

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

G. Gaudig, M. Krebs and H. Joosten

Department of Peatland Studies and Palaeoecology, Institute of Botany and Landscape Ecology,
University of Greifswald, partner in the Greifswald Mire Centre, Germany

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*

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

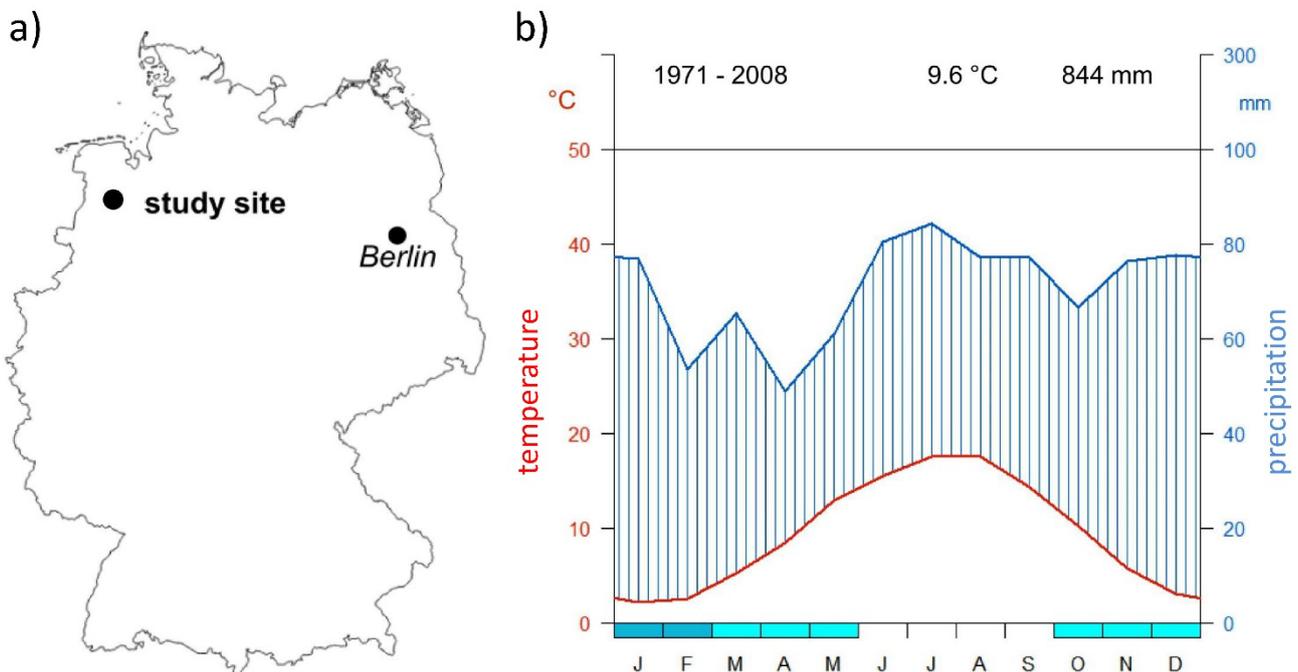


Figure 1. a) Location of the study site at Ramsloh, north-west Germany and b) climate graph (Walter & Lieth 1967) for the meteorological stations at Saterland-Ramsloh (precipitation, mm) and Dörpen (temperature, °C), which are located 4 km and 26 km from the site, respectively. The right-hand vertical 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).

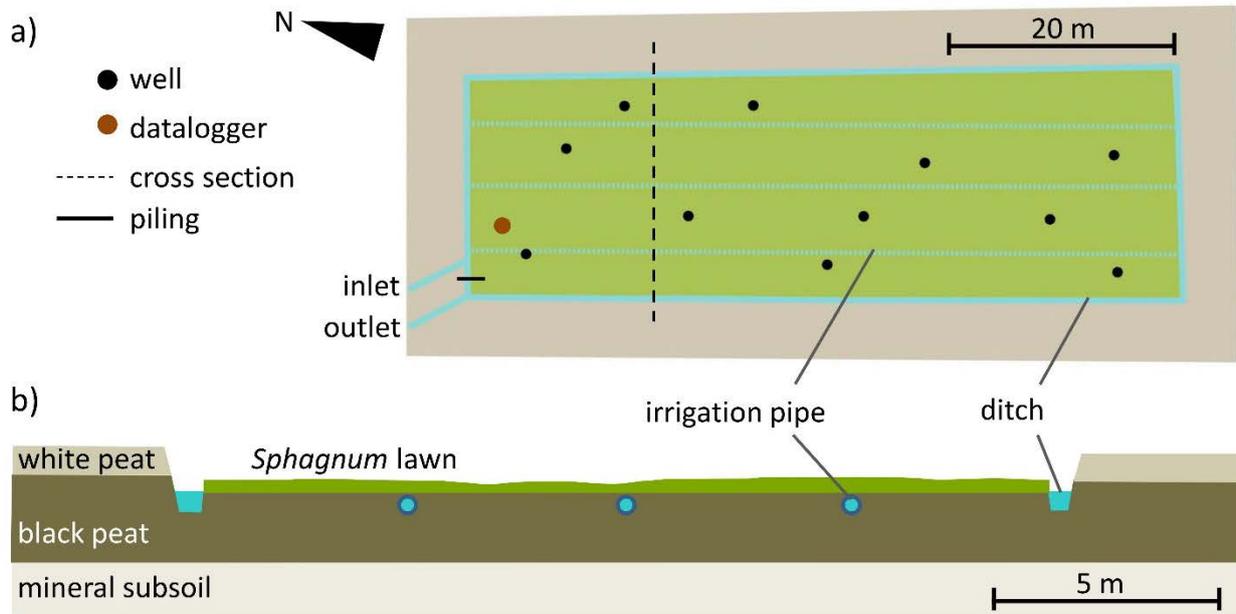


Figure 2. a) Schematic plan view and b) cross-section of the Ramsloh Sphagnum farming study site at the start of the experiment (after Kamermann & Blankenburg 2008).



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 cm³) 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 CaCl₂ 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 (NH₄⁺) and nitrate (NO₃⁻) 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 $\sim 2.5 \text{ m} \times 2.5 \text{ m}$ 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 pgrimess (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

Table 1. Characterisation of the 'black peat' of the Ramsloh site over the duration of the study (mean value \pm 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 ($\mu\text{S cm}^{-1}$)	122	n.d.	8–180

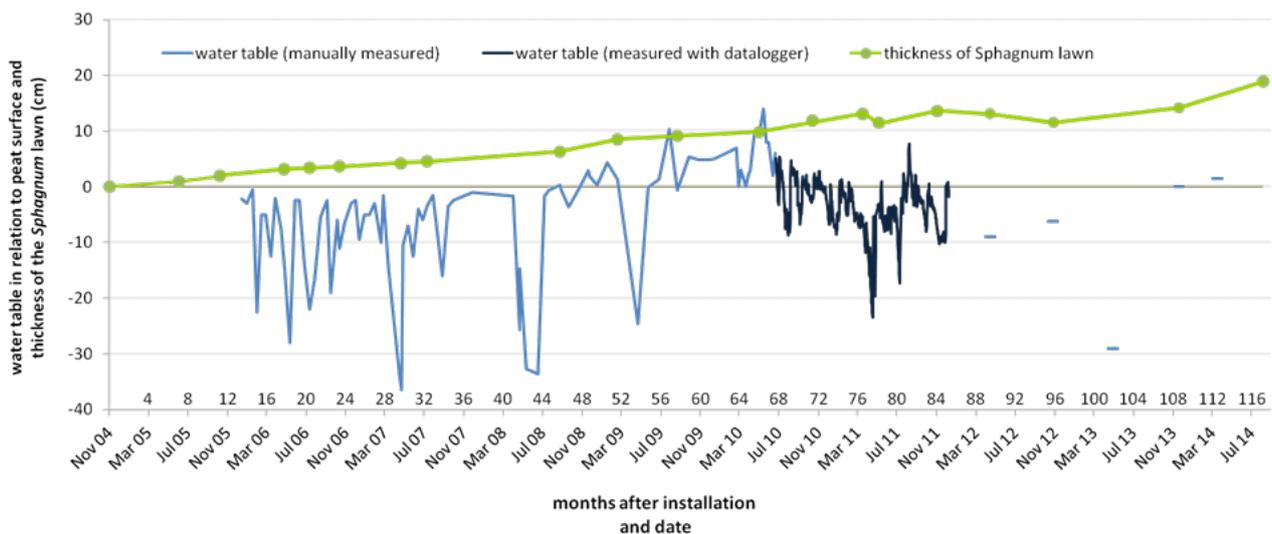


Figure 4. Fluctuations of water table relative to peat and peatmoss surface, and mean thickness (in cm) of *Sphagnum* lawn within 5 m of the water table measurement points. Water table position was determined manually (light blue) in the most northernmost well (near the datalogger) or by datalogger (dark 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.

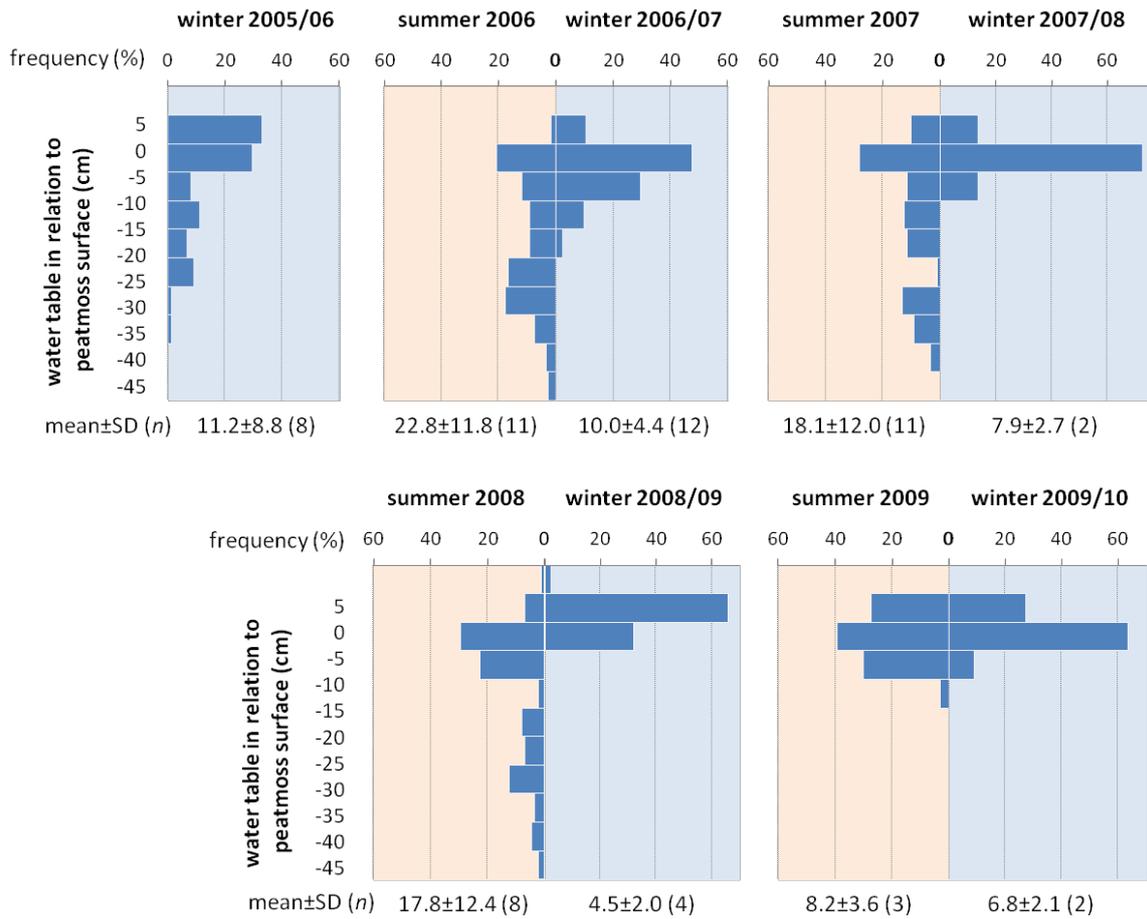


Figure 5. Water table frequency distribution (grouped into classes of 5 cm) and mean water table in relation to peatmoss surface in winter (October–March, blue) and summer (April–September, pink) for the period December 2005 to December 2009. Water table position was determined in eleven wells (see Figure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

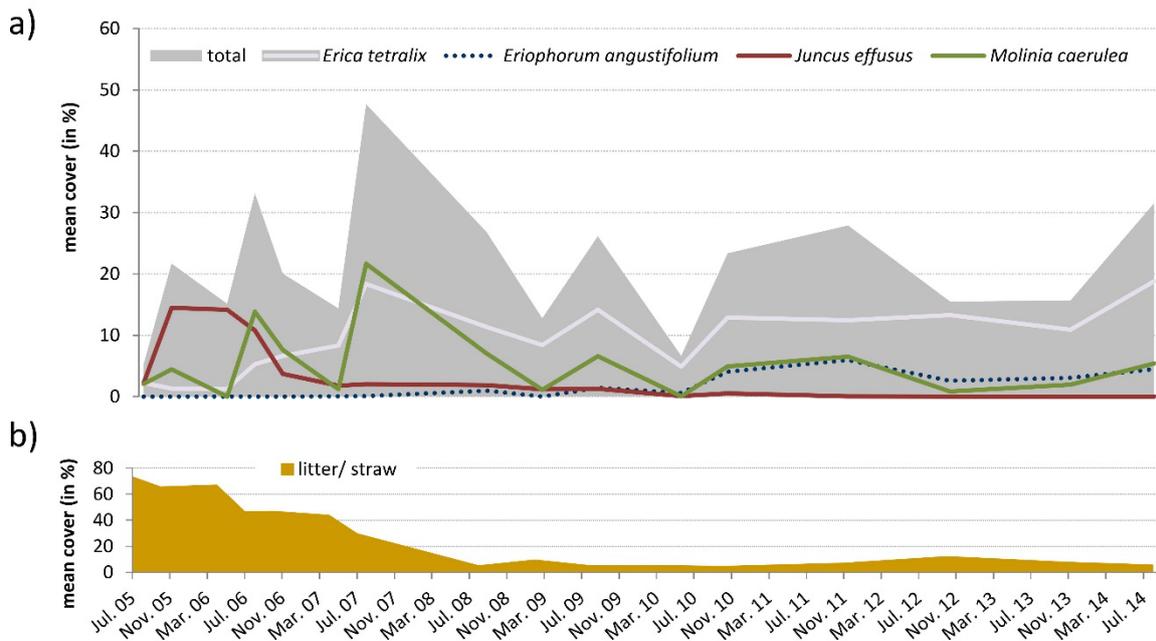


Figure 6. Development through time of a) mean total cover of vascular plants and selected species (%) and b) mean cover of litter including straw and mowed material, at the study site.

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

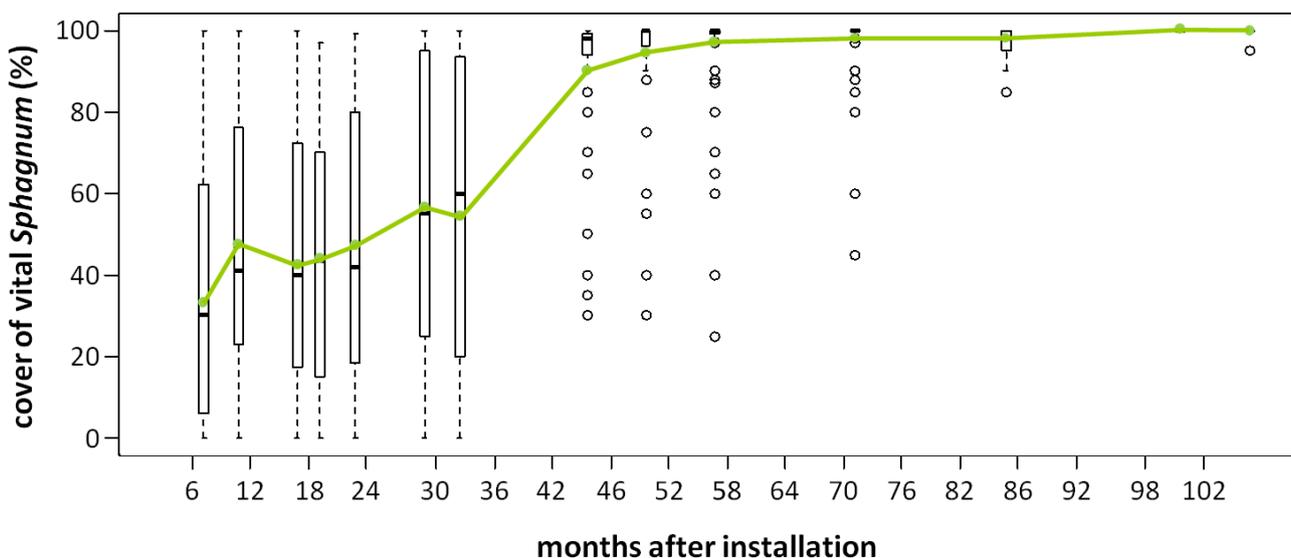


Figure 7. Cover of vital *Sphagnum* (%) at the study site for a period of 105 months after installation. For each observation date the plot shows the median (bold line), the upper and lower quartiles (the box includes 50 % of the data), the lowest value within 1.5 interquartile range (IQR) of the lower 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* ($1,950 \text{ g m}^{-2}$) 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 $1 \text{ t ha}^{-1} \text{ yr}^{-1}$) than between

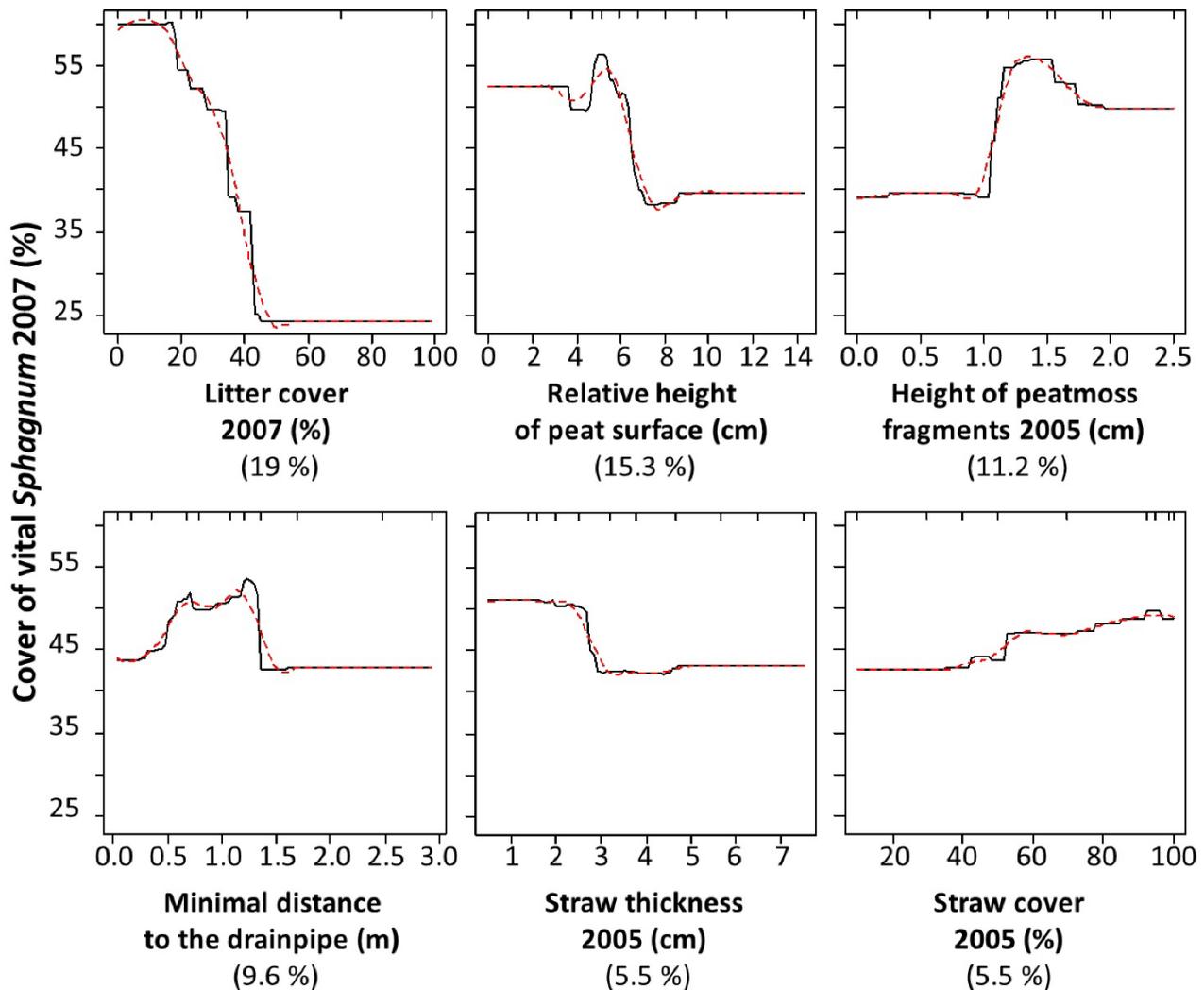


Figure 8. Boosted regression tree model of establishment expressed as cover (%) of vital *Sphagnum papillosum* 32 months after installation (July 2007, response variable) and its predictor/explanatory variables litter cover (%), relative height of peat surface (cm above the lowest peat surface altitude), 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).

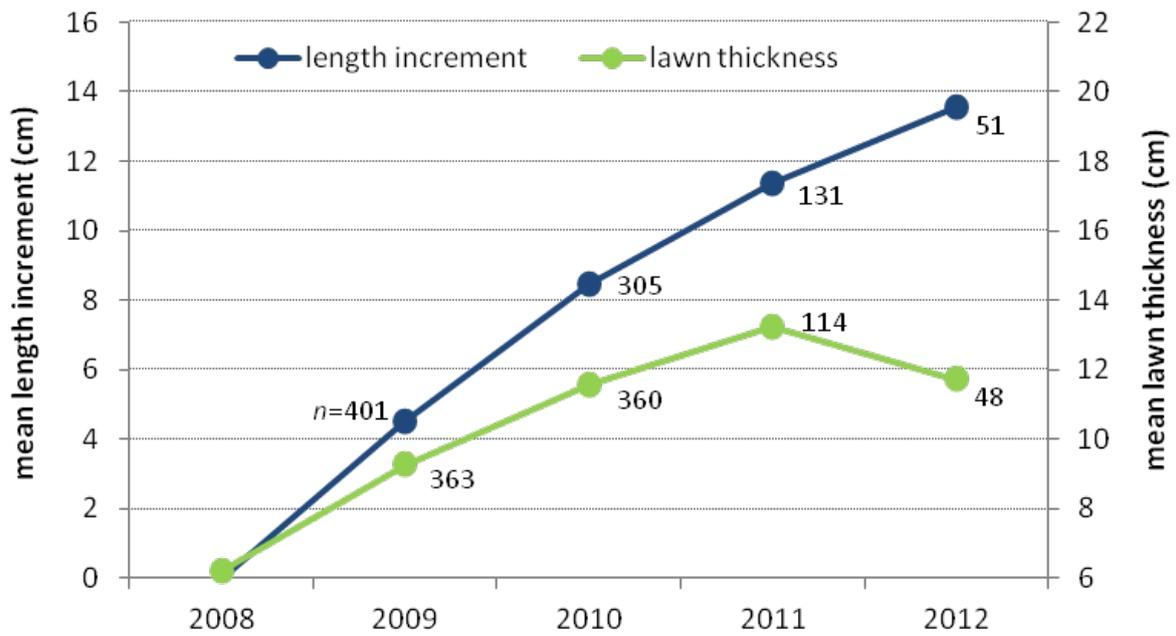


Figure 9. Mean cumulative length increment and mean lawn thickness of *Sphagnum papillosum* (in cm, mean thickness 6.2 cm in August 2008) at the study site between 2008 and 2012. Number of samples (*n*) for each measurement is written next to the mean value.

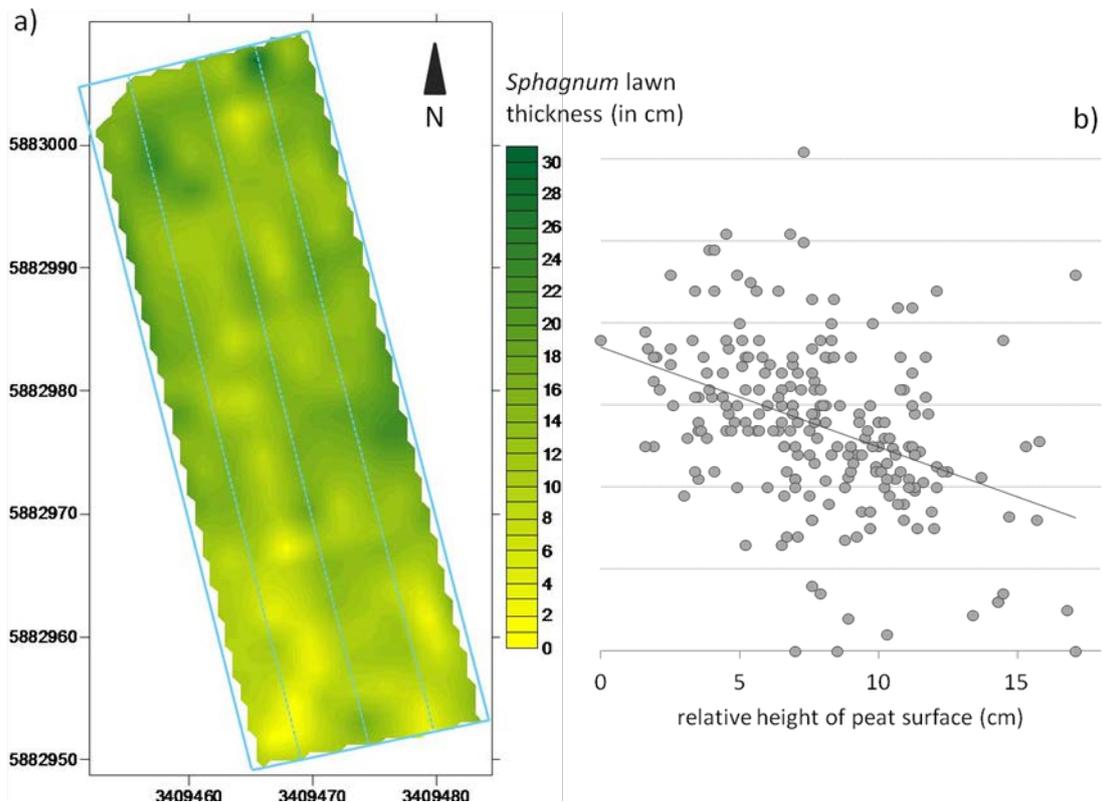


Figure 10. a) *Sphagnum papillosum* lawn thickness (cm) at the study site 6.5 years after installation, measured at points on a 2.5 m grid. Blue lines represent the irrigation system with ditches (solid lines) and subsurface pipes (dotted lines). b) Relationship between *Sphagnum* lawn thickness and 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

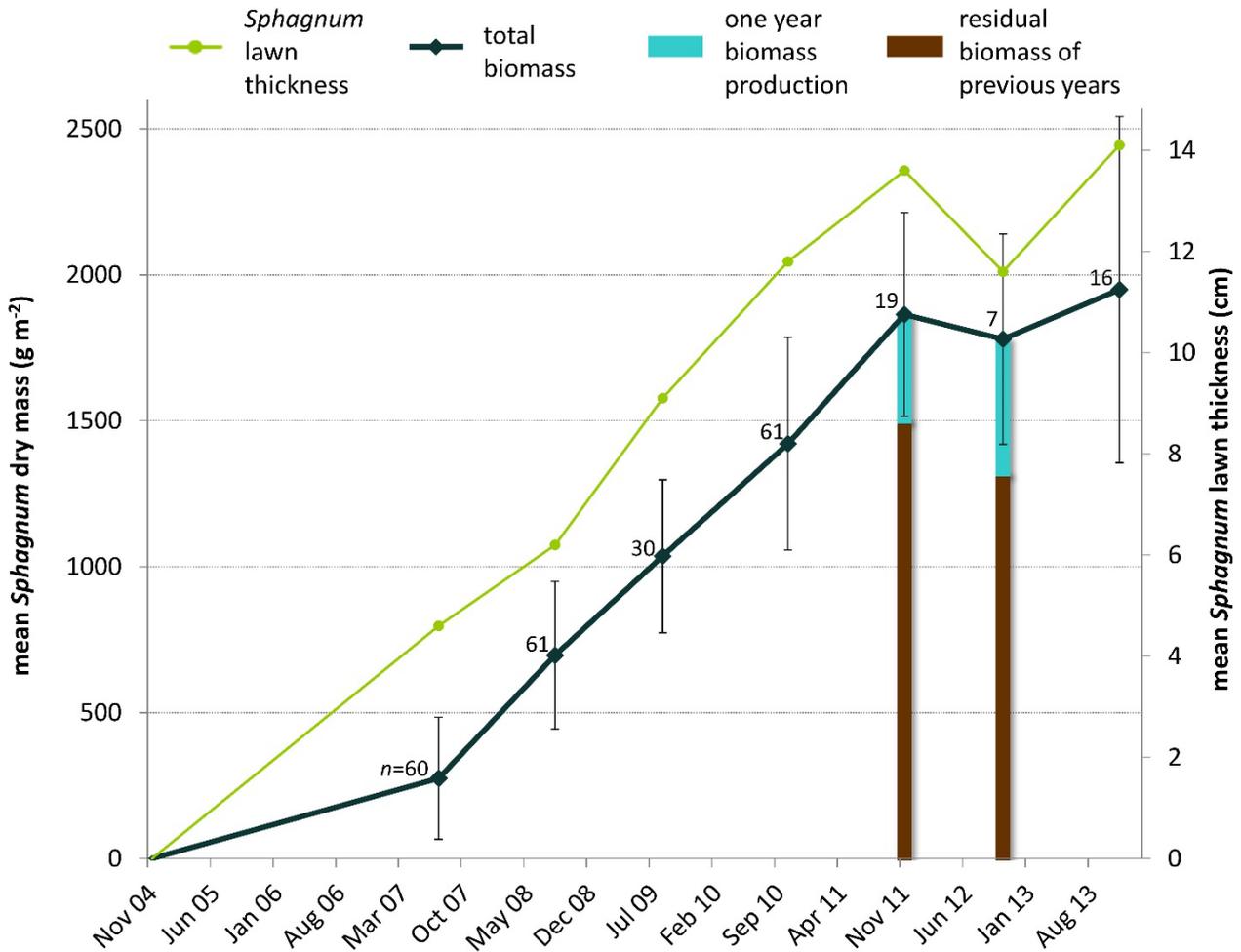


Figure 11. Development of mean *Sphagnum papillosum* lawn thickness measured at five points in each plot (green) and mean total *Sphagnum* biomass (dry mass ± SD) over time (dark blue) at the Ramsloh study site. The bars (left bar 2010–2011, right bar 2011–2012) are divided into one-year biomass production (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

was highest. Dry biomass productivity decreased at capitula N concentrations $>12 \text{ mg g}^{-1}$ and N/P quotients >18.5 , as well as at P concentrations in surface peat $>1.6 \text{ mg g}^{-1}$ 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).

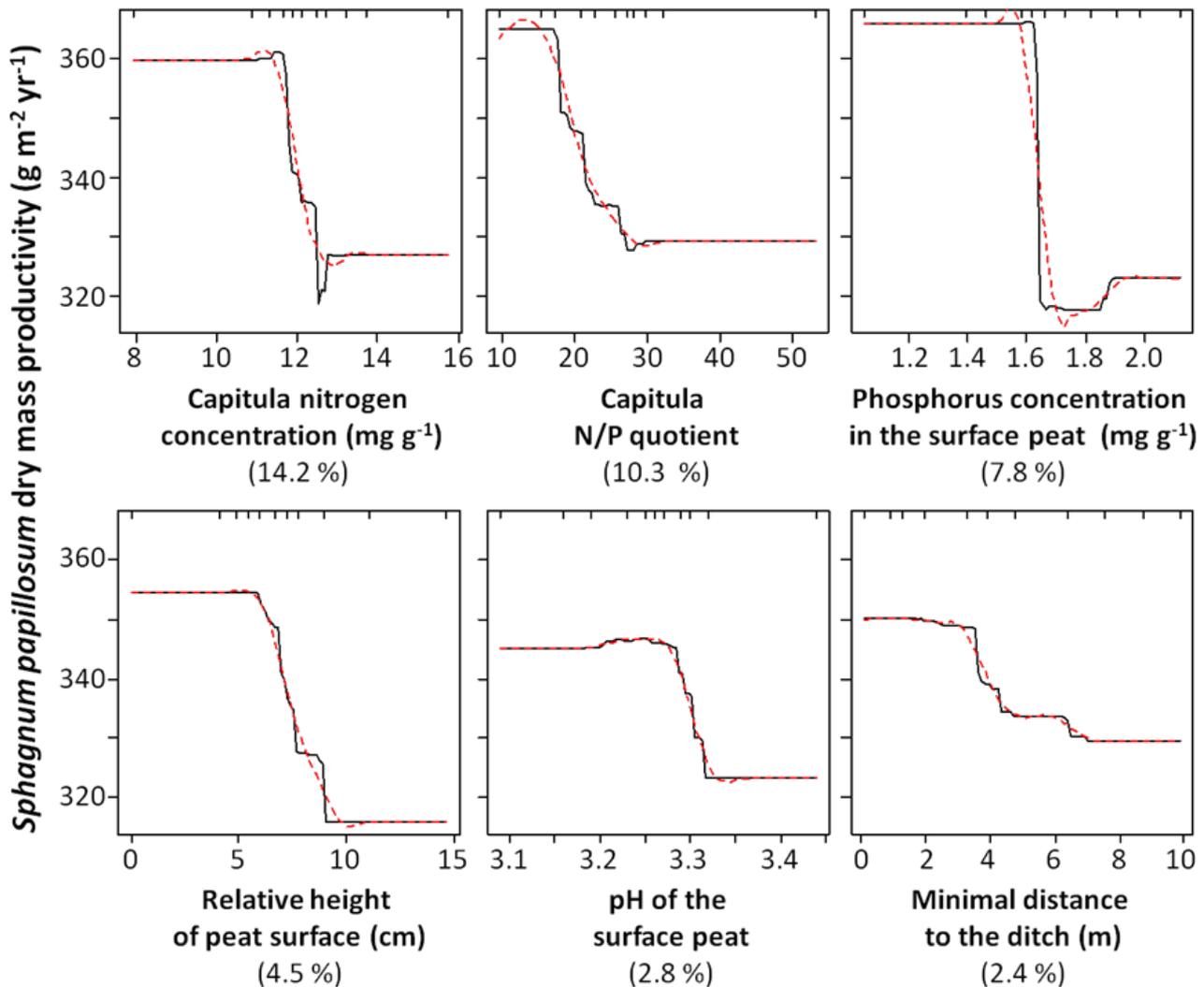


Figure 12. Boosted regression tree model of *Sphagnum papillosum* biomass productivity in $\text{g m}^{-2} \text{ yr}^{-1}$ (response variable) between 2008 and 2010 and its predictor/explanatory variables dry mass nitrogen concentration (mg g^{-1}) in capitula, capitula N/P quotient, dry mass phosphorus 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 %).

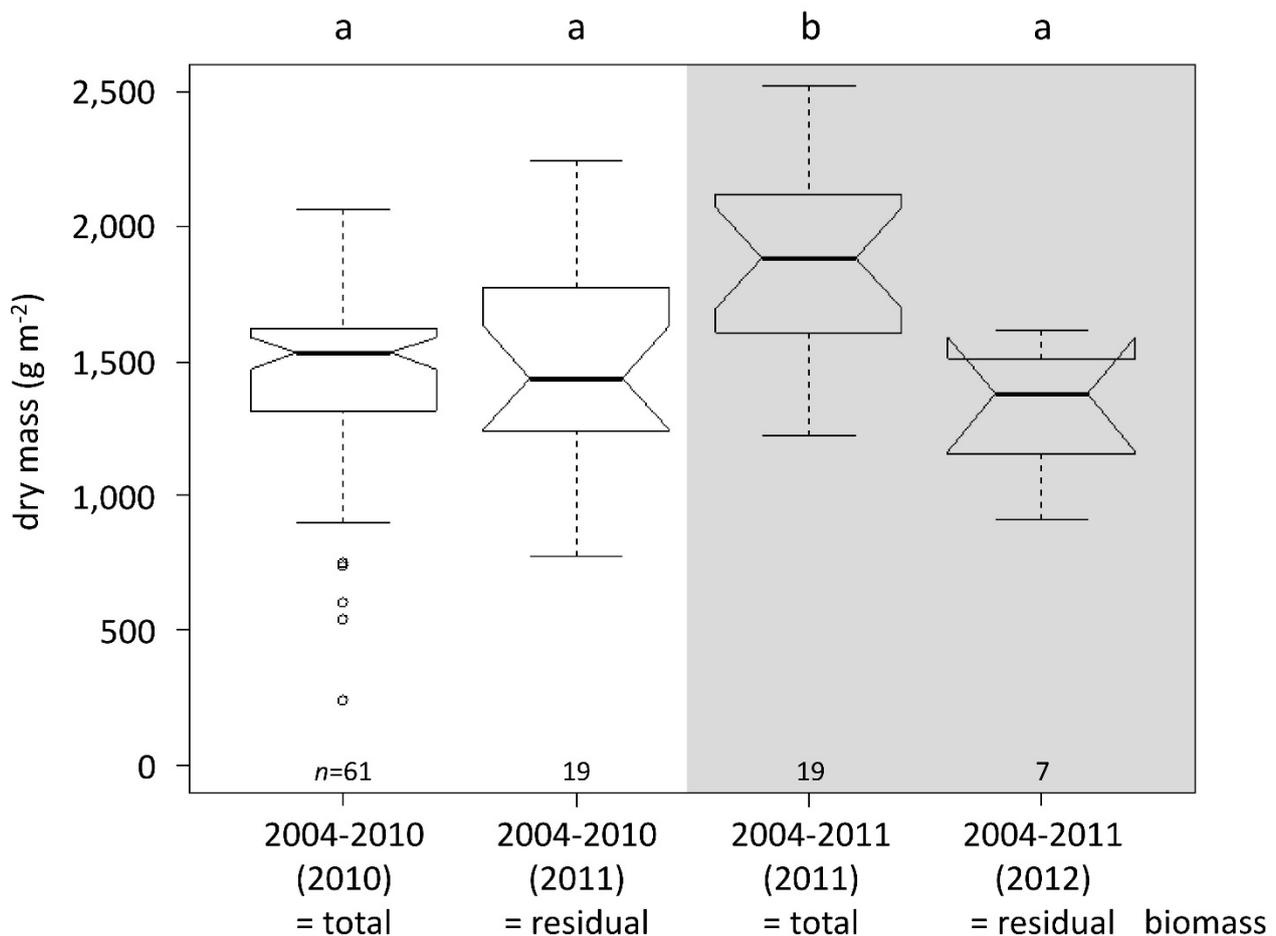


Figure 13. Biomass accumulation of peatmoss for 2004–2010 (white) and 2004–2011 (grey), as determined at the ends of these periods (2010 or 2011 = total biomass) and one year later (2011 or 2012 = residual biomass). Number of samples is written below each boxplot. Values with different letters differ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

DISCUSSION

Sphagnum productivity and biomass accumulation

At 365 and 461 $\text{g m}^{-2} \text{yr}^{-1}$ 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 $\text{g m}^{-2} \text{yr}^{-1}$. Higher values (up to 550 $\text{g m}^{-2} \text{yr}^{-1}$) 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 \pm 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 ($787 \pm 86 \text{ g m}^{-2}$) 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 recommended 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 (Guetegeinschaft 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.

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).

ACKNOWLEDGEMENTS

This study has been facilitated by the German Federal Ministry of Food, Agriculture and Consumer Protection (BMELV) and Torfwerk Moorkultur Ramsloh Werner Koch GmbH & Co. KG, whose financial and in-kind support is gratefully acknowledged. We thank our project partners for the fruitful co-operation. Furthermore, we thank Dörte Kamermann and Joachim Blankenburg for initiating the study and monitoring its development in the first three years, Ulrich Möbius and his team for laboratory support, and many student assistants for their patience and accuracy in sorting the mountains of biomass samples.

REFERENCES

- Altmann, M. (2008) *Socio-economic Impact of the Peat and Growing Media Industry on Horticulture in the EU*. Report to the European Peat and Growing Media Association (EPAGMA), 126 pp. Online at: http://www.epagma.eu/sites/default/files/growing%20media/socio_economic_study2008.pdf
- Aerts, R., Wallen, B. & Malmer, N. (1992) Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. *Journal of Ecology*, 80, 131–140.
- Baden, W. & Eggelsmann, R. (1963) Zur Durchlässigkeit der Moorböden (On the permeability of mire soils). *Zeitschrift für Kulturtechnik*, 4, 226–254 (in German).
- Berendse, F., van Breemen, N., Rydin, H., Buttler, A., Heijmans, M.M.P.D., Hoosbeek, M.R., Lee, J.A., Mitchell, E., Saarinen, T., Vasander, H. & Wallen, B. (2001) Raised atmospheric CO₂ levels and increased N deposition cause shifts in plant species composition and production in *Sphagnum* bogs. *Global Change Biology*, 7, 591–598.
- Beyer, C. & Höper, H. (2015) Greenhouse gas exchange of rewetted bog peat extraction sites and a *Sphagnum* cultivation site in northwest Germany. *Biogeosciences*, 12, 2101–2117.
- Blievernicht, A., Irrgang, S., Zander, M. & Ulrichs, C. (2013) *Sphagnum* biomass - the next generation of growing media. *Peatlands International*, 1/2013, 32–35.
- Bragazza, L., Tahvanainen, T., Kutnar, L., Rydin, H., Limpens, J., Hájek, M., Grosvernier, P., Hájek, T., Hajkova, P., Hansen, I., Iacumin, P. & Gerdol, R. (2004) Nutritional constraints in ombrotrophic *Sphagnum* plants under increasing atmospheric nitrogen deposition in Europe. *New Phytologist*, 163, 609–616.
- Campeau, S., Rochefort, L. & Price, J.S. (2004) On the use of shallow basins to restore cutover peatlands: Plant establishment. *Restoration Ecology*, 12/ 4, 471–482.
- Clymo, R.S. (1973) The growth of *Sphagnum*: some effects of environment. *Journal of Ecology*, 61, 849–869.
- Clymo, R.S. & Hayward, P.M. (1982) The ecology of *Sphagnum*. In: Smith, A.J.E. (ed.) *Bryophyte Ecology*, Chapman and Hall, London, 229–289.
- Crawley, M.J. (2005) *Statistics - An Introduction Using R*. John Wiley & Sons, Chichester, 342 pp.
- Crompton, T.R. (1996) *Determination of Anions: A Guide for the Analytical Chemist*. Springer-Verlag Berlin Heidelberg, XV+583 pp.
- Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology*, 77, 802–813.
- Emmel, M. (2008) Growing ornamental plants in *Sphagnum* biomass. *Acta Horticulturae*, 779, 173–178.
- Friedman, J.H. (2001) Greedy function approximation: a gradient boosting machine. *The Annals of Statistics*, 29, 1189–1232.
- Friedman, J.H. & Meulman, J.J. (2003) Multiple additive regression trees with application in epidemiology. *Statistics in Medicine*, 22, 1365–1381.
- Fritz C., van Dijk G., Smolders A.J.P., Pancotto V.A., Elzenga, T.J.T.M., Roelofs, J.G.M. & Grootjans, A.P. (2012) Nutrient additions in pristine Patagonian *Sphagnum* bogs: Can phosphorus addition alleviate (the effects of) increased nitrogen loads. *Plant Biology*, 14, 491–499.

- Gaudig, G., Fengler, F., Krebs, M., Prager, A., Schulz, J., Wichmann, S. & Joosten, H. (2014) Sphagnum farming in Germany - a review of progress. *Mires and Peat*, 13(08), 1–11.
- Giraudoux, P. (2010) pgrimess: Data analysis in ecology. R package version 1.4.9. Online at: <http://CRAN.R-project.org/package=pgrimess>
- Granath, G., Wiedermann, M.M. & Strengbom, J. (2009) Physiological responses to nitrogen and sulphur addition and raised temperature in *Sphagnum balticum*. *Oecologia*, 161, 481–490.
- Guetegemeinschaft Substrate fuer Pflanzen e.V. (2015) Gütekriterien für Kultursubstrate (RAL-GZ 250/2) (Quality criteria for growing media (RAL-GZ 250/2)). Online at: <http://www.substrate-ev.org/wp-content/uploads/2015/12/KultursubstrateGuetekriterien2015-01.pdf>, accessed 01 Apr 2017 (in German).
- Gunnarsson, U. (2005) Global patterns of *Sphagnum* productivity. *Journal of Bryology*, 27, 269–279.
- Günther, A., Jurasinski, G., Albrecht, K., Gaudig, G., Krebs, M. & Glatzel, S. (2017) Greenhouse gas balance of an establishing *Sphagnum* culture on a former bog grassland in Germany. *Mires and Peat*, 20(02), 1–16.
- Hayward, P.M. & Clymo, R.S. (1982) Profiles of water content and pore size in *Sphagnum* and peat, and their relation to peat bog ecology. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 215, 299–325.
- Hayward, P.M. & Clymo, R.S. (1983) The growth of *Sphagnum*: experiments on, and simulation of, some effects of light flux and water-table depth. *Journal of Ecology*, 71, 845–863.
- Hendry, G.A.F. & Grime, J.P. (eds.) (1993) *Methods in Comparative Plant Ecology: a Laboratory Manual*. Chapman and Hall, London, 276 pp.
- Hurlbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, 54, 187–211.
- IVG (2014) Zahlen, Daten, Fakten - Deutschland: Einsatz und Verfügbarkeit alternativer Ausgangsstoffe (Numbers, data, facts - Germany: use and availability of alternative raw materials). Online at: <http://www.warum-torf.info/zahlen-daten-fakten/daten-deutschland/deutschland-einsatz-und-verfuegbarkeit>, accessed 31 Mar 2017 (in German).
- Jobin, P., Caron, J. & Rochefort, L. (2014) Developing new potting mixes with *Sphagnum* fibers. *Canadian Journal of Soil Science*, 94, 585–593.
- Johnson, L.C. & Damman, A.W.H. (1991) Species-controlled *Sphagnum* decay on a South Swedish raised bog. *Oikos*, 61, 234–242.
- Kamermann, D. & Blankenburg, J. (2008) Erfahrungen und Ergebnisse eines Feldversuchs im Projekt „Torfmoos als nachwachsender Rohstoff“ (Experiences and results of a field experiment in the project “Peat moss as renewable raw material”). *Telma*, 38, 121–144 (in German).
- Kennedy, G.W. & Price, J.S. (2005) A conceptual model of volume-change controls on the hydrology of cutover peats. *Journal of Hydrology*, 302, 13–27.
- Krebs, M. & Gaudig, G. (2005) Torfmoos (*Sphagnum*) als nachwachsender Rohstoff - Untersuchungen zur Maximierung der Produktivität von *Sphagnum papillosum* im Regendurchströmungsmoor Ispani 2 (Georgien) (Peatmoss (*Sphagnum*) as a renewable resource - investigations on maximising the productivity of *Sphagnum papillosum* in the percolation bog Ispani 2 (Georgia)). *Telma*, 35, 171–189 (in German).
- Krebs, M., Gaudig, G. & Joosten, H. (2016) Record growth of *Sphagnum papillosum* in Georgia (Transcaucasus): rain frequency, temperature and microhabitat as key drivers in natural bogs. *Mires and Peat*, 18(04), 1–16.
- Krom, M.D. (1980) Spectrophotometric determination of ammonia: A study of a modified Berthelot reduction using salicylate and dichloroisocyanurate. *The Analyst*, 105, 305–316.
- Lamers, L.P.M., Bobbink, R. & Roelofs, J.G.M. (2000) Natural nitrogen filter fails in polluted raised bogs. *Global Change Biology*, 6, 583–586.
- Landry, J. & Rochefort, L. (2009) *Experimental Sphagnum Farming Station Shippagan, New-Brunswick. Activity Report 2003–2008*. Peatland Ecology Research Group, Université Laval, Québec, Canada, 50 pp. Online at: http://www.gret-perg.ulaval.ca/uploads/tx_centre_recherche/Report_SphFarm_2003_2008_final_04.pdf, accessed 08 Apr 2017.
- Li, Y., Glime, M. & Liao, C. (1992) Responses of two interacting *Sphagnum* species to water level. *Journal of Bryology*, 17, 59–70.
- Limpens, J., Berendse, F. & Klees, H. (2003) N deposition affects N availability in interstitial water, growth of *Sphagnum* and invasion of vascular plants in bog vegetation. *New Phytologist*, 157, 339–347.
- Limpens, J., Granath, G., Gunnarsson, U., Aerts, R., Bayley, S., Bragazza, L., Bubier, J., Buttler, A., van den Berg, L.J.L., Francez, A.-J., Gerdol, R., Grosvernier, P., Heijmans, M.M.P.D., Hoosbeek, M.R., Hotes, S., Ilomets, M., Leith, I., Mitchell, E.A.D., Moore, T., Nilsson, M.B., Nordbakken, J.-F., Rochefort, L., Rydin, H., Sheppard, L.J.,

- Thormann, M., Wiedermann, M.M., Williams, B.L. & Xu, B. (2011) Climatic modifiers of the response to nitrogen deposition in peat-forming *Sphagnum* mosses: a meta-analysis. *New Phytologist*, 191, 496–507.
- Limpens, J. & Heijmans, M.M.P.D. (2008) Swift recovery of *Sphagnum* nutrient concentrations after excess supply. *Oecologia*, 157, 153–161.
- Londo, G. (1976) The decimal scale for relevés of permanent quadrats. *Vegetatio*, 33(1), 61–64.
- Luthardt, V. & Wichmann, S. (2016) Ecosystem services of peatlands. In: Wichtmann, W., Schröder, C. & Joosten, H. (eds.) *Paludiculture - Productive Use of Wet Peatlands*. Schweizerbart Science Publishers, Stuttgart, 13–20.
- Lütt, S. (1992) *Produktionsbiologische Untersuchungen zur Sukzession der Torfstichvegetation in Schleswig-Holstein (Production Biological Studies of the Succession of Peat Pit Vegetation in Schleswig-Holstein)*. Volume 43, Mitteilungen der Arbeitsgemeinschaft Geobotanik in Schleswig-Holstein und Hamburg, Kiel, 250 pp. (in German).
- Malmer, N., Svensson, B.M., & Wallén, B. (1994) Interactions between *Sphagnum* mosses and field layer vascular plants in the development of peat-forming systems. *Folia Geobotanica & Phytotaxonomica*, 29(4), 483–496.
- McCarter, C.P.R. & Price, J.S. (2014) Ecohydrology of *Sphagnum* moss hummocks: mechanisms of capitula water supply and simulated effects of evaporation. *Ecohydrology*, 7, 33–44.
- McCorry, M.J. & Renou, F. (2003) *Ecology and Management of Juncus effusus (Soft Rush) on Cutaway Peatlands*. Forest Ecosystem Research Group Report 69, Dublin, 66 pp. Online at: http://www.ucd.ie/ferg/Research/Projects/BOGF-OR/Juncus_McCorry_Renou.pdf, accessed 01 Apr 2017.
- Oberpaur, C., Puebla, V., Vaccarezza, F. & Arévalo, M.E. (2010) Preliminary substrate mixtures including peat moss (*Sphagnum magellanicum*) for vegetable crop nurseries. *Ciencia e Investigación Agraria*, 37, 123–132.
- Ohlson, M., Økland, R.H., Nordbakken, J.-F. & Dahlberg, B. (2001) Fatal interactions between Scots pine and *Sphagnum* mosses in bog ecosystems. *Oikos*, 94, 425–432.
- Oleszczuk, R. & Brandyk, T. (2008) The analysis of shrinkage-swelling behaviour of peat-moorsh soil aggregates during drying-wetting cycles. *Agronomy Research*, 6(1), 131–140.
- Pedersen, A. (1975) Growth measurements of five *Sphagnum* species in South Norway. *Norwegian Journal of Botany*, 22, 277–284.
- Pouliot, R., Hugron, S. & Rochefort, L. (2015) Sphagnum farming: A long-term study on producing peat moss biomass sustainably. *Ecological Engineering*, 74, 135–147.
- Pouliot, R., Rochefort, L., Karofeld, E. & Mercier, C. (2011) Initiation of *Sphagnum* moss hummocks in bogs and the presence of vascular plants: Is there a link? *Acta Oecologica*, 37, 346–354.
- Quinty, F. & Rochefort, L. (2003) *Peatland Restoration Guide, Second Edition*. Canadian Sphagnum Peat Moss Association (St. Albert, AB) & New Brunswick Department of Natural Resources and Energy (Fredericton, NB), Canada, 106 pp. Online at: http://www.gret-perg.ulaval.ca/uploads/tx_centrecherche/Peatland_Restoration_guide_2ndEd_01.pdf, accessed 01 Apr 2017.
- R Development Core Team (2009) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. Online at: <http://www.R-project.org>
- Reinikainen, O., Korpi, J., Tahvonen, R., Näkkilä, J., Silvan, N. & Silvan, K. (2012) Harvesting of *Sphagnum* biomass and its use as a growing medium constituent. Abstract No. 137, *Proceedings of the 14th International Peat Congress*, International Peat Society, Stockholm, Sweden, 6 pp.
- Ridgeway, G. (2007) Generalized boosted regression models. Documentation for the R Package ‘gbm’, version 1.6-3.
- Robert, É.C., Rochefort, L. & Garneau, M. (1999) Natural revegetation of two block-cut mined peatlands in eastern Canada. *Canadian Journal of Botany*, 77, 447–459.
- Robroek, B.J.M., Limpens, J., Breeuwer, A. & Schouten, M.G.C. (2007) Effects of water level and temperature on performance of four *Sphagnum* mosses. *Plant Ecology*, 190, 97–107.
- Robroek, B.J.M., Schouten, M.G.C., Limpens, J., Berendse, F. & Poorter, H. (2009) Interactive effects of water table and precipitation on net CO₂ assimilation of three co-occurring *Sphagnum* mosses differing in distribution above the water table. *Global Change Biology*, 15, 680–691.
- Rydin, H. & Jeglum, J.K. (2013) *The Biology of Peatlands*. Second edition, Oxford University Press, 400 pp.
- Schouwenaars, J.M. (1995) The selection of internal and external water management options for bog restoration. In: Wheeler, B.D., Shaw, S., Fojt, W.J. & Robertson, R.A. (eds.) *Restoration of Temperate Wetlands*, John Wiley & Sons Ltd., Chichester, 331–346.
- Siegel, S. & Castellan, N.J.Jr. (1988) *Nonparametric Statistics for the Behavioral Sciences*. McGraw

- Hill, New York, 399 pp.
- Strack, M. & Price, J. (2009) Moisture controls on carbon dioxide dynamics of peat-*Sphagnum* monoliths. *Ecohydrology*, 2, 34–41.
- Temminghoff, E.E.J.M. (ed.) (2004) *Plant Analysis Procedures*. Second edition, Kluwer Academic Publishers, Dordrecht, The Netherlands, 178 pp.
- Temmink, R., Fritz, C., van Dijk, G., Hensgens, G., Lamers, L., Krebs, M., Gaudig, G. & Joosten, H. (2016.) Sphagnum farming in a eutrophic world: the importance of optimal nutrient stoichiometry. *Ecological Engineering*, 98, 196–205.
- Titus, J.E. & Wagner, D.J. (1984) Carbon balance for two *Sphagnum* mosses: water balance resolves a physiological paradox. *Ecology*, 65, 1765–1774.
- UBA (2016) *Hintergrundbelastungsdaten Stickstoff, Bezugsjahr 2009 (Background Nitrogen Exposure Data, Reference Year 2009)*. Interactive map, Umwelt Bundesamt (UBA), Dessau-Rosslau. Online at: <http://gis.uba.de/website/depo1/>
- Van den Akker, J.J.H., Hendriks, R., Hoving, I. & Pleijter, M. (2010) *Toepassing van Onderwaterdrains in Veenweidegebieden. Effecten op Maaiveldddaling, Broeikasgasemissies en het Water (Application of Underwater Drains in Peatland Areas. Impacts on Subsidence, Greenhouse Gas Emissions and Water)*. Landschap 27/3, Werkgemeenschap voor Landschapsonderzoek (WLO), Utrecht, 137–149 (in Dutch). Online at: <http://veenweiden.nl/wp-content/uploads/2012/04/Toepassing-van-drains-in-veenweidegebieden.pdf>, accessed 01 Apr 2017.
- van der Heijden, E., Verbeek, S.K. & Kuiper, P.J.C. (2000) Elevated atmospheric CO₂ and increased nitrogen deposition: effects on C and N metabolism and growth of the peat moss *Sphagnum recurvum* P. Beauv. var. *mucronatum* (Russ.) Warnst. *Global Change Biology*, 6, 201–212.
- von Post, L. (1924) Das genetische System der organogenen Bildungen Schwedens (The genetic system of the organogenic deposits in Sweden). In: Comité International de Pédologie, IVème commission (commission pour la nomenclature et la classification des sols, commission pour l'Europe, président: B. Frosterus) (ed.) *Mémoires sur la Nomenclature et la Classification des Sols*, Helsingfors/Helsinki, 287–304 (in German).
- Walter, H. & Lieth, H. (1967) *Klimadiagramm-Weltatlas (World Atlas of Climate Diagrams)*. Gustav Fischer Verlag, Jena, 256 pp. (in German).
- Wichmann, S., Prager, A. & Gaudig, G. (2017) Establishing *Sphagnum* cultures on bog grassland, cut-over bogs, and floating mats: procedures, costs and area potential in Germany. *Mires and Peat*, 20(03), 1–19.
- Wichtmann, W., Schröder, C & Joosten, H. (eds.) (2016) *Paludiculture - Productive Use of Wet Peatlands*. Schweizerbart Science Publishers, Stuttgart, 272 pp.
- Zegers, G., Larraín, J., Díaz, F. & Armesto, J. (2006) Impacto ecológico y social de la explotación de pomponales y turberas de *Sphagnum* en la Isla Grande de Chiloé (Ecological and social impact of the exploitation of pomponales and *Sphagnum* bogs on the Greater Island of Chiloé). *Revista Ambiente y Desarrollo de CIPMA*, 22(1), 28–34 (in Spanish). Online at: <http://uniciencia.ambientalex.info/revistas/Impactoecologicoysocial.pdf>, accessed 01 Apr 2017.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, 573 pp.

Submitted 13 May 2016, final revision 09 May 2017
Editor: Stephan Glatzel

Author for correspondence:

Greta Gaudig, Department of Peatland Studies and Palaeoecology, Institute of Botany and Landscape Ecology, University of Greifswald, partner in the Greifswald Mire Centre, Soldmannstraße 15, D-17487 Germany. Tel. +49 3834 4204692; Fax. +49 3834 4204114; E-Mail: gaudig@uni-greifswald.de