and Werner Härdtle (Institute of Ecology, Leuphana University Lüneburg) and Kristin Ludewig (Applied Plant Ecology Group, Biocenter Klein Flottbek, University of Hamburg). I conducted the experiment, the field work and laboratory analyses as well as data preparation and statistical analyses and further, I wrote the whole chapter.

Chapter three

I designed the experiment in cooperation with Marion Vanselow-Algan, Claudia Fiencke and Eva-Maria Pfeiffer (Institute of Soil Science, University of Hamburg). Marion Vanselow-Algan conducted gas flux measurements, laboratory analyses and carried out gas flux calculations. I collected meteorological and hydrological data as well as vegetation data. Further, I conducted all statistical analyses. I wrote the chapter except of the methods describing gas flux measurements and calculations.

Chapter four

The experiment was designed in cooperation with Peter Müller and Christoph Reisdorff (Applied Plant Ecology Group, Biocenter Klein Flottbek, University of Hamburg). I conducted field work and laboratory analyses as well as data preparation and statistical analyses and further I wrote the whole chapter. Peter Müller contributed to gas flux measurements as well as field work. Furthermore, Peter Müller and Christoph Reisdorff gave helpful comments on the manuscript.

Chapter five

The experiment was designed in cooperation with Christian Knoblauch (Institute of Soil Science, University of Hamburg). I conducted field work as well as the laboratory experiment. Furthermore, I carried out data preparation and statistical analyses and wrote the whole chapter.

Eidesstattliche Versicherung

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

Hamburg, den 13.12.2013