Sphagnum regrowth after cutting

M. Krebs[1], G. Gaudig[1], I. Matchutadze[2] and H. Joosten[1]

[1]Institute of Botany and Landscape Ecology, University of Greifswald, partner in the Greifswald Mire Centre, Germany
[2]Department of Conservation of Kolkheti Peatlands and Water Ecosystems, Batumi Shota Rustaveli State University, Georgia

SUMMARY

Sphagnum biomass is commercially harvested from semi-natural and natural peatlands. In this article we analyse the effects of harvesting *Sphagnum* by cutting off the top parts of the plants and leaving the cut stems to regenerate. We tested regrowth of *Sphagnum palustre* and *Sphagnum papillosum* in natural peatlands with high *Sphagnum* productivity in Kolkheti (Georgia, Transcaucasus) using two cutting depths (5, 10 cm) and two cutting intervals (1, 2 years). In Germany we measured regrowth of *S. papillosum* in an experimental Sphagnum farming field 2.5 years after cutting off the top 5 cm. Regrowth of *Sphagnum* was similar in both regions, with new capitula attaining 80 % cover one year after cutting and similar biomass productivities (Kolkheti: *S. palustre* 169–329 g m^{-2} yr^{-1}, *S. papillosum* 152–246 g m^{-2} yr^{-1}; Germany: *S. papillosum* 249 g m^{-2} yr^{-1}). In Kolkheti, regrowth was independent of cutting depth. No relationship between site conditions and biomass regrowth was identified in either Kolkheti or Germany, probably because of the overarching effect of favourable hydrological conditions. This study shows that cutting is an appropriate method for harvesting *Sphagnum* and allows repeated harvests with fast *Sphagnum* regrowth. For *S. palustre*, it may even be possible to harvest annually without reducing yields.

KEY WORDS: productivity, recovery yield, Sphagnum farming, *Sphagnum palustre*, *Sphagnum papillosum*

INTRODUCTION

Fresh *Sphagnum* (peatmoss) biomass is of high economic value (Johnson & Maly 1998, Stokes *et al.* 1999, Díaz *et al.* 2008) for producing high-quality horticultural growing media (Whinam *et al.* 2003, Emmel 2008, Oberpaur *et al.* 2010, Blievernicht *et al.* 2013, Jobin *et al.* 2014) and a wide range of further applications (Hotson 1918, Elling & Knighton 1984). Since various countries, including the United Kingdom, Switzerland and Germany, have decided to restrict or phase out the use of peat (Joosten *et al.* 2015, BMUB 2016, Bonn *et al.* 2015), the demand for *Sphagnum* biomass as a renewable substitute for peat is expected to increase.

Sphagnum biomass is collected commercially from semi-natural and natural areas in Chile, New Zealand, Australia/Tasmania, Finland, USA and China (Elling & Knighton 1984, Buxton *et al.* 1996, Johnson & Maly 1998, Esposito 2000, Whinam *et al.* 2003, Díaz & Silva 2012, Domínguez 2014, Silvan *et al.* 2017), using various methods. In New Zealand and Chile the *Sphagnum* is collected manually using pitchforks (Stokes *et al.* 1999). In North America small 'crawler tractors' scrape living and partly decomposed *Sphagnum* material from the frozen peat surface in winter (Elling & Knighton 1984, mossman381 2012), while in Finland *Sphagnum* mosses are collected using mechanical excavators (Silvan *et al*. 2017).

Collection intervals range from three to ten years (Johnson & Maly 1998, Esposito 2000, Whinam *et al.* 2003, Díaz *et al.* 2008) depending on residual moss cover (parts of or whole moss plants), collection method, growth rate and site conditions (Buxton *et al.* 1996, Whinam & Buxton 1997, Whinam *et al.* 2003). For Finland, Silvan *et al.* (2017) suggest a collection interval of ~30 years when removing the uppermost 30 cm of moss.

Regrowth of *Sphagnum* has been found to be faster at warmer and wetter sites and can be accelerated by leaving behind (or re-spreading) 30 % of the actively growing *Sphagnum* (Buxton *et al.* 1996, Whinam *et al.* 2003). Re-spreading combined with fertiliser application allowed a collection interval of ten years in Tasmania (Whinam & Buxton 1997). *Sphagnum* regrowth is reportedly also stimulated by partial shade and a water table close to the moss surface (Whinam *et al*. 2003), but further insight on how site conditions influence *Sphagnum*

 DOI: 10.19189/MaP.2017.OMB.298

regrowth is still missing. Under optimal conditions, collection intervals of 3–5 years may be attainable (Whinam *et al.* 2003).

Various studies suggest that the number of newly grown shoots ('innovations') decreases with increasing distance from the capitulum. Sobotka (1976) and Poschlod (1990) showed that green (chlorophyll containing) *Sphagnum* parts have a greater ability to regenerate than the brown parts deeper in the moss layer. In various *Sphagnum* species including *Sphagnum magellanicum*, Campeau & Rochefort (1996) observed most innovations in plant parts taken from depths of less than 10 cm below the *Sphagnum* surface. In another resprouting experiment, Díaz & Silva (2012) found that 90 % of new shoots in single *S. magellanicum* plants developed within 12 cm of the capitulum, and most formed in the first 6 cm. In contrast, when Clymo & Duckett (1986) tested *Sphagnum papillosum* regeneration from contiguous 3 cm thick slices, they found the best regeneration at depths of 6–12 cm below the *Sphagnum* surface and very few new shoots in the first 6 cm, suggesting some sort of 'apical dominance'. Hitherto, no study has systematically addressed biomass regrowth and productivity of the *Sphagnum* layer that remains after cutting off the top parts of *Sphagnum* plants as a regular harvesting procedure in Sphagnum farming. Therefore, in this article we test the following hypotheses:

1. cutting of *Sphagnum* allows fast regrowth;
2. *Sphagnum* regrowth is faster under warmer and wetter climatic conditions;
3. *Sphagnum* regrowth is faster when the harvesting depth is shallower; and
4. annual harvesting of *Sphagnum* from the same site is possible, with consistently high yields.

METHODS

Site descriptions

The experiments were set up in naturally established *Sphagnum* lawns on the Ispani 1 and Grigoleti peatlands in the Kolkheti Lowlands of Georgia, Transcaucasia (short name 'Kolkheti'), *i.e.* the region with the highest natural productivity of *Sphagnum papillosum* Lindb. and *Sphagnum palustre* L. globally (Krebs *et al.* 2016). For comparison, we analysed regrowth of *S. papillosum* in an experimental Sphagnum farming field on the Ramsloh peatland in north-west Germany (Figures 1a, 1c). In all of these peatlands the living *Sphagnum* layer was clearly separate from the underlying strongly decomposed peat.

The Ispani 1 peatland (41° 50.3' N, 41° 47.5' E, ~1 m a.s.l.) is located east of Kobuleti (South Kolkheti) at a distance of 0.5 km from the Black Sea, and comprises a 500 ha open area partly surrounded by alder (*Alnus glutinosa* ssp. *barbata* (C.A.Mey.) Yalt.) forest. The peatland has been damaged by peat extraction which commenced in the 1960s (Tavadze 1963) and continued until the 1980s, although the mire vegetation has now recovered. The area currently consists of dense lawns of *S. papillosum* (90–100 % cover) with *Molinia caerulea* ssp. *arundinacea* and *Carex elata* (30–40 % cover), and *S. palustre* (90–100 % cover) with *Juncus effusus* (30 % cover).

The Grigoleti peatland (42° 3.2' N, 41° 44.3' E, 1–1.5 m a.s.l.) is located in Central Kolkheti at a distance of 0.35 km from the Black Sea and comprises 150 ha of open mire and 270 ha of alder forest (Krebs *et al.* 2016, Figure 1a). The open part of the peatland is dominated by *S. palustre* (80 % cover) with some *S. papillosum* and 60 % cover of vascular plants (*M. caerulea* ssp. *arundinacea*, *Carex lasiocarpa*, *Rhynchospora caucasica*, *Cladium mariscus*).

Recently, these peatlands - in particular their margins - have been locally affected by cattle trampling and fires started by hunters (Krebs *et al.* 2016, 2017). We installed fences and, each autumn, removed vascular plants and litter from 5 m wide strips around our study plots to protect them from cattle and fire. Despite these measures, disturbance by hunters, jackals (*Canis aureus*) and cattle increased over the study period, and some of our plots and sampling squares were badly damaged (see later).

The climate of Central and South Kolkheti is warm temperate (Walter 1974). Mean annual temperature in Kobuleti is 14.1 °C, and precipitation is evenly distributed over the year with an annual average of 2,338 mm (Figure 1b). Air humidity is almost continuously high (70–83 %) and frost is rare (Krebs *et al.* 2016, Figure 1b). In South Kolkheti the year 2007/08 had more precipitation than the 1955–2005 average; and fewer rain days, longer periods without rain and a 0.5 °C lower mean annual temperature than 2008/09 (Table 1). In 2008/09, Central Kolkheti had fewer rain days, longer periods without rain and higher mean temperatures than South Kolkheti (Table 1).

The Ramsloh Sphagnum farming field was established in November 2004 on cut-over bog in north-west Germany (53° 4.31' N, 07° 38.90' E; dimensions 61.5 × 20.5 m; Figure 1c) and equipped with an irrigation and overflow system to ensure constantly high water table (Gaudig *et al.* 2017). In August 2008 *Sphagnum* cover (predominantly *S. papillosum*) was 90 % and vascular plant cover was 27 % (mainly *Erica tetralix* and *M. caerulea*) (Gaudig *et al*. 2017).

The climate of Ramsloh is (cool) temperate with a mean annual temperature of 9.6 °C and mean annual precipitation 844 mm (Figure 1d). Summer (June to August) is the warmest and wettest period, while the lowest monthly rainfall is recorded for February to May (Figure 1d). Frosts occur mainly in January and February, when mean minimum temperature is - 0.2 °C.

Experimental design

At all three peatlands the experiments were set up in a factorial and randomised block design (*cf*. Hurlbert 1984) of 1.5 × 1.5 m plots, laid out on areas with closed *Sphagnum* cover. Treatments included two *Sphagnum* species (*S. papillosum*, *S. palustre*), two initial cutting depths (5, 10 cm) and three cutting intervals (1, 2, 2.5 years) (Figure 2).

At Ispani 1, treatments for *S. papillosum* included two initial cutting depths (5, 10 cm) and two cutting intervals (1, 2 years; Figure 2) resulting in four treatments, each with five replicates (20 plots in total); and treatments for *S. palustre* included one initial cutting depth (10 cm) and two cutting intervals, resulting in two treatments with three replicates (6 plots in total). The treatment for *S. palustre* at Grigoleti involved one initial cutting depth (10 cm) and a one-year cutting interval (3 replicates, 3 plots in total). At Ramsloh, the treatment for *S. papillosum* again involved a single initial cutting depth (5 cm, as the minimum *Sphagnum* lawn thickness was 8 cm) and one cutting interval (second cut 30 months after first cut).

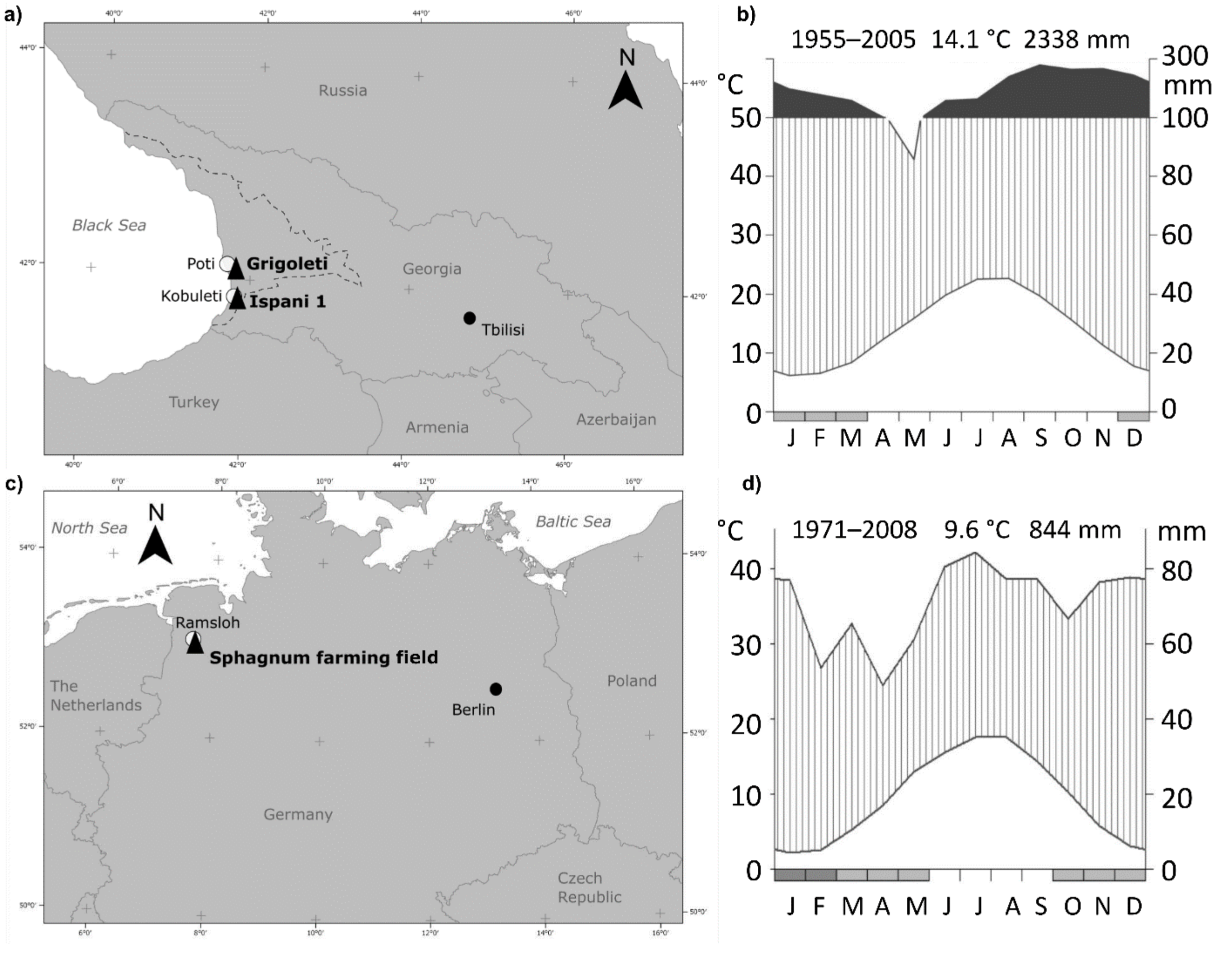


Figure 1. Locations of the study areas (▲) in Georgia (a) and north-west Germany (c) with nearby settlements (○). The dark grey dashed line in (a) indicates the extent of the Kolkheti Lowlands. The climate graphs (Walter & Lieth 1967) for Kobuleti (b, after Krebs *et al.* 2016) and Ramsloh (d, after Gaudig *et al*. 2017) show mean monthly temperature (°C) on the left-hand axis and precipitation (mm *per* calendar month) on the right-hand axis. The numbers at the top of the diagram show the period of data recording followed by mean annual temperature and mean annual precipitation for that period. The bar at the bottom of the diagram is shaded dark grey for months with frost, and light grey for months with possible frost. Note the break in scale of the precipitation axis in b).

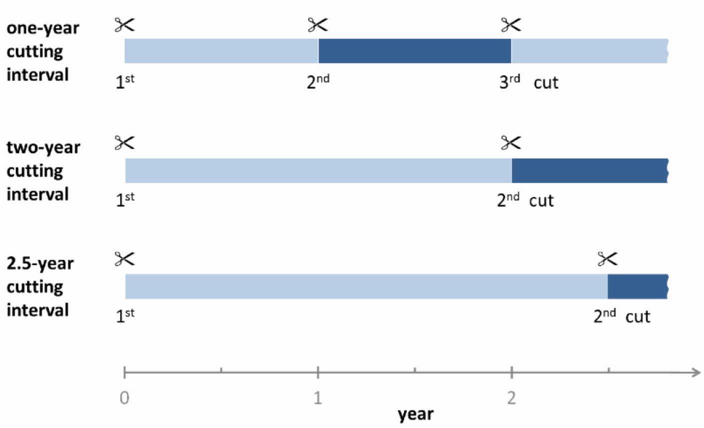
Regrowth measurements

The experiments were initiated by manually cutting off the biomass from the 1.5 × 1.5 m plots using scissors, removing the material, and measuring the thickness of the residual *Sphagnum* layer to the underlying strongly decomposed peat (five points *per* plot in Kolkheti, 30 points *per* plot in Germany). Subsequently, *Sphagnum* capitula at the plots were estimated by eye every six months (with an extra observation for Kolkheti in February 2009) and vascular plant cover was recorded in August/ September of each year, *i.e.* at the time of maximum cover.

Immediately after the first cut, ten 10 × 10 cm sampling squares were randomly located within each plot and ten single *Sphagnum* stems within each

Table 1. Climatic variables for the study years 2007/08 (01 Apr 2007–31 Mar 2008) and 2008/09 (01 Apr 2008–31 Mar 2009) in South Kolkheti (climate station Kobuleti) and for 2008/09 (01 Apr 2008–31 Mar 2009) in Central Kolkheti (climate station Poti) in Georgia, after Krebs *et al.* 2016; and for the study years 2008/09 (01 Aug 2008–31 Jly 2009), 2009/10 (01 Aug 2009–31 Jly 2010) and 2010/11 (01 Aug 2010–15 Mar 2011) at Ramsloh (climate station Ramsloh), after Gaudig *et al*. 2017. Note that the length of the 'study year' 2010/11 at Ramsloh was 226 days (all other study years were 365 days long).

	South Kolkheti (Kobuleti)		Central Kolkheti (Poti)	Germany (Ramsloh)		
Study year	2007/08	2008/09	2008/09	2008/09	2009/2010	2010/2011
Number of days	365	365	365	365	365	226
Precipitation sum (mm)	2787	2416	2515	803	641	541
Rain days (no.)	167	186	160	183	194	130
Contiguous days without rain (mean/max)	3.8/16	2.9/11	3.4/11	3.0/14	2.9/12	2.4/11
Mean temperature (°C)	14.1	14.6	15	9.6	9.2	6.5
Days without frost (no.)	362	364	364	338	311	180
Mean relative humidity (%)	81	82	83	82	82	89



Region	Peatland	*Sphagnum* species	Initial cutting depth	Study period
Kolkheti, Georgia	Ispani 1	*S. papillosum* *S. palustre*	5, 10 cm 10 cm	04/2007 – 03/2009
	Grigoleti	*S. palustre*	10 cm	04/2008 – 03/2009
Kolkheti, Georgia	Ispani 1	*S. papillosum* *S. palustre*	5, 10 cm 10 cm	04/2007 – 03/2009
NW-Germany	Ramsloh	*S. papillosum*	5 cm	08/2008 – 03/2011

Figure 2. Overview of the study treatments (*Sphagnum* species, initial cutting depth and cutting interval), peatlands and timescales.

sampling square were marked by attaching a nylon cable tie (2 mm wide, 100 mm long) directly below the cut *Sphagnum* surface (*cf*. Krebs *et al*. 2016). Regrowth was measured as the *in situ* (fresh) length between the cable tie and the tops of the new capitula. After one and/or two years (April 2008 and April 2009 in Kolkheti) or 2.5 years (March 2011 in Germany) of regrowth, the newly grown parts (as indicated by the cable ties) of all sampling squares were cut off and collected, after which the entire 1.5 × 1.5 m plot was cut down to the level of the cable ties and the cut vegetation was removed. The biomass samples were separated into *Sphagnum* species, other mosses, vascular plants and litter. The *Sphagnum* biomass was dried at 80 °C for 24 hours and weighed (accuracy 1 mg; Hendry & Grime 1993). Additionally, both *Sphagnum* capitula and litter cover (%) were estimated at each sampling square immediately before the second and third cuts.

The *Sphagnum* capitula (shoot apex excluding fully developed branches, Clymo 1973) from each biomass sample were dried and ground in a centrifugal ball mill (18,000 rpm for 1–2 min; FRITSCH pulverisette 14, Idar-Oberstein). The resulting material was analysed for total carbon (C) and nitrogen (N) (CHNOS element analyser Vario EL III, Elementary Analytical Systems Hanau) after microwave digestion (START 1500, MLS Enterprises), for potassium (K) with an atomic absorption flame spectrometer (CD-ContrAA 300, Analytic Jena), and for total phosphorus (P) with a UV/Visible spectrophotometer (Cecil CE 1021, 890 nm wavelength) using the 'molybdenum blue method' after Murphy & Riley (1962).

Site conditions

Because site conditions cannot be kept identical under field conditions, we measured environmental variables to assess their effects on regrowth. In Kolkheti, water table (phreatic surface) depth below *Sphagnum* surface (Schouwenaars 1995), together with pH and electrical conductivity (EC) of the interstitial water (multi variable tester Hanna Combo HI 98129), were measured in one well *per* plot at intervals of 3–6 weeks. In Germany, water table level was recorded monthly from September 2008 to December 2009 and once every five months from January 2010 until March 2011 (Gaudig *et al*. 2017) in wells located at distances of 2.5, 3.0 or 5.0 m from the three plots (one well *per* plot).

For determination of C, N, P and K in the top 5 cm of peat directly below the *Sphagnum* lawn, the same methods were used as for biomass (see above). Peat was sampled with an Eijkelkamp half-circular (5 cm diameter) chamber auger. In Kolkheti, sampling occurred at each plot during installation; in Germany, sampling for K was carried out on 13 plots in September 2007 (D. Kamermann, unpublished data) and for C, N and P on 61 plots spread randomly over the Ramsloh Sphagnum farming field in February 2011 (Gaudig *et al*. 2017).

In the second study year, seven plots of *S. papillosum* and four of *S. palustre* (in Kolkheti) were severely damaged (disturbance > 50 % cover) by trampling (cattle, hunters and jackals). Data from these plots were excluded from analysis.

Data analysis

All biomass values were, where relevant, standardised to $m^{-2}\,yr^{-1}$. After detailed data exploration (Zuur *et al*. 2009), the effects of treatments and site conditions on regrowth (dry mass) were analysed with mixed effect models containing fixed and random effects, taking into account possible spatial auto-correlation within single plots (Pinheiro *et al*. 2009, Zuur *et al*. 2009).

To analyse *Sphagnum* biomass regrowth (dry mass) we used cover of *Sphagnum* capitula and litter (%) directly before harvest, mean water table level (cm), pH and EC of the interstitial water, element concentrations in *Sphagnum* capitula (N) and surface peat (N, P, K), and the C/N quotient of the surface peat as explanatory variables (fixed components of the model) and the single plots as random components. We analysed the effects of site conditions on regrowth of *S. papillosum* at Ispani 1 separately for one-year cutting interval and the second and third cuts. For the analysis of one-year cutting interval, third cut, we included P and K concentrations and N/P and N/K quotients for the *Sphagnum* capitula as additional explanatory variables.

We applied a likelihood-based boosting approach in fitting generalised linear mixed models with a component-wise boosting method, as this allows high-dimensional settings with a large number of potentially influential explanatory variables (Tutz & Groll 2010).

Group differences for biomass regrowth and length increase were analysed using the non-parametric Kruskal Wallis test and a multiple comparison test after Siegel & Castellan (1988); R package pgirmess, Giraudoux 2010) to accommodate the unequal sample sizes caused by removal of the damaged plots from the analysis. The Kruskal Wallis test was also applied to test differences between natural growth without cutting (data from Krebs *et al.* 2016) and regrowth after cutting (biomass, length increase, element concentration in the capitula) for the same period and the same peatlands. Statistical data exploration, computation and preparation of

Figures were performed with R software (R Development Core Team 2009) and the packages AED (Zuur *et al.* 2009), GMMBoost (Groll 2015), nlme (Pinheiro *et al.* 2009), pgirmess (Giraudoux 2010) and stats (R Development Core Team 2009).

RESULTS

Development of new *Sphagnum* capitula after cutting

While regrown *Sphagnum* capitula reached 58–87 % cover six months after cutting in Kolkheti, regrowth reached only 11 % cover after six months in Germany (mean values, Figures 3a, 4). After one year, however, regrowth had converged to 80 % in both regions. After two years, cover was > 97 % in Kolkheti and > 90 % in Germany (Figures 3a, 4). In the case of one-year cutting interval in Kolkheti, capitula cover was 60–65 % six months after the second cut (Figure 3a). Three months later, *S. papillosum* cover was nearly 100 % but then rapidly declined again to 70 %, which was close to the values for *S. palustre* (Figure 3a).

Regrowth of *Sphagnum* in biomass and length

Average length increase ranged from 0.9 to 6.6 cm yr^{-1}, with a maximum of 15.4 cm yr^{-1} (*S. palustre*, 10 cm initial cutting depth, one-year cutting interval, directly before the second cut, Grigoleti) (Figure 5c). Average *Sphagnum* biomass regrowth ranged from 152 to 329 g m^{-2} yr^{-1} with a minimum of 54 g m^{-2} yr^{-1} (*S. papillosum*, 5 cm cutting depth, one-year cutting interval, third cut, Ispani 1) and a maximum of 549 g m^{-2} yr^{-1} (*S. palustre*, 10 cm initial cutting depth, two-year cutting interval, second cut, Ispani 1) (Figure 5b). Highest mean annual biomass values (> 246 g m^{-2} yr^{-1}) were recorded for *S. palustre* at Grigoleti (10 cm initial cutting depth, one-year cutting interval, second cut), for *S. papillosum* in Kolkheti (5 cm initial cutting depth, two-year cutting interval, second cut) and for *S. papillosum* in Germany (5 cm initial cutting depth, 2.5-year cutting interval, second cut, Figure 5b). Biomass regrowth was (only partly significantly) lower and similar between the other treatments (Figure 5b). The lowest values were recorded for *S. papillosum* at Ispani 1 (10 cm initial cutting depth, one-year cutting interval, third cut).

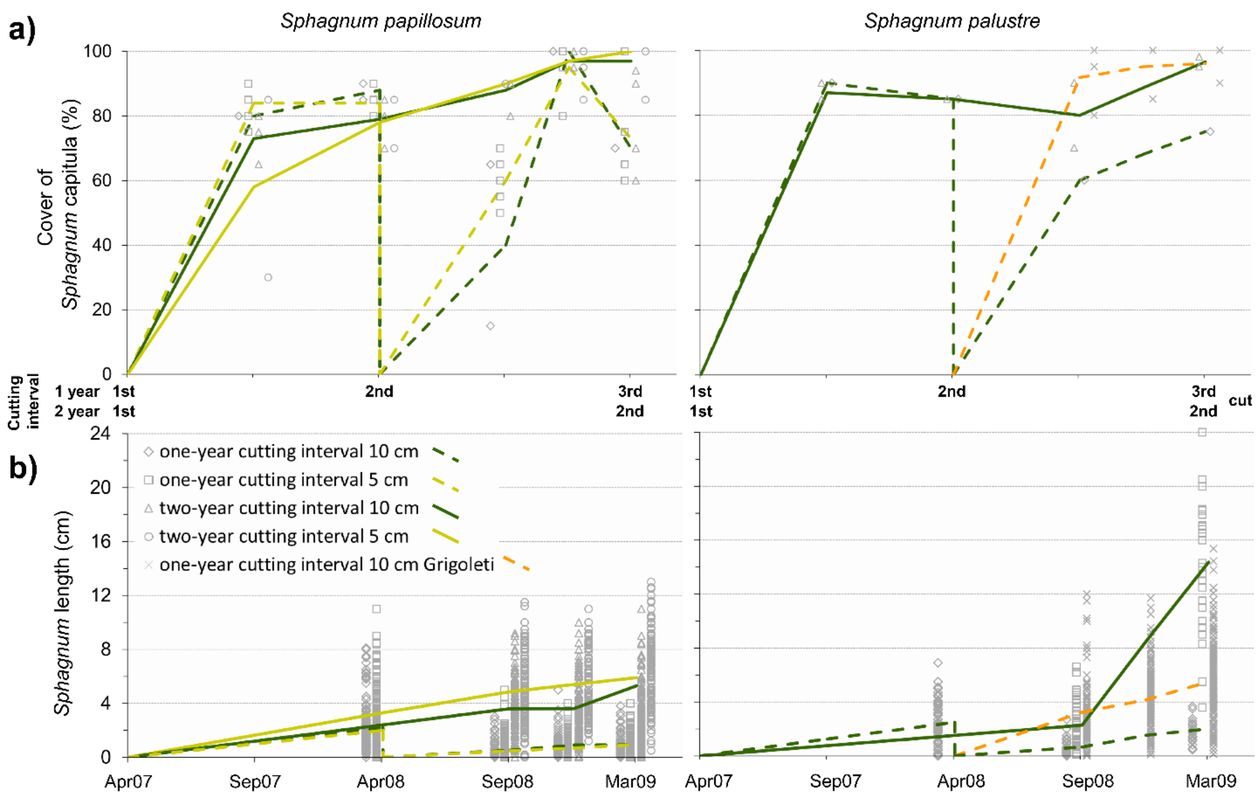


Figure 3. Development of regrown capitula cover (a) and length increase (b) after cutting of *S. papillosum* and *S. palustre* at different initial cutting depths (5, 10 cm) and intervals (1, 2 years) on the plots (cover) and sampling squares (length) at Ispani 1 and Grigoleti (Georgia). Each column of grey symbols represents the measurements on one treatment and date, and the lines represent means for different treatments (see key).

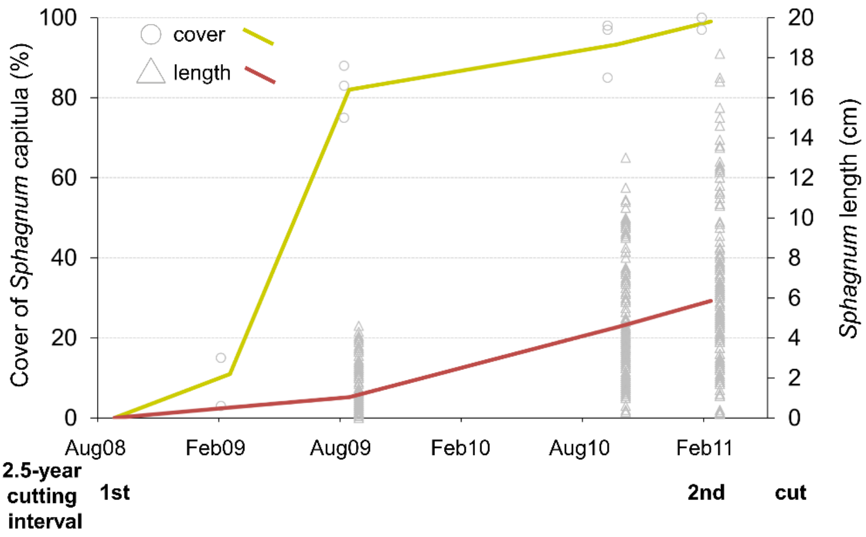


Figure 4. Development of mean *Sphagnum* capitula cover and mean length after cutting *S. papillosum* at depth 5 cm on plots (cover) and sampling squares (length) at the Ramsloh Sphagnum farming field (Germany). Each column of grey symbols represents the individual measurements on one date, and the lines represent mean values (see key).

Cutting depth had no significant effect on biomass regrowth of *S. papillosum* or *S. palustre* at Ispani 1, whereas cutting interval was important - annual biomass regrowth was significantly higher with a two-year cutting interval than with a one-year cutting interval (see Table A1 in Appendix). Biomass regrowth of *S. papillosum* at Ispani 1 decreased significantly with increasing number of cuts (Table A1). We also observed slower regrowth in cover (for 5 cm cutting depth) and length for *S. papillosum* after the second cut (measured immediately before the third cut) (Figures 3b, 5a, 5c).

N, P and K concentrations in *Sphagnum* capitula

The highest N and P concentrations in *Sphagnum* capitula were observed for *S. papillosum* in Germany (Table A2). In Kolkheti, P and K concentrations in the capitula tended to be higher for *S. palustre* than for *S. papillosum*. N and P concentrations were in the ranges 4.8–14.6 mg g^{-1} and 0.09–0.42 mg g^{-1}, respectively, with lowest values for the two-year cutting interval. Mean quotients of N/P and N/K in the *Sphagnum* capitula were 23.1–37.5 and 1.2–2.7, respectively (Table A2).

Site conditions

In Kolkheti, water table levels in the treatment plots were similar and ranged from 67 to 6 cm below the *Sphagnum* surface (with lowest and highest values in *S. palustre* plots at Ispani 1, Figure 6a). In Germany the water table was higher (mean water table level 3.8 cm below the *Sphagnum* surface) and the mosses were partly flooded (Figure 6a). In Kolkheti the EC of interstitial water was 55–99 µS cm^{-1} and its pH was 4.80–5.21 with lowest values in *S. palustre* plots (Table A3).

Residual *Sphagnum* thickness directly after the first cut was larger for *S. palustre* (14.0–21.0 cm) than for *S. papillosum* (9.0–15.5 cm in Kolkheti, 2.5–13.8 cm in Germany, Table A3) and did not differ significantly between the 5 cm and 10 cm cutting depths for *S. papillosum* in Kolkheti (Kruskal-Wallis $\chi^2 = 0.0136$, df = 1, $P = 0.91$). The highest litter cover was recorded for *S. papillosum* plots in Kolkheti (Table A3). Vascular plant cover was similar in all Kolkheti plots, the highest values being recorded in *S. palustre* plots at Grigoleti. *S. papillosum* plots in Germany had the lowest cover, but were not significantly different from *S. palustre* plots at Ispani 1 (Table A3).

In Kolkheti, mean P and K concentrations in the surface peat were similar at the different peatlands and N concentration was lowest in the *S. palustre* plots at Ispani 1 (13.7 mg g^{-1}, Table A3). The lowest mean N and highest mean P concentrations were recorded in Germany (*S. papillosum*, Table A3). The mean C/N quotient for surface peat ranged from 17 to 34 in Kolkheti, while in Germany it was 56 (Table A3).

Variables influencing regrowth

At Ispani 1, capitula cover of *S. papillosum* was positively correlated with biomass regrowth after the first and second cuts in the one-year cutting interval treatment (Table A4). Biomass regrowth after the first cut was negatively correlated with N concentration in the *Sphagnum* capitula (Table A4).

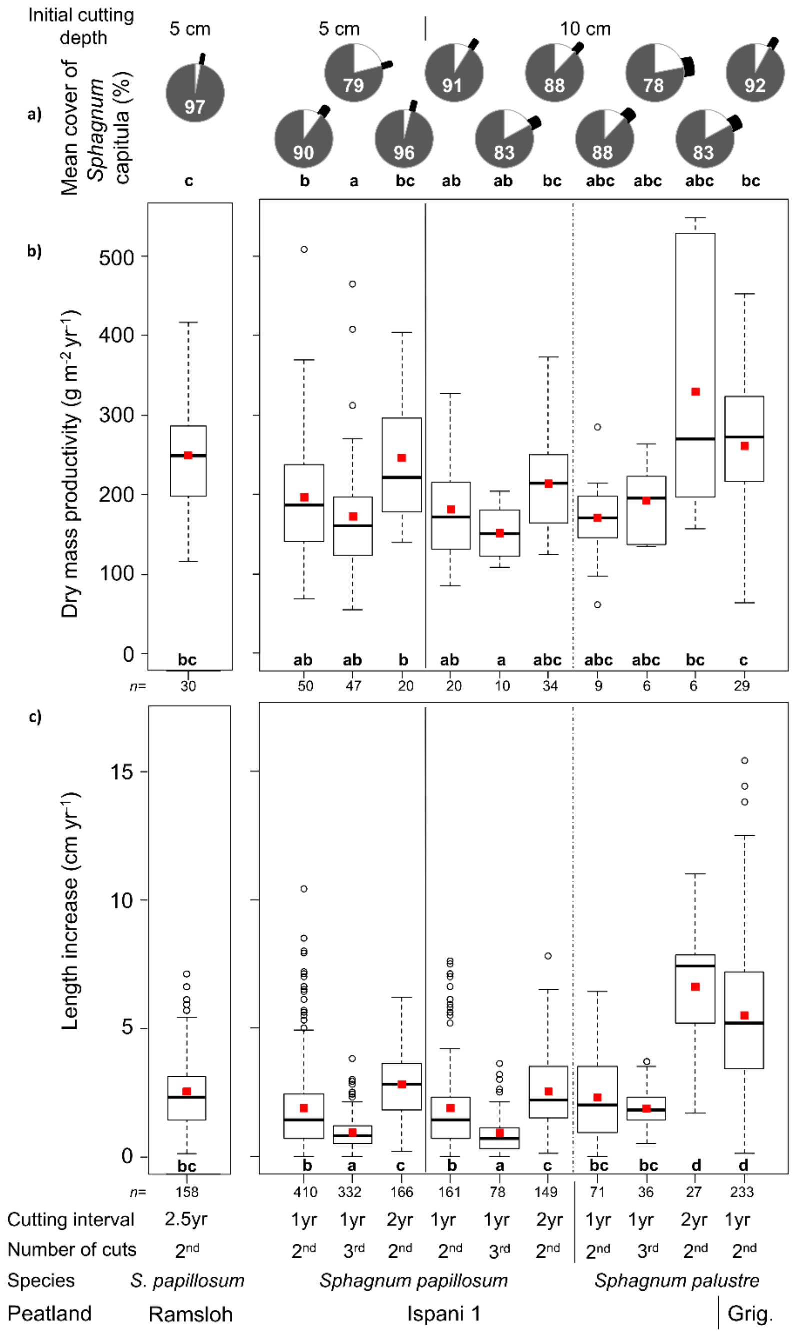


Figure 5. Regrowth of *S. papillosum* and *S. palustre* expressed as a) mean cover of *Sphagnum* capitula directly before cutting (the black strip adjacent to each pie chart is the 95 % confidence interval), b) dry mass productivity and c) length increase, for treatments with different combinations of initial cutting depth (5, 10 cm), cutting interval (1, 2 years) and number of cuts (second or third cut) at the Ramsloh Sphagnum farming field in Germany (Sep 2008–Mar 2011), and at Ispani 1 (Apr 2007–Mar 2009) and Grigoleti (Apr 2008–Mar 2009) in Georgia. *n* = number of measurements (on 10 × 10 cm sampling squares); a) and b) have the same numbers of measurements. The 'box and whisker' graphs in b) and c) show the median (bold line), the mean (red square), 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). Values with different letters differ significantly ($P \leq 0.05$). Differences between sites (peatlands), treatments and species were analysed using the non-parametric Kruskal Wallis test after Siegel & Castellan (1988) after a significant overall Kruskal Wallis test for a) cover of *Sphagnum* capitula: $\chi^2 = 84.1081$, df = 10, *P*-value <0.001; b) biomass: $\chi^2 = 59.3225$, df = 10, *P*-value < 0.001; c) length: $\chi^2 = 735.6477$, df = 10, *P*-value < 0.001.

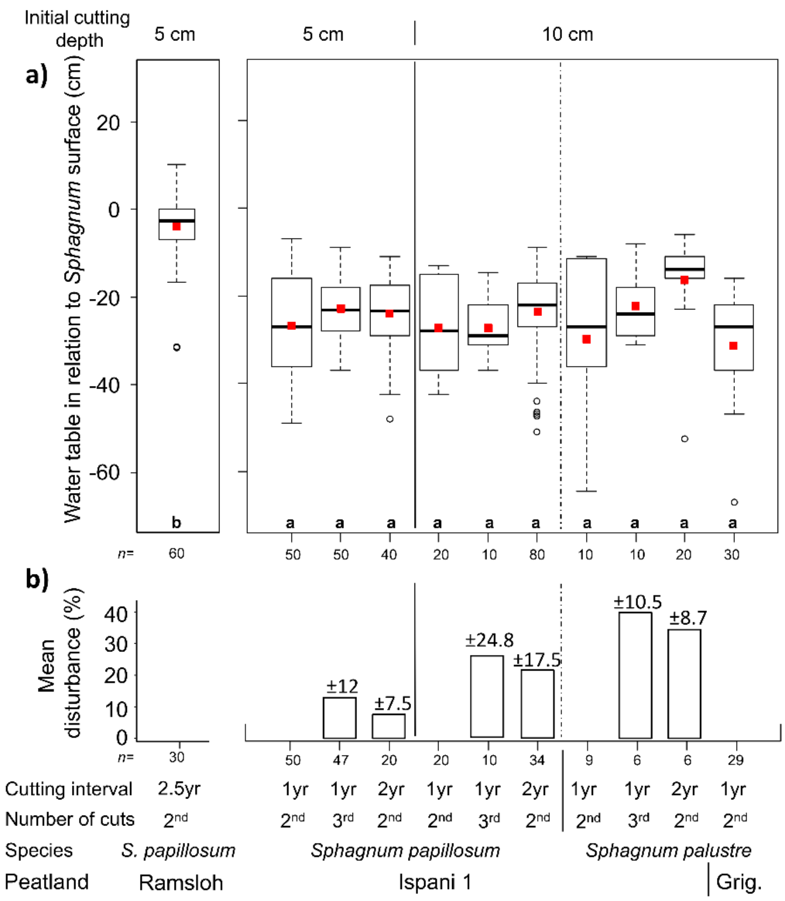


Figure 6. a) Position of water table relative to *Sphagnum* surface (= 0 cm), and b) mean disturbance (standard deviation written above each bar), for treatments with different combinations of initial cutting depth (5, 10 cm), cutting interval (1, 2 years) and number of cuts (second or third cut) at the Ramsloh Sphagnum farming field in Germany (Sep 2008–Mar 2011), and at Ispani 1 (Apr 2007–Mar 2009) and Grigoleti (Apr 2008–Mar 2009) in Georgia. n = number of measurements. For an explanation of the 'box and whisker' graph format, see the caption to Figure 5. Statistically significant differences in a) are indicated by different letters ($P \leq 0.05$).

Initial cutting depth, litter cover, mean water table level, pH and EC of the interstitial water, N, P, K concentrations in *Sphagnum* capitula (P, K analysed only after the second cut), and surface peat C/N quotient had no effect on *S. papillosum* biomass regrowth at Ispani 1. A weak positive correlation was found between *S. papillosum* capitula cover and litter cover one year after the second cut in the one-year cutting interval treatment ($P = 0.09$, Table A4).

DISCUSSION

Sphagnum growth and regrowth in different regions

The cover of new *S. papillosum* capitula six months after cutting was much lower in Germany (11 %) than in Kolkheti (75 %). The difference is attributable to the time of cutting (at the beginning of the growing season in Kolkheti and at the end of the growing season in Germany) and the seasonality of *Sphagnum* growth (lower rates in winter, Krebs *et al*. 2016). However, capitula cover no longer differed between Kolkheti and Germany one year after cutting (Figures 3a, 4). Also, biomass and length regrowth did not differ significantly between regions for similar treatments (initial cutting depth 5 cm, two-year or 2.5-year cutting interval) (Figure 5b, c).

Uncut *S. papillosum* achieved significantly higher biomass productivity and length increase than *Sphagnum* re-growing after cutting, over the same periods and at the same peatlands (Table 2).

In both Kolkheti and Germany, the *S. papillosum* biomass regrowth rate was similar to mean global natural productivity (230 ± 140 g m^{-2} yr^{-1}; Krebs *et al*. 2016). Biomass regrowth in the Kolkheti peatlands is attributable to high and evenly distributed precipitation allowing *Sphagnum* to reach the highest

Table 2. Comparison of uncut growth with regrowth after cutting of *Sphagnum papillosum* over the same periods on the same peatlands (Ispani 1 and Grigoleti in Kolkheti, Georgia; Ramsloh Sphagnum farming field in north-west Germany). Kruskal Wallis test (degrees of freedom =1 for each test), [1] Krebs *et al*. 2016, [2] Gaudig *et al*. 2017.

			Uncut	Regrowth after cutting	χ^2	*P*
S. papillosum	Ispani I	Mean biomass productivity (g m^{-2} yr^{-1})	360 ± 206 [1]	196 ± 74	5.65	≤ 0.05
		Mean length increase (cm yr^{-1})	3.6 ± 2.3 [1]	2.5 ± 1.6	16.06	≤ 0.001
	Ramsloh	Mean biomass productivity (g m^{-2} yr^{-1})	341 ± 92 [2]	250 ± 69	22.12	≤ 0.001
		Mean length increase (cm yr^{-1})	4.2 ± 1.7 [2]	2.5 ± 1.5	68.21	≤ 0.001
S. palustre	Ispani I	Mean biomass productivity (g m^{-2} yr^{-1})	565 ± 228 [1]	221 ± 120	13.61	≤ 0.001
		Mean length increase (cm yr^{-1})	10.4 ± 3.8 [1]	3.2 ± 2.4	161.70	≤ 0.001
	Grigoleti	Mean biomass productivity (g m^{-2} yr^{-1})	584 ± 144 [1]	260 ± 83	21.16	≤ 0.001
		Mean length increase (cm yr^{-1})	17.5 ± 3.4 [1]	5.5 ± 2.9	162.23	≤ 0.001

natural productivity recorded globally (Krebs *et al.* 2016). Similar biomass regrowth rates at the Ramsloh Sphagnum farming field in Germany show that its hydrological management was successful in creating and maintaining conditions that were as favourable for *Sphagnum* growth as those in Kolkheti.

In Kolkheti the recovery of capitula tended to be faster and biomass regrowth larger for *S. palustre* than for *S. papillosum*. Nevertheless, *S. palustre* regrowth reached less than half of the global natural productivity for that species (470 ± 190 g m^{-2} yr^{-1}; Krebs *et al.* 2016) and only 40–44 % of the productivity of uncut *S. palustre* at Ispani 1 and Grigoleti (Table 2).

Initial cutting depth and residual *Sphagnum* thickness

In Kolkheti, *Sphagnum* regrowth was similar for both initial cutting depths (Figure 5), with fast regeneration even after cutting at 10 cm depth. Sobotka (1976) and Poschlod (1990) observed faster growth of new shoots from green *Sphagnum* parts than from brownish moss segments, but did not report sampling depths. Our results indicate that brownish parts are capable of fast regrowth after cutting, as the *Sphagnum* in our study was already brownish at 5 cm depth. Campeau & Rochefort (1996) reported most regrowth (new capitula) of *Sphagnum* from fragments originating from the surface layer (0–10 cm), whereas Clymo & Duckett (1986) found the best regeneration in fragments from 6–12 cm below surface and on this basis suggested that there may be some kind of hormonal control of innovations akin to apical dominance in vascular plants. While less regrowth might be expected after cutting at greater depths, our study shows that there is no difference in growth reduction between 10 cm and 5 cm harvesting depths.

Regrowth of *S. papillosum* and *S. palustre* in Kolkheti was independent of residual *Sphagnum* thickness after harvesting (on average 11–16 cm, Table A3). In Germany we observed least regrowth (both length and biomass) at the plot where average residual thickness was 6.3 cm, *i.e.* only 2.2 cm (but significantly) shorter than at the other two plots (differences in thickness between the three plots: χ^2 = 21.86, df = 2, $P \leq 0.001$). It is possible that a thicker residual *Sphagnum* layer fosters *Sphagnum* regrowth, at least in the case of shallow layers. Further research is needed.

Harvesting method

We harvested *Sphagnum* mosses by cutting and removing the cut-off parts, leaving a closed lawn of

Sphagnum stems without capitula. This harvesting method differs from the common practice of removing most of the moss entirely and optionally leaving or re-spreading some of the material to stimulate regrowth (Elling & Knighton 1984, Buxton *et al*. 1996, Domínguez 2014). In Tasmania and New Zealand (with mean January temperature >12 °C and > 2,000 mm annual precipitation), where the moss was harvested by picking it up manually using a pitchfork, *Sphagnum* cover reached 50 % three years after complete removal of *Sphagnum* leaving a bare peat surface, and 90 % at plots where 30 % of the *Sphagnum* had been left or re-spread (Whinam & Buxton 1997, Whinam *et al*. 2003). In Minnesota (North America; mean annual temperature 4.5 °C, mean annual precipitation 715 mm), where *Sphagnum* (green material and some underlying, partly decomposed parts) was scraped off by 'crawler tractors' leaving some green *Sphagnum* on the exposed peat surface, *Sphagnum* had recovered to its former dominance after 7–8 years (Elling & Knighton 1984). In our study, new *Sphagnum* capitula had already reached > 80 % cover one year after harvesting (Figures 3a, 4) and *Sphagnum* dry mass productivity was higher. The productivity of *S. papillosum* in Minnesota reached 170 g m^{-2} yr^{-1} (763 ± 374 g m^{-2} over five years; Elling & Knighton 1984) and that of *Sphagnum cristatum* in New Zealand (sites without re-spreading) 100 g m^{-2} yr^{-1} (Denne 1983). In our study, the dry mass productivity of *S. palustre* was 169–329 g m^{-2} yr^{-1} (in Kolkheti) whilst that of *S. papillosum* was 181–245 g m^{-2} yr^{-1} in Kolkheti and 250 g m^{-2} yr^{-1} in Germany (mean of treatments).

Harvest number and harvesting interval

In Kolkheti, using a one-year cutting interval, regrowth of *S. palustre* was similar after the first and second cuts, indicating that annual harvesting is possible without growth reduction. *S. papillosum* had lower biomass and slower length growth after the second cut (Table A1, Figure 5), indicating that a one-year cutting interval reduces *S. papillosum* regrowth. The capitula cover of both species was lower immediately before the third cut than it had been before the second cut (Figures 3, 5a), but this may have been caused by minor disturbance, mainly trampling, just before the third harvest (Figure 6b). The effects on biomass and length growth were minor as the mosses were only compressed, and the results represent regrowth up to the time of the disturbance. For both species, annual regrowth two years after cutting was higher than one year after cutting (Table A1, Figure 5), indicating that *Sphagnum* growth increases after full capitula cover has been re-established, as has been found when establishing a new Sphagnum farming field (Gaudig *et al*. 2017). This effect seems more explicit for *S. palustre* than for *S. papillosum*. Moreover, regrowth in the second year after cutting may have been fostered by warmer and wetter weather conditions in Kolkheti (fewer contiguous days without rain, Table 1, *cf*. Krebs *et al*. 2016).

Growth is more distinctly seasonal in Germany because it is arrested by winter frost (Lütt 1992, Asada *et al*. 2003). The *S. papillosum* at Ramsloh regrew only during the two seasons with temperatures > 0 °C, whereas growth continued almost year-round in Kolkheti (Table 1). Nonetheless, the fast and extensive regrowth of *S. papillosum* in Germany indicates that a two-year harvesting interval might be achievable even there. Collection intervals are (3–)5–8 years in New Zealand (Buxton *et al*. 1996) and 3–5 years in Chile (Díaz *et al*. 2008). When *Sphagnum* removal is too intensive (leaving < 30 % *Sphagnum*, using heavy machinery, leaving < 20 % protective shade) or too early (before complete recovery of the moss carpet), *Sphagnum* regeneration may be slow or fail completely (Whinam *et al*. 2003). In New Zealand, *Sphagnum* yields decreased after repeated collections without re-spreading (Buxton *et al*. 1996). On the other hand, at least for *S. palustre*, if the *Sphagnum* is harvested by cutting so as to leave a residual layer of moss *in situ*, it seems that it will be possible to harvest at intervals of one to two years in both Kolkheti and Germany.

Effects of site conditions on *Sphagnum* regrowth

Water supply and temperature

The development of new *Sphagnum* capitula and subsequent *Sphagnum* growth depend on water supply (Clymo & Hayward 1982). Water table level at the Kolkheti peatlands during this study was 24 cm on average and 67 cm at maximum below the *Sphagnum* surface (Figure 6a); observations similar to those reported by Krebs & Gaudig (2005). McCarter & Price (2014) noted desiccation of the uppermost 5 cm of *S. magellanicum*, which would hamper photosynthesis, at a water table level of 40 cm below *Sphagnum* surface. The *S. papillosum* and *S. palustre* in Kolkheti had similar structure and capitula density to *S. magellanicum* (Krebs *et al*. 2016) and yet regrew optimally with water table sometimes deeper than 40 cm, implying that an additional water source must be available. As for natural productivity (Krebs *et al*. 2016), regrowth of *Sphagnum* in Kolkheti is probably facilitated by the evenly distributed precipitation, which regularly rewets the capitula without necessarily leading to higher water table. At

Ramsloh the water table level was kept constantly high (on average 3.8 cm below the *Sphagnum* surface) by irrigation. The residual moss layer with newly growing *Sphagnum* shoots was sometimes flooded (Figure 6a), but we found no evidence that temporary flooding was harmful (*cf*. Rochefort *et al.* 2002).

If the water supply is sufficient, temperature is a major factor for *Sphagnum* growth (Asada *et al.* 2003, Krebs *et al.* 2016). High precipitation frequency combined with high temperatures (mean ~14.5 °C) facilitates *Sphagnum* productivity in Kolkheti (Krebs *et al.* 2016) and probably also *Sphagnum* regrowth. However, water supply seems to be more important for *Sphagnum* regrowth than temperature, as regrowth rates of *S. papillosum* are similar in north-west Germany where mean annual temperature is substantially lower (Table 1, Figures 1b, 1d).

Vascular plant cover

Vascular plants may, together with litter cover, prevent excessive surface temperatures, evaporation (Pedersen 1975, Sliva 1997) and photoinhibition (Murray *et al.* 1993). Although the correlation between vascular plant cover and *Sphagnum* regrowth was not statistically significant, we assume that fast regrowth of vascular plants (reaching a mean cover of up to 48 % in autumn, Table A3) fosters *Sphagnum* regrowth in Kolkheti, where summers are hot and light-intensive. This hypothesis is supported by our observation that the greatest regrowth in length and biomass was associated (although without significant correlation) with the highest vascular plant cover (*S. palustre* at Grigoleti; Figure 5, Table A3). In contrast to cutting as applied in our set-up, pulling out vascular plants completely (including their roots) was detrimental to *Sphagnum* regrowth mainly because of desiccation in summer (Whinam & Buxton 1997).

Beside regrown vascular plants, newly accumulated litter (mean cover up to 29 %) seems to have promoted regrowth of *Sphagnum* capitula in Kolkheti. Total cover of vascular plants and litter remained lower than 75 % and did not limit regrowth by too-intense shading (Clymo & Duckett 1986).

In our study, Ramsloh (Germany) had the lowest cover of vascular plants because of regular mowing (Gaudig *et al.* 2017). Litter cover was similar to that in Kolkheti because the mown material was not removed. The litter cover will have been less important for *Sphagnum* regrowth at Ramsloh because of lower surface temperatures and less solar radiation compared to Kolkheti.

Nutrient availability

The concentrations of N, P, and K in the peat and *Sphagnum* capitula in Kolkheti and Germany correspond to those in natural bogs (Aerts *et al.* 1992, Succow & Joosten 2001, Bragazza *et al.* 2004, Fritz *et al.* 2012). Krebs *et al.* (2016) concluded that, for natural productivity at the Kolkheti peatlands, *S. papillosum* was K- and partly P-colimited while *S. palustre* had an optimal nutrient balance. In our study, dry mass N concentration in the capitula indicated regular N-limitation (< 9 mg g^{-1}; Lamers *et al.* 2000) in Kolkheti and N-saturation (>12 mg g^{-1}) in Germany. We observed decreasing N concentrations with increasing length of cutting interval because of higher *Sphagnum* productivity in the second regrowth year (Tables A2, A4) leading to ‘dilution’ (Malmer 1990, Temmink *et al*. 2017).

In Kolkheti, K concentrations in the surface peat are more than twice those observed elsewhere in the same peatland (Krebs *et al.* 2016), in particular at the Ispani 1 *S. papillosum* plots. These higher K concentrations may be attributable to the better accessibility of our regrowth plots and the consequently more frequent fires leading to an increase in K availability (Tallis 1983). The N/K quotients of the *Sphagnum* capitula are below 3.3 (Table A3), which precludes K-limitation (Bragazza *et al.* 2004). The P concentrations of regrown *S. papillosum* capitula in Kolkheti were significantly lower (on average 0.24 mg P $g^{-1} \pm 0.06$, SD) than those of uncut areas (0.31 mg P $g^{-1} \pm 0.07$, SD, $\chi^2 = 7.94$, $P \leq 0.01$; Krebs *et al.* 2016) and similar to those of P-limited peatlands (Aerts *et al.* 1992, Limpens & Heijmans 2008). The N/P quotients of the capitula (> 30; Bragazza *et al.* 2004) and the low P-concentrations indicate that *S. papillosum* regrowth after cutting in Kolkheti is P-limited.

With N/K quotients < 3.3 and N/P quotients < 30, optimal nutrient supply is approached for *S. palustre* regrowth (Bragazza *et al*. 2004); higher N/P quotients (mean 31.9 ± 3.3 SD) after the second cut at Ispani 1 and partly low N and P concentrations in the capitula, however, also imply some growth constraints due to N- or P-limitation.

Mean N concentrations in *Sphagnum* capitula of 15.9 mg g^{-1} (Table A2) and atmospheric N deposition of 21 kg ha^{-1} yr^{-1} (UBA 2016) imply that *S. papillosum* regrowth in Germany is not N-limited (Lamers *et al.* 2000). P values in peat and *Sphagnum* capitula which correspond to values in P-limited peatlands (Limpens & Heijmans 2008), along with N/P quotients > 30, indicate that *S. papillosum* regrowth at Ramsloh is P-limited (Bragazza *et al.* 2004). This was also concluded for *Sphagnum* productivity at Ramsloh when *Sphagnum* mosses were not harvested (Gaudig *et al.* 2017).

Natural *Sphagnum* habitats are characterised by low nutrient availability (Malmer 1993). Elements such as N, P and K are supplied by atmospheric deposition and relocation from the lower moss parts and the peat below (Rydin & Clymo 1989, Succow & Joosten 2001). Under such conditions, repeated biomass removal by multiple *Sphagnum* harvests may result in a decrease in nutrient availability and, in time, may lessen *Sphagnum* regrowth. P-limitation of *S. papillosum* may increase with increasing harvest frequency.

CONCLUSIONS

Compared with conventional methods, cutting off the top parts of *Sphagnum* while leaving residual stems to regenerate is the most promising *Sphagnum* harvesting method because it allows fast regrowth and frequent harvests.

The hypothesis that *Sphagnum* regrows faster under warmer and wetter climatic conditions was not confirmed. Regrowth was similar in Kolkheti and north-west Germany. Regrowth is probably favoured in both regions by the sufficient water supply: in Kolkheti by abundant, evenly distributed precipitation, and in Germany by artificial irrigation. Further study is needed to determine whether regrowth in Kolkheti can be increased by keeping the water table high.

As *S. palustre* has higher natural productivity and higher regrowth rates than *S. papillosum*, and does not seem to be adversely affected by repeated harvesting, the former species is probably more suitable for Sphagnum farming.

Harvesting in spring allows regrowth during the immediately following main growing season and may, thus, be optimal for Sphagnum farming. Trampling may damage *Sphagnum* and reduce its growth, so should be kept to a minimum during management and harvesting.

The optimal harvesting depth depends on the regeneration capacity of the residual *Sphagnum* layer. The hypothesis that *Sphagnum* regrowth is faster with shallower harvesting depths was not confirmed for depths of 5 cm and 10 cm. Regrowth seems to be influenced by the thickness of the residual *Sphagnum* layer, at least for layers thinner than 9 cm (at Ramsloh). In Kolkheti, a harvesting depth of 10 cm did not reduce regrowth. Further studies must be undertaken to determine whether and how *Sphagnum* regrowth decreases after harvesting to greater depths and whether *Sphagnum* fragments $\geq$15 cm long can be harvested to satisfy one of the quality demands of commercial markets (*cf*. Stokes *et al.* 1999).

The hypothesis that high yields can be maintained with annual *Sphagnum* harvesting from the same site was not disproved for Kolkheti. However, the decline in regrowth of *S. papillosum* with increasing number of harvests indicates a need for long-term study of the effects of frequent harvesting. Also, longer intervals between harvests should be tested, as annual biomass regrowth was higher with a two-year cutting interval than with a one-year interval.

Frequent harvesting may change or intensify nutrient limitations because nutrients, in particular P, are removed with the harvested *Sphagnum*. Whether and how fertiliser applications may stabilise and enhance *Sphagnum* regrowth under regimes of repeated harvesting remains to be clarified.

ACKNOWLEDGEMENTS

We thank Martin Theuerkauf for preparing the maps; Franziska Fengler and Mindia Komakhidze for fieldwork; Vasha and Maradi Vashakhmadze for helping with fence installation; and Ulrich Möbius for chemical analyses. Peter Meffert is gratefully acknowledged for his assistance in statistics to analyse the data with generalised mixed effect models. We thank the Scholarship Programme of the German Federal Environmental Foundation (DBU) for funding MK. We acknowledge the two anonymous referees and the editors for useful comments on this manuscript.

REFERENCES

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.

Asada, T., Warner, B.G. & Banner, A. (2003) Growth of mosses in relation to climate factors in a hypermaritime coastal peatland in British Columbia, Canada. *The Bryologist*, 106, 516–527.

Blievernicht, A., Irrgang, S., Zander, M. & Ulrichts, C. (2013) *Sphagnum* biomass – the next generation of growing media. *Peatlands International*, 1/2013, 32–35.

BMUB (2016) *Klimaschutzplan 2050: Klimaschutz-politische Grundsätze und Ziele der Bundes-regierung* (*Climate Action Plan 2050: Principles and Goals of the German Government's Climate Policy*). Kabinettbeschluss vom 14. November

2016, Bundesministerium für Umwelt, Naturschutz, Bau und Reaktorsicherheit (BMUB) (Cabinet Decision of 14 November 2016, Federal Ministry for the Environment, Nature Conservation, Building and Nuclear Safety), Berlin, 91 pp. Online at: http://www.bmub.bund.de/fileadmin/Daten_BMU/Download_PDF/Klimaschutz/klimaschutzplan_2050_bf.pdf (in German); Executive Summary in English at: http://www.bmub.bund.de/fileadmin/Daten_BMU/Download_PDF/Klimaschutz/klimaschutzplan_2050_kurzf_en_bf.pdf, accessed 17 Jul 2017.

Bonn, A., Berghöfer, A., Couwenberg, J., Drösler, M., Jensen, R., Kantelhardt, J., Luthard, V., Permien, T., Röder, N., Schaller, L., Schweppe-Kraft, B., Tanneberger, F., Trepel, M. & Wichmann, S. (2015) Klimaschutz durch Wiedervernässung von kohlenstoffreichen Böden (Climate protection by rewetting carbon-rich soils). In: Hartje, V., Wüstemann, H. & Bonn, A. (eds.) *Naturkapital Deutschland - TEEB DE: Naturkapital und Klimapolitik - Synergien und Konflikte (Natural Capital Germany - TEEB DE: Natural Capital and Climate Politics - Synergies and Conflicts)*. Helmholtz Centre for Environmental Research - UFZ, Technical University of Berlin, Berlin/Leipzig, 124–147 (in German). ISBN: 978-3-944280-15-8.

Bragazza, L., Tahvanainen, T., Kutnar, L., Rydin, H., Limpens, J., Hajek, M., Grosvernier, P., Hajek, 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.

Buxton, R.P., Johnson, P.N. & Espie, P.R. (1996) *Sphagnum Research Programme: The Ecological Effects of Commercial Harvesting*. Science for Conservation 25, Department of Conservation, Wellington, New Zealand, 34 pp. Online at: https://www.doc.govt.nz/Documents/science-and-technical/Sfc025.pdf, accessed 23 Jly 2018.

Campeau, S. & Rochefort, L. (1996) *Sphagnum* regeneration on bare peat surfaces: Field and greenhouse experiments. *Journal of Applied Ecology*, 33, 599–608.

Clymo, R.S. (1973) The growth of *Sphagnum*: some effects of environment. *Journal of Ecology*, 61, 849–869.

Clymo, R. & Duckett, J. (1986) Regeneration of *Sphagnum*. *New Phytologist*, 102, 589–614.

Clymo, R.S. & Hayward, P.M. (1982) The ecology of *Sphagnum*. In: Smith, A.J.E. (ed.) *Bryophyte Ecology*, Springer Netherlands, Dordrecht, 229–289.

Denne, T. (1983) *Sphagnum on the West Coast, South Island, New Zealand. Resource Characteristics, the Industry and Land Use Potential*. MSc thesis, Centre for Resource Management, University of Canterbury and Lincoln College, Christchurch, New Zealand, 178 pp. Online at: https://www.researchgate.net/publication/48333115, accessed 23 Jly 2018.

Díaz, M.F. & Silva, W. (2012) Improving harvesting techniques to ensure *Sphagnum* regeneration in Chilean peatlands. *Chilean Journal of Agricultural Research*, 72, 296–300.

Díaz, M.F., Tapia, C. & Armesto, J.J. (2008) *Sphagnum* moss harvesting in southern Chile: Capacity building for peatland management and conservation. Archived Abstracts, 93rd ESA Annual meeting (Milwaukee, Wisconsin), Ecological Society of America, Washington DC. Online at: http://esameetings.allenpress.com/2008/P11946.HTM, accessed 21 Jan 2015.

Domínguez, E. (2014) *Manual de Buenas Prácticas para el Uso Sostenido del Musgo* Sphagnum magellanicum *en Magallanes, Chile.* (*Manual of Good Practices for Sustainable Use of* Sphagnum magellanicum *in Magallanes Region*). Boletín INIA Nº 276, Instituto de Investigaciones Agropecuarias, Centro Regional de Investigación Kampenaike, Punta Arenas, Chile, 113 pp. (in Spanish).

Elling, A.E. & Knighton, D.M. (1984) *Sphagnum* moss recovery after harvest in a Minnesota bog. *Journal of Soil and Water Conservation*, 39, 209–211.

Emmel, M. (2008) Growing ornamental plants in *Sphagnum* biomass. *Acta Horticulturae*, 779, 173–178.

Esposito, K. (2000) Bringing in nature's bounty. *Wisconsin Natural Resources Magazine*, April 2000, Wisconsin Department of Natural Resources, Madison, Wisconsin, USA. Online at: https://dnr.wi.gov/wnrmag/html/stories/2000/apr00/mossy.htm, accessed 23 Jly 2018.

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* bog vegetation: can phosphorus addition alleviate (the effects of) increased nitrogen loads. *Plant Biology*, 14, 491–499.

Gaudig, G., Krebs, M. & Joosten, H. (2017) Sphagnum farming on cut-over bog in NW Germany: Long-term studies on *Sphagnum* growth. *Mires and Peat*, 20(04), 1–19.

Giraudoux, P. (2010) pgirmess: Data analysis in ecology. R package version 1.4.9. Online at:

http://CRAN.R-project.org/package=pgirmess.

Groll, A. (2015) Likelihood-based boosting for generalized mixed models. Online at: https://cran.r-project.org/web/packages/GMMBoost/GMMBoost.pdf.

Hendry, G.A.F. & Grime, J.P. (1993) *Methods in Comparative Plant Ecology: A Laboratory Manual*. Springer Netherlands, Dordrecht, 252 pp.

Hotson, J.W. (1918) *Sphagnum* as a surgical dressing. *Science*, *New Series*, 48(1235), 203–208.

Hurlbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, 54, 187–211.

Jobin, P., Caron, J. & Rochefort, L. (2014) Developing new potting mixes with *Sphagnum* fibers. *Canadian Journal of Soil Sciences*, 94, 585–593.

Johnson, K.W. & Maly, C.C. (1998) Greenhouse studies of *Sphagnum papillosum* for commercial harvest and peatland restoration in Minnesota. In: Malterer, T., Johnson, K.W. & Stewart, J. (eds.), *Proceedings of the Peatland Restoration and Reclamation Symposium, Duluth, Minnesota, USA, 14–18 July 1998*, International Peat Society, Jyskä, Finland, 49–55.

Joosten, H., Gaudig, G., Krawczynski, R., Tanneberger, F., Wichmann, S. & Wichtmann, W. (2015) Managing soil carbon in Europe: paludicultures as a new perspective for peatlands. In: Banwart, S.A., Noellemeyer, E. & Milne, E. (eds.) *Soil Carbon: Science, Management and Policy for Multiple Benefits*, SCOPE Series Vol. 71, CABI, Wallingford, UK, 297–306.

Krebs, M. & Gaudig, G. (2005) Torfmoos (*Sphagnum*) als nachswachsender Rohstoff - Untersuchungen zur Maximierung der Produktivität von *Sphagnum papillosum* im Regendurchströmungsmoor Ispani 2 (Georgien) (Peat mosses (*Sphagnum*) as a renewable resource - Investigations on maximising 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.

Krebs, M., Matchutadze, I., Bakuradze, T. & Kaiser, R. (2017) Georgia. In: Joosten, H., Tanneberger, F. & Moen, A. (eds.) *Mires and Peatlands of Europe: Status, Distribution and Conservation*. Schweizerbart Science Publishers, Stuttgart, 403–412.

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.

Limpens, J. & Heijmans, M.P.D. (2008) Swift recovery of *Sphagnum* nutrient concentrations after excess supply. *Oecologia*, 157, 153–161.

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. (1990) Constant or increasing nitrogen concentrations in *Sphagnum* mosses on mires in Southern Sweden during the last few decades. *Aquilo Serie Botanica*, 28, 57–65.

Malmer, N. (1993) Mineral nutrients in vegetation and surface layers of *Sphagnum*-dominated peat-forming systems. In: Miller, N.G. (ed.) *Advances in Bryology*, Volume 5. Cramer, Berlin, 223–248.

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.

mossman381 (2012) *Harvesting Wisconsin Long Fiber Sphagnum: Moss Harvesting with an Oliver OC-6 Crawler with a Cab*. Online at: https://www.youtube.com/watch?v=piw3S3td1YY&list=PLZwy_pK9cqiPzP0eY1WGpP_HboxehPV8P, accessed 08 Aug 2018.

Murphy, J. & Riley, J.P. (1962) A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta*, 27, 31–36.

Murray, K.J., Tenhunen, J.D. & Nowak, R.S. (1993) Photoinhibition as a control on photosynthesis and production of *Sphagnum* mosses. *Oecologia*, 96, 200–207.

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.

Pedersen, A. (1975) Growth measurements of five *Sphagnum* species in South Norway. *Norwegian Journal of Botany*, 22, 277–284.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core team (2009) *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3, R Foundation for Statistical Computing, Vienna, 96 pp. Online at: http://www.R-project.org

Poschlod, P. (1990) *Vegetationsentwicklung in* *abgetorften Hochmooren des bayerischen Alpenvorlandes unter besonderer Berücksichtigung standortskundlicher und populationsbiologischer Faktoren (Development of the Vegetation in Cut-over Bogs of the Bavarian Alpine Foreland with Special Consideration of Site Conditions and Plant Population Biology).* Dissertationes Botanicae 152, Cramer, Berlin, 331 pp. (in German).

R Development Core Team (2009) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, 409 pp. Online at: http://www.R-project.org

Rochefort, L., Campeau, S. & Bugnon, J.-L. (2002) Does prolonged flooding prevent or enhance regeneration and growth of *Sphagnum*? *Aquatic Botany*, 74, 327–341.

Rydin, H. & Clymo, R.S. (1989) Transport of carbon and phosphorus compounds about *Sphagnum*. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, 237, 63–84.

Schouwenaars, J.M. (1995) The selection of internal and external water management options for bog restoration. In: Wheeler, B.D., Shaw, S.C., Fojt, W.J. & Robertson, R.A. (eds.) *Restoration of Temperate Wetlands*. John Wiley and Sons, Chichester, New York, 321–346.

Siegel, S. & Castellan, N.J. (1988) *Nonparametric Statistics for the Behavioral Sciences*. Second edition, McGraw-Hill, New York, 399 pp.

Silvan, N., Jokinen, K., Näkkilä, J. & Tahvonen, R. (2017) Swift recovery of *Sphagnum* carpet and carbon sequestration after shallow *Sphagnum* biomass harvesting. *Mires and Peat*, 20(1), 1–11.

Sliva, J. (1997) *Renaturierung von industriell abgetorften Hochmooren am Beispiel der Kendlmühlfilzen* (*Restoration of Industrial Cut-over Bogs by the Example of the Kendlmühlfilzen*). Utz, München, 221 pp. (in German).

Sobotka, D. (1976) Regeneration and vegetative propagation of *Sphagnum palustre* as factor of population stability. *Acta Societatis Botanicorum Poloniae*, 45, 357–368.

Stokes, J.R., Alspach, P.A. & Stanley, J. (1999) Effect of water table on growth of three New Zealand *Sphagnum* species: implications for *S. cristatum* management. *Journal of Bryology*, 21, 25–29.

Succow, M. & Joosten, H. (2001) *Landschaftsökologische Moorkunde. (Landscape Ecology of Mires).* Second edition, Schweizerbart, Stuttgart, 622 pp. (in German).

Tallis J.H. (1983) Changes in wetland communities. In: Gore, A.J.P. (ed.) *Mires: Swamp, Bog, Fen and Moor, General Studies*. Ecosystems of the World 4A, Elsevier, Amsterdam, 311–347.

Tavadze, F.N. (1963) *Prirodnije Resursij Grusinskoi SSR (Natural Resources of the Georgian SSR)*. Volume 5, Isdatelstwo Akademii Nauk SSSR, Moscow, 272 pp. (in Russian).

Temmink, R.J.M., Fritz, C., van Dijk, G., Hensgens, G., Lamers, L.P.M., Krebs, M., Gaudig, G. & Joosten, H. (2017) Sphagnum farming in a eutrophic world: The importance of optimal nutrient stoichiometry. *Ecological Engineering*, 98, 196–205.

Tutz, G. & Groll, A. (2010) Generalized linear mixed models based on boosting. In: Kneib, T. & Tutz, G. (eds.) *Statistical Modelling and Regression Structures*, Physica, Heidelberg, 197–215.

UBA (2016) *Karte Hintergrundbelastungsdaten Stickstoff, Bezugsjahr 2009* (*Map of Background Exposure Data for Nitrogen, Reference Year 2009*). Umwelt Bundesamt (Federal Environment Office), Dessau-Roßlau, Germany. Online at: http://gis.uba.de/website/depo1/

Walter, H. (1974) *Die Vegetation Osteuropas, Nord- und Zentralasiens* (*The Vegetation of East Europe, North and Central Asia*). Fischer, Stuttgart, 452 pp. (in German).

Walter, H. & Lieth, H. (1967) *Klimadiagramm-Weltatlas* (*World Atlas of Climate Diagrams*). Fischer, Jena, 256 pp. (in German).

Whinam, J. & Buxton, R. (1997) *Sphagnum* peatlands of Australasia: an assessment of harvesting sustainability. *Biological Conservation*, 82, 21–29.

Whinam, J., Hope, G.S., Clarkson, B.R., Buxton, R.P., Alspach, P.A. & Adam, P. (2003) *Sphagnum* in peatlands of Australasia: their distribution, utilisation and management. *Wetlands Ecology and Management*, 11, 37–49.

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, 524 pp.

Submitted 21 Sep 2017, revision 21 May 2018
Editor: Stephan Glatzel

Author for correspondence:
Matthias Krebs, Institute of Botany and Landscape Ecology, University of Greifswald, partner in the Greifswald Mire Centre, Soldmannstr. 15, 17487 Greifswald, Germany. Email: krebsm@uni-greifswald.de

Appendix

Table A1. Results of boosted generalised linear mixed modelling of the response variable dry mass regrowth of *Sphagnum papillosum* and *S. palustre* at Ispani 1, tested for the treatments initial cutting depth, cutting interval and number of cuts. *CI* = confidence interval.

Species, peatland	Response variable	Factor	Estimate of the slope	95 % *CI*	*P*	Random effect 'plots'
Sphagnum papillosum, Ispani 1	Dry mass regrowth	n=181				0.18
		Cutting interval	$4.67e^{-4}$	$-0.71e^{-4}$–$8.63e^{-4}$	< 0.05	
		Number of cuts	-0.171	-0.04–0.30	< 0.05	
Sphagnum palustre, Ispani 1	Dry mass regrowth	n=50				0.25
		Cutting interval	0.154	-0.137–0.171	< 0.001	

Table A2. *Sphagnum* capitula element concentration (dry mass basis) after cutting (N, P and K, mean values with standard deviation) in the various treatments for the study periods Apr 2007–Mar 2009 (Ispani 1), Apr 2008–Mar 2009 (Grigoleti) and Aug 2008–Mar 2011 (Ramsloh). Values with different superscripts (a–d) differ significantly ($P \leq 0.05$); n.d. = not determined. Differences between treatments were analysed using the non-parametric Kruskal Wallis test after Siegel & Castellan (1988), following a significant overall Kruskal Wallis test for each variable (P-value < 0.001) - Nitrogen: $\chi^2 = 157.96$; Phosphorus: $\chi^2 = 87.07$; Potassium: $\chi^2 = 71.69$; N/P quotient: $\chi^2 = 21.37$; N/K quotient: $\chi^2 = 24.02$.

Region	Germany	Kolkheti, Georgia									
Peatland	Ramsloh	Ispani 1						Ispani 1			Grigoleti
Sphagnum species	*S. papillosum*	*Sphagnum papillosum*						*Sphagnum palustre*			*S. palustre*
Initial cutting depth (cm below original *Sphagnum* surface)	5	5			10			10			10
Cutting interval	2.5 years	one year		two years	one year		two years	one year		two years	one year
Number of cuts	2	2	3	2	2	3	2	2	3	2	2
No. of capitula samples (*n*)	30	50	47	20	20	10	34	9	6	6	29
Nitrogen (mg g^{-1})	15.9 ± 2.0^{c}	9.9 ± 1.0^{b}	9.0 ± 1.2^{b}	7.3 ± 1.4^{a}	10.2 ± 0.9^{b}	9.5 ± 1.4^{b}	7.2 ± 1.0^{a}	9.5 ± 0.5^{b}	11.8 ± 1.6^{b}	6.0 ± 1.3^{a}	9.3 ± 2.1^{b}
Phosphorus (mg g^{-1})	0.51 ± 0.08^{c}	n.d.	0.25 ± 0.04^{b}	0.19 ± 0.04^{a}	n.d.	0.28 ± 0.06^{b}	0.23 ± 0.06^{ab}	n.d.	0.37 ± 0.05^{bc}	0.27 ± 0.02^{b}	0.40 ± 0.12^{bc}
Potassium (mg g^{-1})	n.d.	n.d.	3.8 ± 0.5^{c}	2.9 ± 0.2^{a}	n.d.	3.5 ± 0.4^{bc}	3.1 ± 0.5^{ab}	n.d.	5.0 ± 0.6^{cd}	5.0 ± 0.8^{cd}	5.4 ± 0.7^{d}
N/P quotient	32.3 ± 4.0^{ab}	n.d.	34.3 ± 9.2^{bc}	37.5 ± 4.9^{c}	n.d.	34.4 ± 6.1^{bc}	32.5 ± 9.8^{ab}	n.d.	31.9 ± 3.3^{b}	23.1 ± 4.6^{a}	23.7 ± 3.1^{a}
N/K quotient	n.d.	n.d.	2.3 ± 0.6^{b}	2.5 ± 0.6^{b}	n.d.	2.7 ± 0.3^{b}	2.4 ± 0.7^{b}	n.d.	2.4 ± 0.4^{b}	1.2 ± 0.3^{a}	1.7 ± 0.5^{ab}

Table A3. Site conditions (mean values with standard deviation) of different peatlands and *Sphagnum* species over the periods Aug 2008–Mar 2011 (Ramsloh), Apr 2007–Mar 2009 (Ispani 1) and Apr 2008–Mar 2009 (Grigoleti). Number of measurements is shown in square brackets and is based on number of plots ($n = 19$ for *S. papillosum* at Ispani 1 and $n = 3$ for *S. palustre* at Ispani 1, *S. palustre* at Grigoleti and *S. papillosum* at Ramsloh) and frequency of sampling ([1] 5 times *per* plot in Kolkheti and 30 times *per* plot at Ramsloh; [2] once *per* plot, except peat chemistry measurements in Germany, see text for details; [3] ten sampling squares *per* plot, fewer for damaged plots; [4] three times *per* plot for one-year cutting interval and six times for two-year cutting interval in Kolkheti, *S. papillosum*: [13 plots × 3 measurements] + [6 × 6] = 75 and *S. palustre*: [2 × 3] + [1 × 6] = 12). Differences from the numbers initially installed are due to removal of damaged plots from the analysis. Statistical significance of differences in site conditions (indicated by different superscripted letters) was tested with the non-parametric Kruskal Wallis test after Siegel & Castellan (1988), following a significant overall Kruskal Wallis test for each variable (P-value < 0.001) - Residual *Sphagnum* thickness: $\chi^2 = 42.96$; Vascular plant cover: $\chi^2 = 42.35$; Litter cover: $\chi^2 = 77.16$; Nitrogen (peat): $\chi^2 = 53.57$; Phosphorus (peat): $\chi^2 = 50.30$; Potassium (peat): $\chi^2 = 20.27$; C/N quotient (peat): $\chi^2 = 54.17$; pH (water): $\chi^2 = 6.52$ P-value < 0.05.

	Region and/or country	Germany	Kolkheti, Georgia		
	Peatland	Ramsloh	Ispani 1		Grigoleti
	Sphagnum species	*S. papillosum*	*S. papillosum*	*S. palustre*	*S. palustre*
Residual *Sphagnum* thickness after first cut (cm) [1]		8 ± 2^{a}[90]	11 ± 2^{a} [95]	16 ± 1^{b} [15]	16 ± 3^{b} [15]
Vascular plant cover (%) [2]		11 ± 7^{a} [30]	36 ± 7^{b} [19]	20 ± 5^{ab} [3]	48 ± 16^{b} [3]
Litter cover (%) [3]		10 ± 9^{a} [30]	29 ± 18^{b} [180]	6 ± 5^{a} [20]	10 ± 8^{a} [30]
Peat [2]	Nitrogen (mg g^{-1})	10.1 ± 1.6^{a} [61]	20.0 ± 2.6^{b} [19]	13.7 ± 1.6^{a} [3]	23.0 ± 0.9^{b} [3]
	Phosphorus (mg g^{-1})	1.7 ± 0.4^{b} [61]	1.05 ± 0.07^{a} [19]	1.09 ± 0.19^{a} [3]	1.45 ± 0.16^{ab} [3]
	Potassium (mg g^{-1})	0.75 ± 0.17^{a}[13]	1.97 ± 0.56^{b} [19]	1.50 ± 0.62^{b} [3]	1.51 ± 0.25^{b} [3]
	C/N quotient	56 ± 9^{b} [61]	22 ± 6^{a} [19]	34 ± 4^{a} [3]	17 ± 1^{a} [3]
Water [4]	pH	-	5.08^{b} [75]	5.21^{b} [12]	4.80^{a} [9]
	ECcorr (μS cm^{-1})	-	55 ± 27 [75]	99 ± 44 [12]	73 ± 10 [9]

Mires and Peat, Volume 20 (2017/18), Article 12, 1–20, http://www.mires-and-peat.net/, ISSN 1819-754X

Table A4. Results of boosted generalised linear mixed modelling of the response variable dry mass regrowth of *Sphagnum papillosum* at Ispani 1 tested separately for the one-year cutting interval at second and third cut on site conditions (cover of *Sphagnum* capitula and litter (%), mean water table level (cm below *Sphagnum* surface), pH and EC of the interstitial water, element concentrations in *Sphagnum* capitula (N) and surface peat (N, P, K), and C/N quotient of surface peat). P and K concentrations and N/P and N/K quotients were included in the dataset for third cut. Results are also presented for the cover of *Sphagnum papillosum* capitula at Ispani 1 directly before the third cut, tested for litter cover in the one-year cutting interval. *CI* = confidence interval.

Species, peatland	Response variable	Factor	Estimate of the slope	95 % *CI*	*P*	Random effect ‘plots’
Sphagnum papillosum, Ispani 1	Dry mass regrowth one year after first cut (one-year cutting interval, second cut)	*n*=68				0.19
		Cover of *Sphagnum* capitula	0.02	-21.89–21.89	< 0.001	
		Nitrogen concentration of capitula	-0.11	-2.77–2.85	< 0.01	
Sphagnum papillosum, Ispani 1	Dry mass regrowth one year after second cut (one-year cutting interval, third cut)	*n* = 60				0.21
		Cover of *Sphagnum* capitula	0.01	-0.006–0.014	< 0.001	
Sphagnum papillosum, Ispani 1	Cover of *Sphagnum* capitula one year after second cut (one-year cutting interval, third cut)	*n* = 60				0.06
		Litter cover	$7.03e^{-5}$	-1.66–1.66	0.09	