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Sphagnum growth

and its perspectives for Sphagnum farming

Novel peatland use approach

Sphagnum growth
and its perspectives for Sphagnum farming

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Für Papi.

… the climate crisis has already been solved. We already have all the facts and solutions. All we need to do is to wake up and change! | … die Klimakrise wurde bereits gelöst. Wir kennen bereits alle Fakten und Lösungen. Alles, was wir jetzt noch tun müssen, ist aufzuwachen und etwas zu verändern!

Greta Thunberg, 2018

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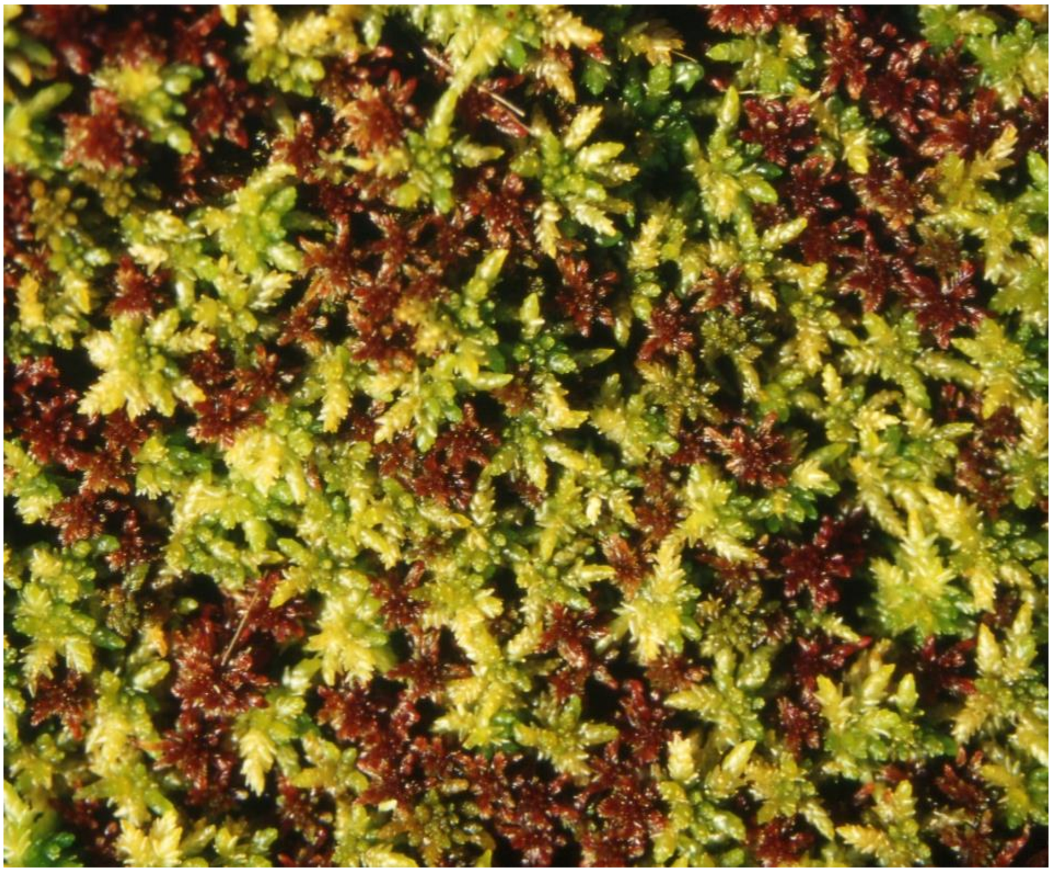
Summaries



Summary

The genus *Sphagnum* (L.) belongs to the Bryophyte plant division and includes 150 to 400 species. As all mosses *Sphagnum* has no roots and can hardly regulate its water uptake. As long as enough water is available *Sphagnum* can grow nearly unlimited while the lower, older parts die off and may accumulate as peat. Single *Sphagnum* species are able to build up an acrotelm as a hydrological self-regulating mechanism of a bog, a type of intact peatland (mire) only fed by precipitation. Because *Sphagnum* dominates nearly half of the peatlands in the world, it is one of the globally most important peat formers.

Sphagnum biomass is an important raw material for many valuable products, but in a much larger scale *Sphagnum* is used in its fossil state – as *Sphagnum* peat. With a consumption of *c.* 40 million m³ per year globally, *Sphagnum* peat is the predominant raw material for horticultural growing media. To get *Sphagnum* biomass it is currently collected from wild populations, to get *Sphagnum* peat it is extracted from bogs.

By far, more peatlands (including bogs) are subjects to drainage for agri- and silvicultural use since centuries, which harms their ecosystem services, including their typical biodiversity, carbon storage capacity, water regulation function and palaeo-environmental archive. In Europe, *c.* 25 % of all peatlands are used for agriculture, in Germany more than 80 %. Globally drained peatlands cover 0.4 % of land surface but produce 5 % of all anthropogenic greenhouse gas emissions.

Sphagnum farming aims to cultivate *Sphagnum* biomass on rewetted degraded bogs as a new agricultural crop. Sphagnum farming is paludiculture and contributes to the protection of bogs and their peat by conserving the peat body through rewetting and by offering a climate-friendly alternative to fossil peat in horticulture. Next to climate change mitigation, Sphagnum farming has benefits for nutrient retention and biodiversity conservation.

This thesis contributes to the development of Sphagnum farming by studying the conditions under which *Sphagnum* may reach maximal growth. Under (semi)controlled glasshouse conditions, we tested the effects of different water regimes and fertilisation levels on the productivity of various *Sphagnum* species. On a 1260 m² large irrigated field on cut-over bog in Lower Saxony (Germany) we studied length increase, biomass productivity and tissue nutrient content of *Sphagnum* over a period of 10 years. Finally, we reviewed all scientific literature and practical experiences with respect to Sphagnum farming worldwide as a first step towards a science-based implementation manual.

The main conclusions of our studies are:

1. It is possible to cultivate *Sphagnum* on rewetted cut-over bog and on rewetted former bog grassland.
2. The rapid establishment of a closed, highly productive *Sphagnum* lawn requires the deployment of a loose, >1(–5) cm thick *Sphagnum* layer (80–100 m³ of *Sphagnum* founder material per hectare) at the start of the growing season (when long frost periods are no longer probable) and adequate water supply.
3. Water table management must be very precise until a dense, well-growing *Sphagnum* lawn has established. For highest yields the water table should rise with *Sphagnum* growth and be kept a few centimetres below the *Sphagnum* capitula. Water supply via open irrigation ditches seems to function better than via subsurface irrigation pipes.
4. Fertilisation does not increase *Sphagnum* productivity on sites with high atmospheric nitrogen deposition and irrigation with phosphate-rich surface water from the agricultural surroundings. To avoid growth reduction a balanced stoichiometry is important.

5. From all studied species, *Sphagnum fallax* has the highest productivity. Its fast decomposition and low water holding capacity, however, may make this species less suitable for use in horticultural substrates.
6. Vascular plant cover on *Sphagnum* production fields can be kept low (<50 % cover) by regular mowing. Higher covers retard *Sphagnum* growth and reduce its quality for growing media.
7. Pathogenic fungi occurred far more in the glasshouse than in the field and have to be controlled for highest *Sphagnum* yields. We found *Sphagnum* vitality and growth rate to be stimulated by high water levels, where *Sphagnum* is less vulnerable to fungal or algal infection despite high nutrient loads.
8. The rate of *Sphagnum* biomass accumulation may remain constant over at least 4–5 years after establishing a *Sphagnum* production field with sufficient water supply. At dry conditions *Sphagnum* biomass accumulation is lower as a result of lower biomass productivity and higher decomposition rates.

Zusammenfassung

Die Gattung *Sphagnum* (L.) gehört zur Abteilung der Bryophyten und umfasst 150 bis 400 Arten. Wie alle Moose hat *Sphagnum* keine Wurzeln und kann seine Wasseraufnahme kaum regulieren. Solange genügend Wasser vorhanden ist, kann *Sphagnum* fast unbegrenzt wachsen, während die unteren, älteren Teile absterben und als Torf akkumulieren können. Einzelne *Sphagnum*-Arten sind in der Lage, ein Akrotelm als hydrologischen Selbstregulierungsmechanismus eines Hochmoores aufzubauen. Hochmoore werden nur durch Niederschläge gespeist. Da *Sphagnum* fast die Hälfte der Moore der Welt dominiert, ist es einer der weltweit wichtigsten Torfbildner.

Sphagnum-Biomasse ist ein wichtiger Rohstoff für viele wertvolle Produkte, aber in viel größerem Umfang wird *Sphagnum* in seinem fossilen Zustand verwendet - als *Sphagnum*-Torf. Mit einem Verbrauch von weltweit ca. 40 Mio. m^3 pro Jahr ist *Sphagnum*-Torf der dominierende Rohstoff für gärtnerische Kultursubstrate. Um *Sphagnum*-Biomasse zu erhalten, wird sie derzeit aus Wildbeständen gesammelt. Um *Sphagnum*-Torf zu erhalten, wird dieser in Hochmooren abgebaut.

Weitaus mehr Moore (einschließlich Hochmoore) werden seit Jahrhunderten für die land- und forstwirtschaftliche Nutzung entwässert mit negativen Folgen für ihre Ökosystemdienstleistungen, einschließlich der typischen Biodiversität, Kohlenstoffspeicherkapazität, Wasserregulierungsfunktion und ihrer Funktion als Paläo-Umweltarchiv. In Europa werden ca. 25 % aller Moore für die Landwirtschaft genutzt, in Deutschland über 80 %. Global bedecken entwässerte Moore 0,4 % der Landoberfläche, verursachen aber 5 % aller anthropogenen Treibhausgasemissionen.

Torfmooskultivierung (‚Sphagnum farming‘) zielt darauf ab, *Sphagnum*-Biomasse auf wiedervernässten, degradierten Hochmooren als neue Nutzpflanze anzubauen. Torfmooskultivierung ist Paludikultur und trägt zum Schutz von Mooren und deren Torf bei, indem sie den Torfkörper durch Wiedervernässung erhält und eine klimafreundliche Alternative zu fossilem Torf im Gartenbau bietet. Neben dem Klimaschutz hat Torfmooskultivierung auch Vorteile für den Nährstoffrückhalt und den Biodiversitätsschutz.

Diese Arbeit trägt zur Entwicklung von Torfmooskultivierung bei, indem die Bedingungen, unter denen *Sphagnum* ein maximales Wachstum erreichen kann, untersucht wurden. Unter (semi-)kontrollierten Gewächshausbedingungen haben wir die Auswirkungen verschiedener Wasserregime und

Düngestufen auf die Produktivität verschiedener *Sphagnum*-Arten getestet. Auf einer 1.260 m² großen, bewässerten Fläche in einem abgetorften Hochmoor in Niedersachsen (Deutschland) untersuchten wir über einen Zeitraum von 10 Jahren Längenzunahme, Biomasseproduktivität und Nährstoffgehalt der ausgebrachten Torfmoose. Schließlich haben wir weltweit die wissenschaftliche Literatur und praktischen Erfahrungen zu Torfmooskultivierung zusammengetragen und geprüft - als einen ersten Schritt hin zu einer wissensbasierten Anleitung zur praktischen Umsetzung von Torfmooskultivierung.

Die wichtigsten Schlussfolgerungen unserer Studien sind:

1. Es ist möglich, *Sphagnum* auf wiedervernässtem, abgetorften Hochmoor und auf wiedervernässtem, ehemaligen Hochmoorgrünland anzubauen.
2. Die schnelle Etablierung eines geschlossenen, hochproduktiven *Sphagnum*-Rasens erforderten die Ausbringung einer losen, >1(-5) cm dicken *Sphagnum*-Schicht (80-100 m³ *Sphagnum*-„Saatgut“ pro Hektar) zu Beginn der Vegetationsperiode (wenn lange Frostperioden nicht mehr wahrscheinlich sind) sowie eine ausreichende Wasserversorgung.
3. Das Wassermanagement muss sehr präzise sein, bis ein dichter, gut wachsender *Sphagnum*-Rasen etabliert ist. Für höchste Erträge sollte der Wasserspiegel mit dem *Sphagnum*-Wachstum ansteigen und einige Zentimeter unter den *Sphagnum*-Köpfchen (Capitula) gehalten werden. Die Wasserversorgung über offene Bewässerungsgräben scheint besser zu funktionieren als über unterirdische Bewässerungsrohre.
4. Düngung erhöht nicht die Produktivität von *Sphagnum* an Standorten mit hoher atmosphärischer Stickstoffdeposition und bei Bewässerung mit phosphatreichem Oberflächenwasser aus der landwirtschaftlichen Umgebung. Um Wachstumsreduktionen zu vermeiden, ist eine ausgewogene Stöchiometrie wichtig.
5. Von allen untersuchten Arten weist *Sphagnum fallax* die höchste Produktivität auf. Aufgrund der schnellen Zersetzung und der geringen Wasserspeicherkapazität könnte diese Art jedoch weniger für den Einsatz in Gartenbausubstraten geeignet sein.
6. Die Gefäßpflanzendeckung auf den *Sphagnum*-Produktionsfeldern kann durch regelmäßige Mahd niedrig gehalten werden (<50 % Deckung). Höhere Deckungen verringern das Torfmooswachstum und die Qualität für Kultursubstrate.
7. Pathogene Pilze traten im Gewächshaus weitaus häufiger auf als im Feld und müssen für höchste Erträge von *Sphagnum*-Biomasse kontrolliert werden. Wir haben festgestellt, dass die Vitalität und Wachstumsrate von *Sphagnum* durch hohe Wasserstände stimuliert wird, bei denen *Sphagnum* trotz hoher Nährstofffracht weniger anfällig für Pilz- oder Algeninfektionen ist.
8. Die Biomasseakkumulationsrate von *Sphagnum* kann über einen Zeitraum von mindestens 4–5 Jahren nach der Etablierung eines *Sphagnum*-Produktionsfeldes mit ausreichender Wasserversorgung konstant bleiben. Bei trockenen Bedingungen ist die Biomasseakkumulation von *Sphagnum* aufgrund der geringeren Biomasseproduktivität und der höheren Zersetzungsraten geringer.

Author's contributions to each chapter

The present dissertation consists of two published peer-reviewed papers (chapters 3 and 4) and one submitted scientific paper (chapter 2) preceded by a general introduction, an overview of the main results and a final discussion. My personal contribution to each of these components is as follows:

Chapter 1: **Introduction, methods, results, discussion, conclusions, outlook**. – I wrote this chapter completely by myself.

Chapter 2: ***Sphagnum* growth under N-saturation: interactive effects of water level and P or K fertilisation**. – I carried out the work in the glasshouse, interpreted the results and wrote the manuscript. The data analysis was conducted mainly by M. Krebs. The manuscript was revised by M. Krebs and H. Joosten.

Chapter 3: **Sphagnum farming on cut-over bog in NW Germany: Long-term studies on *Sphagnum* growth**. – M. Krebs and I jointly carried out the fieldwork under my leadership (during the last seven years of the experiment). M. Krebs and I analysed the data and I wrote the manuscript. It was revised by M. Krebs and H. Joosten.

Chapter 4: **Sphagnum farming from species selection to the production of growing media: a review** – All 34 authors (except L. Rochefort) participated in the 3rd International Sphagnum farming workshop in Germany (September 2017), mainly conceived, organised and moderated by me. Their contributions to the workshop provided the basis for this article. Authors from the Greifswald Mire Centre (GMC) wrote under my leadership the first draft, which was then iteratively revised by all authors.

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I confirm the author contribution statements.

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(date) Prof. Dr. Dr. h.c. Hans Joosten

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Introduction,

methods, results, discussion,

conclusions, outlook

Greta Gaudig

1.1 Introduction

1.1.1 *Sphagnum* – the plant

The genus *Sphagnum* (L.) is a phylogenetically isolated genus within the Bryophyte plant division (Michaelis 2011). *Sphagnum* is characterised by a unique combination of dimorphisms with respect to its branches (standing and hanging branches), leaves (stem and branch leaves), and cells within leaves (living chlorocytes and empty hyalocytes) (*ibid*.). Because of morphological plasticity and different species concepts the estimated number of *Sphagnum* species ranges between 150 and 450 (*ibid*.).

Sphagnum does not survive prolonged desiccation and without roots (as all mosses) it can hardly regulate its water uptake. Additionally, many species do not survive prolonged inundation. Next to precipitation also capillary transport from deeper layers provides water to the capitulum – the apical part of the mosses with highest photosynthesis activity and productivity. As long as water is available to keep the capitula moist, *Sphagnum* is able to grow nearly unlimited while the lower and older parts die off.

Sphagnum efficiently takes up even low concentrations of cations by direct exchange against hydrogen ions. This process acidifies the surrounding of *Sphagnum* and enhances its competitiveness in nutrient poor ecosystems (Clymo & Hayward 1982). As soon as more nutrients are available, more competitive species establish and may outcompete *Sphagnum* by light competition (Berendse *et al.* 2001).

Natural productivity of *Sphagnum* varies widely among species. Global average dry mass production is 260 g m^{-2} yr^{-1}, while the maximum value measured is 1450 g m^{-2} yr^{-1} (Gunnarsson 2005).

1.1.2 *Sphagnum* biomass

Sphagnum biomass is an important raw material for many valuable products. Dried it is used for orchid propagation, as growing medium for hanging baskets, vertical “living walls” or roof gardening, and for specialised products like biodegradable flowerpots. Living *Sphagnum* is used as ornamental moss (“floral moss”), for green sculptures and as ingredient in turf roofs, as packaging material (*e.g.* for fish and orchids), in terrariums as bedding for egg clutches, as moist hiding places or for hibernation and transport of amphibians, reptiles and spiders, and as founder material for peatland restoration (Glatzel & Rochefort 2017). *Sphagnum* biomass can also be used as material for bandages and sanitary items with high absorption properties, as insulating material in buildings such as log cabins, as absorbent material for decontamination of pollutants (*e.g.* oil, chemicals), for water filtering, and for pharmaceuticals or cosmetics (*e.g.* Wichmann *et al.* in press).

To acquire the biomass, *Sphagnum* mosses are collected from wild populations generally without management to maintain or increase yields (‘*Sphagnum* gathering’, **Chapter 4**). *Sphagnum* gathering takes place *e.g.* in Chile, New Zealand, Tasmania and recently also with increasing amounts in Finland. In 2013 Chile exported 5,200 tons *Sphagnum* biomass mainly to Taiwan. These amounts decreased to 3,750 tons in 2018, but with a constant value of approx. 15.3 million US$ (Instituto Forestal 2019).

For fast regrowth, it has been recommended to collect at most every fifth year only the uppermost parts of the mosses preferably manually and leave behind (or re-spread) 30 % of the actively growing *Sphagnum* (Buxton *et al.* 1996, Whinam *et al.* 2003, Zegers *et al.* 2006, Díaz *et al.* 2008, FIA 2009, Díaz & Silva 2012). Despite of regrowth, *Sphagnum* gathering in living peatlands is not climate-neutral because part of the collected *Sphagnum* would otherwise be permanently stored as peat and contribute to an effective carbon sink (Joosten 2017).

1.1.3 *Sphagnum* peatlands

Sphagnum has a high resistance to decay because of the phenolic metabolites it produces (Clymo & Hayward 1982). This, in combination with the permanent water-saturated conditions in which many *Sphagnum* species prefer to grow, allows biomass production to exceed decay and thus dead plant material to accumulate as peat. *Sphagnum* dominated peatlands span an area of 2 million km² (Laine *et al.* 2009), *i.e.* nearly half of the peatlands worldwide (*c.* 4.4 million km² = 3 % of the terrestrial surface, Yu *et al.* 2010).

Some *Sphagnum* species are "key species" for the creation and maintenance of raised bog (Joosten 1995 – a type of mire only fed by precipitation (Joosten *et al.* 2017). These typical bog species are able to build up an 'acrotelm' with special hydraulic properties, which facilitate constant water availability in a rainwater infiltration environment (Joosten 1993). Such acrotelm allows a peat dome to emerge far above the water level of the surrounding landscape (*ibid.*). The surprisingly wide climatic distribution of *Sphagnum* acrotelm bogs (from strongly oceanic to slightly continental and from subarctic to temperate) illustrates the effectiveness of this hydrological self-regulation mechanism (Joosten *et al.* 2017, Joosten & Couwenberg 2019).

1.1.4 *Sphagnum* peat

The properties described above have made *Sphagnum* to one of the most important peat formers globally (Clymo 1970) – faithful to its English name peat moss. Clymo & Hayward (1982) speculate that *Sphagnum* contains - with worldwide *c.* 300 Gt C - more carbon in its living and dead tissues than any other plant genus. The same properties have also made *Sphagnum* peat to the prevalent resource for a wide variety of applications.

Globally about 40 million m³ of *Sphagnum* peat are used annually in horticulture (Block *et al.* 2019). Decisive properties for that purpose are its structural stability, low bulk density, high porosity, and low pH, nutrient and nitrogen immobilisation levels, which allow easy adjustment to the requirements of individual crops. Small differences in these properties are caused by the degree of humification, which varies from not to moderately humified (H1–H5 after von Post 1924 = 'white peat') to strongly humified (H6–H10 = 'black peat') (Schmilewski 2008, 2019).

With a reported volume of 25.35 million m³ (15.50 million m³ for the professional and 9.85 million m³ for the hobby market) *Sphagnum* peat is the predominant raw material for horticultural growing media in the European Union (Schmilewski 2017). Professional substrates consist in the EU for 80 %, in Germany for 90 % and in the Baltic States for up to 96 % of peat (Schmilewski 2017). Germany and The Netherlands are with 6.8 and 2.9 million m³ yr^{-1}, respectively, the main users (and importers) of *Sphagnum* peat (Schmilewski 2017). *Sphagnum* peat is mainly extracted in the Baltic States, Germany, Ireland and in Canada (Salo 2019). In Germany, domestic peat extraction volumes are decreasing as a result of expiring permits and conservation constraints. Whereas in 2012 still 7.3 million m³ were extracted on 11,500 hectares, extracted volume and area are expected to decrease by 2040 to 0.73 million m³ from 840 hectares (Schmatzler 2012).

Slightly humified *Sphagnum* peat is furthermore in smaller volumes used as animal bedding material (*e.g.* litter in horse or poultry stables), filter and absorbent material, and insulation material (Joosten & Clarke 2002). Strongly humified *Sphagnum* peat is mainly used as a fuel – nowadays especially in Finland, Ireland, Sweden, and Belarus (Joosten & Tanneberger 2017).

1.1.5 Environmental consequences of peat extraction and drainage-based agriculture

Peat extraction and associated drainage have a severe negative impact on peatlands and the ecosystem services they provide, including their typical biodiversity, carbon storage capacity, water regulation function and palaeo-environmental archive. In Germany, living (peat accumulating) peatlands (= mires) are strictly protected and new peat extraction is only allowed on agriculturally used peatlands. However, also peat extraction from these degraded sites has negative environmental effects because of continued drainage and the fact that the extracted peat fully decomposes after a short period of use. As a result, peat extraction causes by far the highest greenhouse gas emissions per area in comparison to other land use categories on organic soils (Joosten *et al.* in prep). In Germany, peat extraction in 2016 caused emissions of 2.2 Mt CO_2 yr^{-1}, *i.e.* 5 % of the total CO_2 emissions from German peatlands (*ibid*., UBA 2018). If the extracted peat is burned for energy, CO_2 emissions are per unit produced energy higher than those of coal. And though peat extraction and use are only responsible for a small part of global greenhouse gas emissions, the peat industry – like every sector and every person – should address its responsibility to reduce its CO_2 emissions to zero until 2050 (cf. 'Paris Agreement', UN 2015, IPCC 2018).

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Next to peat extraction, *Sphagnum* peat deposits are threatened by continued drainage for agriculture. Drainage allows oxygen to enter the soil, microbial peat decomposition to accelerate, and substantial amounts of CO_2 (and N_2O) to be emitted to the atmosphere (as a rule of thumb: 5 t CO_2 per hectare more with every 10 cm deeper mean annual water level, *cf*. Jurasinski *et al.* 2016). Drainage also leads to the mobilisation and discharge of nutrients as well as to soil subsidence of 1–2 cm per year, which results in increasing drainage costs, higher flood risks and eventually a loss of cultivated land (GMC 2018). In Europe *c.* 25 % of all peatlands are in agricultural use (GPD 2019). In Germany, more than 80 % of all peatlands are in agricultural use (21 % arable land, 60 % grassland), which causes 37 % of all agricultural greenhouse gas emissions (GMC 2019, UBA 2019). Altogether, in Germany peatlands emit 47 million t CO_{2e} per year, corresponding to 5.4 % of total greenhouse gas emissions (*ibid*.), which makes Germany the second largest greenhouse gas emitter from peatlands in the European Union (Wetlands International 2015).

In a global context drained peatlands cover 0.4 % of the land but cause 5 % of global anthropogenic greenhouse gas emissions (Joosten *et al.* 2016). In terms of climate change, protection and rewetting of peatlands are of particular importance.

1.1.6 Peat and peatland conservation

Peat substitutes

Urged by decreasing domestic supplies and increasing climatic concerns, science and industry have since more than 30 years been looking for substitutes for peat in growing media. A variety of raw materials has been explored and implemented, most importantly compost, coir (coconut fibres), wood fibres and bark. Within the European Union 18.7 % of all reported constituents of growing media (6,467,000 m^3) are organic materials other than peat (Schmilewski 2017), but with major differences between the professional and the hobby market. So far, only limited volumes of environmentally friendly, qualitatively and economically competitive alternatives are available to replace peat in professional substrates (Schmilewski 2008) and consequently the share of other constituents than peat in professional substrates in Germany is only 10 %, against 47 % in the hobby market (BMEL 2019). However, the first step to reduce the demand for high-quality but fossil peat is to avoid its use for low quality applications like hobby gardening. Renewable peat substitutes may largely or completely replace the use of peat on the hobby and professional landscape gardening market (BMEL 2019).

The United Kingdom and Switzerland have already decided to reduce and eventually phase out the use of peat entirely (Secretary of State for Environment, Food and Rural Affairs 2011, Schweizerische Eidgenossenschaft 2012). In Germany, the federal government currently finances a research programme to reduce the use of peat substantially ("Torfminderungsstrategie") (BMEL 2019). A 'peat substitute forum' ("Torfersatzforum") was installed in 2015 in the federal state of Lower Saxony to advise the government on knowledge and implementation gaps to reach that aim.

The necessity to substitute fossil peat by environment-friendly substitutes of sufficient quality inspired Joosten (1998) to revive the centuries old idea of sustainable peat cultivation ("peat farming", *cf*. Schoockius 1658, Dau 1823) by stimulating *Sphagnum* growth and peat accumulation through active management.

Under natural conditions *Sphagnum* peat accumulation rates are among the highest in kettle-shaped basins (Wilcox & Simonin 1988, Couwenberg *et al.* 2001). Here peat accumulation takes place either downwards (top down) from a floating mat under stable water level conditions (terrestrialisation), or upwards (bottom up) when the water level progressively rises as humus colloids seal off the basin (self-sealing) (Gaudig *et al.* 2006). While average long-term peat (dry weight) accumulation rates in natural bogs amount to 30–60 g m^{-2} yr^{-1} (Turunen & Tolonen 1996), Joosten (1995) found rates of 100–500 g m^{-2} yr^{-1} in floating mats in peat pits after peat extraction, whereas Gaudig (2000) found rates of 75–190 g m^{-2} yr^{-1} in 'self-sealing' kettle hole mires. These observations supported the idea that high and stable water levels, as are realized either by floating mats or under conditions of a progressive rise of the water level, may to be a viable option for maximising *Sphagnum* (peat) yields (Joosten 1998, Joosten & Timmermann 1999, Gaudig *et al.* 2006).

Peat accumulates when biomass production exceeds its decomposition. In the long run, however, more and more of the primary production material gets lost by decomposition (Clymo 1984, Gaudig 2001). To achieve maximum yields, one should harvest the newly grown peat as early as possible, which led to the idea to use fresh *Sphagnum* biomass instead of young peat (Gaudig 2001). Numerous experiments have since proven that *Sphagnum* biomass has similar properties to slightly humified *Sphagnum* peat ('white peat') and is suitable for producing high-quality horticultural growing media (*e.g.* Grantzau 2002, 2004, Emmel 2008, Oberpaur *et al.* 2010, Reinikainen *et al.* 2012, Blievernicht *et al.* 2013, Jobin *et al.* 2014). This changed the focus on the cultivation of *Sphagnum* ('Sphagnum farming') instead of 'peat farming'.

Sustainable bog use

Major parts of European bogs are drained and used for agriculture and forestry with numerous negative effects (see above). The only way to protect their peat body (and carbon storage capacity) is to rewet them.

Rewetting without continued production is the first step in bog restoration - aiming at stimulation of bog regeneration, the process of renewed development towards a living (peat accumulating) bog (Joosten 1992). Bog restoration - albeit mainly of cut-over bogs, only previously used for agriculture - has achieved only limited success (Rosinski 2012), because suboptimal hydrological and hydrochemical conditions as well as the lack of diaspores often hamper the re-establishment of key *Sphagnum* species (Joosten 1998).

In order to preserve the production function at the same time as rewetting, the concept of paludiculture was developed, and elaborated for bogs by the University of Greifswald. Paludiculture is defined as the productive use of wet peatlands in a way that stops subsidence and minimises emissions (Wichtmann *et al.* 2016). Appropriate paludiculture crops are wetland plants with (new) production and utilisation options (*cf*. Abel *et al.* 2013). Plants that can be cultivated in bogs – mainly fed by rain – are *e.g.* sundew, *Ericaceae* shrubs or peatmosses (*Sphagnum*). In this thesis we describe studies into the cultivation of peatmosses ('Sphagnum farming').

1.2 Aims of the thesis

Sphagnum farming aims at cultivating *Sphagnum* biomass, originally as a founder material for bog restoration in nature conservation (Money 1994), but nowadays increasingly as an agricultural crop. This new type of wet peatland agriculture comes with many questions, several of which are addressed in this thesis.

Indeed, *Sphagnum* is a very well-studied species but most studies focus on natural mires. Furthermore, many publications deal with the restoration of *Sphagnum* vegetation cover on degraded bogs (especially after peat extraction), however without the intention to harvest the re-established *Sphagnum* vegetation. In contrast, Sphagnum farming aims to maximise yields for later harvest of the biomass. This dissertation reports on studies into the effect of different water regimes and levels of nutrient supply (especially of the macro elements nitrogen, phosphorus and potassium) on the establishment and growth of different *Sphagnum* species in a glasshouse experiment (**Chapter 2**). Because promising sites for Sphagnum farming in Western-Europe often are situated in regions with high atmospheric nitrogen deposition, the experiment was carried out under nutrient rich conditions. In parallel, Sphagnum farming was studied on a rewetted cut-over bog in a long-term (10 years) pilot study (**Chapter 3**). Next to cut-over bogs also rewetted bog grasslands and floating mats on acidic water bodies seem appropriate for Sphagnum farming (Gaudig *et al.* 2014, Wichmann *et al.* 2017).

Since the first efforts to cultivate *Sphagnum* as a peat substitute in growing media (Gaudig & Joosten 2002) and first field trials in Germany and Canada from 2004 onwards, much progress has been made. Recent results and experiences in *Sphagnum* vegetation restoration, *Sphagnum* gathering and Sphagnum farming from all over the world were discussed in a workshop and summarised in a review paper (**Chapter 4**) as a first step towards a science-based Sphagnum farming manual. The review covers the entire production cycle and deals with topics like the selection of highly productive *Sphagnum* species, active management to maximise yields, and the production of growing media from *Sphagnum* biomass.

Sphagnum farming is a new agricultural activity and still in its infancy. This thesis underlines the necessity of Sphagnum farming and discusses opportunities, challenges and remaining research questions of large-scale commercial implementation (**Chapters 1 and 4**).

1.3 Methods

We tested *Sphagnum* growth under different site conditions in a glasshouse and in the field. Under (semi)controlled conditions in the glasshouse, pure patches of four *Sphagnum* species, collected from natural lawns (10 cm deep), were cultivated in plant containers (12×12 cm) with perforated bottom and placed in boxes filled with a culture medium (**Chapter 2**). Three water regimes (rising, fluctuating, static) and three fertilisation levels (control, fivefold deposition of phosphorus and a double deposition of both phosphorus and potassium, using atmospheric deposition levels (also for nitrogen) of Northwest Germany) were applied in combination. To measure *Sphagnum* growth five moss shoots per container were marked with nylon zip ties fixed between the capitulum and the subjacent branches at the beginning of the experiment and cut at the level of the zip ties at the end of the experiment (day 280). Length increase was measured and the biomass (above zip tie) gain of each marked moss shoot and each container were determined after drying. Annual dry mass productivity was calculated by extrapolating the subcapitulum weight of each entire container to hectare and year. Additionally, weight per length unit was calculated for each marked moss shoot to characterize compactness. Nutrient concentrations (carbon, nitrogen, phosphorous and potassium) were determined in the dry mass of all capitula per container and in the culture medium at the end of the experiment.

The field experiment on a cut-over bog was established in Lower Saxony (Germany) at Ramsloh (1260 m², 53° 4.31′ N, 07° 38.90′ E) in November 2004 (**Chapter 3**). To characterise the study site, we determined the thickness of residual peat layer and the degree of humification, bulk density, pH, and carbon, nitrogen and phosphorous concentration in the surface peat. After site preparation *Sphagnum* fragments were spread manually on the even, bare black peat surface and covered with straw mulch after which the site was rewetted. Water levels were kept close below the peatmoss surface by subsurface irrigation pipes connected with a perimeter ditch and an active water table regulation. The phreatic water level was measured regularly and adjusted when necessary. Cover and abundance of vascular plant and moss species, *Sphagnum* lawn thickness and yearly species biomass growth were determined in randomly distributed permanent plots (25×25 cm). The irrigation water was analysed on pH, EC, phosphorus, potassium, calcium, sodium, ammonium, and nitrate concentration, the moss capitula biomass on carbon, nitrogen, phosphorus and potassium content. To control the growth of vascular plants, the site was mowed 1–3 times per growing season with a handheld petrol strimmer.

Statistical analysis, including data exploration, computation and figure design were carried out using R software (R Development Core Team 2009) and the packages nlme (Pinheiro *et al.* 2009), mgcv (Wood 2006) and stats (R Development Core Team 2009). In the glasshouse experiment (**Chapter 2**) effects of the treatments (including possible interactions) were analysed with linear mixed effect models to accommodate for induced correlation structures. The correlation between *Sphagnum* dry mass productivity and N/P quotient was analysed with a generalized additive model with integrated smoothness estimation. To identify the effect of site variables on *Sphagnum* establishment and *Sphagnum* biomass productivity in the field experiment (**Chapter 3**) boosted regression trees were applied. In all experiments strength and direction of association between *Sphagnum* growth (*e.g.* dry mass productivity or lawn thickness) and other parameters were tested with Spearman rank-order correlation or Pearson product-moment correlation ('standard' correlation). Due to different sample sizes, differences between treatments were tested with the non-parametric Kruskal Wallis test and a multiple comparison test after Siegel & Castellan (1988) using R package pgirmess (Giraudoux 2010).

For a comprehensive overview of the state-of-the-art of Sphagnum farming in praxis we reviewed the literature and summarised the results of an international workshop held in 2017 (**Chapter 4**).

1.4 Results

1.4.1 Site conditions

Water table: In the glasshouse we tested water regimes with very precisely regulated water levels (from constant 2 cm below the top of the capitula to max. 9 cm below) (**Chapter 2**), whereas the water table in the field fluctuated over the 10 years of study between 4 cm and 40.5 cm below the peatmoss surface (**Chapter 3**).

Water quality: Water quality of the irrigation water in the field and the culture medium in the glasshouse was similar to that of pore water in natural bogs (Lütt 1992), except for nitrogen which had 15-fold (field) or 8-fold (glasshouse) higher concentrations than in natural habitats (**Chapters 2 and 3**). Nitrogen was applied by fertilisation (38 kg ha^{-1} yr^{-1}, **Chapter 2**) or by atmospheric deposition (ca. 21 kg ha^{-1} yr^{-1}, **Chapter 3**).

1.4.2 *Sphagnum* establishment

While in the glasshouse experiment peatmosses started in their natural lawn structure (**Chapter 2**), spreaded fragments in the field experiment first had to establish a new lawn (**Chapter 3**). After 3.75 years (45 months) the average cover of green, vital *Sphagnum* in the field was 91 %. *Sphagnum* established better where a) the cover of litter/straw (32 months after installation) was less than 20 %, b) the initial peatmoss layer was more than 1 cm thick and c) the peat surface was low (shallow depressions). The distance to the nearest irrigation pipe was less important, with the highest *Sphagnum* cover occurring at a distance of 1 m from the pipe. Initial straw thickness and cover had only little effects on *Sphagnum* establishment.

1.4.3 Nutrient concentration in *Sphagnum* capitula

In the field experiment the range of nitrogen concentrations in the peatmoss capitula was 7.9–15.8 (mean 12.2) mg g^{-1} DW, of P 0.3–1.2 (mean 0.5) mg g^{-1} DW, and of K 2.0–10.1 (mean 3.5) mg g^{-1} DW (**Chapter 3**). In the glasshouse experiment nutrient concentrations in the peatmoss capitula were higher as a result of higher nutrient supply: N 9.4–26.2 (mean 14.4) mg g^{-1} DW, P 0.63–2.36 (mean 1.3) mg g^{-1} DW, and K 2.9–11.9 (mean 6.0) mg g^{-1} DW (**Chapter 2**).

1.4.4 *Sphagnum* growth

The thickness of the *Sphagnum* lawn in the field increased from 2004 to 2014 continuously on average to 19 cm, with a stagnation period (in thickness increase) between October 2010 and October 2012 (**Chapter 3**). For the stagnation period we determined a mean length growth for *Sphagnum papillosum* of 5 cm (2.5 cm yr^{-1}). From 2008 to 2012, length growth was 13.5 cm (3.4 cm yr^{-1}) whereas lawn thickness increased by 5.5 cm. In the glasshouse experiment length increase of *S. papillosum* was with 0.4–22 (mean 8.8) cm yr^{-1} larger than in the field but smaller in comparison to the other three tested species (**Chapter 2**). Differences in length increase were significant, with *S. fallax* having the fastest length growth (max. 48 cm yr^{-1}).

After nine years *Sphagnum papillosum* dry mass was on average 19.5 t per hectare (1950 g m^{-2}), corresponding to a dry mass productivity of 2.2 t ha^{-1} yr^{-1} (**Chapter 3**). During the establishment phase (first three years) dry mass accumulation was with 1 t ha^{-1} yr^{-1} lower than during the following four years (mean value 3.7 t ha^{-1} yr^{-1}). Annual *Sphagnum* dry mass productivity in years six and seven after installation reached 6.9 t ha^{-1}. In the glasshouse *S. papillosum* produced with 0.7–7 (mean 4.5) t ha^{-1} yr^{-1} as much dry mass as in the field but significantly less compared to the other three tested species

(**Chapter 2**). *S. fallax* produced most dry mass (2.7–10.8, mean 6.4 t ha^{-1} yr^{-1}) but grew significantly less compact than *S. papillosum* and *S. palustre*. In the field we determined eight years after installation 30 % less biomass for the first seven years than one year before, indicating considerable loss (**Chapter 3**).

Generally, *Sphagnum* grew best under wet conditions (**Chapters 2 and 3**). In the field the distance to the irrigation system and peat surface height, as indicators for water supply, clearly determined the growth of *S. papillosum* (**Chapter 3**): The closer to the irrigation system (ditch or pipe), the thicker the peatmoss lawns. Also dry mass productivity was higher close to the irrigation ditch, but irrigation pipes had no influence on productivity. The higher the peat surface (thus the deeper the water table), the lower *Sphagnum* lawn thickness and dry mass productivity. In the glasshouse, length increase and dry mass productivity of all *Sphagnum* species were highest with the water table staying constantly 2 cm below capitula (*i.e.* rising with moss growth) (**Chapter 2**). Moss growth decreased with lower water tables, even if lowering was only periodically and concerned a few centimetres. The latter conditions also led to a more compact growth.

Sphagnum dry mass productivity decreased with increasing N-concentration in the capitulum (**Chapters 2 and 3**), with a rapid decline at capitula N concentrations > 12 mg g^{-1} DW in the field. Similarly, dry mass productivity decreased with increasing N/P quotients with highest N/P quotients reached in the field (max. 53). In the field P concentrations in the surface peat of > 1.6 mg g^{-1} DW and surface peat pH values of > 3.29 led to decreased *Sphagnum* dry mass productivity (**Chapter 3**). N/K quotients in the *Sphagnum* capitula ranged between 1.1 and 5.3 in the glasshouse, and between 1.2 and 6.9 in the field, but had no relation to dry mass productivity (**Chapters 2 and 3**). Fertilisation influenced neither N, P and K concentrations in the capitula nor growth, compactness and occurrence of necrosis and algae (**Chapter 2**).

1.4.5 *Sphagnum* growth restraints: vascular plants, necrosis and algae

While in the glasshouse experiment single vascular plants were removed manually immediately after their germination such procedure was not possible in the 1260 m² large field experiment. As a result, vascular plant cover reached 50 % in the summer of 2007 (**Chapter 3**), but declined in the long term as a result of regular mowing. *Juncus effusus* had disappeared already 5.5 years after installation.

Seasonally we observed single small plots with necrosis in the field (probably due to fungal infection), but with negligible effects. In contrast, both necrosis and algae in 38 % of the containers in the glasshouse (**Chapter 2**) led to dry mass productivity decreasing with increasing percentage of necrosis or algae, particularly at ‘rising’ water table. At these higher water tables necrosis and algae were, however, less than in the other water regimes, where a clear relation with productivity could not be found.

1.5 Discussion

The following discussion is structured along the implementation steps of Sphagnum farming (setting up, management, harvest, *cf*. **Chapter 4**) and integrates the results of our own studies (**Chapters 2 and 3**).

1.5.1 Setting up a Sphagnum farming site

Site selection

Chapter 3 demonstrates the feasibility of Sphagnum farming on low-permeable 'black peat' in a bog after milled peat extraction. Experiences with Sphagnum farming have also been gained on bogs after block-cut peat extraction, on former bog grassland, on artificial floating mats and in rice paddy fields (**Chapter 4**). For successful soil-based Sphagnum farming, climatic conditions (precipitation, temperature), characteristics of the residual peat layer (chemistry, hydraulic conductivity) and the availability and quality of water are of major importance. In our field experiment (**Chapter 3**) main reasons for successful *Sphagnum* growth were the 844 mm mean annual precipitation supplemented by extra water supply via irrigation system and an outflow to avoid flooding in wet periods. Also the low nutrient input (except nitrogen) was beneficial, whereas the strong humification of the surficial peat might have been unfavourable for *Sphagnum* establishment (hydraulic conductivity not determined).

Surface levelling

Site preparation must create an even, horizontal surface to ensure optimal water levels over the entire *Sphagnum* production field after rewetting. In our field experiment surface was levelled with an excavator (**Chapter 3**), but large extracted areas can also be prepared by tracked vehicles equipped with grading blades (**Chapter 4**). The costs of surface levelling of a cut-over bog are much lower than of a former bog grassland, especially when the degraded top soil of the bog grassland has to be removed (**Chapter 4**, Wichmann *et al.* 2017).

Infrastructure for water management

Effective Sphagnum farming requires water tables to be permanently close below the moss surface, which has to be enabled by infrastructure for both irrigation (to avoid droughts) and drainage (to avoid prolonged flooding and washing away of moss fragments). In the field experiment, we used a windmill to pump groundwater into the ditch and a bended pipe as an adjustable outflow (**Chapter 3**). Other sources of irrigation water may include streams, ditches, wells, ponds or artificial water reservoirs (**Chapter 4**). For pumping irrigation water, electric pumps have the advantage that they can be switched on and off at preset minimum and maximum water levels, monitored by sensors in the irrigation ditches. Power for the electric pumps can be provided by the electricity net, wind turbines or solar panels. Wind pumps are comparatively cheap, but risky in periods with little wind and high evapotranspiration.

Small ditches, subsurface pipes, drip systems or sprinklers (for filtered water) can be used for transporting the irrigation water from the pump to the *Sphagnum* production fields (**Chapter 4**). The maximum distances between the irrigation elements depend on the hydraulic conductivity of the upper peat layer, *e.g.* 5 m in strongly humified ('black') (**Chapter 3**) or 10–20 m in slightly humified ('white') peat (Gaudig *et al.* 2014). Observations in our field experiment indicate that ditches have a farther-reaching influence than irrigation pipes because they are larger water reservoirs with a greater area of contact with peat than irrigation pipes (**Chapter 3**). As ditches are easier to install and manage, they seem to be more suitable than pipes for irrigating Sphagnum farming sites.

Introduction of Sphagnum

Rapid and successful establishment of a closed *Sphagnum* lawn is the key in Sphagnum farming. To accelerate *Sphagnum* establishment founder material must be applied on the bare peat surface. In our field experiment the founder material was chopped into fragments (0.5–2 cm), since *Sphagnum* may regenerate from the smallest plant parts (Clymo & Duckett 1986). Gaudig *et al.* (2014) found, however, lawn thickness and cover to increase faster if large (5–10 cm) rather than small (0.1–0.3 cm) fragments were used. Especially, application of a loose >1(–5) cm thick layer with a high cover encourages the establishment of *Sphagnum* (**Chapter 3**, Campeau & Rochefort 1996, Quinty & Rochefort 2003). Such layer corresponds to 80–100 m³ vegetative *Sphagnum* founder material per hectare (**Chapter 4**). Our field experiment showed that *Sphagnum* fragments should best be applied at the start of the growing season (when long frost periods are no longer probable), provided that sufficient water is available (**Chapter 3**). When optimal water tables cannot be ensured, it might be better to bring out a mixture of *Sphagnum* species with different water table demands (**Chapter 4**).

Of the four *Sphagnum* species studied in the glasshouse experiment (*S. palustre*, *S. papillosum*, *S. fimbriatum*, *S. fallax*), *S. fallax* had the highest productivity, which corresponds to results from a global meta-analysis (Gunnarsson 2005). On the other hand, *S. fallax* decomposes faster than *S. papillosum* and has a lower water holding capacity, which might make the species less suitable for use in horticultural substrates, at least for various applications (**Chapter 2**). In our field experiment we tested only *S. papillosum* (**Chapter 3**). More research into the selection of highly productive (and slowly decomposing) *Sphagnum* taxa is needed.

Protective cover

Quinty & Rochefort (2003) recommend to cover the *Sphagnum* fragments with loose straw mulch (minimum 3,000 kg ha^{-1}) to improve microclimate (higher relative humidity, more stable temperatures, less exposure to intense radiation and wind). We applied more than twice this recommended minimum amount in our field experiment, which appeared to impede *Sphagnum* establishment when straw thickness (eight months after installation) exceeded 3 cm, probably because the fragments received insufficient light (**Chapter 3**). *Sphagnum* fragments covered with geotextile (50 % shade) grew much slower compared to cover with straw, probably because the water-saturated geotextile led to anaerobic conditions (Graf *et al.* 2017). If sufficient water supply can be ensured, covering *Sphagnum* fragments to improve microclimate might be redundant (**Chapter 4**).

1.5.2 Managing a Sphagnum farming site

Water table management

Water table management must be very precise in the establishment phase, because *Sphagnum* fragments lying on bare peat surface are sensitive to desiccation (more vulnerable to water losses than a dense *Sphagnum* lawn) and inundation (washing away) (**Chapter 4**). Our field experiment irrigation system (ditch and pipes) worked well during the establishment phase but the wind pump failed to maintain constantly high water tables. Water tables fluctuated, with lowest values (up to 36.5 cm below peat surface, equivalent to 40.5 cm below peatmoss surface) being observed at the driest times of the years (**Chapter 3**). However, after 3.75 years (45 months) a well-growing closed *Sphagnum* lawn had established and growth became better at sites where the water table was closer to the peat surface.

During the production phase constantly high water tables, *i.e.* rising with the growing moss, should be maintained since all four tested *Sphagnum* species show highest growth rates at this water regime (**Chapter 2**). As soon as the relative water table sinks only a few centimetres, *Sphagnum* growth was significantly hampered. This happened with a 'static' water level (*i.e.* relatively sinking compared to the up-growing moss) more than with a 'fluctuating' water level, probably because the former caused a decreased water availability in the capitula leading to less CO_2 assimilation (*cf*. Robroek *et al.* 2009). A high water table does not only lead to an optimal water supply, but also to a better nutrient supply of the capitulum (*cf*. Clymo & Hayward 1982), to a higher vitality (indicated by less necrosis and algae infestation) and to a looser growth form allowing light to penetrate deeper into the *Sphagnum* lawn resulting in an increased active assimilation area (Sliva 1997, *cf*. Robroek *et al.* 2009).

The water supply was not quantified in our field experiment (**Chapter 3**), but was estimated in other studies. Annually required irrigation volumes at another Sphagnum farming site in NW-Germany amounted to, on average, 1600 m³ per hectare of *Sphagnum* production field (160 mm) (Brust *et al.* 2018). Brown (2017) estimated substantially lower irrigation demands (74–130 mm) for a Sphagnum farming site in Canada, which had, however, much smaller evapotranspiration and seepage losses (**Chapter 4**). Water losses can be reduced by several measures (see **Chapter 4**).

Water quality

Nutrients are supplied to the up-growing *Sphagnum* by atmospheric deposition, by release from the (mineralized and formerly fertilized) peat soil, and by irrigation water. Irrigation water can originate *e.g.* from natural peatland lakes, artificial (rain) water reservoirs, drainage ditches from peat extraction fields, drainage ditches from the agricultural surroundings, or from groundwater (**Chapter 4**).

In our experiments nitrogen input was very high, simulating the loads in NW-Germany. In comparison to pore water in natural bogs nitrogen concentrations in the irrigation water were 8-fold in the culture medium in the glasshouse and 15-fold in the field (**Chapters 1–3**). In addition, nitrogen was applied by fertilisation in the glasshouse (38 kg ha^{-1} yr^{-1}, **Chapter 2**) and by atmospheric deposition in the field (ca. 21 kg ha^{-1} yr^{-1}, **Chapter 3**). *Sphagnum* growth, therefore, was not N limited. Resulting N tissue concentrations of up to 15.8 (field) and 26.2 mg g^{-1} DW (glasshouse) led to growth reduction only for *S. papillosum*, but at different levels (> 12 mg g^{-1} DW in the field, > 20 mg g^{-1} DW in the glasshouse) possibly because of different durations of the experiments and different conditions. For the other species high N tissue concentration (up to 22.8 mg g^{-1} DW in *S. fimbriatum*) had no effect on growth (**Chapter 2**, *cf*. Limpens & Berendse 2003).

The negative effect of N can be reduced by high availability of P and K and optimisation of other growth factors (*e.g.* light and moisture levels) so that N-accumulation to toxic levels is prevented by dilution through increased biomass growth (**Chapter 4**). While in the field experiment P-limitation cannot be excluded (**Chapter 3**), tissue N/P quotients and the failing correlation between tissue P concentrations, fertilisation and *Sphagnum* growth indicate the absence of P-limitation in the glasshouse experiment (**Chapter 2**). In both experiments K was not limiting. In the glasshouse *Sphagnum* dry mass productivity significantly decreased with increasing N/P quotient (**Chapter 2**). Because neither P nor N limitation is plausible we assume for the N/P quotients (and similar for the N/K quotients) that conclusions from studies of natural systems cannot be simply transferred to systems with high nutrient loads and high nutrient concentrations in the moss tissue. However, our results confirm that *Sphagnum* species grow optimally when their species-specific nutrient stoichiometry is balanced, *i.e.* without under- or oversupply of any nutrient (**Chapter 4**, *e.g.* Temmink *et al.* 2017), as long as an optimal water supply is guaranteed (**Chapter 2**).

The quality of the irrigation water is determined by its origin. Drainage water from agriculturally used surroundings may have high loads of nitrogen (N), phosphorus (P), and potassium (K) (Temmink *et al.*

2017). This may cause a shift in *Sphagnum* species composition at the expense of less competitive, but for a specific application more favoured *Sphagnum* species (*ibid.*) as different *Sphagnum* species have different growth responses to nutrient supply, pH, and bicarbonate concentration in the water that surrounds the mosses (Hájek *et al.* 2006). Most *Sphagnum* species are sensitive to high concentrations of calcium (Ca) and bicarbonate (HCO^{3-}) (**Chapter 4**). However, in our experiments Ca concentrations were very low, similar to pore water in natural bogs. Various measures to avoid solute concentrations that would be damaging for *Sphagnum* are described in **Chapter 4**.

Management of vascular plant growth

The presence of vascular plants and brown mosses is almost inevitable because their diaspores are continuously introduced from the surroundings or were already present in the founder material. Vascular plants may facilitate, but - when they dominate - may also retard *Sphagnum* growth (**Chapter 4**). Furthermore, the quantity of vascular plant biomass and seeds in the produced *Sphagnum* biomass has to be minimised for its usage as a raw material for growing media. Therefore, vascular plant cover on *Sphagnum* production fields should be kept at a low level (<50 % cover), *e.g.* by regular mowing. Vascular plant cover was kept below 20–30 % in our field experiment and did not affect *Sphagnum* growth (**Chapter 3**). While high-growing plants (*e.g. Juncus effusus*) were effectively suppressed, *Erica tetralix* became the most frequent species because this low-growing plant could not be effectively mowed without damaging the mosses. The competitive pressure of vascular plants normally decreases once a closed *Sphagnum* lawn has established and seeds can no longer germinate (**Chapter 3**).

Next to a strimmer also a single-axle mower equipped with cutter bar and triple tyres, a mowing robot and an excavator with an elongated arm with mowing bucket were already tested for mowing (**Chapter 4**). Only the excavator could mow from the causeway without causing compaction by driving on the *Sphagnum* production fields and could remove the mown material so that a mulch layer - which may hamper moss growth by shading - did not develop.

Control of fungal pests

Fungi are common in *Sphagnum* mires and peatlands (Thormann 2011, Kostka *et al.* 2016). Mosses grow together with many fungal species, some of them growth stimulating, others growth retarding. Necrotic diseases of peatmosses are often caused by pathogenic fungi. Although no molecular identification of the fungal mycelium was conducted in our glasshouse experiment, the typical pattern of damage and sporocarps indicated the occurrence of *Sphagnurus paluster* (**Chapter 2**). We found a negative effect of infection on dry mass production of *Sphagnum* and less necrosis at higher water levels, but no relationship between necrosis or algae occurrence and fertilisation or N/P quotient. Our results indicate that *Sphagnum* vitality and growth rate are stimulated by high water levels, where they are less vulnerable to fungal or algal infection despite high nutrient loads.

While fungal pest in our field experiment were negligible (**Chapter 3**), parasitic or pathogenic fungal species of the genera *Galerina* and *Sphagnurus* have been identified at the Sphagnum farming site on former bog grassland (**Chapter 4**). Since Sphagnum farming sites on rewetted bogs are artificial systems, the risk potential for diseases by fungi and algae has to be assessed. Effective measures for limiting *Sphagnurus paluster* without affecting *Sphagnum* are the fungicide Myclobutanil (Landry *et al.* 2011) or *Trichoderma virens* as an antagonist (Irrgang *et al.* 2012), which were only tested and might only be applicable in the glasshouse.

1.5.3 Harvest

Dry mass productivity of *Sphagnum* in Sphagnum farming sites in Germany mainly ranges between 3 and 6 t ha^{-1} yr^{-1} (Gaudig *et al.* 2014) with higher rates for *Sphagnum papillosum* than on natural bogs and on Sphagnum farming sites in Canada (**Chapter 3**). However, decomposition of *Sphagnum* biomass is a continual process and, in a typical peatland environment, only 85 % of the primary production is preserved after one year (Lütt 1992). Nonetheless, the rate of *Sphagnum* biomass accumulation may remain constant over some (at least 4–5) years in an established *Sphagnum* production field with sufficient water supply. At dry conditions *Sphagnum* biomass accumulation is lower as a result of lower biomass productivity and higher decomposition rates (**Chapter 3**). At the latest when annual decomposition of the accumulated biomass starts to approach annual biomass production, it is time to harvest. The choice of harvesting time needs to balance the accumulation rate with several other factors (**Chapter 3**). A harvesting frequency of once every 3–5 years seems to be feasible (Gaudig *et al.* 2014, Krebs *et al.* 2018).

To harvest a Sphagnum farming site an excavator with long arm and mowing bucket has already been successfully tested (**Chapter 4**). Other machines are used for *Sphagnum* gathering in Finland and USA. So far, no *Sphagnum* harvesting machinery is available that operates directly on (unfrozen) very wet *Sphagnum* production fields without damaging them. There is a need for further development of devices to cut, collect and transport the wet moss biomass.

1.6 Conclusions, recommendations, outlook

Sphagnum farming contributes to the protection of bogs in two ways: it leads to the conservation of the peat body by rewetting degraded bogs and it offers a climate friendly renewable alternative to the fossil peat, which is currently extracted in bogs and used for growing media.

The suitability of *Sphagnum* biomass as a raw material for horticultural growing media has been proven many times and for numerous cultivated plants (see **Chapters 1 and 4**). In addition, benefits for climate change mitigation (Beyer & Höper 2015, Günther *et al.* 2017), nutrient retention (Temmink *et al.* 2017), and biodiversity (Muster *et al.* 2015, Gaudig & Krebs 2016) have been quantified (for Germany). Improved management and harvest techniques may further enhance these benefits.

Economic studies of setting up Sphagnum farming sites in Germany (on cut-over bog and on former bog grassland) arrive at high investment costs, especially attributable to the costs of founder material, but with large potential for reduction (Wichmann *et al.* 2017). The economics of the entire production cycle on the farm level shows that in the current situation the production costs of *Sphagnum* biomass cultivated on former bog grassland are (much) higher than the current market prices of ‘white peat’. However, an end consumers’ willingness-to-pay a top up of 10 % for plants cultivated in peat free growing media would lead to cost-covering prices for *Sphagnum* biomass (Wichmann *et al.* in press).

In Germany, Sphagnum farming is currently operational on 14 ha former bog grassland (= 5.6 ha netto *Sphagnum* production field). Furthermore, smaller scaled experiences exist on cut-over bog (**Chapter 3**, Graf *et al.* 2017) and artificial floating mats (Gaudig *et al.* 2014, Wichmann *et al.* 2017). Assuming that a) *Sphagnum* biomass with a bulk density of 30 g L^{-1} can replace ‘white peat’ at a volume ratio of 1:1, and that b) an average *Sphagnum* dry mass productivity is achieved of 3.25 t ha^{-1} yr^{-1}, a net moss production area comprising *c*. 35,000 ha could produce sufficient *Sphagnum* biomass to completely replace the ‘white peat’ demands of the German growing media industry (*c*. 3.5 million m^3 per year) (Wichmann *et al.* 2017). This area corresponds to approximately 40 % of the current bog grassland area in NW-Germany.

To achieve the goals of the Paris Agreement (UN 2015) all mires have to be kept wet and all drained peatlands have to be rewetted to the surface (“Moor muss nass!”), the sooner the better. A pathway scenario for Germany (with 1.8 million hectare organic soils) postulates a replacement of all peat by renewable alternatives and a complete fade out of peat extraction and consumption as well as a stop of all cropland use on organic soils by 2030 (Joosten *et al.* in prep.). Water levels have to be progressively raised also in grassland and forested areas (*ibid*.). Sphagnum farming can provide both, a renewable peat alternative in horticulture and a wet peatland use option.

For the large-scale implementation of Sphagnum farming more research is needed to reach technological maturity and to reduce costs, *e.g.* research into highly productive *Sphagnum* taxa, production of founder material, optimisation of site conditions, production and processing, development of machinery, and implementation in growing media (**Chapter 4**). Also the (farmers’) interest in Sphagnum farming has to be increased, through education and knowledge transfer, but also by adaptating the policy frameworks. First of all, the new European Union’s Common Agriculture Policy (CAP) should include the phasing-out of CAP funding for drainage-based peatland utilisation and should establish eligibility of paludicultures for 1st and 2nd CAP pillar payments as well as for the remuneration of ecosystem services like for reducing greenhouse gas emissions (GMC 2018).

Sphagnum farming offers the opportunity to contribute to tackling pressing societal challenges. We should seize this opportunity and join forces (research, industry, policy) to intensify efforts to upscale Sphagnum farming.

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2

Sphagnum growth under N-saturation: interactive effects of water level and P or K fertilisation

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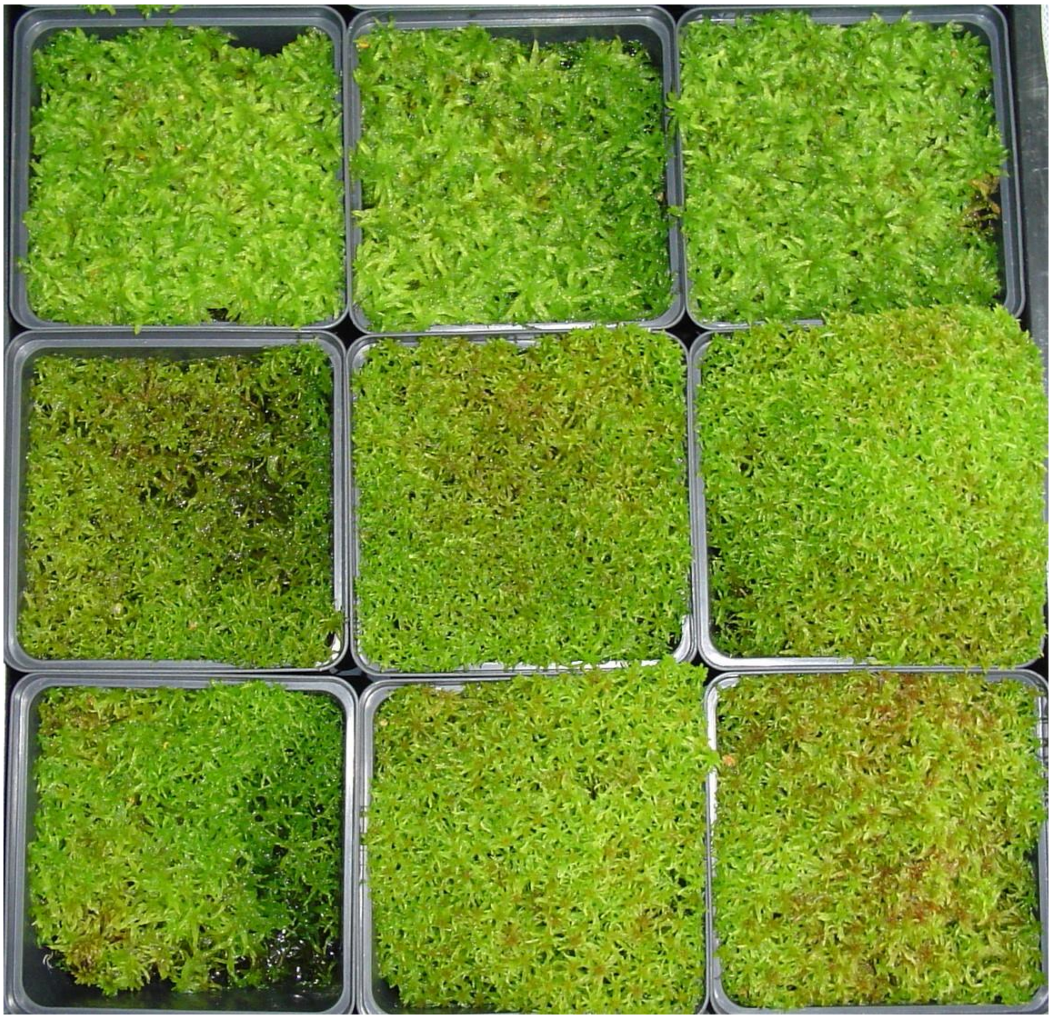

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RESEARCH PAPER

Sphagnum growth under N saturation: interactive effects of water level and P or K fertilization

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ABSTRACT

- *Sphagnum* biomass is a promising material that could be used as a substitute for peat in growing media and can be sustainably produced by converting existing drainage-based peatland agriculture into wet, climate-friendly agriculture (paludiculture). Our study focuses on yield maximization of *Sphagnum* as a crop.
- We tested the effects of three water level regimes and of phosphorus or potassium fertilization on the growth of four *Sphagnum* species (*S. papillosum*, *S. palustre*, *S. fimbriatum*, *S. fallax*). To simulate field conditions in Central and Western Europe we carried out a glasshouse experiment under nitrogen-saturated conditions.
- A constant high water table (remaining at 2 cm below capitulum during growth) led to highest productivity for all tested species. Water table fluctuations between 2 and 9 cm below capitulum during growth and a water level 2 cm below capitulum at the start but falling relatively during plant growth led to significantly lower productivity. Fertilization had no effect on *Sphagnum* growth under conditions with high atmospheric deposition such as in NW Germany (38 kg N, 0.3 kg P, 7.6 kg K·ha^{-1}·year^{-1}).
- Large-scale maximization of *Sphagnum* yields requires precise water management, with water tables just below the capitula and rising with *Sphagnum* growth. The nutrient load in large areas of Central and Western Europe from atmospheric deposition and irrigation water is high but, with an optimal water supply, does not hamper *Sphagnum* growth, at least not of regional provenances of *Sphagnum*.

2

INTRODUCTION

Sphagnum biomass is an important renewable raw material that can be used in various products (Pouliot *et al*. 2015; Glatzel & Rochefort 2017). It can substitute for fossil peat, especially for slightly humified *Sphagnum* peat (Emmel 2008; Reinikainen *et al*. 2012; Blievernicht *et al*. 2013; Jobin *et al*. 2014), which, with an annual worldwide consumption of 30 million m^3, is the major constituent of growing media used in professional horticulture (Schmilewski 2017). Its cultivation on rewetted peatlands (‘Sphagnum farming’) contributes to reducing greenhouse gas emissions from formerly drained agricultural land (Beyer & Höper 2015; Wichtmann *et al*. 2016; Günther *et al*. 2017). Replacing peat with *Sphagnum* biomass, however, requires a substantial expansion of the area under cultivation and of the yield per hectare (Gaudig *et al*. 2014, 2018; Wichmann *et al*. 2017). Maximizing yield implies that conditions for optimal *Sphagnum* growth should be identified.

Sphagnum growth rate is, next to climate factors, determined by water and nutrient availability as well as the *Sphagnum* species (Gunnarsson 2005). Under natural conditions, atmospheric water supply in NW Germany used to provide sufficient water to cover water losses, in particular through evapotranspiration in summer. This is, however, no longer the case. In the present situation of higher atmospheric water demand and larger seepage losses as a result of extensive drainage in the surrounding land, Sphagnum farming now requires an additional water supply (Brust *et al*. 2018) to keep the photosynthetically most active apical capitulum continuously moist (cf. Robroek *et al*. 2007). Several studies have shown that the growth rate of most *Sphagnum* species is highest at water tables just below the capitula, independent of the species (Clymo & Reddaway 1971; Hayward & Clymo 1983; Campeau & Rochefort 1996; Robroek *et al*. 2009; Brown *et al*. 2017).

In NW Germany, with a total atmospheric N deposition of ca. 38 kg·ha^{-1}·year^{-1} (Gauger *et al*. 2002), *Sphagnum* growth is not N-limited, and the N pool of the *Sphagnum* layer is saturated (cf. Malmer 1990; Lamers *et al*. 2000; Berendse *et al*. 2001; Bragazza *et al*. 2004). Additional N input would not result in extra *Sphagnum* growth and could even negatively affect growth, both directly (*e.g*. by lower photosynthesis, increased metabolic costs) and indirectly (by vascular plants increasingly competing with *Sphagnum* for light and water; Berendse *et al*. 2001; Tomassen *et al*. 2004; Limpens *et al*. 2011; Fritz *et al*. 2014). Under high N loads *Sphagnum* growth may furthermore become limited by phosphorus (P) (Aerts *et al*. 1992; Verhoeven *et al*. 1996; Lund *et al*. 2009) and potassium (K) (Bragazza *et al*. 2004). The addition of P may then substantially increase *Sphagnum* biomass production (Limpens *et al*. 2004; Fritz *et al*. 2012), but this effect disappears with insufficient water availability (Aerts *et al*. 2001; Limpens *et al*. 2004; Fritz *et al*. 2012). High *Sphagnum* biomass production was indeed observed in a Sphagnum farming field experiment in NW Germany under high N loads, balanced supply of P and K in irrigation water, and year-round water tables just below the moss surface (Temmink *et al*. 2017). However, the water table varied up to 20 cm over time and around 10 cm in space because of differences in micro-relief (cf. Brust *et al.* 2018).

In this study we address the relationship between nutrient supply, high water level regimes and growth of different *Sphagnum* species for the first time in a glasshouse factorial experiment. We hypothesize that under N-saturated conditions, the highest *Sphagnum* growth rates can be achieved by combining a constantly high water table with extra P and K fertilization.

MATERIAL AND METHODS

The experiment was set up in a full factorial design with three replicates and repeated twice with the same combination of water regime and fertilization level. A total of 216 moss containers (4 species × 3 water regimes × 3 fertilization levels × 3 replicates × 2 repetitions) were placed in 18 (2 repetitions × 9 combinations of water regime and fertilization level) boxes (4 × 60 × 23 cm) filled with culture medium after Rudolph *et al.* (1988) (Table 1). Each box contained 12 containers: three of each species (with the exception of *S. palustre* with lower availability) distributed randomly within the box. To ensure similar conditions within the boxes, 'gaps' due to the lack of *S. palustre* were filled using containers with *S. papillosum* (same section).

Sphagnum species

Pure patches (12 × 12 cm and 10-cm deep) of *Sphagnum papillosum*, *S. palustre*, *S. fimbriatum* and *S. fallax* were collected from natural lawns in Lower Saxony (Esterweger Dose, NW Germany) and placed in containers (12 × 12 × 12 cm) with a perforated base, within the boxes filled with a culture medium.

Water regimes

Three water regimes were applied by adjusting water levels in the boxes each week: (i) water level rising with moss growth and remaining 2 cm below the top of the capitulum ('rising'), (ii) water level alternating between 2 cm (1 week duration) and 8 cm (3 weeks duration) below the top of the capitulum ('fluctuating'), (iii) water level starting 2 cm below the top of the capitulum and remaining at the same absolute level in spite of moss growth ('static').

Fertilization levels

Water with a composition according to Rudolph *et al.* (1988) for microelements and to Gauger *et al.* (2002) for macroelements was sprayed every third week (2 h after sprinkling the mosses with demineralized water in the morning) to control the level to the average annual (1990–1999) atmospheric deposition of Ramsloh (Lower Saxony 53°04′ N, 7°38 O). The other treatments were a five-fold deposition of P (5P: 1.5 kg P·ha^{-1}·year^{-1}) and a twofold deposition of both P and K (2P2K: 0.6 kg P·ha^{-1}·year^{-1} and 15 kg K·ha^{-1}·year^{-1}) (cf. Table 1). All fertilization treatments received the same amount of N (38 kg·ha^{-1}·year^{-1}).

Cultivation conditions

The mosses were cultivated in a glasshouse with a light regime of 12-h light (mostly sunlight, but at light flux densities < 15 klx, supplemented with a sodium vapour lamp – Philips Son-T Agro 400 W – of 80 µmol·m^{-2}·s^{-1}) and 12-h dark. Air temperatures in the glasshouse were 18–21 °C during the day and 12 °C at night, without active cooling. Temperatures at the moss surface never exceeded 35 °C and were thus not detrimental to the mosses (cf. Clymo & Hayward 1982). After 2 weeks of adaptation, the experiment ran from September 2006 to June 2007 (280 days). Sprinkler irrigation (~0.25 mm demineralized water·m^{-2}) was applied twice a day (06:00 and 18:00 h) for 1 min, simulating morning dew and rain (Rudolph 1963). Different growth rates between containers within a box were corrected weekly by adjusting the height position of the containers. After 54 and 146 days, all mosses of the 'rising' and 'fluctuating' treatments were cut back from the base to a length of 10 cm to maintain similar water levels within a box for all containers. In the 'static' treatment, container walls were regularly elongated to avoid interaction between the growing mosses.

Table 1. Nutrient availability during the experiment (280 days) – calculated from nutrient concentrations in the boxes at the beginning of the experiment ('culture medium', pH 5.8) and the nutrients added by fertilization (fertilization solution: pH 8.7–9.0, weakly buffered) – depending on fertilization treatment compared to mean concentration of the culture medium in the boxes at the end of the experiment (in kg·ha^{-1} ± SEM, n = 6 for each fertilization treatment). N availability was the same for all treatments, with N at 6.67 kg·ha^{-1} by culture medium + 28.98 kg·ha^{-1} by adding fertilizer = 35.65 kg·ha^{-1} total. C = control, P5 = five-fold addition of phosphorus, 2P2K = double addition of both phosphorus and potassium.

		fertilization treatment								
		C			5P			2P2K		
	culture medium start	applied by fertilization	total nutrient availability	culture medium end	applied by fertilization	total nutrient availability	culture medium end	applied by fertilization	total nutrient availability	culture medium end
K	1.64	5.81	7.45	3 ± 1	5.81	7.45	2 ± 1	11.61	13.25	3 ± 1
NO_3-N	2.86	7.02	9.88	n.d.	7.02	9.88	n.d.	7.02	9.88	n.d.
NH_4-N	3.81	21.96	25.77	1 ± 0.5	21.96	25.77	1 ± 0.6	21.96	25.77	1 ± 0
PO_4-P	0.55	0.23	0.78	0.5 ± 0	1.15	1.70	0.4 ± 0	0.46	1.01	0.5 ± 0
N/P	12.1	126	45.7		25.2	21		63	35.3	
N/K	4.1	5	4.8		5	4.8		2.5	2.7	

Growth measurements

At the beginning of the experiment, five moss shoots per container were marked with nylon zip ties (width 2 mm, length 100 mm) fixed between the capitulum and the subjacent branches (cf. Overbeck & Happach 1957; Clymo 1970). At the end of the experiment (day 280) all mosses were cut at the level of the zip ties and at 1 cm below the surface to separate the capitula (0–1 cm). Length increase was measured, and biomass weight of each marked moss shoot and each container determined after drying for at least 48 h at 60 °C. Annual biomass productivity was calculated by extrapolating the subcapitulum weight (dry mass) of each entire container to hectares and year, assuming that the biomass of the capitula had not changed since the end of the initial adaptation period. Weight per length unit was calculated for each marked moss shoot to characterize compactness.

Fruiting bodies of the fungus *Sphagnurus paluster* were removed from 28 of the 216 containers during the experiment to prevent further distribution of the fungus. The cover (% of the container area) of *Sphagnum* tissue with necrosis (bleached capitula) and with algal infestation (dark green capitula) was estimated at the end of the experiment.

Nutrient measurements

The biomass of all capitula per container was dried and milled in a centrifugal ball mill (Pulverisette 14, Fritsch Idar-Oberstein; for 1–2 min at RCF: 15,580 *g*), and total N concentration and C/N ratio determined with a dry-combustion C/N analyser (CHNOS element analyser; Vario EL III, Elementar Analysensysteme, Hanau, Germany). After dry ashing (in a muffle furnace at 550 °C for 4 h), the ash was dissolved in 10% H_2SO_4 (Kalra 1998) and the solution treated with an acidic molybdate solution containing ascorbic acid (modified molybdenum blue method; Temminghoff 2004) to measure total P using a UV/Visible spectrophotometer (Cecil CE 1021, 890 nm wavelength). Potassium (K) was determined with an atomic absorption flame spectrometer (CD-ContrAA 300, analytic Jena) directly after microwave digestion (START 1500, MLS Enterprises). The K concentration of the water in the boxes was determined as described for the biomass samples but without digestion. Orthophosphate (ortho-P) in the water was measured after filtration (cellulose acetate filter with 0.45-µm pore size) using the modified molybdenum blue method (Temminghoff 2004), and ammonium (NH_4^+) was measured spectrophotometrically using the salicylate method (Krom 1980).

Data analysis

We analysed the effects and possible interactions of the treatments, *Sphagnum* species, water regime and fertilization level, on *Sphagnum* dry mass productivity and length increase, moss compactness, N, P and K concentrations and N/P and N/K quotients ratios in the *Sphagnum* capitula, and cover of necrosis and algae (dependent variable). As we had different sample sizes (number of replicates) and no homogeneity among the datasets, assumptions necessary for applying linear regression models (including ANOVA models) were not met (Zuur *et al.* 2009). To accommodate possible spatial correlation of *Sphagnum* containers of the same species in one box, we thus applied linear mixed effect models with fixed and random components (Pinheiro *et al.* 2009; Zuur *et al.* 2009). We also applied linear mixed effect models to compare the results of dry mass productivity ($t \cdot ha^{-1} \cdot year^{-1}$), rate of increase in length ($cm \cdot year^{-1}$), compactness ($mg \cdot cm^{-1}$) and cover of necrosis and algae (% per container) for each *Sphagnum* species (*S. fallax*, *S. fimbriatum*, *S. palustre* and *S. papillosum*) with regard to the treatments water regime and fertilization level.

Restricted maximum likelihood estimation (REML) was used to calculate estimates of coefficients for the models (Zuur *et al.* 2009). To identify the optimal model, we used the Akaike information criterion (AIC), which measures goodness-of-fit and model complexity (the lower the AIC value, the better the model).

Furthermore, we measured the strength and direction of association between dry mass productivity and necrosis, algae and N, P and K concentrations in the *Sphagnum* capitula using Pearson product-moment ('standard') or Spearman rank-order correlation, depending on whether the data were normally or not normally distributed, respectively. Correlation between *Sphagnum* dry mass productivity and N/P ratio was analysed with a generalized additive model with integrated smoothness estimation (Wood 2006).

Data exploration, computation and figure design were done with the software R (R Development Core Team 2009) and the packages' 'nlme' (Pinheiro *et al.* 2009), 'mgcv' (Wood 2006) and 'stats' (R Development Core Team 2009).

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RESULTS

Length increase and biomass productivity

Differences in productivity between *Sphagnum* species were significant (Fig. 1; Table 2). Most values of dry mass productivity ranged between 4 and 8 $t \cdot ha^{-1} \cdot year^{-1}$. Differences in length increase were also significant (Fig. 1; Table 2), with *S. fallax* growing fastest (max. 48$\cdot cm \cdot year^{-1}$ and 10.8 $t \cdot ha^{-1} \cdot year^{-1}$) and *S. papillosum* slowest (max. 22 $cm \cdot year^{-1}$ and 7 t $ha^{-1} \cdot year^{-1}$).

Length increases and biomass productivity of all *Sphagnum* species were highest with the water table staying constantly 2 cm below the capitulum (treatment 'rising'; Table 2). Moss growth decreased with lower water tables, even if lowering was only periodic and only a few centimetres. As long as high water tables (2 cm below capitulum) occurred periodically, *S. palustre* grew better than with a water level not rising with moss growth (treatment 'static', *i.e.* water table sinking relative to the moss growth; $P = 0.027$). At the end of the experiment, the water level in the 'static' water level treatment was: *S. fallax* 1–9 cm (mean 5.6 cm), *S. fimbriatum* and *S. palustre* 4.0–8.5 cm (mean 6.3 cm) and *S. papillosum* 3.0–7.5 cm (mean 5.3) cm below the capitulum. The 'static' water level led to the lowest biomass and length values for all species, except biomass productivity of *S. fallax*, which was similar to that with a fluctuating water table (Fig. 1, Table 2).

Fertilization with P or with P and K had no effect on *Sphagnum* growth (Table 2).

Compactness

Compactness, *i.e.* dry mass per unit moss length, determines water-holding capacity and capillarity (cf. Hayward & Clymo 1982; Titus & Wagner 1984). Compactness was used as a proxy

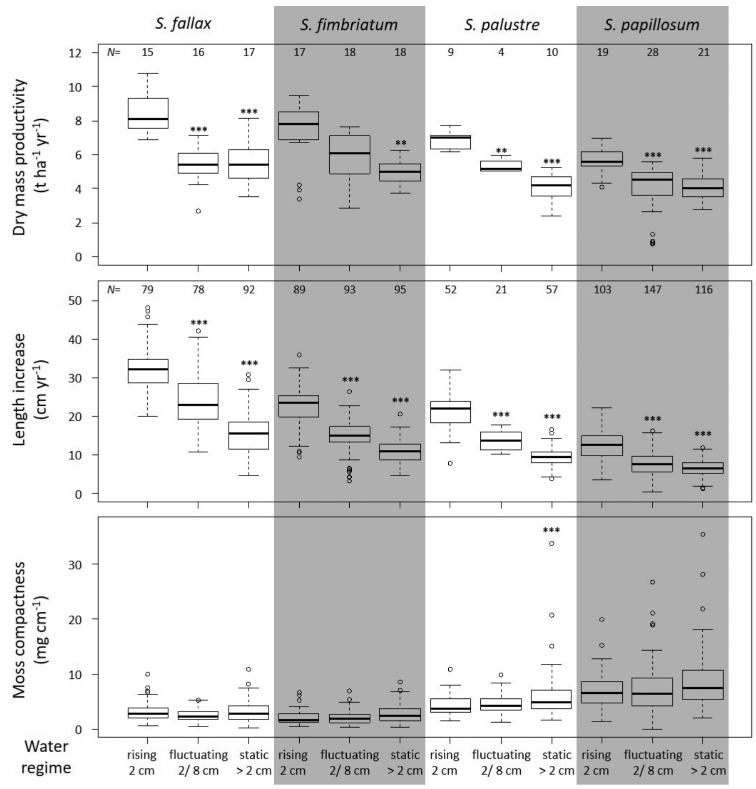

Fig. 1. Dry mass productivity ($t \cdot ha^{-1} \cdot year^{-1}$), length increase ($cm \cdot year^{-1}$) and compactness ($mg \cdot cm^{-1}$) of *Sphagnum fallax*, *S. fimbriatum*, *S. palustre* and *S. papillosum* as a function of water regime (see text for details), with levels of significance for comparison to 'rising' water level within one species (*$P \le 0.05$, **$P \le 0.01$, ***$P \le 0.001$) and total number of measurements (*N* compactness is similar to *N* length increase). The 'box and whisker' graphs show the median (bold line), the upper and lower quartiles (which include 50% of the data and create the box), whiskers representing the lowest value within 1.5 IQR (=interquartile range) of the lower quartile and the highest value within 1.5 IQR of the upper quartile, and outliers (o, *i.e.* values outside these ranges).

for the suitability of *Sphagnum* biomass as a raw material for growing media (cf. Jacobs *et al.* 2009).

Sphagnum papillosum and *S. palustre* were significantly more compact than *S. fallax* and *S. fimbriatum* (Fig. 1; Table 2). A 'static' water level resulted in more compact growth of all species, but this was only significant for *S. palustre* (Fig. 1; Table 2). Fertilization had no significant influence on the morphological characteristics of these peat mosses.

Nutrient concentrations in *Sphagnum* capitula

The N concentrations in all *Sphagnum* species were similar (mean N 14.4 $mg \cdot g^{-1}$ DW). Generally, biomass productivity decreased with increasing N concentration in the capitulum (Pearson correlation: $r = -0.23$, $n = 190$, $P \le 0.01$). *Sphagnum papillosum* had the lowest biomass production with highest N values (max. 26.2 $mg \cdot g^{-1}$ DW).

The P concentrations ranged between 0.63 and 2.36 $mg \cdot g^{-1}$ DW (mean 1.3 $mg \cdot g^{-1}$ DW), K concentrations were between 2.9 and 11.9 $mg \cdot g^{-1}$ DW (mean 6.0 $mg \cdot g^{-1}$ DW). While lowest P concentrations were in *S. papillosum* (mean 1.1 $mg \cdot g^{-1}$ DW), the highest K concentrations were in *S. palustre* and *S. fallax* with 'rising' water level (Table 3). Fertilization did not influence N, P or K concentrations in the capitula nor the growth (Tables 2 and 3). Both P and K concentrations were lowest at the 'static' water level (Table 2). Biomass productivity decreased with increasing N/P values (Table 2; Fig. 3), with highest N/P ratio reached in *S. papillosum* (N/P = 7–24).

The N/K ratio ranged between 1.1 and 5.3 but had no relationship to biomass productivity. On the other hand, N/K values were significantly lowest in the 'rising' water table, except for *S. fallax* (Table 3).

Necrosis and algae

Algae (leading to dark green capitula) were recorded in 38% of the containers. Also, in 38% of the containers, more than 5% of the *Sphagnum* plants suffered from necrosis, probably because of fungal infection. With higher water tables there were fewer necrosis and algal infections (Fig. 2). Containers with *S. fimbriatum* experienced the highest level of necrosis per container (up to 92%), but proportionally more containers of *S. palustre* were affected. *Sphagum fallax* experienced the highest level of algal infestations (up to 55% of the moss; Fig. 2).

We excluded six containers with *S. fallax* from data analysis because these mosses collapsed and lost their structure, making further measurements impossible. The reasons for the die-off are unclear. There was no link between die-off and treatment.

Biomass productivity values as a function of cover of necrosis (% per container) were wide ranging (Fig. 4), but decreased

Table 2. Results of linear modelling of the response variables biomass productivity, length increase and compactness.

variable	factor	estimate of the slope	SE	*t*-value	*P*
Dry mass	*S. fimbriatum*[a]	−0.26	0.16	−1.65	0.099
productivity	*S. palustre*[a]	−0.96	0.21	−4.56	**<0.001**
n = 192, df 186	*S. papillosum*[a]	−1.24	0.16	−7.96	**<0.001**
	Water regime 'fluctuating'[b]	−1.51	0.33	−4.55	**<0.001**
	Water regime 'static'[b]	−1.71	0.33	−5.16	**<0.001**
Length	*S. fimbriatum*[a]	−7.64	0.38	−20.06	**<0.001**
increase	*S. palustre*[a]	−8.37	0.48	−17.26	**<0.001**
n = 1022, df: 1016	*S. papillosum*[a]	−14.56	0.36	−40.40	**<0.001**
	Water regime 'fluctuating'[b]	−7.26	1.02	−7.09	**<0.001**
	Water regime 'static'[b]	−11.21	1.02	−10.98	**<0.001**
Moss	*S. fimbriatum*[a]	−0.59	0.05	−5.05	**<0.001**
compactness	*S. palustre*[a]	2.08	0.06	8.91	**<0.001**
n = 1021, df: 1015	*S. papillosum*[a]	4.65	0.05	21.49	**<0.001**
	Water regime 'fluctuating'[b]	0.03	0.07	−0.50	0.615
	Water regime 'static'[b]	0.96	0.07	2.24	**<0.05**
Phosphorus	*S. fimbriatum*[a]	−0.04	0.04	−0.79	0.42
concentration	*S. palustre*[a]	−0.11	0.05	−1.89	0.06
in *Sphagnum*	*S. papillosum*[a]	−0.39	0.04	−9.03	**<0.001**
capitula	Water regime 'fluctuating'[b]	−0.05	0.11	−0.53	0.59
n = 192, df: 186	Water regime 'static'[b]	−0.27	0.11	−2.57	**<0.05**
Potassium	*S. fimbriatum*[a]	−0.53	0.23	−2.31	**<0.05**
concentration in	*S. palustre*[a]	1.20	0.29	−4.07	**<0.001**
Sphagnum	*S. papillosum*[a]	−0.15	0.22	−0.66	0.50
capitula	Water regime 'fluctuating'[b]	−1.71	0.54	−3.15	**<0.05**
n = 184, df: 178	Water regime 'static'[b]	−2.44	0.54	−4.49	**<0.001**

Generalized least squares fitted by REML, Correlation structure (boxes): biomass productivity Rho = 0.149; rate of increase in length Rho = 0.134; compactness Rho = 0.026; phosphorus concentration Rho = 0.359; potassium concentration Rho = 0.389.
df, degrees of freedom; *P*, level of significance; significant values are marked in bold.
[a]Compared with *S. fallax*.
[b]Compared with the water regime 'rising'.

with increasing percentage of necrosis, particularly in the 'rising' water table, were less distinct in the 'fluctuating' water table, whereas in the 'static' water level biomass productivity was independent of necrosis (Fig. 4). We observed an association between decreasing *Sphagnum* dry mass and an increase in algae (Spearman correlation: $r_s = -0.42$, $n = 191$, $P \leq 0.001$). Fertilization had no significant effect on necrosis or algae, but algal occurrence was higher in the 5P treatment. Furthermore, there was no relationship between nutrient concentration (N, P, K) in the moss capitula and percentage of necrosis or algae.

DISCUSSION

Water level

Our results show that constantly high water tables, *i.e.* continuously rising with the growing moss, lead to the highest growth rates for all four *Sphagnum* species. As soon as the relative water table falls by only a few centimetres, *Sphagnum* growth is significantly hampered. The 'static' water level, which sank relative to the up-growing moss, apparently hampered *Sphagnum* growth more than an alternating water level (treatment 'fluctuating'). This concurs with the results of Robroek *et al.* (2007), who found a lower capitulum water content and a consequent growth reduction in lawn species growing with a water table of 15 cm compared to a water table 5 cm below the top of the capitulum. In contrast, Breeuwer *et al.* (2009) found the productivity of the lawn species *Sphagnum magellanicum* increased with summer water table fluctuations of between 7 and 23 cm in comparison to somewhat wetter conditions (water table 3–15 cm below moss surface), and they attributed this to a competitive advantage of *S. magellanicum* in the drier conditions over the co-occurring *S. cuspidatum*. Without competition, growth of lawn species is generally highest at high water levels (Hayward & Clymo 1983; Grosvernier *et al.* 1997; Johnson 1998; Stokes *et al.* 1999).

Despite their more dense and compact growth form, our mosses obviously could not compensate for lower water levels through more effective capillarity (cf. Clymo & Hayward 1982). The water content of the capitulum is a good indicator of whether water supply is sufficient for optimal CO_2 assimilation (cf. Robroek *et al.* 2009). We did not measure capitulum water content in our study, but several other studies have found a rapid decrease when lowering water levels by only a few centimetres (Hayward & Clymo 1982; Robroek *et al.* 2009; Strack & Price 2009). On the other hand, even small amounts of precipitation (0.5–1.0 mm) may rewet the capitulum sufficiently to reduce the negative effect of low water levels (Robroek *et al.* 2009; Strack & Price 2009; Nijp *et al.* 2014; Krebs *et al.* 2016). As we sprinkled water on our mosses twice a day, with 0.5 mm per day, and each week replenished water loss in the boxes, capitulum water content will only have varied very slightly.

Table 3. Mean nitrogen, phosphorus and potassium concentrations (mg·g^{-1} dry mass ± SEM) and N/K quotient in capitula of different *Sphagnum* species as a function of water regime and fertilization level.

Sphagnum species	*S. fallax*	*S. fimbriatum*	*S. palustre*	*S. papillosum*
mg N·g^{-1} dry mass				
Water regime				
Rising	14.2 ± 0.07 (14)[a]	15.2 ± 0.10 (17)[a]	14.6 ± 0.11 (9)[a]	14.3 ± 0.06 (19)[a]
Fluctuating	16.7 ± 0.06 (15)[b]	16.3 ± 0.07 (18)[a]	13.2 ± 0.14 (4)[a]	15.3 ± 0.07 (27)[a]
Static	12.6 ± 0.07 (17)[a]	13.1 ± 0.07 (18)[a]	13.8 ± 0.15 (10)[a]	12.7 ± 0.04 (21)[a]
Fertilization level				
C	14.7 ± 0.08 (14)[a]	16.3 ± 0.07 (18)[a]	14.6 ± 0.26 (6)[a]	14.1 ± 0.06 (23)[a]
5P	14.6 ± 0.11 (15)[a]	15.0 ± 0.09 (18)[a]	14.5 ± 0.13 (6)[a]	14.6 ± 0.09 (20)[a]
2P2K	14.0 ± 0.07 (17)[a]	13.3 ± 0.07 (17)[a]	13.4 ± 0.11 (11)[a]	14.0 ± 0.06 (24)[a]
mg P·g^{-1} dry mass				
Water regime				
Rising	1.6 ± 0.01 (14)[a]	1.5 ± 0.01 (17)[a]	1.7 ± 0.01 (9)[b]	1.2 ± 0.01 (19)[a]
Fluctuating	1.6 ± 0.01 (15)[a]	1.6 ± 0.01 (18)[a]	1.2 ± 0.02 (4)[a]	1.1 ± 0.00 (27)[a]
Static	1.3 ± 0.01 (17)[a]	1.3 ± 0.01 (18)[a]	1.2 ± 0.01 (10)[a]	1.0 ± 0.01 (21)[a]
Fertilization level				
C	1.5 ± 0.01 (14)[a]	1.5 ± 0.01 (18)[a]	1.3 ± 0.03 (6)[a]	1.1 ± 0.00 (23)[a]
5P	1.6 ± 0.01 (15)[a]	1.6 ± 0.01 (18)[a]	1.6 ± 0.03 (6)[a]	1.2 ± 0.01 (20)[a]
2P2K	1.4 ± 0.01 (17)[a]	1.3 ± 0.01 (17)[a]	1.3 ± 0.01 (11)[a]	1.0 ± 0.00 (24)[a]
mg K·g^{-1} dry mass				
Water regime				
Rising	6.0 ± 0.02 (14)[a]	6.7 ± 0.03 (17)[b]	9.6 ± 0.07 (9)[b]	8.1 ± 0.05 (19)[b]
Fluctuating	6.3 ± 0.02 (15)[a]	5.3 ± 0.03 (17)[a]	6.1 ± 0.02 (4)[ab]	5.4 ± 0.02 (27)[a]
Static	5.8 ± 0.05 (12)[a]	4.7 ± 0.04 (18)[a]	5.4 ± 0.06 (10)[a]	4.7 ± 0.02 (21)[a]
Fertilization level				
C	5.9 ± 0.03 (14)[a]	5.9 ± 0.04 (17)[a]	6.6 ± 0.24 (6)[a]	6.3 ± 0.06 (23)[a]
5P	6.2 ± 0.03 (10)[a]	5.2 ± 0.04 (18)[a]	7.7 ± 0.21 (6)[a]	5.7 ± 0.04 (20)[a]
2P2K	6.1 ± 0.03 (17)[a]	5.6 ± 0.04 (17)[a]	7.2 ± 0.08 (11)[a]	5.7 ± 0.03 (24)[a]
N/K quotient				
Water regime				
Rising	2.4 ± 0.01 (14)[ab]	2.3 ± 0.01 (17)[a]	1.5 ± 0.01 (9)[a]	1.8 ± 0.01 (19)[a]
Fluctuating	2.7 ± 0.01 (15)[b]	3.1 ± 0.01 (17)[b]	2.2 ± 0.03 (4)[ab]	2.9 ± 0.01 (27)[b]
Static	2.2 ± 0.02 (12)[a]	3.0 ± 0.02 (18)[b]	2.6 ± 0.04 (10)[b]	2.8 ± 0.01 (21)[b]
Fertilization level				
C	2.5 ± 0.01 (14)[a]	2.9 ± 0.02 (17)[a]	2.4 ± 0.06 (6)[a]	2.6 ± 0.02 (23)[a]
5P	2.5 ± 0.02 (10)[a]	3.0 ± 0.02 (18)[a]	2.1 ± 0.08 (6)[a]	2.7 ± 0.02 (20)[a]
2P2K	2.3 ± 0.01 (17)[a]	2.5 ± 0.02 (17)[a]	2.0 ± 0.02 (11)[a]	2.5 ± 0.01 (24)[a]

Number of replicates per water level or fertilization treatment of each species are in brackets.
Different letters indicate significant differences within single treatments (water regime, fertilization level) for each single species. $P \leq 0.05$.

A high water level not only leads to optimal water supply to the capitulum, but also to an improved nutrient supply (cf. Clymo & Hayward 1982), higher vitality (indicated by less necrosis and algal infestation) and a looser growth form, allowing light to penetrate deeper into the *Sphagnum* lawn, resulting in an increased active assimilation area (Sliva 1997; cf. Robroek *et al.* 2009). Continuous optimal growth requires a high water table that continuously rises with the growing moss. A water drawdown would result in a growth reduction or – in the case of low stem density – even death of the peat mosses (Fritz *et al.* 2012).

Fertilization

Since *Sphagnum* growth is not N-limited at atmospheric deposition rates exceeding 18 kg·ha^{-1}·year^{-1} (Malmer 1990; Aerts *et al.* 1992; Verhoeven *et al.* 1996 Lamers *et al.* 2000) and our control (38 kg·ha^{-1}·year^{-1}; Gauger *et al.* 2002; Table 1) far exceeded this value, we refrained from testing additional N fertilization. The mean *Sphagnum* tissue N concentration of 14.4 mg·g^{-1} DW found at the end of our experiment, indeed confirms the prevalence of N-saturated conditions (Lamers *et al.* 2000).

Over the entire dataset there was a negative correlation between N tissue concentration and biomass productivity, but this effect was most distinct in *S. papillosum* ($r = -0.53$, $P \leq 0.01$). Its growth strongly decreased at capitulum N concentrations >20 (max. 26.2) mg·g^{-1} DW, resulting in the lowest biomass productivity values measured in this study. For the other species, N tissue concentration had no effect on growth (cf. Limpens & Berendse 2003). Berendse *et al.* (2001) proposed a maximum N concentration in *Sphagnum* tissues of 20 mg·g^{-1} DW, which was exceeded in both the study of Breeuwer *et al.* (2009) and in our study. According to van der Heijden *et al.* (2000), a capitulum N concentration in *S. fallax* of 15 mg·g^{-1} DW indicates N pollution stress in bogs. However, our study shows that even a maximum N value of 20.5 mg·g^{-1} DW has no negative effect on growth of *S. fallax*.

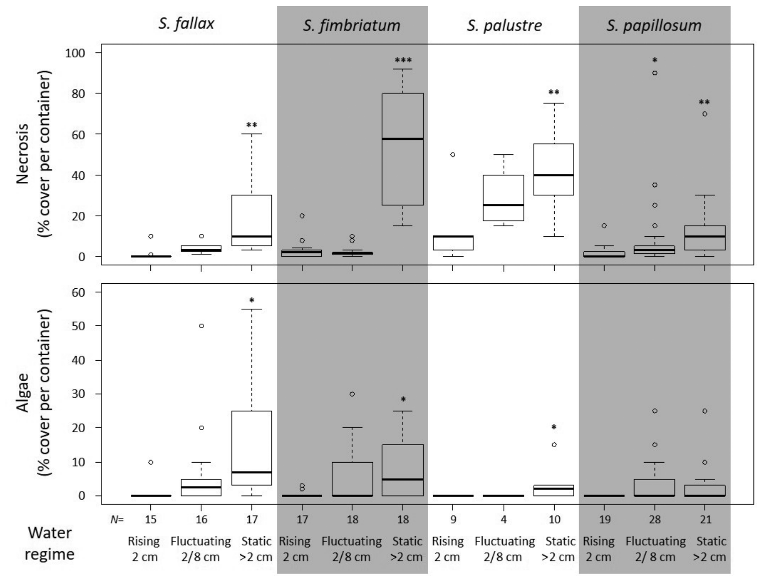

Fig. 2. Cover of necrosis and algae (% per container) on *Sphagnum fallax*, *S. fimbriatum*, *S. palustre* and *S. papillosum* as a function of water regime (see text for details and caption of Fig. 1 for further explanation).

Similarly, Granath *et al.* (2009) found no detrimental effects on the photosynthetic apparatus at N tissue concentrations up to 20 mg·g^{-1} DW in *S. balticum* (a species of the *Cuspidata* section, like *S. fallax*). Bragazza *et al.* (2005) suggested that *Sphagnum* plants in polluted regions have a metabolic adaptation (with lower rates of N absorption) to high N supply, which was confirmed by Fritz *et al.* (2014). This ability seems, however, to be differently developed between species, as also suggested in Fig. 3. In our study (as in Temmink *et al.* 2017 with N concentrations >18 mg·g^{-1} DM), a toxic effect (growth reduction) of a high N tissue concentration >20 mg·g^{-1} DM was observed only in *S. papillosum*. Chiwa *et al.* (2016) found that an *S. capillifolium* lawn can filter wet N deposition of up to 32 kg N·ha^{-1}·year^{-1} for least a decade, leading to N concentrations in the capitula of around 14 mg·g^{-1} DM.

In our study, P fertilization had no significant effect on *Sphagnum* growth, indicating the absence of P limitation. This is corroborated by the failing correlation between P concentration in the capitula (mean 1.3 up to 2.4 mg·g^{-1} DW) and fertilization (cf. Li *et al.* 1993, Table 2), as well as N/P ratio <30 (cf. Bragazza *et al.* 2004). In other studies, with low P concentrations in the pore water, similarly high P concentrations in the mosses were found only after P fertilization (Chiwa *et al.* 2018, Limpens *et al.* 2003b; Limpens *et al.* 2004; Limpens & Heijmans 2008; Fritz *et al.* 2012). As in our study, *Sphagnum* did not respond significantly to additional P (Li *et al.* 1993; Limpens *et al.* 2004) at sites with similar water P concentrations as in our experiment (0.23 mg·l^{-1}) and in natural bogs in Lower Saxony (Bertram 1988; Lütt 1992). Only at 'rising' water level (remaining 2 cm below the capitulum) did P fertilization (5P) slightly (but not significantly) increased growth of *Sphagnum palustre*, *S. fimbriatum* and *S. fallax* in our study. The P concentrations in the culture medium were similar at the end of the experiment irrespective of the treatment (see Table 1). This can be explained by P fixation into forms that are unavailable to the plants, as only orthophosphate was determined in the solutions.

The N/P ratios in the *Sphagnum* capitula at the end of the experiment ranged between 7.2 and 23.6, with a mean value of 11.3, indicating optimal nutrient supply (cf. Aerts *et al.* 1992). With increasing N/P ratio, biomass productivity significantly decreased (Fig. 3). Nevertheless, no P

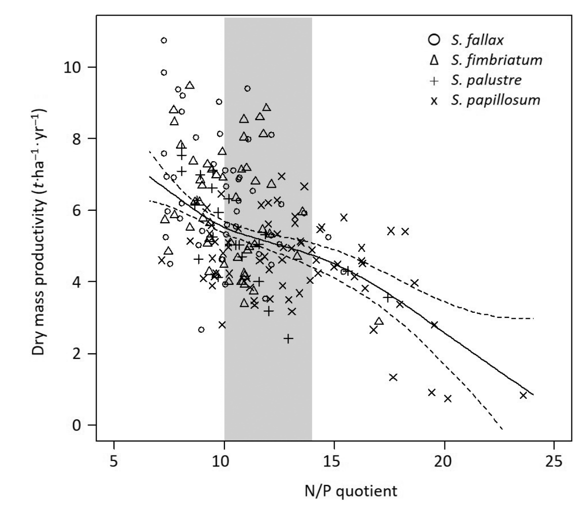

Fig. 3. Correlation between dry mass productivity (t·ha^{-1}·year^{-1}) and N/P quotient for different *Sphagnum* species; grey: N/P quotient with optimal *Sphagnum* growth (after Aerts *et al.* 1992). Model results (generalized additive model), $N = 191$: estimated degrees of freedom for the smoother = 3.23, explained deviance (R^2) = 30.5%, variance of the residuals = 1.25, $P < 0.001$. The curve is estimated using LOESS smoother and point-wise 95% confidence bands (dotted lines) (Zuur *et al.* 2009).

limitation can be found in our study (see above). According to Aerts *et al.* (1992), N/P ratios below ten indicate N limitation, which would apply to about 40% of our values. As all mosses received the same (high) N amount, P fertilization had no influence, and *Sphagnum* species did not differ in N/P ratios, the suggestion of N limitation is implausible.

Compared to studies in natural habitats with 2.5–5.2 mg K·g^{-1} DW (Bragazza *et al.* 2004; Fritz *et al.* 2012), the K concentration in the capitula in our study (mean 4.7–9.6 g·g^{-1} DW; Table 3) was higher, but similar to a Sphagnum farming site (irrigated with eutrophic water) with 4.5–10.3 g K·g^{-1} DW (Temmink *et al.* 2017). Bragazza *et al.* (2004) suggest K limitation at N/K ratios above 3.3, which was only found in a single case in our study (N/K 1.1–5.3, mean 2.6). However, K fertilization did not lead to either significantly higher biomass productivity nor higher K concentrations or lower N/K ratios in the moss capitula. Similarly, the K concentration in the culture medium at the end of the experiment was independent of the fertilization treatment. These facts indicate K-saturated conditions.

Higher N, P and K concentrations in the capitula at constantly high water levels ('rising' treatment) may result from increased nutrient uptake by the larger moss surface with permanent water contact (cf. Clymo & Hayward 1982). The values for N, P and K are known to be more concentrated in the *Sphagnum* capitula (Malmer 1988), but under nutrient-saturated conditions their accumulation in stems cannot be ruled out (cf. Chiwa *et al*. 2018); unfortunately, this was not measured in our study. Li *et al.* (1993), however, we did not find changes in P concentration either in the capitula (0–1 cm) or in the stem (1–4 cm) of *S. papillosum* at different P fertilization levels. Nevertheless, nutrients will have been removed from the rather closed box system in our study through the cutting and removal of the basal parts (see Methods).

Both the N/P and N/K ratios in our study indicate that conclusions from studies of natural systems cannot simply be transferred to systems with high nutrient loads and high nutrient concentrations in the moss tissue.

We used the culture medium of Rudolph *et al.* (1988), which is optimized for *Sphagnum* growth and was apparently sufficient and had a favourable stoichiometry, thus no stimulating effect of additional P and K fertilization on *Sphagnum* growth was found. In practice, even larger amounts of nutrients, in particular N, P and K, are supplied to the moss layer when the irrigation water of the Sphagnum farming site is obtained from the surrounding fertilized agricultural areas (Krebs *et al.* 2012; Temmink *et al.* 2017). Nutrient-rich conditions (as in our study) are representative for extensive areas of Western and Central Europe. Our study demonstrates that *Sphagnum* grows well under nutrient-rich conditions, as long as an optimal water supply is guaranteed. These results might also be useful for bog restorations. The long-term effects of such site conditions, *e.g.* on *Sphagnum* growth and species composition, still have to be investigated.

In contrast to the results of Fritz *et al.* (2012) for a nutrient-poor site, we did not find changes in *Sphagnum* morphology as a result of fertilization since N, P and K supply in our study were apparently sufficient for *Sphagnum* growth, including in the control.

Sphagnum species

Of the four studied *Sphagnum* species (*S. palustre*, *S. papillosum*, *S. fimbriatum*, *S. fallax*), *S. fallax* had the highest productivity, which corresponds to results from a global meta-analysis (Gunnarsson 2005). Both high water level and an adequate nutrient supply promote growth of all four tested species, but the minerotrophic species *S. fallax* profits most (cf. Lee & Studholme 1992; Twenhöven 1992; Limpens *et al.* 2003b). On the other hand, *S. fallax* decomposes faster than *S. papillosum* (Limpens & Berendse 2003) and has a lower water-holding capacity (Overbeck & Happach 1957), which might make this species less suitable for use in horticultural substrates, at least for some applications (Emmel & Kennett 2007).

Necrosis and algae

Necrotic diseases of peat mosses are often caused by pathogenic fungi, such as *Sphagnurus paluster* (syn. *Lyophyllum palustris*, *Tephrocybe palustris*) (Redhead 1981; Untiedt & Müller 1985; Limpens *et al.* 2003a); this parasitic basidiomycete is only found on *Sphagnum* (Untiedt & Müller 1985). Although no molecular identification of the fungal mycelium was conducted, the typical pattern of damage and sporocarps in our study indicate the occurrence of *Sphagnurus paluster*.

In contrast to Limpens *et al.* (2003a), our study found a negative effect of infection on biomass production of *Sphagnum* (Fig. 4). This contradiction may be explained by the increased fungal biomass being included in the biomass values of Limpens *et al.* (2003a) and by the intensity of necrosis being lower at high water levels (Fig. 2). Similarly, in contrast to Limpens *et al.* (2003a), we did not find any relationship between necrosis or algae and fertilization treatment or N/P ratio. The N/P ratio in our study, however, did not exceed 25, *i.e.*

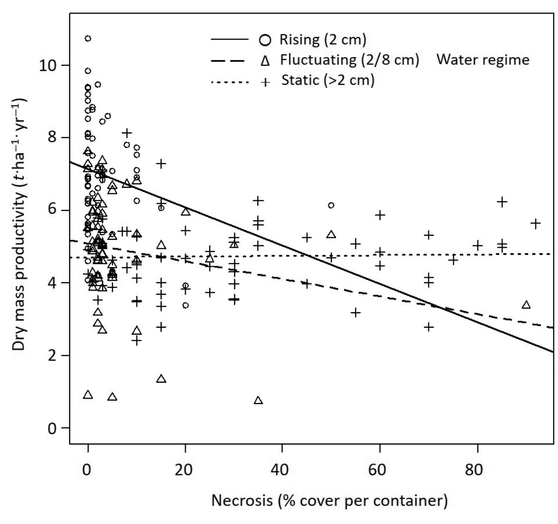

Fig. 4. Relation between dry mass productivity (t·ha^{-1}·year^{-1}) and necrosis (% cover per container) for different water regimes with regression lines, including all species. Overall model with dry mass productivity (dependent variable) and necrosis (explanatory variable) and its interaction with the different water regime model results (linear mixed effect model), $N = 192$: degrees of freedom = 188, F-value = 3.58, $P < 0.05$, Rho (induced correlation structure of containers of the same moss species within a box) = 0.53.

remained in the range where Limpens *et al.* (2003a) also failed to see any correlation. Our results indicate that *Sphagnum* vitality and growth rate are stimulated by high water levels, where they are less vulnerable to fungal or algal infection despite high nutrient loads.

While *Sphagnurus paluster* infects only small areas in nature, it often kills most peat mosses in glasshouses where there is a favourable environment for rapid fungal dispersal (Untiedt & Müller 1985; Landry *et al.* 2011). Since *Sphagnum* farming sites on rewetted bogs are also artificial systems, the risk potential for diseases from fungi and algae must be assessed. Effective measures to limit *Sphagnurus paluster* without affecting *Sphagnum* are the fungicide Myclobutanil (Landry *et al.* 2011) or *Trichoderma virens* as an antagonist (Irrgang *et al.* 2012), which have only been tested and might only be applicable in glasshouse cultivation.

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Sphagnum farming on cut-over bog in NW Germany: Long-term studies on *Sphagnum* growth

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Sphagnum farming on cut-over bog in NW Germany: Long-term studies on *Sphagnum* growth

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SUMMARY

Sphagnum farming allows sustainable and climate-friendly land use on bogs while producing a renewable substitute for peat in horticultural growing media. We studied *Sphagnum* productivity on an experimental *Sphagnum* culture established on a cut-over bog in Germany with strongly humified peat at the surface. Preparation of the site included levelling of the peat surface, construction of an irrigation system, spreading of *Sphagnum papillosum* fragments, covering them with straw, and finally rewetting. Provided there was an adequate (95 %) initial cover of *Sphagnum* fragments, the most relevant variables for *Sphagnum* productivity were found to be water supply and regular mowing of vascular plants. As long as sufficient water was supplied, the dry biomass accumulation of the established *Sphagnum* lawn remained high, reaching 3.7 t ha^{-1} yr^{-1} between 2007 and 2011. Annual dry *Sphagnum* biomass productivity over the period 2010–2011 was up to 6.9 t ha^{-1}. During periods when high water table could not be maintained, substantial decomposition of the previously accumulated biomass occurred. After nine years the net accumulated dry mass *per* hectare was on average 19.5 t of pure *Sphagnum* and 0.7 t of subsurface vascular-plant biomass. Nitrogen deposition in the study region is apparently sufficient to support fast *Sphagnum* growth, whereas phosphorus and potassium may be limiting.

KEY WORDS: biomass, degraded bog, growing media, paludiculture, *Sphagnum papillosum*

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INTRODUCTION

Sphagnum farming is the commercial cultivation of *Sphagnum* species (‘peatmoss’) for harvest as living biomass. *Sphagnum* biomass is used in a variety of applications (Zegers *et al.* 2006, Pouliot *et al.* 2015) including, importantly, as a substitute for ‘white peat’ in horticultural growing media (Emmel 2008, Oberpaur *et al.* 2010, Reinikainen *et al.* 2012, Blievernicht *et al.* 2013, Jobin *et al.* 2014). White peat is slightly humified *Sphagnum* peat (also known as ‘blond peat’ and, confusingly, ‘peat moss’) which is mined from peatlands. Currently, peat provides 86 % of the raw material required by the European Union for horticultural substrates (Altmann 2008) and 92 % of the German demand (IVG 2014). In Germany, approximately 4 million cubic metres of white peat is used annually for professional horticulture and hobby gardening (IVG 2014). This high demand creates great potential for replacing fossil white peat with renewable *Sphagnum* biomass as an environmentally friendly and high quality raw material for horticulture (Gaudig *et al*. 2014).

Sphagnum farming on rewetted bogs is a promising example of paludiculture, which allows agricultural use of wet peatlands while halting degradation of the peat layer (Wichtmann *et al*. 2016). In addition to biomass production, paludiculture provides a range of other ecosystem services including climate regulation, water purification/nutrient retention, regulation of the water cycle, and provision of habitats for specialised biodiversity (Luthardt & Wichmann 2016).

The first pilot field study on Sphagnum farming in Germany, installed in 2004, was inspired by the Canadian moss layer transfer technique for ecological restoration of cut-over bogs (Quinty & Rochefort 2003). Sphagnum farming experiments on cut-over bogs have also been conducted since 2004 in Canada (Landry & Rochefort 2009, Pouliot *et al*. 2015). In contrast to the slightly humified residual peat in Canada (Robert *et al.* 1999), the highly humified ‘black peat’ of cut-over bogs in Germany has very low permeability (*cf*. Baden & Eggelsmann 1963). Consequently, our Sphagnum farming method differs from the Canadian one in that we have installed water management systems to stabilise the water table (Wichmann *et al*. 2017).

In this article we discuss the results of a long-term study of Sphagnum farming on a cut-over bog in

Germany (Gaudig *et al.* 2014), addressing the following questions:

1. Which variables accelerate the establishment of a *Sphagnum* culture on 'black peat'?
2. Which variables increase *Sphagnum* productivity and yields?

METHODS

Site

The Sphagnum farming pilot plot (approximately 61.5 m × 20.5 m, total area 1,260 m²) was established on cut-over bog at Ramsloh in Lower Saxony, Germany (53° 4.31′ N, 07° 38.90′ E) (Figure 1a) within the Esterweger Dose, which was formerly one of the most extensive bog areas in western Europe. It was used as grassland for 30 years before peat extraction by the 'milled peat' method (described by Altmann 2008) commenced in 2000.

The oceanic climate is (cool) temperate with mean annual temperature 9.6 °C and mean annual precipitation 844 mm (Figure 1b). Summer (June–August) is the warmest and wettest season, while the lowest rainfall is recorded for February–May (Figure 1b). Mean monthly minimum temperature is **-** 0.2 °C for both January and February, and frosts occur mainly during these two months.

Establishment of the Sphagnum farming field

Site preparation included removal of the white peat layer (~ 65 cm thick), levelling of the surface with an excavator, and installation of underground irrigation pipes (depth 30 cm, spacing 5 m) connecting with a perimeter ditch (Figures 2 and 3, Kamermann & Blankenburg 2008, Wichmann *et al.* 2017). Because optimal *Sphagnum* growth requires high and stable water levels (Hayward & Clymo 1982, 1983), we installed active water table regulation. Natural precipitation was supplemented with groundwater pumped into the ditch by a windmill. Flooding of the site was prevented by installing an overflow. In November 2004, fragments of *Sphagnum papillosum* (0.5–2 cm long) with small proportions of other mosses (*S. fallax, S. cuspidatum, S. fimbriatum*) and vascular plant species (*Erica tetralix*, *Molinia caerulea*) were spread manually over the bare peat surface to achieve ~ 95 % cover and mulched with a layer of straw (*cf.* Quinty & Rochefort 2003), after which the site was rewetted. To control the growth of

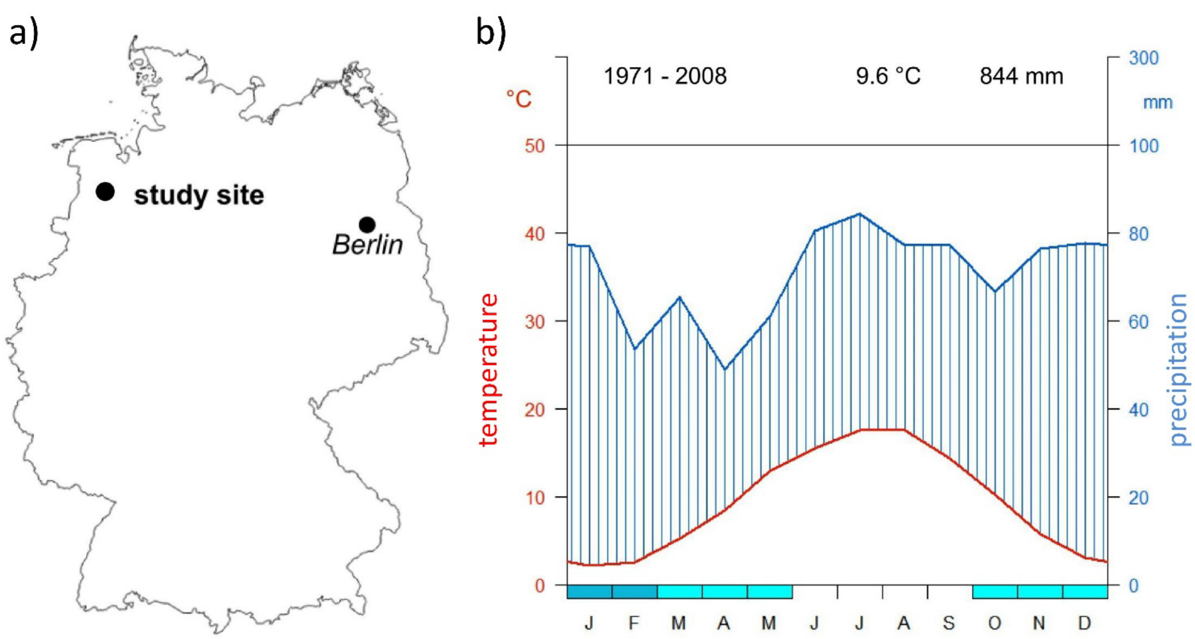

Figure 1. a) Location of the study site at Ramsloh, north-west Germany and b) climate graph (Walter & Lieth 1967) for the meteorological stations at Saterland-Ramsloh (precipitation, mm) and Dörpen (temperature, °C), which are located 4 km and 26 km from the site, respectively. The right-hand vertical axis indicates precipitation in mm *per* calendar month. On the horizontal axis, dark blue panels indicate months during which frost events certainly occur, and light blue panels those when frost may occur. Data provided by the German Weather Service DWD (Deutscher Wetterdienst).

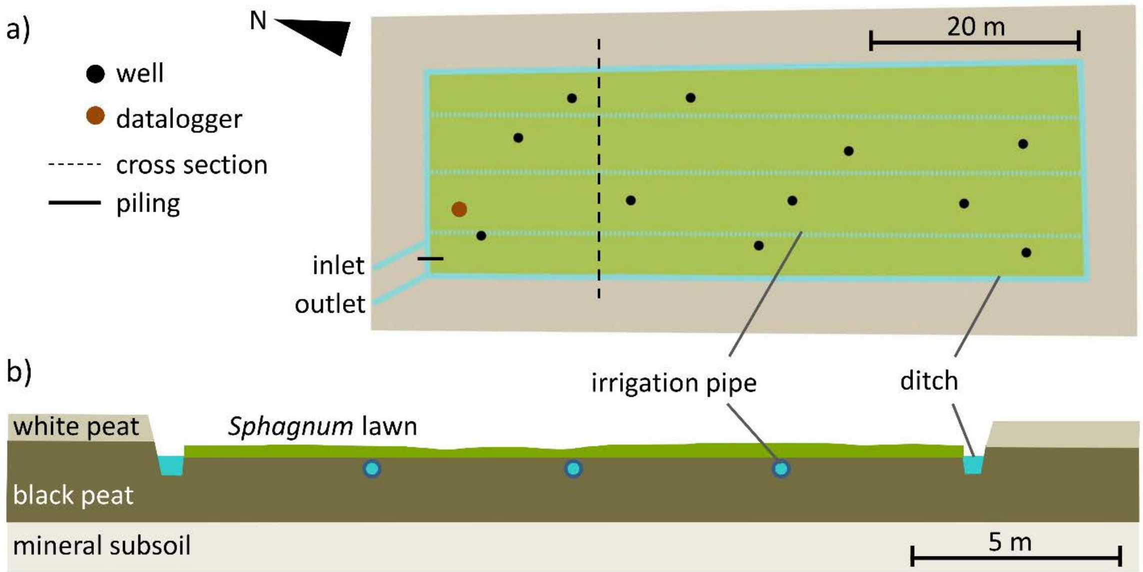

Figure 2. a) Schematic plan view and b) cross-section of the Ramsloh Sphagnum farming study site at the start of the experiment (after Kamermann & Blankenburg 2008).

Figure 3. The Sphagnum farming study site at Ramsloh, Germany. a) Aerial view directly after installation in November 2004 within a peat cutting field; b) established *Sphagnum* lawn five years after installation (March 2010); c) established *Sphagnum* lawn with fruiting *Eriophorum angustifolium* and *E. vaginatum* (May 2010); d) *Sphagnum* lawn thickness six years after installation (October 2010). Photos: G. Block.

vascular plants, the site was mowed 1–3 times *per* growing season with a handheld petrol strimmer starting in August 2005.

Site conditions

The thickness of the residual peat layer was determined at 44 evenly distributed points across the site, using a gouge auger (diameter 3 cm). To characterise the surface peat the uppermost 5 cm of peat was sampled three times during the experiment using a Russian pattern 'D'-corer (chamber diameter 4.5 cm, length 50 cm, made by Eijkelkamp) and analysed for degree of humification (after von Post 1924), bulk density, pH, carbon (C), nitrogen (N) and phosphorous (P). Bulk density was determined by drying a 5 cm slice (39.76 cm^3) of the core to constant weight at 80 °C (at least 48 h; Hendry & Grime 1993). The pH of a mixture of 10 ml fresh peat and 25 ml $CaCl_2$ was measured after 24 hours using a WTW 315i pH meter with SenTix41 electrode. Total N content and C/N quotient were determined with a dry-combustion CN analyser (CHNOS element analyser vario EL III). To measure total phosphorus (P), 300 mg of dry peat was microwave digested (START 1500, MLS Enterprises) and treated with an acidic molybdate solution containing ascorbic acid (modified molybdenum blue method, Temminghoff 2004) before determination of P using a UV/visible spectrophotometer (Cecil CE 1021, wavelength 890 nm).

The phreatic level of the interstitial water (Schouwenaars 1995) was measured in eleven wells evenly distributed over the site, manually as the distance between water table and peat or moss surface at intervals of two weeks to four months from December 2005 until June 2010, automatically every half hour with a data collector (Schlumberger MiniDiver; Beyer & Höper 2015) from June 2010 to Dec 2011, and again manually twice a year from 2012 until the end of the experiment (Figure 2). Water quality in the ditch was analysed twice during the experiment. pH and electrical conductivity (EC) were measured with a multi variable tester Hanna Combo HI 98129. Orthophosphate (ortho-P) was determined by the modified molybdenum blue method (Temminghoff 2004) after filtering the samples (cellulose acetate filter with pore size 0.45 µm), and total phosphorus was measured similarly after microwave digestion (START 1500, MLS Enterprises). Potassium (K), calcium (Ca), and sodium (Na) were determined directly after microwave digestion using an atomic absorption flame spectrometer (CD-ContrAA 300, analytic Jena). Ammonium (NH_4^+) and nitrate (NO_3^-) in the water were measured photometrically after Krom (1980, salicylate method) and Crompton (1996, UV/visible spectrophotometer), respectively.

Vegetation development and *Sphagnum* growth

We monitored cover of vascular plants, moss species, open water, bare peat, and litter (including the applied straw) using the scale of Londo (1976), as well as *Sphagnum* lawn thickness (at five points *per* plot), in 25 cm × 25 cm plots located at random over the study site (*cf*. Hurlbert 1984). For *Sphagnum* we differentiated 'vital' (green, "healthy") and 'subvital' (white to brownish) mosses.

To determine the annual development of total biomass accumulation since installation, a varying number of entire plots was harvested with scissors each year, starting three years after installation. For each plot *Sphagnum* species, other mosses, vascular plants and litter were separated and dried to constant weight (80 °C for 48 h, Hendry & Grime 1993). In 2010/11 and 2011/12 five single *Sphagnum* shoots *per* plot were marked by attaching a nylon cable tie (width 2 mm, length 100 mm) directly below the moss capitulum (0–1 cm, *cf*. Clymo 1973). Then, after harvesting, the plot sample was divided into two parts, the upper part (= one year's biomass production) above the cable ties and the lower part (= the residual biomass of previous years) below them. The difference between the total biomass sample in one year and the part below the cable ties one year later indicated the loss by decomposition.

In March 2011 (6.5 years after installation) we recorded *Sphagnum* lawn thickness and peat surface altitude (Trimble TSC 3 differential GPS) at 222 points on a ~ 2.5 m × 2.5 m grid covering the entire area, starting at the western irrigation ditch.

Nutrient concentrations in the moss capitula were measured for each plot ($n = 61$) in 2010. Carbon (C), nitrogen (N), phosphorous (P) and potassium (K) were determined, using the methods described above for peat and water.

Data analysis

We used R software (R Development Core Team 2009) and the packages AED (Zuur *et al.* 2009) and stats (R Development Core Team 2009) for statistical data exploration, computation and graphics.

Boosted regression trees (BRTs; Friedman 2001, Elith *et al.* 2008) were used to identify the effect of site variables on *Sphagnum* establishment and *Sphagnum* biomass productivity. We chose this method because BRTs can fit complex nonlinear relationships and reduce the problem of 'overfitting' (Elith *et al.* 2008), whilst highly correlated explanatory variables do not cause numeric aberrations (Friedman & Meulman 2003).

We tested the dependence of the cover of vital *Sphagnum papillosum* (%, July 2007, 32 months after installation) on litter cover (%, July 2007, 32 months after installation), relative height of the peat surface (cm above the lowest peat surface altitude), layer thickness of peatmoss fragments (cm, June 2005, eight months after installation), minimum distance to an irrigation pipe (m), straw layer thickness and cover, as well as the cover of vital peatmoss (%, June 2005, eight months after installation). Additionally, we used BRT to test the dependence of annual biomass productivity of *Sphagnum papillosum* (period 48–72 months after installation) on capitula N, P and K concentrations (mg g^{-1}, dry mass basis), capitula N/P and N/K quotients, P concentration of the surface peat (mg g^{-1}, dry mass basis), relative height of peat surface (cm above the lowest surface altitude), pH, C/N quotient, degree of decomposition and dry bulk density (g L^{-1}) of the surface peat, minimal distance to the ditch and irrigation pipes (m), and cover of litter and vascular plants (%).

The BRT tool calculates multiple regression models (regression trees) and includes an adaptive method for combining many simple models to give improved predictive performance (boosting). The final additive regression model is fitted forward with increasing numbers of trees (Elith *et al.* 2008). As this method does not deliver *P*-values, but uses internal validation processes, we used ten-fold cross validation for model development and validation. Within the BRT model, three terms are used to optimise predictive performance: bag fraction, learning rate, and tree complexity (Friedman 2001, Elith *et al.* 2008). Explanatory variables with explaining deviances below 1 % were excluded from the final model. We used R package gbm (version 1.6-3) (Ridgeway 2017).

Sphagnum lawn thickness, measured at points on a ~ 2.5 m × 2.5 m grid in March 2011 (6.5 years after installation), was tested for association with minimum distance to an irrigation ditch or pipe (in metres) and height of the peat surface because the distances of grid points from the irrigation system varied due to the irregular shape of the pilot study site (width 19.9–21 m; length 60.5–62.7 m). For this analysis we calculated the Pearson's product moment correlation coefficient (Crawley 2005). Relationships were visualised using Surfer (Golden Software).

Differences in dry mass accumulation of *Sphagnum* were analysed using the non-parametric Kruskal Wallis test and a multiple comparison test after Siegel & Castellan (1988), using R package pgirmess (Giraudoux 2010) because sample sizes were unequal.

RESULTS

Site conditions

Peat layer

When the experiment had been set up, the thickness of the peat layer was 160–195 cm. The peat was a strongly humified (mainly H7) 'black peat'. Nitrogen concentration remained constant over time, whereas phosphorous concentration increased (Table 1). Bulk density varied between 71 and 115 g L^{-1}.

Water

Irrigation water quality was similar in June 2006 and two years later (Table 2). The water table fluctuated between 14 cm above and 36.5 cm below the peat surface, corresponding to 4 cm above to 40.5 cm below the peatmoss surface (Figures 4, 5). During the first five winters the water table did not drop below 25 cm depth (below peatmoss surface), except during

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Table 1. Characterisation of the 'black peat' of the Ramsloh site over the duration of the study (mean value ± SD). Data from September 2004 derived from Kamermann & Blankenburg (2008). n.d. = data not determined.

	Sep 2004	Aug 2007	Feb 2011
phosphorous (%)	0.01 ± 0	0.02 ± 0.01	0.17 ± 0.04
nitrogen (%)	1.24 ± 0.13	1.08 ± 0.08	1.01 ± 0.16
organic carbon (%)	58.1 ± 0.6	57.3±0.9	55.5 ± 1
C/N quotient	47 ± 5	53 ± 4	56 ± 9
dry bulk density (g L^{-1})	76 ± 8	115 ± 18	71 ± 11
pH	n.d.	n.d.	3.3 ± 0.1
number of samples	5	11	61

the first winter (2005/2006) (Figure 5). The deepest water tables in single years occurred in the summer half-years (Figure 5), in particular in spring (Figure 4). From June 2009 to July 2010 the water table was continuously above the peat surface (Figure 4), and during the summer of 2009 it was less than 20 cm below the peatmoss surface (Figure 5).

Development of vascular plants and litter

The total cover of vascular plants varied over the year, and was lowest in spring. The highest values were observed in summer and reached almost 50 % on average in July 2007 (Figure 6a). Mean total plant cover declined in the long term. *Juncus effusus* dominated in the first two years but had disappeared

Table 2. Comparison of irrigation water quality at the study site in June 2006 (after Kamermann & Blankenburg 2008) and June 2008 ($n = 1$) with the characteristics of pore water in a natural bog (Lütt 1992). n.d. = data not determined. Unless otherwise indicated, units are mg L^{-1}.

	Ramsloh Sphagnum farming site		natural bog
	14 June 2006	20 June 2008	Lütt 1992
NH_4^+	4.4	2.00	0.048–0.31
NO_3^-	< 0.5	0.67	0–0.018
orthophosphate (PO_4)	0.18	0.15	n.d.
total phosphate (PO_4)	0.15	0.16	0.078–0.231
K^+	1.59	1.26	0.45–3.14
Ca^{2+}	2.06	3.12	0.87–1.69
Na^+	14.7	14.77	7.6–14.0
pH	6.04	n.d.	3.5–5.8
EC (µS cm^{-1})	122	n.d.	8–180

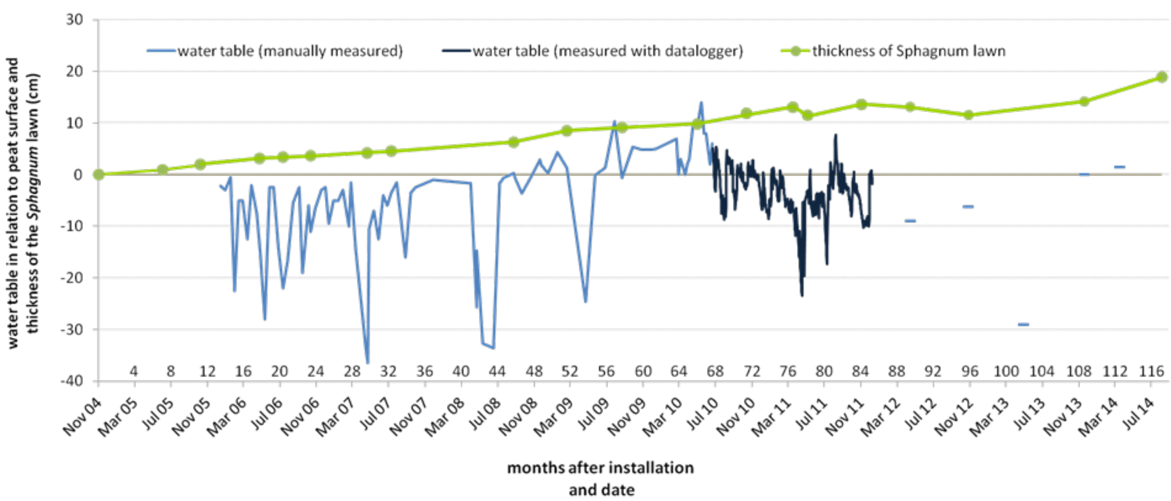

Figure 4. Fluctuations of water table relative to peat and peatmoss surface, and mean thickness (in cm) of *Sphagnum* lawn within 5 m of the water table measurement points. Water table position was determined manually (light blue) in the most northernmost well (near the datalogger) or by datalogger (dark blue, Beyer & Höper 2015). For locations of the measurement points see Figure 2. Water table data from 2012 onwards are shown as discrete points because measurements were made on only two occasions *per* year.

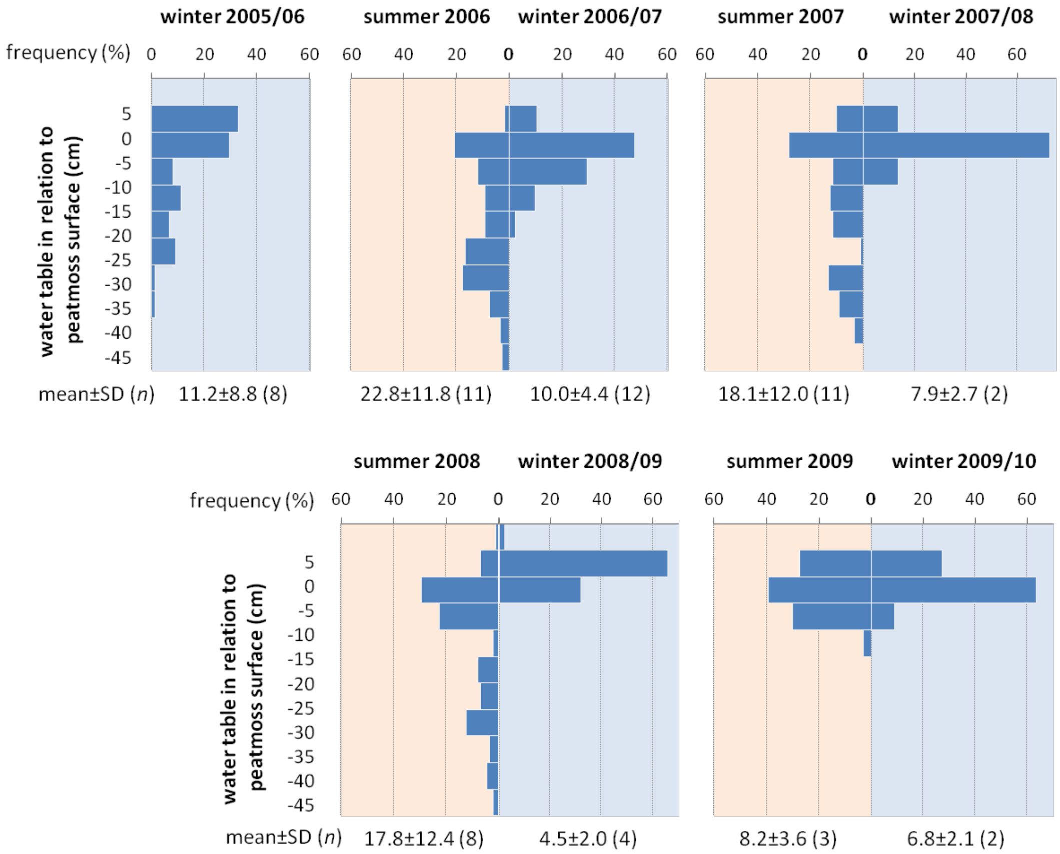

Figure 5. Water table frequency distribution (grouped into classes of 5 cm) and mean water table in relation to peatmoss surface in winter (October–March, blue) and summer (April–September, pink) for the period December 2005 to December 2009. Water table position was determined in eleven wells (see Figure 2a) on each observation date. The number of observations is given in brackets below each diagram.

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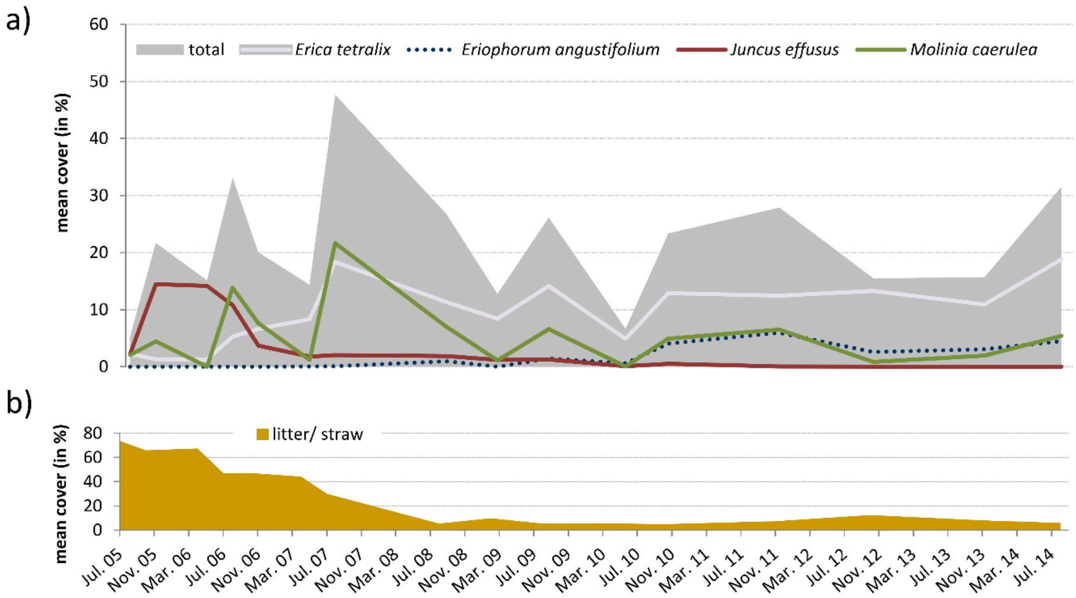

Figure 6. Development through time of a) mean total cover of vascular plants and selected species (%) and b) mean cover of litter including straw and mowed material, at the study site.

5.5 years after installation, whereas *Eriophorum angustifolium* colonised after 2.5 years and covered up to ~ 4.5 % of the site at the end of the experiment. The most frequent species was *Erica tetralix* with maximum cover values of 19 % in summer.

The mean cover of litter (mainly mowed material), including the applied straw mulch, decreased continuously from 73 % eight months after installation to ~ 5 % in August 2008 and remained more or less constant for the last six years of the experiment (Figure 6b).

***Sphagnum* establishment**

Eight months after installation, vital peatmoss had grown out of the fragments and covered on average 36 % of the study site (Figure 7). After 3.75 years (45 months) the average cover value for *Sphagnum papillosum* lawn was 91 %. Other *Sphagnum* species occurred only in small quantities. The cover of *S. fallax*, *S. cuspidatum* and *S. fimbriatum* remained below 1 %, and that of *S. magellanicum* below 5 %.

The cover of litter/straw was identified as the most relevant variable for successful *Sphagnum* establishment (Figure 8). A dense *Sphagnum* lawn (at least 90 % cover) occurred only when litter cover was less than 20 %. As soon as litter cover exceeded 20 %, the cover of vital peatmoss (including moss growing below the litter) decreased rapidly (Figure 8). Peat surface height also influenced establishment - the higher the peat surface, the lower the *Sphagnum* cover. Distance to the nearest irrigation pipe was less important, with the highest *Sphagnum* cover occurring at a distance of 1 m from the pipe. The thickness of the layer of peatmoss fragments eight months after spreading (up to 2.5 cm) also affected the success of establishment. *Sphagnum* cover after 32 months was highest at sites where the peatmoss layer was initially more than 1 cm thick. The initial thickness of the straw layer had little effect on *Sphagnum* establishment three years after installation, although a thick (> 3 cm) straw layer led to significantly lower peatmoss cover. Peatmoss cover half a year after installation had no effect on the cover of vital peatmoss two years later (2007).

***Sphagnum* growth**

The thickness of the *Sphagnum* lawn increased continuously to 19 cm, on average, ten years after installation, with a stagnation period between October 2010 and October 2012 (Figures 4, 9). For the latter period we determined a mean growth in length for *Sphagnum papillosum* of 5 cm (Figure 9). From 2008 to 2012, length growth was 13.5 cm whereas lawn thickness increased by 5.5 cm (Figure 9).

The greatest lawn thicknesses (up to 30.5 cm 6.5 years after installation) were measured in the northern part of the study area and adjacent to the irrigation system (Figure 10a, dark green areas). The closer to the irrigation system (ditch or pipe), the thicker the *Sphagnum* lawns that were formed ($P < 0.001$, $r = -0.3$). Additionally, *Sphagnum* growth

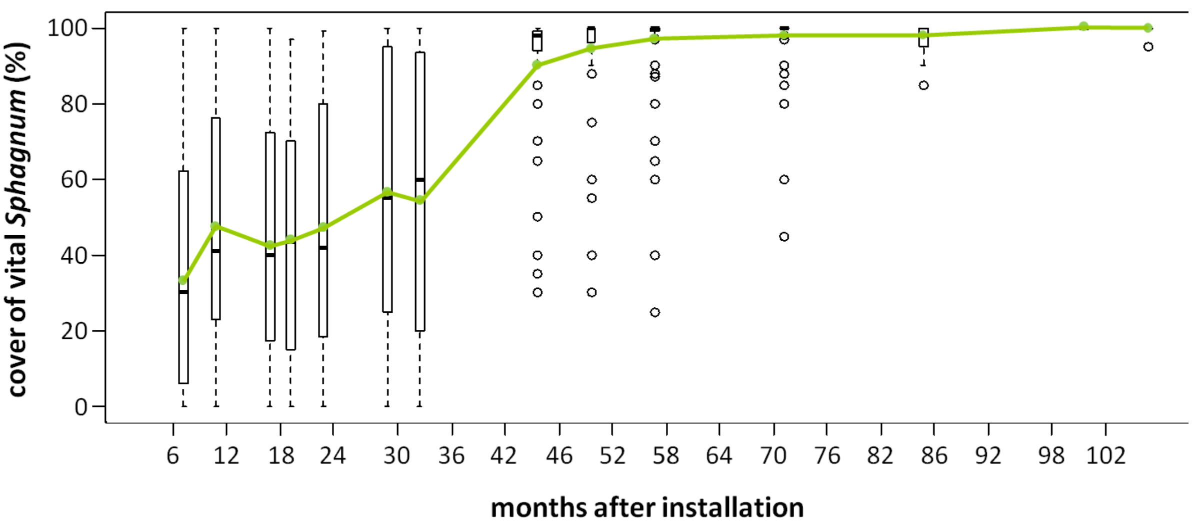

Figure 7. Cover of vital *Sphagnum* (%) at the study site for a period of 105 months after installation. For each observation date the plot shows the median (bold line), the upper and lower quartiles (the box includes 50 % of the data), the lowest value within 1.5 interquartile range (IQR) of the lower quartile (lower whisker), the highest value within 1.5 IQR of the upper quartile (upper whisker), and the outliers (i.e. values outside these ranges) (o). The green line connects the mean values.

was affected by peat surface height. Despite accurate levelling of the peat surface at installation, there were height differences of up to 17 cm 6.5 years after installation (Figure 10b). The higher the peat surface, the lower the *Sphagnum* lawn thickness ($P < 0.001$, $r = -0.4$). The peat surface was generally lower where irrigation pipes were installed ($P < 0.05$, $r = 0.2$).

After nine years the dry biomass *per* hectare was, on average, 19.5 t of pure *Sphagnum* (1,950 g m^{-2}) and 0.7 t of vascular plants growing within the *Sphagnum* lawn. Total *Sphagnum* dry biomass accumulation (including initially applied moss material) was lower in the first three years after installation (mean value 1 t ha^{-1} yr^{-1}) than between

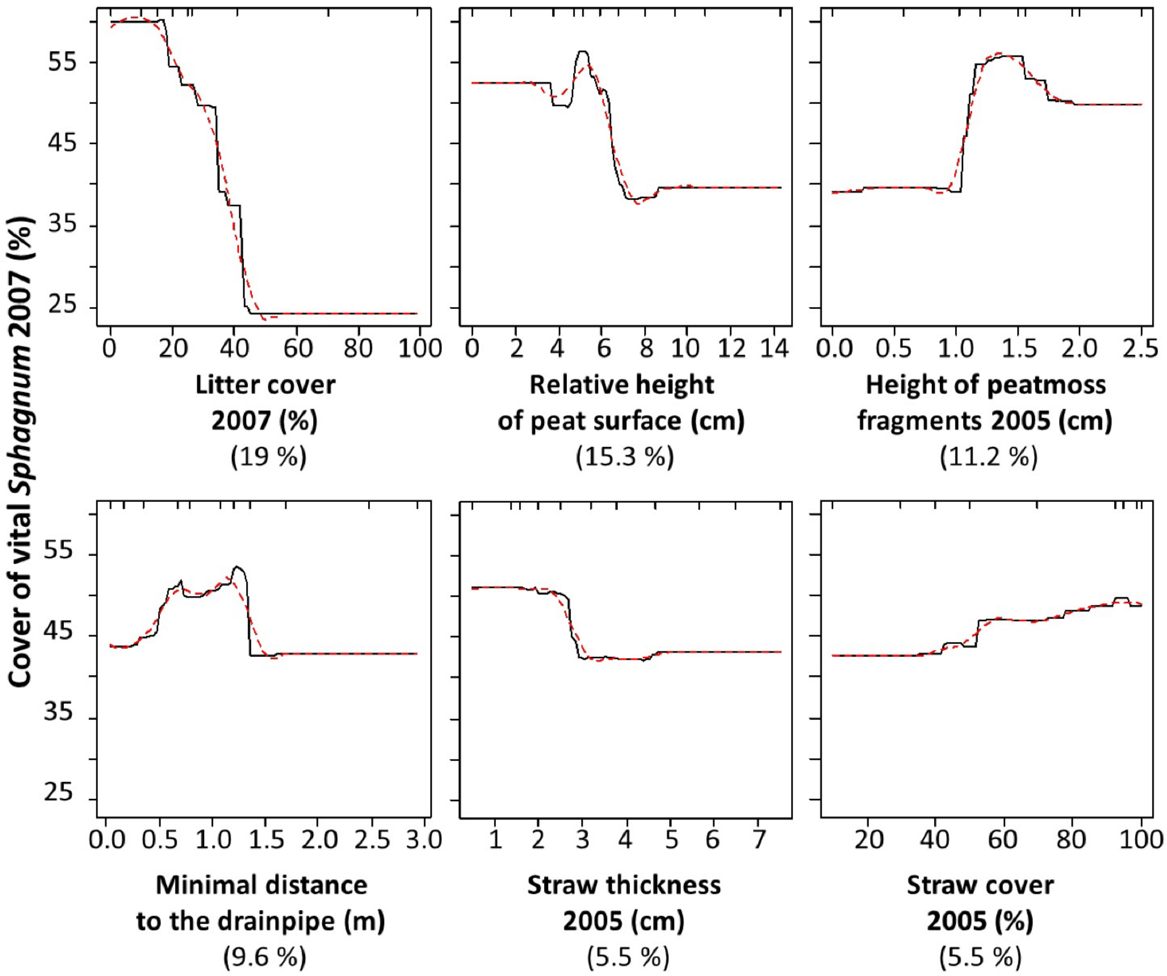

Figure 8. Boosted regression tree model of establishment expressed as cover (%) of vital *Sphagnum papillosum* 32 months after installation (July 2007, response variable) and its predictor/explanatory variables litter cover (%, July 2007), relative height of peat surface (cm above the lowest peat surface altitude), layer thickness of peatmoss fragments (cm, June 2005, 8 months after installation), minimum distance to an irrigation pipe (m), straw layer thickness (cm) and cover (%, June 2005). Percentages in the abscissa labels (in brackets) give the absolute contributions of individual variables to biomass productivity. The red (dashed) line is the smoothed relationship between the cover of vital peatmoss in 2007 and the individual explanatory variable. The vertical markers on the 'box' line at the top indicate real observations. The boosted regression tree model was performed with 60 observations and six predictors, using the Poisson distribution, with tree complexity = 2 (sets the complexity of individual trees, interaction order), learning rate = 0.005 (sets the weight applied to individual trees, shrinkage factor), and bag fraction = 0.75 (sets the proportion of observations used in selecting variables). The final model was fitted with 1050 trees and explained deviance = 0.66. No relationship was observed for cover of vital *Sphagnum* (%, June 2005, eight months after installation).

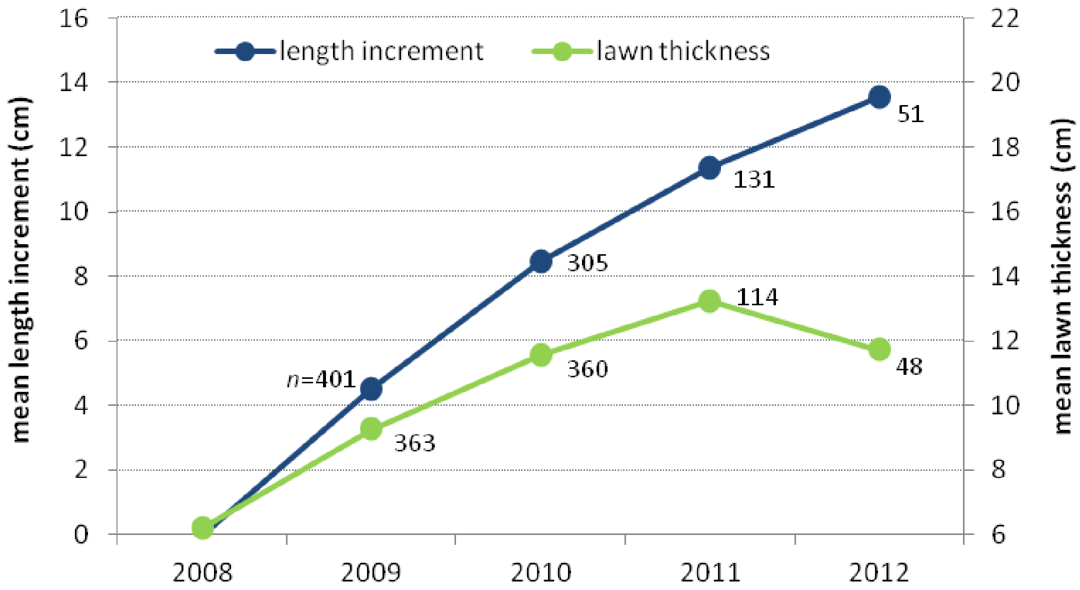

Figure 9. Mean cumulative length increment and mean lawn thickness of *Sphagnum papillosum* (in cm, mean thickness 6.2 cm in August 2008) at the study site between 2008 and 2012. Number of samples (n) for each measurement is written next to the mean value.

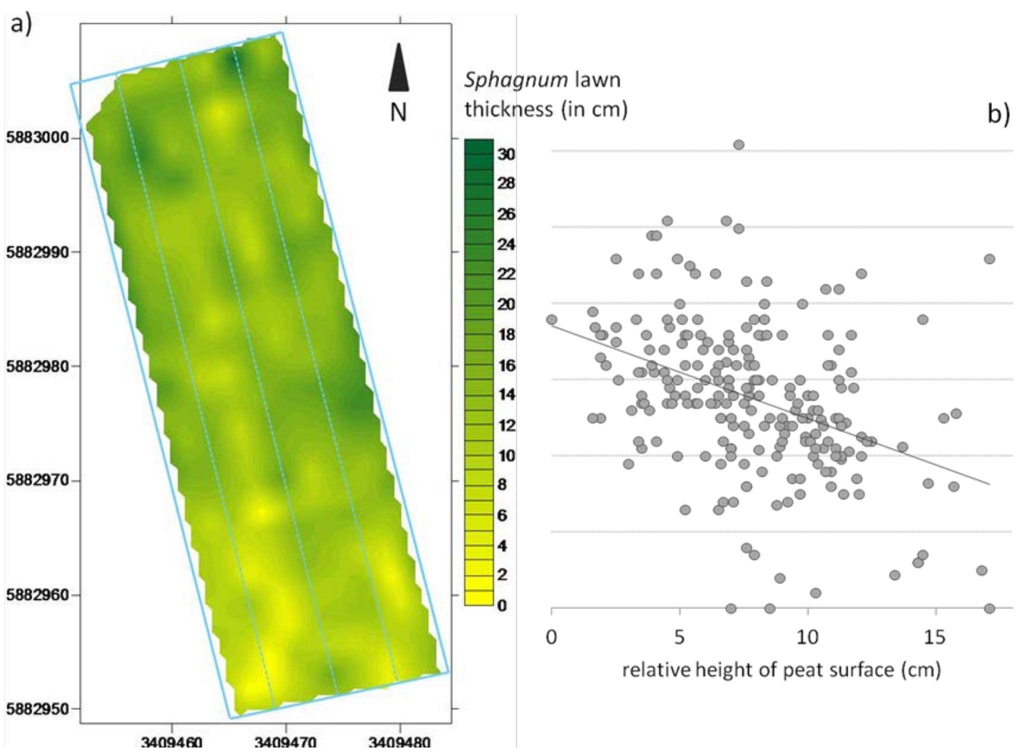

Figure 10. a) *Sphagnum papillosum* lawn thickness (cm) at the study site 6.5 years after installation, measured at points on a 2.5 m grid. Blue lines represent the irrigation system with ditches (solid lines) and subsurface pipes (dotted lines). b) Relationship between *Sphagnum* lawn thickness and relative height of the peat surface (cm above the lowest peat surface altitude) ($P < 0.001$, $r = -0.4$).

2007 and 2011 (mean value 3.7 t ha^{-1} yr^{-1}), and stagnated after 2011 (Figure 11). Annual dry *Sphagnum* biomass productivity over the period 2010–2011 reached 6.9 t ha^{-1}.

In October 2010, nitrogen (N) concentration in the peatmoss capitula (dry mass basis) ranged from 7.9 to 15.8 (mean 12.2) mg g^{-1}, phosphorus (P) concentration was 0.3–1.2 mg g^{-1}, and potassium (K) concentration was 2.0–10.1 mg g^{-1} (Table 3).

To identify the driving variables for *Sphagnum* productivity we used data from the period October 2008 to October 2010 (48–72 months after installation), i.e. after the peatmoss lawn had reached > 90 % cover and when its biomass accumulation rate

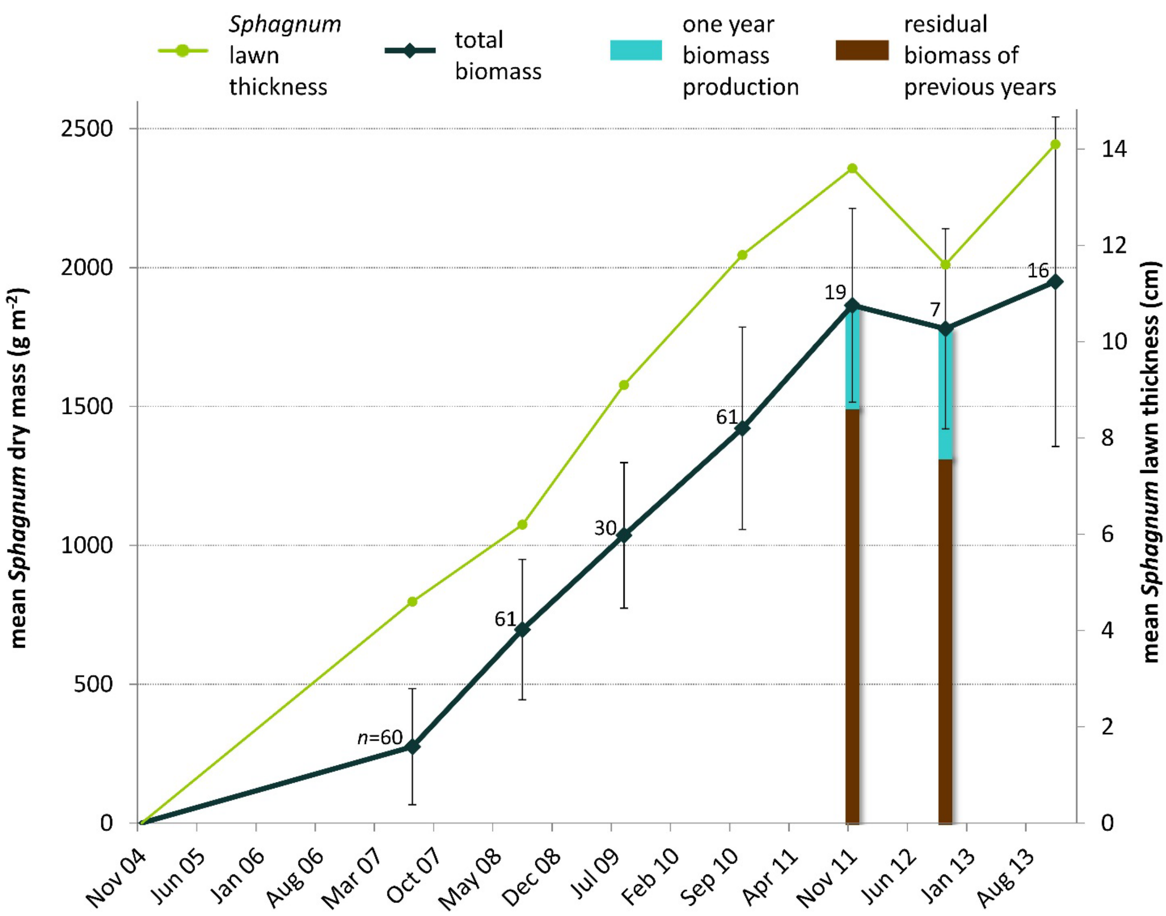

Figure 11. Development of mean *Sphagnum papillosum* lawn thickness measured at five points in each plot (green) and mean total *Sphagnum* biomass (dry mass ± SD) over time (dark blue) at the Ramsloh study site. The bars (left bar 2010–2011, right bar 2011–2012) are divided into one-year biomass production (light blue) and residual biomass of previous years (brown) (in g m^{-2}). The number of samples is written next to each mean value.

Table 3. Nutrient concentrations (mg g^{-1}, dry mass basis) and quotients in the capitula of *Sphagnum papillosum* (uppermost 1 cm) in October 2010, six years after installation of the Sphagnum farming site (*n* = 61).

	N	P	K	N/P	N/K
mean ± SD	12.2 ± 1.3	0.5 ± 0.2	3.5 ± 1.2	24.6 ± 7.8	3.8 ± 0.9
minimum	7.9	0.3	2.0	9.6	1.2
maximum	15.8	1.2	10.1	53.2	6.9

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was highest. Dry biomass productivity decreased at capitula N concentrations > 12 mg g^{-1} and N/P quotients > 18.5, as well as at P concentrations in surface peat > 1.6 mg g^{-1} and surface peat pH values > 3.29 (Figure 12). It was higher at lower-lying plots and close to the irrigation ditch. Irrigation pipes had no influence on productivity.

Total biomass accumulation for the period 2004–2010 determined in 2010 was similar to the residual biomass of 2004–2010 determined in 2011, indicating no biomass loss; whereas residual biomass for 2004–2011 determined in 2012 was, on average, 30 % lower than total biomass determined in 2011, indicating considerable loss (Figure 13).

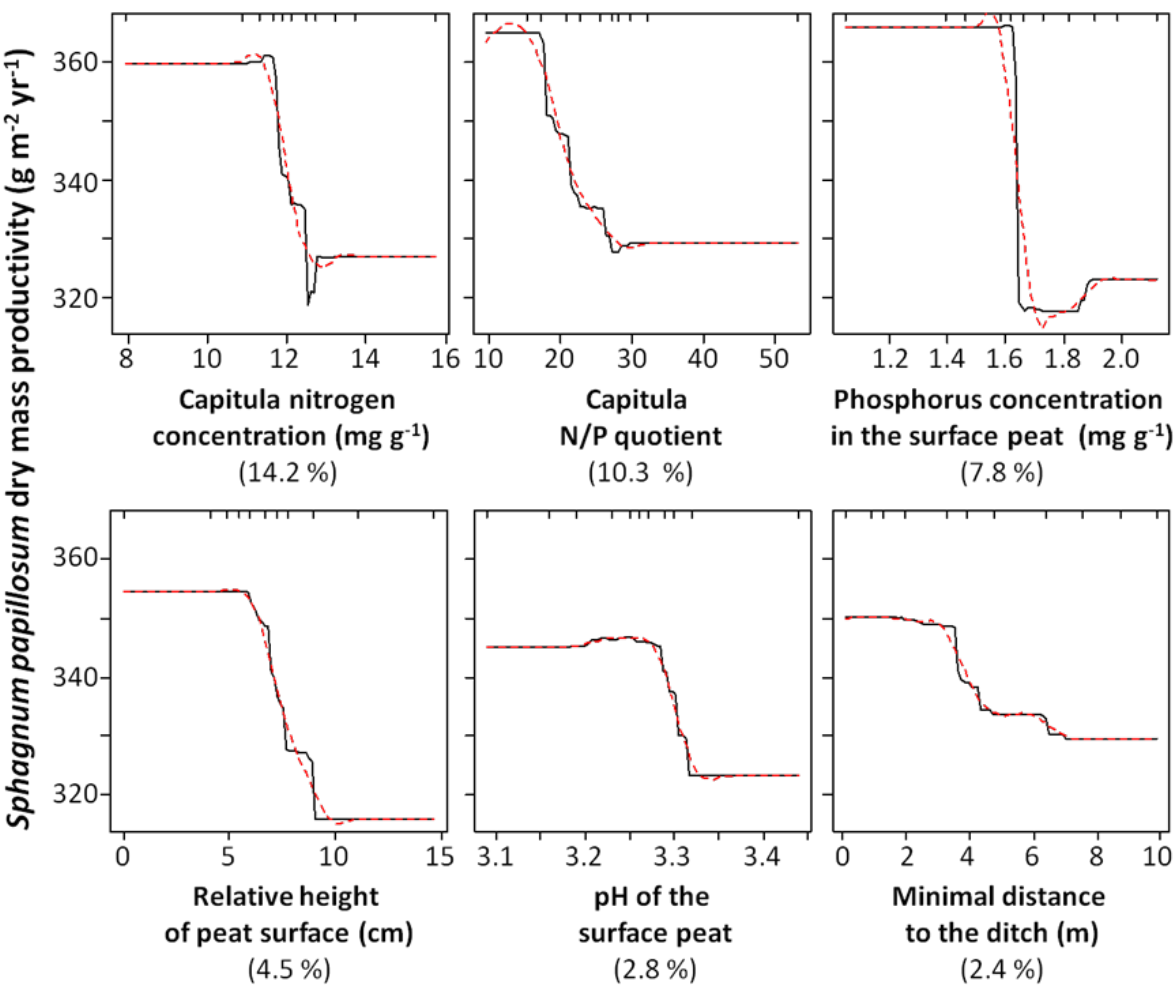

Figure 12. Boosted regression tree model of *Sphagnum papillosum* biomass productivity in g m^{-2} yr^{-1} (response variable) between 2008 and 2010 and its predictor/explanatory variables dry mass nitrogen concentration (mg g^{-1}) in capitula, capitula N/P quotient, dry mass phosphorus concentration (mg g^{-1}) of the surface peat, relative height of the peat surface (cm above lowest peat surface altitude), pH of the surface peat, and minimal distance to the ditch (m). Percentages in the abscissa labels (in brackets) give the absolute contributions of individual variables to biomass productivity. The red (dashed) line is the smoothed relationship between the *Sphagnum papillosum* biomass productivity and the individual explanatory variable. The vertical markers on the 'box' line at the top indicate real observations. The boosted regression tree model was performed with 61 observations and six predictors, using the Poisson distribution, with tree complexity = 2, learning rate = 0.001, and bag fraction = 0.75. The final model was fitted with 2850 trees and explained deviance = 0.42. No relationship was observed for minimal distance to the irrigation pipes (m), dry bulk density (g L^{-1}), dry mass nitrogen concentration (mg g^{-1}), C/N quotient and degree of humification of the surface peat, dry mass phosphorus and potassium concentrations (mg g^{-1}) and N/K quotient of the peatmoss capitula, cover of litter and vascular plants (both %).

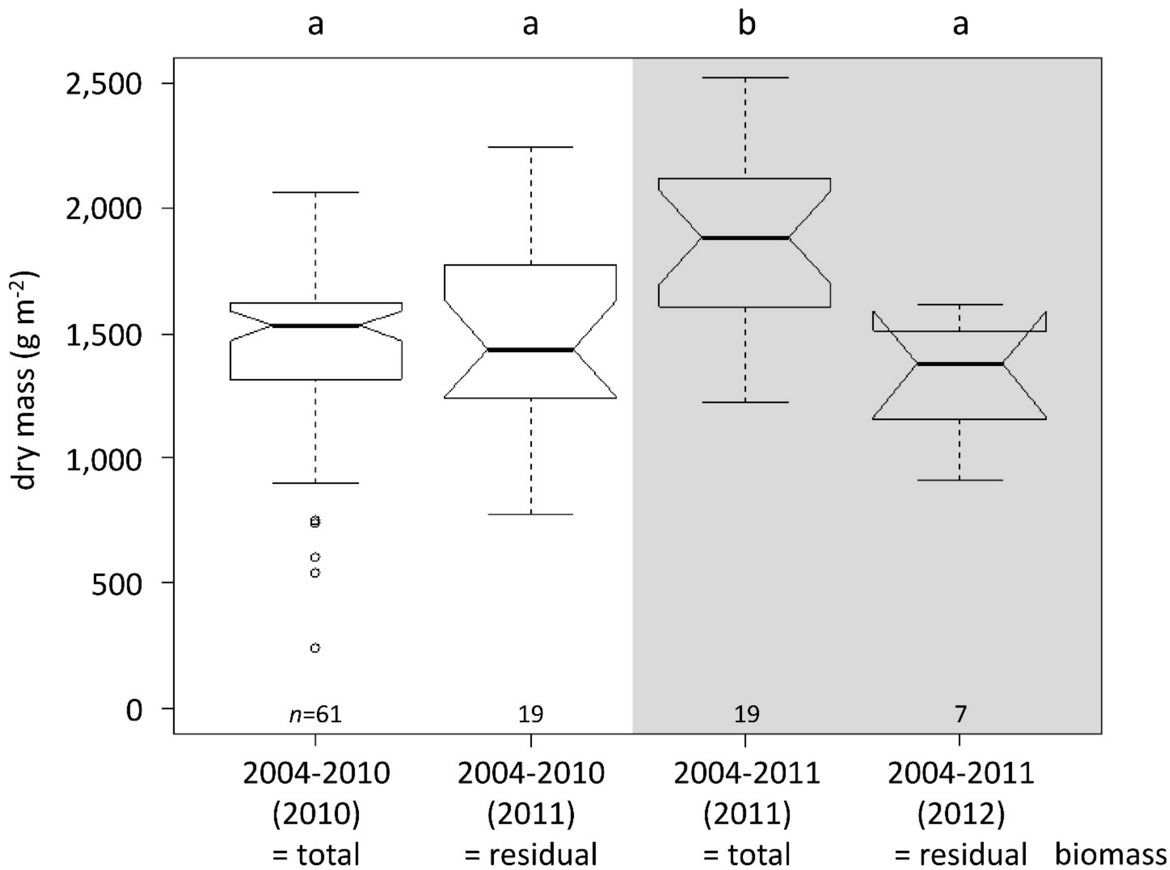

Figure 13. Biomass accumulation of peatmoss for 2004–2010 (white) and 2004–2011 (grey), as determined at the ends of these periods (2010 or 2011 = total biomass) and one year later (2011 or 2012 = residual biomass). Number of samples is written below each boxplot. Values with different letters differ significantly ($P \leq 0.05$). Differences were analysed using the non-parametric Kruskal Wallis test after Siegel & Castellan (1988).

3

DISCUSSION

Sphagnum productivity and biomass accumulation

At 365 and 461 g m^{-2} yr^{-1} on average for 2010/11 and 2011/12, respectively, the dry mass productivity of *Sphagnum papillosum* measured here was higher than on natural bogs (*cf*. Gunnarson 2005, Krebs *et al*. 2016), in particular those in north-west Germany studied by Lütt (1992) where the average dry mass productivity was 202 g m^{-2} yr^{-1}. Higher values (up to 550 g m^{-2} yr^{-1}) have been found only under the year-round warm and humid conditions of the Kolkheti Lowlands in Georgia (Krebs *et al.* 2016). At the Sphagnum farming site in Ramsloh 1.864 ± 349 g m^{-2} of *Sphagnum* dry mass accumulated between 2004 and 2011, *i.e.* during seven growing seasons. In a long-term Sphagnum farming experiment in Shippagan (Canada) *Sphagnum* biomass accumulation was nearly two-and-a-half times smaller (787 ± 86 g m^{-2}) over the same period (Pouliot *et al.* 2015). Although different *Sphagnum* species were cultivated (*S. papillosum* in Ramsloh; mainly *S. rubellum, S. fuscum, S. flavicomans* and *S. magellanicum* in Canada), the productivity of these species in natural bogs is similar (Gunnarson 2005). We assume that better water supply and longer growing seasons are the main reasons for the faster establishment and higher biomass accumulation rates observed in Ramsloh.

Decisive role of water supply

Optimal *Sphagnum* growth requires a constantly high water table (Hayward & Clymo 1982, 1983; Titus & Wagner 1984, Li *et al.* 1992, Robroek *et al.* 2009), which, in our study, the wind pump failed to achieve. The water table fluctuated, with lowest values (up to

36.5 cm below peat surface, equivalent to 40.5 cm below peatmoss surface) being observed at the driest time of the year. As soon as the water table drops below the *Sphagnum* capitulum, moisture content decreases (McCarter & Price 2014) leading to reduced growth rates (Robroek *et al.* 2007, Strack & Price 2009).

As we had not monitored the water table at each permanent plot, we used the dry bulk density of surface peat, peat surface height, and distance to the nearest irrigation element (ditch or pipe) as proxies for water supply. The pipes irrigated well during the establishment phase, but six years later their positive influence on *Sphagnum* lawn thickness was observed only up to a distance of 0.5 m from the pipes (Figure 10a) where the peat surface was lower-lying and closer to the water table, probably as a result of subsidence and compaction of peat over the years. Because the wetter conditions in these locations may also be explained by ponding of rain and inlet water, it is unclear whether the pipes have maintained their functionality. However, *Sphagnum* lawn thickness was significantly lower with increasing distance from the pipes. This relationship was not found for *Sphagnum* biomass productivity, which was greatest within 3.5 m of the ditches (Figure 12). This observation indicates a farther-reaching influence of the ditches, which possibly arises because the ditches (50 cm deep and 50 cm wide) are a larger water reservoir with a greater area of contact with peat than the irrigation pipes (~ 10 cm diameter). As ditches are easier to install and manage, they seem more suitable than pipes for irrigating *Sphagnum* cultures.

Whereas the peat surface level was very similar across the whole site at installation, its height varied by up to 17 cm after 6.5 years, *inter alia* as a result of uneven peat swelling (*cf*. Kennedy & Price 2005, Oleszczuk & Brandyk 2008). The closer the peat surface was to the water table, the wetter the site and the better the establishment and growth of peatmoss became. Differences in peat surface height should be minimised for uniform growth and easier management of the *Sphagnum* lawn. Despite drainage of the surrounding peat extraction site, vertical water loss was probably low because of the > 160 cm thick residual layer of highly decomposed peat. At the start of the experiment the site was situated in a shallow basin (Figure 2, *cf*. Campeau *et al*. 2004). Because of continued peat extraction in the surroundings the site protruded increasingly through time, and lay up to half a metre above the surroundings by the end of the experiment. The increasing water losses by downward and lateral leakage could be only partly compensated by irrigation water provided by the wind pump (*cf*. Figure 4). Unfortunately, we did not quantify this water supply.

Initial *Sphagnum* and straw cover

Although *Sphagnum* fragments were applied evenly with a cover of approximately 95 %, the average cover of vital peatmoss eight months later was only 36 %, ranging from 0 to 100 %. The low establishment success is probably attributable to the season of application (in November). This was close to the beginning of winter, when *Sphagnum* growth rates are low (Lütt 1992, *cf*. Krebs *et al*. 2016), and the fragile moss fragments might be particularly affected by frost. The start of the growing season (without long frost periods) could be a better time for establishing a *Sphagnum* culture, provided that sufficient water is supplied.

Peatmoss cover eight months after installation (2005) did not affect cover two years later (in 2007). The presence of a > 1 cm thick peatmoss layer (determined eight months after establishment) appeared to promote *Sphagnum* establishment significantly (Figure 8). This corresponds with the findings of Quinty & Rochefort (2003), who recommend the application of a fluffy layer of plant (including *Sphagnum*) fragments, initially 1–5 cm thick, for best restoration results. As mowing started in August 2005, the cover of litter/straw in 2005 (eight months after installation = July 2005) still consisted almost exclusively of applied straw. Over time the proportion of litter increased but the components could not be clearly distinguished. Straw cover is reported to improve the growing conditions of *Sphagnum* fragments (Quinty & Rochefort 2003). At the Ramsloh site around 6,500 kg of straw was applied *per* hectare (Kamermann & Blankenburg 2008), which is more than twice the minimum amount recommend by Quinty & Rochefort (2003). Our results show that straw thickness > 3 cm during establishment impedes the development of peatmoss, probably because the fragments receive insufficient light for growth.

Management of vascular plants

Vascular plants may facilitate *Sphagnum* growth by improving microclimate (increase of relative humidity, more stable temperatures) and by providing mechanical support (Pedersen 1975, Pouliot *et al.* 2011, Rydin & Jeglum 2013). When vascular plants dominate, however, they retard *Sphagnum* growth by shading, litterfall, and water and nutrient consumption (Malmer *et al.* 1994, Berendse *et al.* 2001; Limpens *et al.* 2003, 2011). Moss growth is reduced when shading exceeds 50 % (Clymo & Hayward 1982). Furthermore, large proportions of vascular plants and their seeds are undesirable in the raw material for growing media production (Guetegemeinschaft Substrate fuer

Pflanzen e.V. 2015). Therefore, it is important to contain vascular plant growth by mowing, and to remove the mowings, in order to achieve maximal high-quality *Sphagnum* yields. During the last six years of the experiment, vascular plant cover in summer could be maintained at around 30 % by regular mowing (Figure 6). Mowing effectively suppressed *Juncus effusus*, whereas *Erica tetralix* became the most frequent species because this low-growing plant could not be effectively mowed without damaging the mosses. The competitive pressure of vascular plants may decrease once a closed *Sphagnum* lawn has established because seeds, especially those of *Juncus effusus*, cannot germinate in the lawn due to lack of light (*cf*. McCorry & Renou 2003) and seedlings are rapidly overgrown by *Sphagnum* (*cf*. Ohlson *et al.* 2001).

Nutrient availability

The quality of the irrigation water in Ramsloh was similar to that of pore water in natural bogs (Table 2) except for ammonium and nitrate, which were much higher. Together with a total nitrogen deposition of 21 kg ha^{-1} yr^{-1} (UBA 2016) the nitrogen availability was very high and *Sphagnum* growth was not N-limited (Lamers *et al.* 2000, Berendse *et al.* 2001, Bragazza *et al*. 2004). The dry mass nitrogen concentration in the capitula of *Sphagnum papillosum* ranged from 7.9 to 15.8 mg g^{-1}, indicating N-saturated conditions (Lamers *et al.* 2000). In our study, the biomass production of *Sphagnum papillosum* decreased at nitrogen concentrations higher than 12 mg g^{-1} (Figure 12), but probably not as a result of toxicity since a capitulum dry mass N concentration of 13 mg g^{-1} is described as optimal for photosynthetic rate (in *S. balticum*, Granath *et al.* 2009) and only concentrations of 15 mg g^{-1} (in *S. fallax*, van der Heijden *et al.* 2000) or more (in *S. papillosum*, Temmink *et al*. 2016) are suggested to be indicative of N pollution stress.

The dry mass concentration of potassium in the capitula of *Sphagnum papillosum* in our study (on average 3.5 mg g^{-1}) corresponds to values in natural peatlands (Bragazza *et al*. 2004, Fritz *et al*. 2012). Since the N/K quotient of 3.8 ± 0.9 was only slightly above the threshold value indicating K limitation (N/K = 3.3, Bragazza *et al.* 2004) and the N/K quotient was not found to be an explanatory variable for biomass production, there was no evidence for K limitation at the Sphagnum farming site in Ramsloh.

The dry mass concentration of phosphorus in the capitula of *Sphagnum papillosum* (on average 0.5 mg g^{-1}) corresponds to values in P-limited peatlands (Limpens & Heijmans 2008, Aerts *et al.* 1992). In our study *Sphagnum* growth seemed to be limited by phosphorus, because biomass production decreased at N/P quotients > 18.5 (Figure 12) and N/P quotients > 14 indicate P limitation (Aerts *et al.* 1992). On the other hand, Bragazza *et al*. (2004) determined N/P quotients > 30 for P limitation in areas with N deposition > 10 kg ha^{-1} yr^{-1}. It has been shown in several experiments that *Sphagnum* biomass production can be stimulated by P fertilisation, but that high and stable water table is the decisive factor (Krebs & Gaudig 2005). The high nitrogen supply from the atmosphere and water, and the management-induced high water tables, make the Ramsloh situation difficult to compare with earlier studies. However, P limitation at the Sphagnum farming site cannot be excluded.

Decomposition

After the establishment phase, *Sphagnum* growth at the Ramsloh study site was constantly high for four years but a stagnation phase of two years (2010/11 to 2011/12) followed (Figure 11). A similar pattern was observed in long-term studies in Canada (Pouliot *et al*. 2015). During the stagnation period, *Sphagnum* biomass productivity increased but the residual biomass decreased, especially after 2011 (Figure 11), probably as a result of increased decomposition under the drier conditions of 2011/12 (Figure 4, *cf*. Johnson & Damman 1991, Lütt 1992). Growth stagnation continued through the dry conditions of 2012/13, but the thickness of the *Sphagnum* lawn increased again under the wetter conditions of 2013/14. As long as sufficient water is supplied, *Sphagnum* biomass accumulation remains high as a result of high productivity and simultaneously low decomposition.

3

CONCLUSIONS

Our study comprises the first long-term investigation of *Sphagnum* productivity under ‘controlled’ paludiculture conditions. To ensure a sufficient water supply for *Sphagnum* growth on low-permeability black peat, irrigation ditches 5 m apart must be installed. In this regard, subsurface irrigation *via* buried drainage pipes (Van den Akker *et al*. 2010) appeared to be less effective than ditching. If the *Sphagnum* is kept wet, its optimal growth is possible without fertilisation, and decomposition losses are restricted.

The choice of optimal harvesting time for *Sphagnum* biomass can be guided by lawn thickness, which is a satisfactory and easily determined indicator. However, the exact choice of harvest timing will have to balance technical feasibility (minimum lawn height), continued growth, increasing decomposition losses, and economic aspects.

Our study demonstrates that high *Sphagnum* yields can be achieved on cut-over (milled) bogs with black peat at the surface. The transferability to large-scale conventionally cut-over sites with the statutory 50 cm minimum thickness of residual peat has still to be tested (Wichmann *et al.* 2017). However, the greatest potential for Sphagnum farming in Germany is on bog grassland ("Hochmoorgrünland", Wichmann *et al.* 2017), where conversion of the current drainage-based peat-consuming agriculture to wet peat-preserving *Sphagnum* paludiculture provides additional benefits in terms of evaporative cooling (climate change adaptation) and reduction of greenhouse gas emissions (climate change mitigation) (Beyer & Höper 2015, Günther *et al.* 2017).

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4

Sphagnum farming from species selection to the production of growing media: a review

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Sphagnum farming from species selection to the production of growing media: a review

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SUMMARY

Sphagnum farming - the production of *Sphagnum* biomass on rewetted bogs - helps towards achieving global climate goals by halting greenhouse gas emissions from drained peat and by replacing peat with a renewable biomass alternative. Large-scale implementation of Sphagnum farming requires a wide range of know-how, from initial species selection up to the final production and use of *Sphagnum* biomass based growing media in horticulture. This article provides an overview of relevant knowledge accumulated over the last 15 years and identifies open questions.

KEY WORDS: bog, founder material, harvest, horticulture, management, paludiculture, Paris Agreement, peatland, peat moss, sustainable land use, water quality

INTRODUCTION

To achieve the aims of the 'Paris Agreement' (UNFCCC 2015) - *i.e.* to limit global average temperature to less than 2 °C above pre-industrial levels - net greenhouse gas emissions must start to decrease in the coming few years and be reduced to zero by 2050 (Figueres *et al*. 2017). Drained peatlands cover only 0.5 % of the Earth's land surface but globally contribute 5 % of anthropic greenhouse gas emissions (Joosten *et al*. 2016) and 32 % of cropland emissions (Carlson *et al*. 2017). The importance of rewetting degraded peatlands for greenhouse gas emissions reduction in the land use sector is widely recognised (Leifeld & Menichetti 2018). Sustainable peatland use concepts, as well as the replacement of peat in growing media, are promulgated by the UN Food and Agriculture Organisation (Biancalani & Avagyan 2014) and included in national climate commitments, *e.g.* in the German Climate Action Plan 2050 (BMUB 2016). Sphagnum farming leads not only to a reduction of greenhouse gas emissions from land use by rewetting drained peatlands, but also to replacement of a strategic fossil resource by a renewable alternative.

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Large-scale implementation of Sphagnum farming requires knowledge encompassing the entire production sequence; from the selection of cultivation material, acquisition of founder material, establishment and management of the production site, up to harvesting, transport and storage of the biomass and its subsequent processing and application in growing media. This article reviews the available information, including experience gained from *Sphagnum* vegetation restoration and *Sphagnum* gathering (see Box 1 and Table 1), and identifies gaps requiring further research.

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BOX 1

In recent times interest in fresh *Sphagnum* moss as a 'product' has been increasing, albeit with different backgrounds and aims. In this respect it is useful to distinguish between the following three types of activity.

***Sphagnum* vegetation restoration** aims to re-establish *Sphagnum* dominated vegetation on degraded bogs (including sites where peat extraction has occurred) for nature conservation, erosion control or carbon sequestration with no intention to harvest the re-established mosses (*e.g*. Wheeler *et al*. 1995, Shuttleworth *et al*. 2015, González & Rochefort 2014, Clarkson *et al*. 2017, Karofeld *et al*. 2016, 2017).

***Sphagnum* gathering** is the collection of *Sphagnum* (*e.g*. for orchid cultivation) from wild populations which are not (or minimally) managed to maintain or increase yields. *Sphagnum* gathering takes place *e.g.* in Chile (Zegers *et al*. 2006, FIA 2009, Díaz & Silva 2012), Australasia (Denne 1983, Buxton *et al*. 1996, Whinam & Buxton 1997) and recently also in Finland (Silvan *et al.* 2012, 2017; Joosten 2017).

Sphagnum farming aims to cultivate *Sphagnum* biomass for harvest, originally as founder material for restoration (Money 1994), but increasingly nowadays as an agricultural crop, *e.g*. as a raw material for horticultural growing media (Gaudig *et al.* 2014, 2017; Pouliot *et al*. 2015). This new type of peatland agriculture includes the selection of highly productive species and active management to maximise yields.

Table 1. Overview of selected *Sphagnum* vegetation restoration projects ≥ 3 ha and Sphagnum farming trials. Smaller *Sphagnum* vegetation restoration projects have been implemented, *e.g*. in Estonia (near Tässi), Germany (peatland Dalumer Moor), Lithuania (Aukštumala peatland) and the United Kingdom (Wales). Further information at www.sphagnumfarming.com.

Location	**Country**	**Former land use**	**Size in ha** total area *(moss area)*	**Duration**
***Sphagnum* vegetation restoration on degraded bogs**				
Quebec (16 sites)	Canada	milled peat extraction	575	since 1995
New Brunswick (10 sites)	Canada	milled peat extraction	167	since 1997
Saskatchewan (2 sites)	Canada	milled peat extraction	83	since 1999
Manitoba (1 site)	Canada	milled peat extraction	220	since 2006
Alberta (4 sites)	Canada	milled peat extraction	92	since 2009
Ilperveld	The Netherlands	grassland	*(3)*	since 2013
Sphagnum farming on cutover bog				
Saint-Marguerite-Marie	Canada	block-cut peat extraction	*(1.6)*	1992–2001
Shippagan 1	Canada	block-cut peat extraction	3.6 *(2.5)*	2004–2012
Ramsloh	Germany	milled peat extraction	*(0.12)*	2004–2014
Shippagan 2	Canada	block-cut peat extraction	2.0 *(0.6)*	since 2012
Twist (Drenth)	Germany	milled peat extraction	5.0 *(2.6)*	since 2015
Twist (Provinzialmoor)	Germany	milled peat extraction	5.0 *(2.3)*	since 2015
Malpils	Latvia	milled peat extraction	*(0.1)*	since 2015
Sphagnum farming on former drained bog grassland				
Rastede	Germany	grassland	14.0 *(5.6)*	since 2011
Sphagnum farming on other degraded bogs				
Saint-Modeste	Canada	remnant of natural bog within milled peat extraction field	1.0 *(0.3)*	since 2013

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SELECTION OF CULTIVATION MATERIAL

Sphagnum farming is similar to other agricultural practices in that it aims to maximise yields and limit costs. A first step is the selection of cultivation material on the basis of productivity and suitability for the intended use of the crop.

Productivity

Natural productivity of *Sphagnum* varies widely among species. Global average dry biomass production is 260 g m^{-2} yr^{-1}, while the maximum measured value is 1450 g m^{-2} yr^{-1} (Gunnarsson 2005). The highest mean values have been reported for *Sphagnum cristatum* (840 g m^{-2} yr^{-1}), *Sphagnum falcatulum* (770 g m^{-2} yr^{-1}) and *Sphagnum subnitens* (590 g m^{-2} yr^{-1}) growing under hyper-oceanic climate conditions in New Zealand (Stokes *et al.* 1999, Gunnarsson 2005), for *Sphagnum fuscum* (800 g m^{-2} yr^{-1}), *Sphagnum magellanicum* (790 g m^{-2} yr^{-1}) and *Sphagnum rubellum* (960 g m^{-2} yr^{-1}) in the German humid Rhoen mountains (Overbeck & Happach 1957), and for *Sphagnum palustre* in the warm temperate, humid Kolkheti Lowlands in Georgia (mean 575 g m^{-2} yr^{-1}; Krebs *et al.* 2016). Species of the *Sphagnum recurvum* group grow under relatively eutrophic conditions with generally high natural productivity (Gunnarsson 2005).

So far, only randomly sampled material from wild populations of a few species (*Sphagnum fallax*, *Sphagnum fimbriatum*, *Sphagnum flavicomans*, *S. fuscum*, *S. magellanicum*, *Sphagnum papillosum*, *S. palustre*, *S. rubellum*) has been tested in Sphagnum farming field trials (Krebs *et al.* 2012, Gaudig *et al.* 2014, 2017; Pouliot *et al.* 2015, Graf *et al.* 2017) and several more species have been tested in the glasshouse (*e.g.* Campeau & Rochefort 1996, Johnson 1998, Picard 2010, Gaudig *et al*. 2014).

Selection of highly productive wild provenances will lead to increased productivity. The existence of a genetic basis for productivity is illustrated by the differences between taxonomical sections of the genus *Sphagnum*. While most species of Sections *Acutifolia* and *Sphagnum* are characterised by low rates of production and decomposition, species of Section *Cuspidata* have higher productivity but also higher decomposition rates (Johnson & Damman 1991). However, productivity is also dependent on site conditions such as water regime and nutrient availability (Rydin & McDonald 1985, Aerts *et al.* 1992, Lamers *et al*. 2000, Limpens & Berendse 2003; see 'Managing a Sphagnum farming site' on pages 10–13 of this review). Cultivation (and research) will be required to optimise between site conditions and genotypes. Apart from genotype, other genetic properties that may influence productivity include sex and ploidy. Several species have dioecious gametophytes (*i.e*. of different sexes), *e.g*. *S. fallax* (Weston *et al.* 2018).

The role of ploidy deserves extra attention. Polyploid varieties of many agricultural crops display higher productivity and resistance than varieties with lower ploidy (Henry & Nevo 2014). About 70 % of all *Sphagnum* species have haploid gametophytes with chromosome number $n = 19$ while a smaller portion have $n = 38$ (Cronberg 1993). Populations of some species, *e.g*. *S. papillosum*, have both chromosome numbers. These species may provide valuable insights into the link between ploidy and yield. Further research is needed on the relationship between *Sphagnum* genotypes (including ploidy) and productivity, as well as the role of sex in this context.

Suitability for the intended purposes

Sphagnum biomass is already an important raw material for many valuable products (Pouliot *et al*. 2015, Glatzel & Rochefort 2017). Requirements for biomass quality depend on the end use.

Compactness, *i.e*. dry mass *per* unit length of moss, as well as the number of open pores in the *Sphagnum* leaves and stems, determines water holding capacity and capillarity (*cf*. Hayward & Clymo 1982, Titus & Wagner 1984), which is an important determinant of suitability as a raw material for growing media (*cf*. Jacobs *et al*. 2009). Plant cultivation experiments show that numerous *Sphagnum* species can be used in growing media (see 'Application of *Sphagnum* biomass in growing media', page 16; also Appendix).

Largely entire *Sphagnum* plants from Sections *Acutifolia*, *Cuspidata*, *Rigida*, *Sphagnum* and *Subsecunda*, partially dried, are suitable for absorbing toxic substances or oil (Hagen *et al*. 1990). Intact, undecomposed *Sphagnum* is also required for hygiene products and surgical dressings. For many years *Sphagnum* was an officially recognised pharmaceutical product in Britain, where surgical dressings were made from "*Sphagnum imbricatum*", *S. palustre*, *S. magellanicum* and *S. papillosum* during World War I, although "*S. recurvum*" was not suitable (Hotson 1918, 1921).

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AVAILABILITY, COLLECTION AND PRODUCTION OF FOUNDER MATERIAL

Sphagnum farming requires that sufficient *Sphagnum* material is available to populate the fields. Various founder materials may be applied, each with their own multiplication procedures.

***Sphagnum* spores**

Using *Sphagnum* spores as founder material has the advantage that the resulting cultures are species-pure and free from weeds. Furthermore, the material is genetically diverse (a result of sexual reproduction). Gahlert *et al*. (2012) found that spreading of *Sphagnum* spores on rewetted bog did not lead to germination, whereas spores germinated within one week if they were spread in petri dishes filled with peat, sterilised *Sphagnum* biomass or nutrient agar in a glasshouse. Plantlets developed from spores established successfully in the field, forming numerous new capitula within three months.

The potential availability of spores as founder material is large, since one capsule holds 18,500 to 240,000 spores (Sundberg & Rydin 1998) and each spore has potential to grow into a new plant. The practicality of using spores as founder material is still limited, however, because dioecious species rarely sporulate (Longton 1992, Cronberg 1993), capsules can only be collected manually, and the factors inducing sporulation and germination are incompletely understood (Sundberg 2000, Gahlert *et al*. 2012).

***Sphagnum* shoots**

Sphagnum may regenerate from the smallest plant parts (and even from brownish-coloured material), but not from single leaves (Clymo & Duckett 1986, Poschlod & Pfadenhauer 1989). This high capacity for vegetative regeneration makes shoots useful for both direct application as founder material and for multiplication prior to application. Campeau & Rochefort (1996) tested directly applied fragment lengths from 0.5 to 2 cm without finding any difference in capitula density after three months of growth. Lawn thickness and cover increased faster if large (5–10 cm) rather than small (0.1–0.3 cm) fragments were used (Gaudig *et al*. 2014).

Gathering Sphagnum *shoots from wild populations*

Shoots for use as founder material may be collected from wild populations by hand (picking, raking or cutting) or machine (excavator equipped with a shovel, a block-cut peat extraction device or a mowing bucket, Figures 1 and 7). In the Canadian ‘moss layer transfer technique’, developed for vegetation restoration purposes, the total vegetation is transferred from a donor site to the restoration site (Quinty & Rochefort 2003).

Collecting depth should not exceed 10 cm to allow satisfactory regeneration of the donor site (Campeau & Rochefort 1996). In North America, collection over frozen ground has proved successful (Quinty & Rochefort 2003). The ideal time is at the onset of thawing after a frost period, when the thawed upper centimetres of vegetation can be scraped off. In various countries, the scarcity and conservation status of *Sphagnum* mosses constrain the availability of donor material from wild populations.

Multiplying shoots for founder material

An alternative to using *Sphagnum* shoots from wild populations to populate new fields is to use shoots from already existing Sphagnum farming fields. For example, the initial Rastede Sphagnum farming site was partly established using cultivated *Sphagnum* from the Ramsloh site (Gaudig & Krebs 2016) and the extension of Rastede, from 4 ha to 14 ha in total, used *Sphagnum* harvested from 0.64 ha of the initial Rastede Sphagnum farming site (after five years’ growth) as founder material for a new 3.8 ha *Sphagnum* production field.

The multiplication rate of *Sphagnum* material can be increased by cultivation under more controlled conditions. By cultivating vegetative *Sphagnum* on horticultural fleece in a shaded open greenhouse with sprinkle irrigation, a tenfold higher multiplication rate of species-pure founder material with fewer weeds was achieved compared to Sphagnum farming fields on bogs (C. Schade[1], personal communication 2014). To increase founder material production even further by allowing growth in all directions, submerged cultivation of *Sphagnum* has been tested. The mosses grew well under non-axenic conditions, but their growth rate did not exceed that of mosses growing on peat (Gaudig *et al.* 2014). The multiplication rate may be much higher under axenic conditions because the absence of faster-growing competitors like algae, fungi and bacteria should eliminate nutrient (including CO_2) and light limitation. However, the creation of axenic conditions is a challenge. Axenic cultivation starting from sterilised spores was tested successfully in bioreactors (Rudolph *et al*. 1988, Beike *et al.* 2014), the latter authors reporting a 30-fold increase in *Sphagnum* dry mass within four weeks. Micropropagation Services (EM) Ltd. specialises in vegetative micropropagation of *Sphagnum* from small samples of source material to produce easily and uniformly applicable juvenile plants embedded in liquid or firm gel or as plugs (Caporn *et al*. 2018).

Storage of shoots

Broad implementation of Sphagnum farming will require storage and transportation of *Sphagnum* shoots. A test with *Sphagnum palustre* showed that

[1] Company Niedersächsische Rasenkulturen NIRA GmbH & Co. KG, Germany, www.ni-ra.de.

fresh shoots are more vital and, thus, better suited as founder material than shoots stored in a refrigerator at 6 °C for more than three months. The latter still develop lawns, but with significantly lower productivity than fresh mosses (Prager *et al*. 2012).

To reduce the abundance of weeds, storing *Sphagnum* in piles in the field for several months was tested in Canada with positive results (Hogue-Hugron & Rochefort, unpublished data), although further tests are needed to provide an explanation.

SETTING UP A SPHAGNUM FARMING SITE

Depending on its initial condition, preparation of a Sphagnum farming site may include surface levelling, creation of infrastructure for water management and the establishment of *Sphagnum* cover.

Site selection

Sphagnum farming may take place on a variety of substrates. Experience of *Sphagnum* cultivation has been gained on cut-over bogs after milled peat extraction, on cut-over bogs after block-cut peat extraction, on former drained bog grassland, on artificial floating mats, in rice paddy fields and in glasshouses (on/in water, on peat) (Figure 2). *Sphagnum* cultivation on artificial floating mats and rafts has been tested in Japan (Hoshi 2017) and Germany (Blievernicht *et al*. 2013). Wichmann *et al*. (2017) describe procedures for large-scale implementation and the associated high costs and risks (damage by wind, waves, ice drift and water birds). Hence, we focus here on soil-based outdoor Sphagnum farming on peat substrate. Climate (precipitation, temperature), characteristics of the peat layer (chemistry, hydraulic conductivity) and the

Figure 1. Manual (a, b) and mechanical (c, d) *Sphagnum* gathering from wild populations, for founder material in Germany (a) and Canada (c) or commercial use in Chile (b) and Finland (d). In (a) only the upper 5 cm of half a *Sphagnum* hummock was cut to favour regrowth. Photos: a) Jan Köbbing, b) Christel Oberpaur, c) Peatland Ecology Research Group and d) Matthias Krebs.

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availability and quality of water are of major importance for successful Sphagnum farming (Brust *et al*. 2018). In addition to site selection, these starting conditions influence the planning, setting-up and management requirements for individual Sphagnum farming sites.

Figure 2. Overviews of Sphagnum farming sites, a) on cut-over bog in Canada; b) on former bog grassland in Germany (Rastede); c) on cut-over bog in Germany (Drenth); and d) on floating mats on a lake in Germany. Photos: a) Peatland Ecology Research Group, b) ASEA aerial, c) Jan Köbbing and d) Matthias Krebs.

Surface levelling

Site preparation must create an even, horizontal surface to ensure optimal water levels over the entire *Sphagnum* production field after rewetting. Sites from which peat blocks have been cut consist of separate depressions (*e.g*. 10–20 m wide, 50 m long in Canada) whose floors must be levelled. Milled peat extraction leaves large areas (several hectares) with more or less plane but often sloping surfaces. Levelling may be effected manually (*e.g*. using rakes and wooden planks) on small areas, or with tracked vehicles equipped with grading blades on larger sites. On sloping sites, terraces with different water level targets must be constructed to ensure water table levels within a few centimetres of the soil surface over the entire area (Quinty & Rochefort 2003, Blankenburg 2004). If the remaining upper peat layer has become hydrophobic after peat extraction (Quinty & Rochefort 2003) or plate-like, it may be necessary to scrape off about 5 cm with a cultivator bulldozer, an endless screw or an excavator before spreading the *Sphagnum* founder material.

On former bog grassland in Rastede, Germany, the fertilised, limed and degraded topsoil (30–50 cm) was removed with an excavator to create an even, horizontal peat surface and to construct causeways for management and harvesting (Wichmann *et al.* 2017, Figure 3). Whether topsoil removal on former bog grassland is necessary, and the depth of soil that should be removed, has not yet been finally clarified. However, topsoil removal should be minimised to reduce cost and carbon losses. An alternative approach adopted in a recent *Sphagnum* vegetation restoration trial on wet grassland in Wales (UK) was to fully invert the topsoil to produce a rougher surface for *Sphagnum* establishment (S.J.M. Caporn, unpublished data).

The peat surface is likely to move differentially over time due to peat swelling or frost action (Groeneveld & Rochefort 2002, Gaudig *et al*. 2017) but must be kept flat during the establishment phase.

Infrastructure for water management

Productive Sphagnum farming sites require water tables that are permanently close to the moss surface, making infrastructure for irrigation (to supply water during droughts) and drainage (to avoid prolonged flooding and erosion of moss fragments) essential. Possible sources of irrigation water, whose suitability depends on water quality (see ‘Water quality’, page 11), include streams, ditches, wells, ponds and artificial water reservoirs. Practical experience of improving water quality, for example using helophyte filters (constructed wetlands stocked with helophytes) which could potentially remove large amounts of solutes (*e.g*. Land *et al*. 2016), is not yet available.

Various types of pumps have been tested for Sphagnum farming (*cf*. Wichmann *et al*. 2017). Electric pumps need power, either from the electricity net (mains supply) or from wind turbines or solar panels with additional batteries to bridge periods of 'dark lull'. Wind pumps are comparatively cheap but may not adequately cover periods with little wind and high evapotranspiration. However, they can be supplemented with a mobile electric pump and generator as an emergency power unit.

Small ditches, subsurface pipes, drip systems or sprinklers (for filtered water) can be used to transport irrigation water from the pump to the *Sphagnum* production fields (Figure 4). The irrigation system must be carefully adjusted to each individual Sphagnum farming site, with maximum distances between the irrigation elements depending on the hydraulic conductivity of the upper peat layer, *e.g*. 5 m in strongly humified ('black') (Gaudig *et al*. 2017) or 10–20 m in slightly humified ('white') peat (Gaudig *et al*. 2014, Brown *et al*. 2017).

To avoid flooding, the maximum water table level in the field must be regulated by an outflow. Simple but effective outflow constructions include pipe bends and weirs (Figure 4). In an 'adjustable ditch', a float valve opens automatically when the water table is too high (used at the Shippagan 2 and Saint-Modeste sites in Canada). Outflows should be easily adjustable to allow the water table to rise as the surface of the *Sphagnum* lawn grows upwards.

Regulation of both inflow and outflow is necessary for optimal water management. Manual water management requires frequent staff attendance, especially during the growing season. Automatic water management has been tested in Germany at the Rastede and Drenth pilot sites (three and seven irrigation units, respectively), and in Canada at Shippagan 2 and Saint-Modeste, but an electronic control centre may require very high investment costs (Wichmann *et al*. 2017). Installing a simple automatic regulation system for every individual irrigation unit seems to be more reliable and cost effective. At Rastede, Shippagan 2 and Saint-Modeste, electric pumps are switched on and off at preset minimum and maximum water levels, monitored by two sensors in the irrigation ditches.

Sphagnum establishment

Rapid and successful establishment of a closed *Sphagnum* lawn is a key early stage in Sphagnum farming. *Sphagnum* productivity increases substantially as soon as vital (live green) *Sphagnum* covers > 90 % of the peat surface (Gaudig *et al*. 2017) and desiccation tolerance of the moss lawn increases. Next to quality and quantity of the *Sphagnum* founder material, site conditions are important factors for *Sphagnum* establishment.

Figure 3. Setting up a Sphagnum farming site on former bog grassland in Germany (Rastede), using an excavator for a) removal of the degraded topsoil and b) construction of causeways and irrigation ditches. Photos: Sabine Wichmann.

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Figure 4. Water management components for Sphagnum farming sites: a) electric pump (Rastede); b) inlet into the irrigation ditches (Rastede); c) drip irrigation (Drenth); d) 'adjustable ditch' with an outlet (Shippagan 2); e) outlet with a data logger (Rastede); f) outlet (Saint-Modeste). Photos: a) and e) Sabine Wichmann, b) Greta Gaudig, c) Dorothea Rammes, d) and f) Peatland Ecology Research Group.

Introduction of Sphagnum

The higher the cover of *Sphagnum* founder material, the faster a closed *Sphagnum* lawn will establish (Campeau & Rochefort 1996). Application of a loose *Sphagnum* layer 1–5 cm thick encourages its establishment (Quinty & Rochefort 2003, Gaudig *et al*. 2017). Quinty & Rochefort (2003) suggest ~ 100 m³ of *Sphagnum* material *per* hectare for successfully re-establishing *Sphagnum* vegetation on cutover bog (area ratio 1:10 between collection and restoration sites with ~ 10 cm collecting depth), a volume that was used by Pouliot *et al*. (2015) for the Shippagan 1 Sphagnum farming site in Canada. At the Rastede Sphagnum farming site in north-west Germany, ~ 80 m³ of *Sphagnum* founder material *per* hectare (70–80 % cover) with manual replenishment of gaps in the developing moss carpets one year after installation (~ 10 m³ *Sphagnum per* hectare) was sufficient for successful establishment within 1.5 years (Gaudig *et al*. 2014, Wichmann *et al*. 2017). *Sphagnum* fragments should be applied at the start of the growing season (when long frosty periods are no longer probable) because the establishment phase is prolonged in winter, when *Sphagnum* grows only slowly (Lütt 1992, *cf*. Krebs *et al*. 2016). Moreover, moss fragments applied in spring are less likely to be washed away by snowmelt water.

Vital fragments or juvenile plants of *Sphagnum* are spread on the newly prepared bare peat surface (see 'Surface levelling', page 6) either by hand (at small scale, in basins or on very wet sites; *e.g*. Ramsloh and both Twist sites) or with a manure spreader mounted on a tracked vehicle (*e.g*. Rastede, *cf*. Wichmann *et al*. 2017) (Figure 5). Machines tend to spread the *Sphagnum* unevenly, making manual reworking necessary to ensure uniform cover.

Micropropagated mosses in liquid gel (see 'Multiplying shoots for founder material', page 4) stick to the peat surface and gain good capillary contact, as in the 'hydroseeding' method of Money (1995). In the last three years, plugs have successfully been applied for *Sphagnum* vegetation restoration in

Figure 5. Spreading of *Sphagnum* and straw mulch: a) manually; b) mechanically by a tractor driving along the edge of the field pulling a manure spreader or a machine that blows the straw onto the site; or by c) loading founder material onto a manure spreader mounted on a tracked vehicle which then d) drives directly on the field. Photos: a) and b) Peatland Ecology Research Group, c) Sabine Wichmann and d) lensescape.org.

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the southern Pennines (England) and in Wales. Techniques to upscale the planting of micro-propagated materials (beads, gel, plugs) are currently being developed (Caporn *et al*. 2018). The use of gel in Sphagnum farming has not yet been tested in the field.

Especially when optimal water tables cannot be ensured, *e.g*. when surface height differences occur even after levelling (Gaudig *et al*. 2017), it might be advantageous to introduce a mixture of *Sphagnum* species with different water table demands (*cf*. Andrus *et al*. 1983). Under conditions of fluctuating water table (mean depth 29–73 cm below surface in summer), Chirino *et al*. (2006) found that *Sphagnum* species established better in monoculture than in mixtures. In Canada, Picard (2010) described mixtures with *S. fallax* as beneficial for improving the yields of targeted species (*S. magellanicum*, *S. papillosum*) during prolonged drought. In contrast, Limpens *et al*. (2003) supposed that a mixture with *S. papillosum* reduced drought stress for *S. fallax* on a hummock, while Robroek *et al*. (2007b) identified intensity and frequency of rain events as important for the expansion of hollow species in hummocks. More research is needed to determine whether and under which conditions a mixture of different *Sphagnum* species promotes biomass production.

If prepared sites cannot immediately be populated with *Sphagnum* material it may be useful to cover the bare peat with geotextile to prevent the establishment of weeds (S. Hogue-Hugron unpublished data).

Protective cover

Quinty & Rochefort (2003) recommend a loose straw mulch cover (minimum 3000 kg ha^{-1}) for improving microclimate (higher relative humidity, more stable temperatures). Straw cover may also support the establishment of micropropagated *Sphagnum* in gel (Caporn *et al*. 2018.). Straw thickness should not exceed 3 cm to allow sufficient light to reach the *Sphagnum* fragments (Gaudig *et al*. 2017) because moss growth is reduced when shading exceeds 50 % (Clymo & Hayward 1982).

Straw can be applied manually, with a tracked manure spreader driving over the field, or with a machine that blows the straw over the field from the side (Figure 5). This technology could be improved in terms of the width and uniformity of spreading.

In a large-scale Sphagnum farming project in Drenth (Germany), *Sphagnum* fragments covered with geotextile (50 % shade) grew much more slowly than *Sphagnum* fragments covered with straw, probably because the water-saturated geotextile led to anoxic conditions (Graf *et al*. 2017). If a sufficient water supply can be ensured, covering the *Sphagnum* fragments is unnecessary for protection against desiccation (Krebs *et al*. unpublished data). On the other hand, a (straw) cover leads to more balanced surface temperatures (lower during daytime and higher at night; Quinty & Rochefort 2003), which may encourage *Sphagnum* growth by avoiding temperatures above 27 °C, which reduce photosynthesis (Johansson & Linder 1980), and by providing higher temperatures at night (Gerdol *et al.* 1998, Robroek *et al*. 2007a). However, this effect has not yet been tested in Sphagnum farming sites with continuously high water tables.

MANAGING A SPHAGNUM FARMING SITE

Commercial Sphagnum farming involves regular on-site controls, precise water management, weed management of production fields, cleaning of irrigation ditches and mowing of causeways.

Water management

Water table management in the establishment phase

Water management must be very precise and, therefore, carefully controlled especially during the establishment phase. *Sphagnum* fragments lying on the peat surface are sensitive to desiccation as they are more vulnerable to water losses than a dense *Sphagnum* lawn (Price & Whitehead 2001, Price *et al*. 2003). Campeau & Rochefort (1996) found highest growth rates of *Sphagnum* fragments at water table level 5 cm below the peat surface. Inundation must be avoided to prevent washing away of founder material (Rochefort *et al*. 2002, Tuittila *et al*. 2003).

Water table management in the production phase

Several studies have shown that the growth of *Sphagnum* is highest at high water tables (close to, but below, the capitula), regardless of the natural ecological niche of the species (Hayward & Clymo 1983, Lütt 1992, Robroek *et al*. 2009). Under natural conditions, *Sphagnum* growth is often reduced in summer because of water deficits (Robroek *et al*. 2009, Rydin & Jeglum 2009). Thus, in Sphagnum farming it may be opportune to overcome this deficit by direct water supply.

Quantitative water demand

Sphagnum farming sites with drained and dry surroundings (*e.g*. in degraded bog landscapes) are subject to downward and sideward seepage and increased evapotranspiration as a result of the 'oasis effect' (Edom 2001). These increased water losses have to be compensated, especially during (warm) periods with already high evapotranspiration losses

(Brust *et al*. 2018). Therefore, *Sphagnum* production fields require irrigation to maintain high water tables and soil moisture levels (suction pressures, *cf*. Price *et al*. 2003). Annual irrigation volumes amounted, on average, to 1600 m^3 *per* hectare of *Sphagnum* production field (160 mm) at the Rastede Sphagnum farming site in north-west Germany (annual means of temperature 9.8 °C, and of precipitation 849 mm) and double this volume in drier years (Brust *et al*. 2018). At Shippagan 2, Canada (annual mean temperature 4.8 °C, precipitation 1077 mm yr^{-1}) the much smaller evapotranspiration and seepage losses resulted in substantially lower irrigation demands of 74–130 mm (Brown 2017). To reduce irrigation water demand, water tables can be lowered, resulting in smaller losses by both evapotranspiration and seepage, but also in lower *Sphagnum* growth rates.

In general, spatially differentiated air humidity as a result of the 'oasis effect' causes evapotranspiration rates to decrease with a) increasing size of the Sphagnum farming site, b) better orientation along the prevailing direction of dry winds, and c) increasing extent of wet surroundings and their wetness. Evapotranspiration might also be reduced by the wind breaking effect of trees (Limpens *et al*. 2014) or shrubs, especially if they are in blocks orientated perpendicular to the prevailing dry wind direction. Additionally, drainage ditches installed to remove excess water from Sphagnum farming sites should not be too close to cultivated areas because they promote seepage losses.

Water quality

Sphagnum species grow optimally when their nutrient stoichiometry is balanced without nutrient limitation or oversupply (Aerts *et al.* 1992, Bragazza *et al.* 2004, Fritz *et al.* 2012, Temmink *et al.* 2017). Solute supplies that would be much too small to maintain conventional crop plants may actually be poisonous to *Sphagnum*, which has extraordinarily small nutrient needs and tolerances.

Solutes are supplied to the upgrowing *Sphagnum* by atmospheric deposition, by release from the (mineralised and formerly fertilised) peat soil, and by irrigation water. In regions with high atmospheric loads, particularly of NH_3 and NH_4^+ (resulting in dry and wet deposition), additional solutes supplied by irrigation water may have detrimental effects on *Sphagnum* growth. The quality of available water may influence species selection as *Sphagnum* species differ in their growth responses to pH, bicarbonate and other solutes (Hájek *et al.* 2006). A high input of solutes may cause a shift in *Sphagnum* species at the expense of less competitive target *Sphagnum* species (Temmink *et al.* 2017).

The quality of the irrigation water is determined by its origin. In Canada, irrigation water is usually taken from natural peatland lakes (Shippagan 2) or water drained from peat extraction fields (Saint-Modeste). Drainage water from agriculturally used surroundings may have high loads of nitrogen (N), phosphorus (P), and potassium (K) (Temmink *et al.* 2017). P and K are mainly accumulated in the *Sphagnum* mosses next to the irrigation ditch, with plant tissue concentrations decreasing sharply with increasing distance from the ditch. High concentrations of single elements in the mosses can be toxic (Limpens *et al.* 2011) and should be avoided. In particular, N levels should be kept low although the negative effect of N can be reduced by high availability of P and K and optimisation of other growth factors (*e.g*. light and moisture levels) so that N is prevented from accumulating to toxic levels by dilution through increased biomass growth (Carfrae *et al*. 2007, Limpens & Heijmans 2008, Fritz *et al.* 2014). Temmink *et al.* (2017) estimated that, when the *Sphagnum* was growing well, the Rastede Sphagnum farming site took up N at 35–56 kg ha^{-1} yr^{-1}.

Groundwater may also be used for irrigation, but in this case calcium (Ca) and bicarbonate (HCO_3^-) must be taken into account. Most *Sphagnum* species are sensitive to high concentrations of Ca and HCO_3^-, and concentrations > 500–800 µM are detrimental (Vicherová *et al.* 2015, Smolders & Fritz unpublished data), in particular when high cation loads are combined with high pH (Clymo & Hayward 1982, Karofeld 1996, Harpenslager *et al.* 2015, Rammes 2016, Vicherová *et al.* 2017).

Short-term use of irrigation water with suboptimal quality may be possible if rainwater dilution sufficiently reduces the concentrations of detrimental solutes (*e.g*. in Malpils, Latvia). In Canada, Latvia and Germany, *Sphagnum* production fields are irrigated in summer, while excess precipitation water is discharged in winter and might be stored off-site for use when irrigation is needed in summer.

Avoiding solute concentrations that would be damaging for *Sphagnum* may be achieved by:

- careful selection of the source of irrigation water;
- regular cleaning of the supply ditches to remove accumulated solutes;
- pre-treatment of the water, *e.g*. by constructed helophyte filters;
- keeping other site conditions optimal so that accumulation is avoided/retarded by maximising *Sphagnum* biomass growth;
- on-site storage of solute-poor surplus water from intense rainfall events during periods with high

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evaporation losses by temporarily allowing higher-than-optimal water levels; and

- designing *Sphagnum* production fields with larger distances between irrigation ditches (although still ensuring a sufficient water supply for the entire field) in order to fully exploit the purification capacity of the *Sphagnum* between the ditch and the centre of the production field (Temmink *et al*. 2017).

Fertilisation

As nutrients are removed with the harvested *Sphagnum* biomass, frequent harvesting may change existing nutrient limitations, in particular for P (Krebs *et al.* 2018), especially in regions with low nutrient inputs by irrigation and atmospheric deposition. Whether and how fertilisation may balance nutrient stoichiometry and stabilise - or even enhance - *Sphagnum* growth demands further study.

Management of vascular plant growth

The presence of vascular plants and mosses (other than those applied) in *Sphagnum* production fields is almost inevitable because their diaspores are continually introduced from the surroundings. Vascular plants may facilitate *Sphagnum* growth by improving microclimate (especially when conditions are hydrologically suboptimal, *e.g.* with low water tables or large water table fluctuations), reducing photoinhibition, and providing mechanical support promoting length increment ('nurse plants'; Pedersen 1975, Murray *et al*. 1993, Rydin & Jeglum 2009, Pouliot *et al*. 2011). Reliable nurse plants are *Eriophorum* species or ericaceous shrubs at dry sites and *Polytrichum* moss species (*e.g. P. strictum*) at sites with frost heaving (Quinty & Rochefort 2003, Groeneveld *et al*. 2007). On sites with optimal hydrology, nurse plants may not be needed to improve microclimate but are probably still important for reducing photoinhibition. The microclimatic effects of nurse plants at sites with insufficient soil moisture deserve further investigation.

On the other hand, vascular plants may retard *Sphagnum* growth by shading, litterfall, and competition for water and nutrients (Tomassen *et al*. 2003). Furthermore, the quantities of vascular plant biomass and seed in the *Sphagnum* biomass product has to be minimised when it is to be used as a raw material for horticultural growing media (see 'Application of *Sphagnum* biomass in growing media', page 16). Therefore, the vascular plant cover on *Sphagnum* production fields should be kept at a low level, *e.g*. by regular mowing.

The frequency of mowing is determined by the species present, the site conditions promoting vascular plant growth, the amount of litter produced, and the end use of the cultivated *Sphagnum* biomass. Vascular plant cover was less than 40 % and decreasing with succession in Canada (Guêné-Nanchen *et al.* 2017), but in Germany it could only be kept below 20–30 % by regular mowing (Gaudig *et al*. 2017). Mowing of vascular plants (mainly *Juncus* species on nutrient-rich sites) was tested at Rastede using a) a strimmer, b) a single-axle mower equipped with cutter bar and triple tyres to adapt to the low bearing capacity of *Sphagnum* production fields, and c) an excavator with mowing bucket on an elongated arm (Figure 6). Only the excavator could mow from the causeway and thus avoid causing compaction by driving on the *Sphagnum* production fields. In contrast to the other devices, the excavator with mowing bucket removed the mown material so that a mulch layer - which possibly hampers moss growth by shading - did not develop. Standard tractors with wide tyres were used for mowing the causeways to prevent seed dispersal. A mowing robot was successfully tested at the Twist sites, although mowing took a long time and the robot was unable to cross the ditches. In Canada (Shippagan 1), mowing is considered to be unnecessary because the rhizomatous dominant vascular plant (*Eriophorum angustifolium*) has low cover and low litter production (Guêné-Nanchen *et al.* 2017).

Control of fungal pests

Fungi are common in *Sphagnum* mires and peatlands (Thormann 2011, Kostka *et al*. 2016). Mosses have many fungal associates, some growth stimulating and others growth retarding. Parasitic or pathogenic fungal species of the genera *Galerina* and *Sphagnurus* have been identified at the Rastede site. Effective measures for controlling *Sphagnurus paluster* without affecting *Sphagnum* are applications of the fungicide Myclobutanil (Landry *et al*. 2011) and use of the fungus *Trichoderma virens* as an antagonist (Irrgang *et al.* 2012), but both have been tested only in the glasshouse so far. Investigation is required into the extent of *Sphagnum* growth reduction by fungi in the field and the impact of fungal infection of the *Sphagnum* biomass on growing media quality.

Control of disturbing animals

Animals may disturb water management infrastructure, cause nutrient inputs and damage the sensitive *Sphagnum* lawn by trampling. Experience at Rastede has shown that a minimum distance of 10 m between irrigation ditches on the *Sphagnum* production fields and drainage ditches in the surroundings is required to prevent muskrats (*Ondatra zibethicus*) from creating connecting drains.

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In some regions migratory birds cause damage *via* trampling and nitrogen input from droppings. Fences may protect against cattle, roe deer (*Capreolus capreolus*), moose (*Alces alces*), boar (*Sus scrofa*) and the general public.

HARVESTING

Timing and frequency of harvests

Dry mass productivity of *Sphagnum* on Sphagnum farming sites mainly ranges between 3 and 6 t ha^{-1} yr^{-1} in Germany (Gaudig *et al*. 2014) or between 0.3 and 2 t ha^{-1} yr^{-1} in Canada (Pouliot *et al*. 2015). Decomposition of *Sphagnum* biomass is a continuous process and, in a typical peatland environment, only 85 % of the primary production is preserved after one year (Lütt 1992). Nonetheless, the rate of *Sphagnum* biomass accumulation may remain constant over some years in an established *Sphagnum* production field (Gaudig *et al*. 2017). At the latest, when decomposition starts to approach production, it is time to harvest. The choice of harvesting time needs to balance technical feasibility (minimum lawn height), site accessibility, growth rate, decomposition losses, regeneration potential and economic aspects,

Figure 6. Weed management at the Rastede Sphagnum farming site using: a) brush cutter / strimmer; b) single-axle mower with cutter bar and triple tyres; c) excavator equipped with an extra-long arm and a mowing bucket, operating from a causeway. Photos: Sabine Wichmann.

i.e. sales prospects (Gaudig *et al*. 2017). Additionally, seasonal variations in *Sphagnum* biomass quality may be pertinent (see 'Application of *Sphagnum* biomass in growing media', page 16). From the first regrowth experiments at the Ramsloh site, a harvesting frequency of once every 3–5 years seems to be feasible (Gaudig *et al*. 2014, Krebs *et al*. 2018).

Harvesting technique

As for the collection of founder material (see 'Gathering *Sphagnum* shoots from wild populations', page 4), various devices can be used to harvest *Sphagnum* biomass. During the first harvest of cultivated *Sphagnum* at Rastede, an excavator with long arm and mowing bucket and a tractor with double or wide tyres towing a dumper for transport of the harvested biomass both operated on the causeways (Figure 7; see also Radio Bremen 2016). Naturally grown *Sphagnum* is collected from Finnish bogs by an excavator when the ground is frozen in winter (Silvan *et al*. 2012, 2017) or with a forestry vehicle ('forwarder') equipped with bogie tracks and a bucket grapple in summer (Anttila 2016). In northern USA, long *Sphagnum* mosses are scraped from wild populations by a small crawler tractor in winter (Elling & Knighton 1984) or are collected using tracked machinery and sledges for haulage (mossman381 2012). So far, no available harvesting machinery is capable of driving on very wet (not frozen) *Sphagnum* production fields without damaging the residual moss layer. The land has low bearing capacity and, although the ground pressure exerted by machinery with wide tracks may be less than 50 g cm^{-2} (Wichmann *et al*. 2016), adding the weight of wet mosses (loading capacity) presents an additional challenge. There is a need for further development and testing of devices to cut, collect and transport the wet moss biomass.

Regrowth and re-establishment after harvest

The regrowth potential of the residual *Sphagnum* lawn requires more study, but seems to depend on the age and/or the thickness of the residual *Sphagnum*,

Figure 7. Harvesting techniques for Sphagnum farming using a) an excavator operating from a causeway, equipped with b) a mowing bucket or c) a modified excavator for block-cut peat extraction, which tests in Canada have shown can also harvest *Sphagnum*. Photos: a) Gerd Block, b) Sabine Wichmann and c) Benoit St-Hilaire).

harvesting technique, *Sphagnum* species, and site conditions after harvest **-** in particular water table. At Ramsloh, manual removal of the uppermost 2–5 cm resulted in the regrowth of new capitula on 80 % of the *Sphagnum papillosum* plants after one year and almost 100 % after 2.5 years, with average water table level 4 cm below the (harvested) *Sphagnum* surface (Gaudig *et al*. 2014, Krebs *et al*. 2018). The decision on whether to harvest only the upper *Sphagnum* biomass or all of it is determined by the expected speed of regrowth of the residual *Sphagnum* compared to the speed of new establishment, and by related costs **-** *i.e*. income foregone due to reduced yield *versus* the additional expense of spreading new *Sphagnum* fragments.

STORAGE AND TRANSPORT OF *SPHAGNUM* BIOMASS

Storing or transporting large volumes of heavy, wet *Sphagnum* may be a problem if compaction affects the physical properties of the lowermost layers and increases the risk of self-heating. Storing the biomass in piles (Germany) or squeezing out the water (Finland) reduces its water content to 70–80 % (Kumar 2017) and makes it dry enough for further processing. To reduce transport costs, it may be appropriate to further reduce the water content by active drying (see 'Processing for growing media', this page). Chilean moss is dried to a moisture content of 19–20 % and compressed to different formats (150 g, 250 g, 500g, 1 kg, 3 kg, 5 kg and 7 kg packs); for example, the 5 kg quantity is compressed into blocks of 30 × 30 × 50 or 30 × 30 × 60 cm for global shipping (Alpha Moss 2015, Lonquén 2018).

PROCESSING FOR GROWING MEDIA

The processing of harvested *Sphagnum* biomass for use in growing media encompasses drying, 'hygienisation' (*i.e.* treatment of the biomass to kill most pathogens and seeds or vegetative parts of vascular plants to phytosanitary standard) and screening (*cf*. Kumar 2017). Active drying can take place in foil tunnels, glasshouses or with heat (stove, conveyor drier, waste heat from biogas plants). Drying with heat (stove) at 70 °C for at least 24 hours resulted in the loss of absorbency properties (B. St-Hilaire, unpublished data). Dry biomass becomes crumbly and electrostatic, and must be moistened before processing in the growing media plant (Kumar 2017). At moisture contents below 20 % the *Sphagnum* biomass became hydrophobic and rewetting was difficult and time-consuming (Kumar 2017). A century ago, many methods for drying peat were studied and it may be worthwhile to revisit these methods for the drying of *Sphagnum* biomass. Further research is needed on the effect of drying temperature and duration on the physical properties of the *Sphagnum* biomass and to discover the minimum and maximum moisture thresholds that should not be exceeded.

Killing the seeds and vegetative parts of vascular plants, together with parasites, in the harvested *Sphagnum* biomass ('hygienisation') is conducted by water vapour treatment or gamma radiation (Kumar 2017, Thieme 2017). Both methods work well, but gamma radiation is rather expensive whereas water vapour treatment is already widely applied in growing media production (Thieme 2017). Alternatively, moist *Sphagnum* can be placed in transparent bags and left in the sun for six weeks in summer (Oberpaur *et al*. 2012).

In Germany, *Sphagnum* biomass was separated into coarse and fine fractions using a standard screening line designed for peat (Kumar 2017). Growing tests with different fragment sizes produced by shredding the biomass with a garden shredder have been conducted in Canada (Aubé *et al*. 2015, St-Hilaire *et al*. 2017). These studies (lengths 0.5–2 mm and > 2–4.75 mm for an experiment with lettuce in substrate compacted into pellets, and < 6.3 mm and 6.3–19 mm for another experiment with *Zinnia* and basil) showed no significant influence of fragment length on plant yields (St-Hilaire *et al*. 2017). Further research is needed to determine the optimal lengths of *Sphagnum* fragments for various applications in growing media.

A growing medium mix containing 50 % *Sphagnum*, dried and packed in 70-litre plastic bags, was stored for seven months without changes in inorganic solute composition (Kumar 2017).

The European standard DIN EN 12580 describes the standard method for determining the volume of traded growing media and constituents. This includes measuring bulk density by passing the material through a mesh screen with defined mesh widths, allowing it to fall into a 20 L cylinder which is finally weighed. It will be difficult to transpose this method to fresh *Sphagnum* biomass. Since *Sphagnum* is loose when dry and more compact when it is wet, moisture content influences its bulk density. Also, the size of *Sphagnum* fragments affects the results. Long (15–20 cm) fragments of *S. palustre* with 91 % water content had a bulk density of 90 g L^{-1}, while dry mosses (with 10 % water content) had a bulk density

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of only 8.5 g L^{-1} (G. Schmilewski, unpublished data). Before they were incorporated into a growing medium, these *Sphagnum* fragments were shredded, leading to a bulk density of 10 g L^{-1} for fragments < 10 mm long (G. Schmilewski, unpublished data). Considerably higher bulk densities ranging from 25 g L^{-1} (water content 29 %) to 283 g L^{-1} (water content 92 %) were determined by S. Kumar (unpublished data).

APPLICATION OF *SPHAGNUM* BIOMASS IN GROWING MEDIA

Suitability of individual *Sphagnum* species

Sphagnum species are grouped into different sections with differing characteristics (Daniels & Eddy 1985, Michaelis 2011). Differences in stem structure and in the sizes of leaves, hyaline cells and pores, and intrinsic properties (*i.e*. decomposition rate, see 'Productivity', page 3) determine their suitability for use in growing media. Various species of different origins have so far been tested for their suitability in substrate (growing media) applications, namely: *S. capillifolium*, *S. fimbriatum*, *S. flavicomans*, *S. fuscum* and *S. rubellum* (Section *Acutifolia*); *S. magellanicum*, *S. palustre* and *S. papillosum* (Section *Sphagnum*); *S. fallax* and *S. riparium* (Section *Cuspidata*); and *S. squarrosum* (Section *Squarrosa*) (see Appendix). All of these species proved to be suitable as growing media constituents in horticultural experiments. However, results differed depending on the proportion of *Sphagnum* in the potting mix and the plant under cultivation (see the next section below).

Substrates based on *S. fallax* seemed to cause chlorosis, reduced growth and die-back of seedlings more often than substrates containing other *Sphagnum* species (Emmel & Kennet 2007), although *Tagetes* seedlings were propagated without problems and lettuce even produced more biomass in substrates containing increasing proportions of *S. fallax* (0–50–100 %), with the best growth in 100 % *Sphagnum* (M. Emmel unpublished data, Thieme 2017). Seedlings of tomato, cucumber and lettuce cultivated in *S. magellanicum*, *S. fuscum* and *Sphagnum* mixes had a significantly greater fresh weight than the controls (white peat or mineral wool), whereas *S. riparium* worked for lettuce but performed less well for tomato and cucumber (Reinikainen *et al*. 2012). As yet, it is not known why substrates containing *S. fallax* and *S. riparium* (both belonging to Section *Cuspidata*) sometimes cause severe damage to the cultivated plants and at other times support excellent growth.

Proportion of *Sphagnum* biomass in a growing medium and suitability for various crops

Sphagnum biomass has been tested in different mixtures with peat or other growing media constituents. Azaleas grown in mixtures of white peat with 0, 25, 50, 75 and 100 % by volume of *Sphagnum palustre* did not show significant differences in fresh weight (Ueber & Gaudig 2014). Also in a weight-replacement series with white peat, substitution by *Sphagnum fuscum* and a mixture of *Sphagnum* species up to 100 % was beneficial for the growth of all tested cultivars (A. Kämäräinen, unpublished data; see Appendix). In contrast, the fresh weight of *Petunia* decreased with increasing proportions of *Sphagnum palustre*, *S. papillosum* and *S. magellanicum* (M. Emmel, unpublished data). Further research is needed on the suitability of various *Sphagnum* species at different proportions in growing media for the cultivation of a range of plants (Schmilewski & Köbbing 2016). Generally, it can be concluded that a proportion up to 50 % by volume of *Sphagnum* biomass in potting substrates is trouble-free for most cultivars. The proportion of *Sphagnum* biomass may be greater for many crops (Blievernicht *et al*. 2012b, 2013).

Horticultural experiments on *Sphagnum* as a growing medium constituent (Appendix) have been carried out for:

- ornamental plants: *Azalea*, *Begonia*, *Cyclamen*, *Fuchsia*, *Impatiens*, Orchideaceae, *Pelargonium*, *Petunia*, *Poinsettia*, *Tagetes*, *Verbena*, *Zinnia*;
- vegetables: seedlings of cauliflower (*Brassica oleracea* var. *botrytis*), Chinese cabbage (*Brassica rapa* ssp. *pekinensis*), cucumber (*Cucumis sativus*), lettuce (*Lactuca sativa*), tomato (*Solanum lycopersicum*);
- herbs: basil (*Ocimum basilicum*); and
- shrubs and trees: apple (*Malus* sp.), *Calluna*, kiwi fruit (*Apteryx* sp.), *Rhododendron*.

Adjustments in crop management, *e.g*. in irrigation, will be necessary because *Sphagnum* and peat have different physical properties (Blievernicht *et al*. 2012b, Kämäräinen *et al*. 2018).

The pressed potting soils used in vegetable propagation must be stable enough for mechanical processing and suitable as substrates for various vegetables. The peat in pressed potting soil can be replaced with *Sphagnum* biomass at a rate of 25 % by volume without loss of quality or stability (Emmel 2017). Chinese cabbage grew similarly in pressed potting soils containing 0–53 % by volume of *Sphagnum* biomass, while lettuce had lower growth rates at higher *Sphagnum* proportions. Pure

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Sphagnum is not a suitable substrate for seedling production, because the wide pores of the substrate do not allow the seeds to be distributed evenly (Thieme 2017).

Quality challenges

Sphagnum biomass may contain secondary metabolites, which may hamper root growth and lower the yield of the cultivated plant. This effect does not seem to depend on *Sphagnum* species, but on the processing method or (more likely) on the origin of the biomass (stress caused by conditions at the production site). Research in Germany (SPHAKO project) identified five phenolic acids originating from secondary metabolism of *Sphagnum* (S. Irrgang, unpublished data) which, according to the literature, may lead to allelopathic effects. Currently, these substances are tested for harm or toxicity to other plants when applied directly. Further research on allelopathic effects is needed.

The effect of growing and harvesting conditions during Sphagnum farming on the properties of the *Sphagnum* biomass is also insufficiently clear as yet. Impurity of harvested material, *i.e.* the inclusion of residues of other moss species and vascular plants, may cause undesired nitrogen immobilisation in the growing medium as a result of higher availability of easily degradable carbon sources and increased microbial activity, which is not a problem with pure *Sphagnum* biomass. Research is needed to determine how much non-*Sphagnum* material and different 'weed' species may be included in the growing media. The biological and physical stability of *Sphagnum* in mixes also requires further investigation.

ENVIRONMENTAL AND ECONOMIC ASPECTS

Sphagnum farming provides a sustainable land use option for degraded bogs. The benefits for climate change mitigation (Beyer & Höper 2015, Günther *et al*. 2017), nutrient retention (Temmink *et al*. 2017), and biodiversity (Muster *et al*. 2015, Gaudig & Krebs 2016) have been quantified for Germany. Adapted management and harvesting regimes may enhance these benefits. For example, harvesting according to the mosaic-cycle concept can increase biodiversity (Muster *et al*. 2015) although it may also lead to reduced yields.

Economic studies of setting up the Sphagnum farming sites in Germany (Ramsloh, Rastede) have revealed that investment costs are high (especially the cost of founder material) but there is large potential for reducing them (Wichmann *et al*. 2017). Further research is needed to evaluate the long-term effects of Sphagnum farming and to assess profitability and environmental benefits in countries other than Germany.

CONCLUSIONS AND OUTLOOK

Since the first efforts towards cultivating *Sphagnum* to substitute for peat in growing media (Gaudig & Joosten 2002) and first field trials in Germany and Canada from 2004 onwards, much progress has been made. An increasing number of researchers explore increasingly detailed questions relating to Sphagnum farming. More and more demonstration sites are being established in various parts of the world (Table 1), and progressively more practical experience is being gained, also through knowledge exchange between practitioners of *Sphagnum* vegetation restoration, *Sphagnum* gathering and Sphagnum farming.

However, Sphagnum farming is still in its infancy and large-scale commercial implementation is still lacking. Currently, the production costs of farmed *Sphagnum* biomass are still too high to compete with peat, especially because the external costs of peat extraction are not accounted for (S. Wichmann, unpublished data). More research into Sphagnum farming is needed to reach technological maturity and to reduce costs, *e.g*. through the selection of highly productive *Sphagnum* taxa as well as *Sphagnum* breeding and mass propagation of founder material, as in the current German research project MOOSzucht. One might expect traditional selection methods to work rapidly because the cropped 'plant' is haploid, meaning that a single beneficial genetic change would immediately reveal itself in the phenotype. Further understanding is likely to emerge from the SPHAGNOME project, which is investigating gene-to-trait relationships in the genus *Sphagnum* (Weston *et al.* 2018). The optimisation of site conditions and production of *Sphagnum* biomass in paludiculture is currently being investigated in several Sphagnum farming projects in Germany (MOOSWEIT, KlimDivMoos, MoosKult), Latvia and Canada (Table 1). These projects include studies on fungal impact, regeneration and harvest frequency, and on the economics of the entire cultivation cycle at farm level (MOOSWEIT). Further research on the processing of *Sphagnum* biomass and the development of machinery is needed. A machine which can harvest *Sphagnum* biomass while driving on the production field is currently being developed in the TESPER project.

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More research is also needed on applications of the cultivated *Sphagnum* biomass. The introduction of *Sphagnum* biomass as a growing media constituent is currently being investigated in the projects SPHAKO (in combination with compost), MoosKult and TeiGa.

Alongside research on technical aspects, the implementation of large-scale Sphagnum farming requires modifications to the political and legal framework that will effectively initiate a paradigm shift in how peatlands are used for agricultural purposes (*cf*. Wichmann 2018). To achieve the climate goals, economic incentives for reducing greenhouse gas emissions are crucial. The recognition of *Sphagnum* as an agricultural crop (to secure subsidies) and payments for the provision of additional ecosystem services would stimulate the expansion of Sphagnum farming.

Sphagnum farming offers a clear opportunity to make a contribution to tackling pressing societal challenges. Research, industry and policy partners should seize this opportunity by joining forces to scale up Sphagnum farming.

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Appendix: List of plant cultivation experiments with *Sphagnum* biomass.

Application	**Plant species cultivated**	***Sphagnum* species tested**	**Fractions (Vol.-%) of *Sphagnum* tested**	**References**
Seedling test	Pak choi (*Brassica napus* var. *chinensis*)	*S. magellanicum*, *S. fimbriatum*, *S. palustre*, *S. papillosum*	0/ 25/ 50/ 75/ 100	Emmel 2008
	Chinese cabbage (*Brassica rapa car. pekinensis*)	not specified	0/ 50/ 80/ 85/ 100	Grantzau & Gaudig 2005
	Chinese cabbage (*Brassica rapa car. pekinensis*)	*S. fimbriatum*, *S. fallax*, *S. palustre*	0/ 50/ 100	Grantzau & Gaudig 2005
	Chinese cabbage (*Brassica rapa car. pekinensis*)	*S. magellanicum*, *S. fimbriatum*, *S. palustre*, *S. papillosum*	0/ 25/ 50/ 75/ 100	Emmel & Kennett 2007
	Chinese cabbage (*Brassica rapa car. pekinensis*)	*S. fallax*, *S. squarrosum*, *S. magellanicum*, *S. papillosum*, *S. capillifolium*, *S. palustre*	5/ 50/ 100	Thieme 2017
	Chinese cabbage (*Brassica rapa car. pekinensis*)	*S. palustre*, *S. fallax*	0/ 25/ 50/ 75/ 100	M. Emmel (unpublished data)
	Kohlrabi (*Brassica oleracea* var. *gongylodes)*	*S. magellanicum*, *S. fimbriatum*, *S. palustre*, *S. papillosum*	0/ 25/ 50/ 75/ 100	Emmel & Kennett 2007

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Application	**Plant species cultivated**	***Sphagnum* species tested**	**Fractions (Vol.-%) of *Sphagnum* tested**	**References**
Seedling test	Lettuce (*Lactuca sativa*)	*S. fallax*, *S. squarrosum*, *S. magellanicum*, *S. papillosum*, *S. capillifolium*, *S. palustre*	5/ 50/ 100	Thieme 2017
	Spinach (*Spinacia oleracea)*	*S. magellanicum*, *S. fimbriatum*, *S. palustre*, *S. papillosum*	0/ 25/ 50/ 75/ 100	Emmel & Kennett 2007
Pressed pot substrate	Chinese cabbage (*Brassica rapa car. pekinensis*)	*S. papillosum*	0/ 25/ 42/ 53	Emmel 2017
	Lettuce (*Lactuca sativa*)	*S. papillosum*	0/ 25/ 42/ 53	Emmel 2017
Pellets	Lettuce (*Lactuca sativa*)	*S. flavicomans*, *S. magellanicum*, *S. rubellum*, *Sphagnum* mix *(S. rubellum/ S. magellanicum)*	0/ 25/ 50	St-Hilaire *et al*. 2017
Seedling cultivation	Cauliflower, lettuce, tomato	*S. magellanicum*	50	Oberpaur *et al*. 2010
	Cucumber (*Cucumis sativus* 'Highmark II')	*S. papillosum*, *S. fallax*	0/ 50/ 100	Emmel & Kennett 2007
	Cucumber	*S. fuscum*, *S. magellanicum*, *S. riparium*, *Sphagnum* mix		Reinikainen *et al*. 2012
	Lettuce	*S. magellanicum*	40/ 50/ 60	Oberpaur *et al*. 2010, 2012

Application	**Plant species cultivated**	***Sphagnum* species tested**	**Fractions (Vol.-%) of *Sphagnum* tested**	**References**
Seedling cultivation	Lettuce	*S. fuscum*, *S. magellanicum*, *S. riparium*, *Sphagnum* mix		Reinikainen *et al*. 2012
	Tagetes	*S. palustre*, *S. fallax*	0/ 50/ 100	M. Emmel (unpublished data)
	Tomato	*S. fuscum*, *S. magellanicum*, *S. riparium*, *Sphagnum* mix		Reinikainen *et al*. 2012
Herbs	Basil	*S. rubellum*, *S. magellanicum*, *Sphagnum* mix (*S. rubellum*/ *S. magellanicum*)	0/ 40/ 80/ 100	St-Hilaire *et al*. 2017
	Sweet basil (*Basilicum occimum*)	*S. fuscum*	0/ 25/ 50/ 100 (dry weight)	A. Kämäräinen (unpublished data)
Fruit nursery	Kiwi fruit seedlings	*S. magellanicum*	33/ 40/ 80	Arévalo *et al*. 2016
Ornamental plants	*Azalea* ‘Sachsenstern’	*S. palustre*	0/ 25/ 50/ 75/ 100	Ueber & Gaudig 2014
	Begonia-Elatior-Gr. ‘Bellona’	*S. magellanicum*, *Sphagnum* mix (*S. fimbriatum*/ *S. palustre*/ *S. magellanicum*; *S. rubellum*/ *S. magellanicum*)	0/ 40	Grantzau 2004
	Begonia-Elatior-Gr. ‘Berseba’ (rooted cuttings)	*S. fuscum*, *Sphagnum* mix (*S. fuscum*/ *S. magellanicum*/ *S. balticum*, *S. papillosum*/ *S. rubellum*)	0/ 25/ 50/ 75/ 100 (dry weight)	A. Kämäräinen (unpublished data)

Application	Plant species cultivated	*Sphagnum* species tested	Fractions (Vol.-%) of *Sphagnum* tested	References
Ornamental plants	*Calluna vulgaris* 'Aphrodite'	*S. fimbriatum*, *S. papillosum*, *S. fallax*	0/ 25/ 50/ 75/ 100	Blievernicht *et al*. 2012b
	Cyclamen 'Leuchtfeuer'	not specified	0/ 20/ 40/ 60	Grantzau 2002
	Dendranthema 'Yellow Marettimo'	*S. fallax*, *S. palustre*, *S. papillosum*, *S. magellanicum*	0/ 50/ 100	Emmel & Kennet 2007
	Erica gracilis	*S. palustre*	0/ 25/ 50/ 75/ 100	Ueber & Gaudig 2014
	Fuchsia 'Beacon'	not specified	0/ 50	Grantzau (personal communication)[1]
	Gaultheria procumbens	*S. palustre*	0/ 25/ 50/ 75/ 100	Ueber & Gaudig 2014
	Impatiens Neug.-Gr. 'Timor'	*S. magellanicum*, *Sphagnum* mix (*S. fimbriatum*/ *S. palustre*/ *S. magellanicum*; *S. rubellum*/ *S. magellanicum*)	0/ 40	Grantzau 2004
	Impatiens walleriana	*S. fallax*, *S. magellanicum*	0/ 50/ 100	Emmel & Kennet 2007
	Pelargonium x hortorum 'Kim'	*S. magellanicum*	0/ 15/ 30	Jobin *et al*. 2014
	Pelargonium zonale 'Silke'	not specified	0/ 50	Grantzau (personal communication)[1]
	Pelargonium zonale 'Victoria'	not specified	0/ 50	Grantzau (personal communication)[1]

[1] E. Grantzau, Chamber of Agriculture Lower Saxony, Horticultural Training and Research Centre Ahlem, Germany, 2005.

Application	**Plant species cultivated**	***Sphagnum* species tested**	**Fractions (Vol.-%) of *Sphagnum* tested**	**References**
Ornamental plants	*Pelargonium zonale* ‘Tango Lavender’ (rooted cuttings)	*S. fuscum*, *Sphagnum* mix (*S. fuscum*/ *S. magellanicum*/ *S. balticum*/ *S. papillosum*/ *S. rubellum*)	0/ 25/ 50/ 75/ 100 (dry weight)	A. Kämäräinen (unpublished data)
	Petunia	*S. palustre*, *S. papillosum*, *S. magellanicum*	0/ 25/ 50/ 75/ 100	M. Emmel (unpublished data)
	Petunia x hybrida ‘Wave’	*S. magellanicum*	0/ 15/ 30	Jobin *et al*. 2014
	Petunia ‘Sublima White’	not specified	0/ 50	Grantzau (personal communication)[1]
	Poinsettia ‘Primero Red’	*S. palustre*	80	Blievernicht *et al*. 2012a, 2013
	Poinsettia ‘Scandic Early’	*S. palustre*	80	Blievernicht *et al*. 2012a, 2013
	Poinsettia ‘SK 79’	*S. palustre*	80	Blievernicht *et al*. 2012a, 2013
	Tagetes patula ‘Hero Spry’	not specified	0/ 50/ 80/ 85/ 100	Grantzau & Gaudig 2005
	Tagetes patula ‘Hero Spry’	not specified	0/ 50/ 100	Emmel 2008
	Verbena hybrida (rooted cuttings)	*S. fuscum*, *Sphagnum* mix (*S. fuscum*/ *S. magellanicum*/ *S. balticum*/ *S. papillosum*/ *S. rubellum*)	0/ 25/ 50/ 75/ 100 (dry weight)	A. Kämäräinen (unpublished data)
	Zinnia	*S. rubellum*, *S. magellanicum*, *Sphagnum* mix (*S. rubellum*/ *S. magellanicum*)	0/ 40/ 80/ 100	St-Hilaire *et al*. 2017

[1] E. Grantzau, Chamber of Agriculture Lower Saxony, Horticultural Training and Research Centre Ahlem, Germany, 2005.

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