How to promote *Sphagnum* lawn establishment in drained bogs: the role of water table and moss vitality

Greta Gaudig, Anja Prager, Matthias Krebs

Institute of Botany and Landscape Ecology, University of Greifswald, partner in the Greifswald Mire Centre, Germany

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SUMMARY

Many *Sphagnum*-dominated peatlands (mainly bogs) in Europe and North America have been drained and degraded by agricultural use or peat extraction, negatively affecting the ecosystem services they provided in their natural state. The goals of bog restoration are: (1) the return of typical bog hydrology; and (2) a vegetation cover dominated by *Sphagnum*. Despite abundant research, spontaneous establishment of *Sphagnum* is often very slow or even fails. However, rapid establishment of *Sphagnum* is essential for both bog restoration and the profitable cultivation of *Sphagnum* in paludiculture. In the present study we focus on how we can enhance the development of *Sphagnum* lawns on drained peatlands by rewetting them and actively adding living *Sphagnum* fragments (founder material). Our glasshouse, mesocosm and field experiments in Germany and Georgia show that the founder material should ideally provide a high initial cover of vital *Sphagnum* (mainly capitula) on a levelled peat surface that is close to the (permanently high) water table. In drier conditions, *Sphagnum* plants can be introduced as plugs or the founder material can be covered with straw mulch to accelerate establishment. Using these methods it is possible to establish *Sphagnum* lawns within 1–2 years, even under nutrient-rich conditions on a former bog grassland in NW Germany.

KEY WORDS: bog restoration, founder material, Georgia, NW Germany, *Sphagnum* paludiculture

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INTRODUCTION

The manufacture of many valuable products requires *Sphagnum* biomass as a main raw material. To supply this, fossil *Sphagnum* peat is extracted from peatlands (mainly drained bogs) and fresh *Sphagnum* is collected from wild populations. The market is currently dominated by peat; globally, about 40 million m^3 of *Sphagnum* peat is used annually in horticulture alone (Blok *et al.* 2021).

After peat extraction, most bog remnants are rewetted. However, spontaneous re-establishment of key *Sphagnum* species (that are able to create and maintain a raised bog; Joosten 1993) can either take decades or fail owing to suboptimal hydrological and hydrochemical conditions and the lack of diaspores (González *et al.* 2013, Lemmer & Graf 2016, Allan *et al.* 2023). Under suboptimal conditions, vascular plants such as *Molina caerulea* and *Juncus effusus* can become dominant, after which the recovery of self-regulating mechanisms and peat formation becomes very difficult in a raised bog.

More peatlands (including bogs) have been drained for agricultural and silvicultural use than for peat extraction (UNEP 2022), and drainage greatly impairs the ecosystem services of these sites (Bonn *et al.* 2016). Around 25 % of the peatland area in Europe, including more than 80 % of the peatland in Germany, is used for agriculture. As almost all drained peatlands must be rewetted during the next few decades in order to reduce global anthropogenic net carbon dioxide (CO_2) emissions to zero by 2050 (Günther *et al.* 2020, Tanneberger *et al.* 2021), new approaches to the use of peatlands must be developed. One promising use for bogs after rewetting is *Sphagnum* paludiculture which involves the cultivation of *Sphagnum*, e.g. as a raw material for horticultural growing media (Gaudig *et al.* 2014, Pouliot *et al.* 2015, Gaudig *et al.* 2017, 2018; Guêné-Nanchen & St-Hilaire 2022).

For both bog restoration and *Sphagnum* paludiculture sites, fast establishment of the *Sphagnum* lawn is essential. The addition of spores to accelerate establishment is not really practicable (Gaudig *et al.* 2018), because:

a) dioecious *Sphagnum* species rarely sporulate (Longton 1992, Cronberg 1993);

b) spore capsules can only be collected manually;

c) the factors inducing sporulation are incompletely understood (Sundberg 2000); and

d) germination of spores in the field requires special site conditions (Sundberg & Rydin 2002, Rydin & Jeglum 2013).

Owing to the distinctive capability of *Sphagnum* to propagate vegetatively by regenerating itself from fragments (all parts of the moss except individual leaves; Poschlod & Pfadenhauer 1989, Cronberg 1993, Rochefort *et al.* 1995), the application of *Sphagnum* founder material is an appropriate method for accelerating *Sphagnum* establishment (Rochefort *et al.* 2003, Caporn *et al.* 2018, Gaudig *et al.* 2018). Successful establishment requires the right quality and quantity of founder material as well as favourable site conditions.

Water supply is decisive for *Sphagnum* growth, specifically to keep its apical parts (capitula) moist (e.g. Schipperges & Rydin 1998, Robroek *et al.* 2009, Strack *et al.* 2009, Gaudig *et al.* 2020). *Sphagnum* mosses are unable to regulate water losses directly (Hayward & Clymo 1982) so are dependent on a constant water supply, which originates from above (precipitation) and below (groundwater) (Robroek *et al.* 2009, Strack & Price 2009). In established *Sphagnum* lawns the water content of the *Sphagnum* capitula decreases with increasing distance above the water table, as capillary water transport is reduced (Hayward & Clymo 1982, Gerdol 1995, Strack & Price 2009). Precipitation mitigates the adverse effects of water table drawdown by re-moistening the *Sphagnum* mosses or sustaining their water content to enhance growth (Robroek *et al.* 2009, Nijp *et al.* 2014, Krebs *et al.* 2016). Whether this effect also occurs in *Sphagnum* fragments spread on bare peat soil has not yet been investigated.

The successful establishment of *Sphagnum* depends on the vitality and size of the founder material. If this is young, its ability to regenerate (Sobotka 1976, Poschlod 1990) and establish is greater than for older parts farther from the capitula (Campeau & Rochefort 1996, Rochefort *et al.* 2003). Diaz & Silva (2012) found that the top 3 cm of *S. magellanicum* developed the greatest number of new shoots, but the role of the capitulum was unclear. Clymo & Duckett (1986) postulated reduced regeneration of fragments with capitula because of the apical dominance, meaning the subcapitulum (the part directly below the capitulum) should probably regenerate best. Fragments cut from 10 cm *Sphagnum* moss stems to uniform lengths ranging from 0.5 cm to 2 cm are comparable in cover development (Campeau & Rochefort 1996). On the other hand, smaller fragments (< 0.3 cm) develop more new regeneration buds (Gaudig *et al.* 2014). It is unclear whether additional regeneration buds will accelerate the development of a closed *Sphagnum* lawn.

The speed of *Sphagnum* establishment depends not only on the quality but also on the quantity of founder material applied to the site. Campeau & Rochefort (1996) used *Sphagnum* plants that were initially 10 cm long including capitula and were cut into fragments 1 cm and 2 cm long, with or without capitula, before they were applied to the peat surface. In a glasshouse experiment with water table 5 cm below the peat surface and initial density of *Sphagnum* plants 450 m^{-2}, an established *Sphagnum* lawn (> 90 % vital *Sphagnum*) was achieved after six months. However, with lower initial densities of *Sphagnum* plants (150 and 300 m^{-2}) under field conditions, only 5–10 % *Sphagnum* capitula cover was achieved within one growing season. For commercial use a much faster establishment of *Sphagnum* cover is necessary. Higher initial covers were tested in a field experiment by Gaudig *et al.* (2017). They applied fragments 0.5–2 cm long at 95 % initial cover and attained an established *Sphagnum* lawn after 3.75 years with a suboptimal water supply. As *Sphagnum* fragments establish better at high water table levels (Campeau & Rochefort 1996), a higher initial cover should be tested for wet site conditions.

Covering the applied *Sphagnum* fragments with straw mulch is recommended to improve the microclimate for restoration (Price *et al.* 1998, Rochefort *et al.* 2003), while covering with geotextile (50 % shading) is detrimental (Grobe *et al.* 2021). Straw mulch may not be necessary for fast establishment if the water supply is sufficient to keep the mosses constantly wet, but research is lacking.

Different methods are available for the introduction of founder material. For installation of *Sphagnum* paludiculture sites in Germany, fragments were simply scattered (spread) to form a *Sphagnum* layer about 1 cm thick (Gaudig *et al*. 2017, Wichmann *et al.* 2017, 2020). For blanket bog restoration projects in the UK, *Sphagnum* has also been applied successfully as plugs (bundles / aggregates of peat moss plants about 5 cm in diameter and 10 cm long) (Caporn *et al.* 2018). However, further testing of introduction methods, in terms of how they influence the success of *Sphagnum* establishment, is needed.

In the study reported here, we performed all experiments using the two *Sphagnum* species *S. papillosum* and *S. palustre*. We carried out glasshouse experiments and tested the results in the first field investigation (to our knowledge) of large-scale *Sphagnum* establishment on bog grassland. Bog grassland has been identified as a German site type with high potential for *Sphagnum* paludiculture (Wichmann *et al.* 2017) where conversion of land use through topsoil removal and rewetting can succeed, even after decades of drainage and fertilisation (Huth *et al.* 2022, Käärmelahti *et al.* 2023).

We tested the following hypotheses:

1. Precipitation can mitigate the adverse effects of water table drawdown on the establishment of *Sphagnum* fragments spread onto bare peat soil.
2. *Sphagnum* lawn establishes faster from subcapitulum material, and from small rather than large fragments.
3. A high initial cover of founder material accelerates *Sphagnum* lawn establishment.
4. Covering of founder material with straw mulch is not necessary for fast *Sphagnum* establishment when the water supply is adequate.
5. *Sphagnum* lawn establishes faster from evenly spread moss than from plugs.
6. Fast establishment of *Sphagnum* on former agricultural grasslands is possible after topsoil removal and rewetting followed by mechanical introduction of founder material.

METHODS

Glasshouse experiments

Glasshouse experiments investigating the effects of plant parts, initial cover, size and type of founder material were performed in Greifswald (Germany) from June to December 2018 (185 days), November 2012 to March 2013 (117 days), August to November 2011 (120 days) and April to August 2011 (113 days). The diurnal light conditions were 12 hours of mostly sunlight augmented with sodium vapour lamps (Philips Son-T Agro 400 W) at light flux densities below 15 klx, and 12 hours of darkness. Air temperature was 18–21 °C during the day and 12 °C at night. Standard seed trays (21 × 35 × 5 cm) were filled with sterile peat (H3–5, after von Post 1924), which was moistened with demineralised water before the *Sphagnum* fragments or plugs were spread or planted.

For the ‘plant parts’ experiment (Hypothesis 2), 50 stems of *Sphagnum palustre*, each 12 cm long, were cut into five parts (0–1 cm = capitulum, 1–3, 3–6, 6–9 and 9–12 cm). Ten plant parts of all variants were placed in each of five seed trays.

For the ‘initial cover’ experiment (Hypothesis 3), moss stems with capitula and a mean length of 3.2 cm were applied at 40 % and 80 % initial cover on 21 × 17.5 cm plots within the seed trays, with six replicas for each of the two *Sphagnum* species. The mean spreading rates were 410 (40 %) and 1,100 (80 %) capitula m^{-2} for *S. palustre*, and 440 (40 %) and 825 (80 %) capitula m^{-2} for *S. papillosum*. The ‘plant parts’ and ‘initial cover’ experiments were set up in a combined randomised block design.

For the ‘size’ experiment (Hypothesis 2) we used 78 g of fresh homogenised *S. palustre* and *S. papillosum* per seed tray. Moss stems of length 10 cm including capitula were chopped into 0.1–0.3 cm (‘tiny’), 0.5–1 cm (‘small’), 1–3 cm (‘medium’) or 5–10 cm (‘large’) pieces, using a food processor for ‘tiny’ fragments and scissors for all other fragment sizes, and applied to the peat at around 70 % total cover on whole-tray (21 × 35 cm) plots, with three replicas per treatment.

For the ‘application method’ experiment (Hypothesis 5), *S. palustre* and *S. papillosum* were grown from spores in 8 cm petri dishes for 142 days (about 20 months) in the glasshouse until they formed cushions that filled the entire petri dish and were 1.72 ± 0.26 cm thick. They were then planted as plugs or separated and spread flat on half-tray (21 × 17.5 cm) plots, with four replicas for each treatment.

The mosses for all glasshouse experiments originated from NW Germany. Twice a week throughout the experiments, they were sprinkled with demineralised water and fertilised with a nutrient solution after Rudolph *et al.* (1988). During the intervals between water/fertiliser applications, the seed trays were covered with transparent plastic lids to prevent them from drying out. After 3–4 months, *Sphagnum* cover was estimated visually and lawn thickness was measured at five points per plot. For the ‘plant parts’ experiment, the number of innovations (filamentous young shoots with a maximum of three branches forming the unmatured capitulum) was counted after six months.

Field experiments in Germany

The field experiments in Germany were conducted from May 2011 to May 2012 (mesocosm experiment) and from November 2012 (large-scale experiment) on 4 ha of the peatland Hankhauser Moor, which is located near the settlement Rastede (53° 15.80' N, 08° 16.05' E; Figure 1). This peatland is strongly degraded after decades of intensive use as grassland with deep drainage that has resulted in subsidence of 1 m since 1958 (Krebs *et al.* 2012). For installation of the trials, the upper highly mineralised peat layer (~ 30 cm thick, humification degree > H9 after von Post 1924) was removed and used to construct bunds (causeways) providing access to level production fields (10 m wide) bordered by irrigation ditches (50 cm wide, 50 cm deep) (Figure 2). After site preparation, *Sphagnum* fragments collected no more than 160 km from the field trial location were spread on the bared ‘white’ peat (humification degree H3–5 after von Post 1924). The site was then rewetted with surface water from an adjacent stream which collects

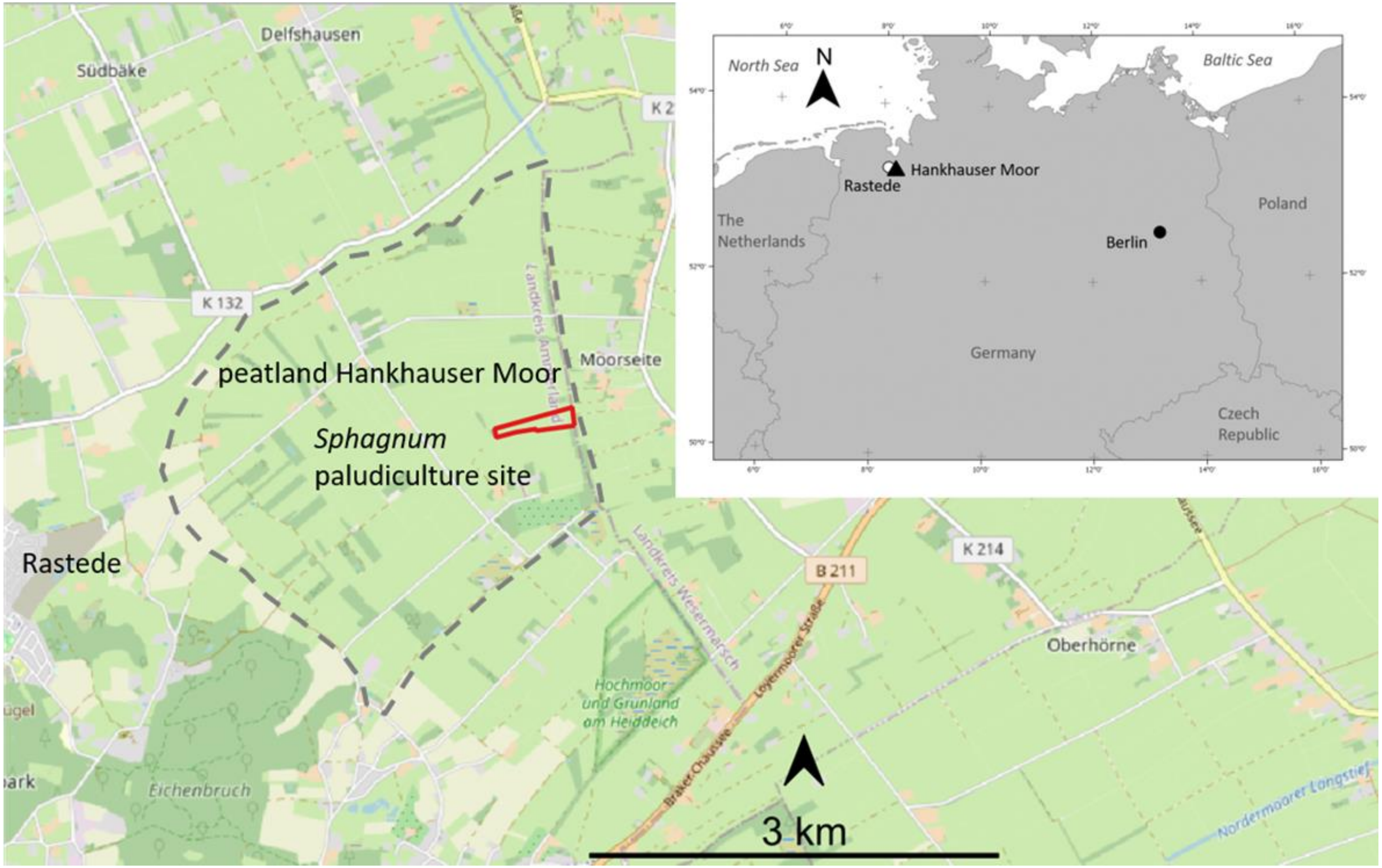

Figure 1. Locations of the study site (red outline) on the Hankhauser Moor peatland (grey dashed line, ▲) and the nearby settlement Rastede (o). Detailed map based on OpenStreetMap contributors (2015a).

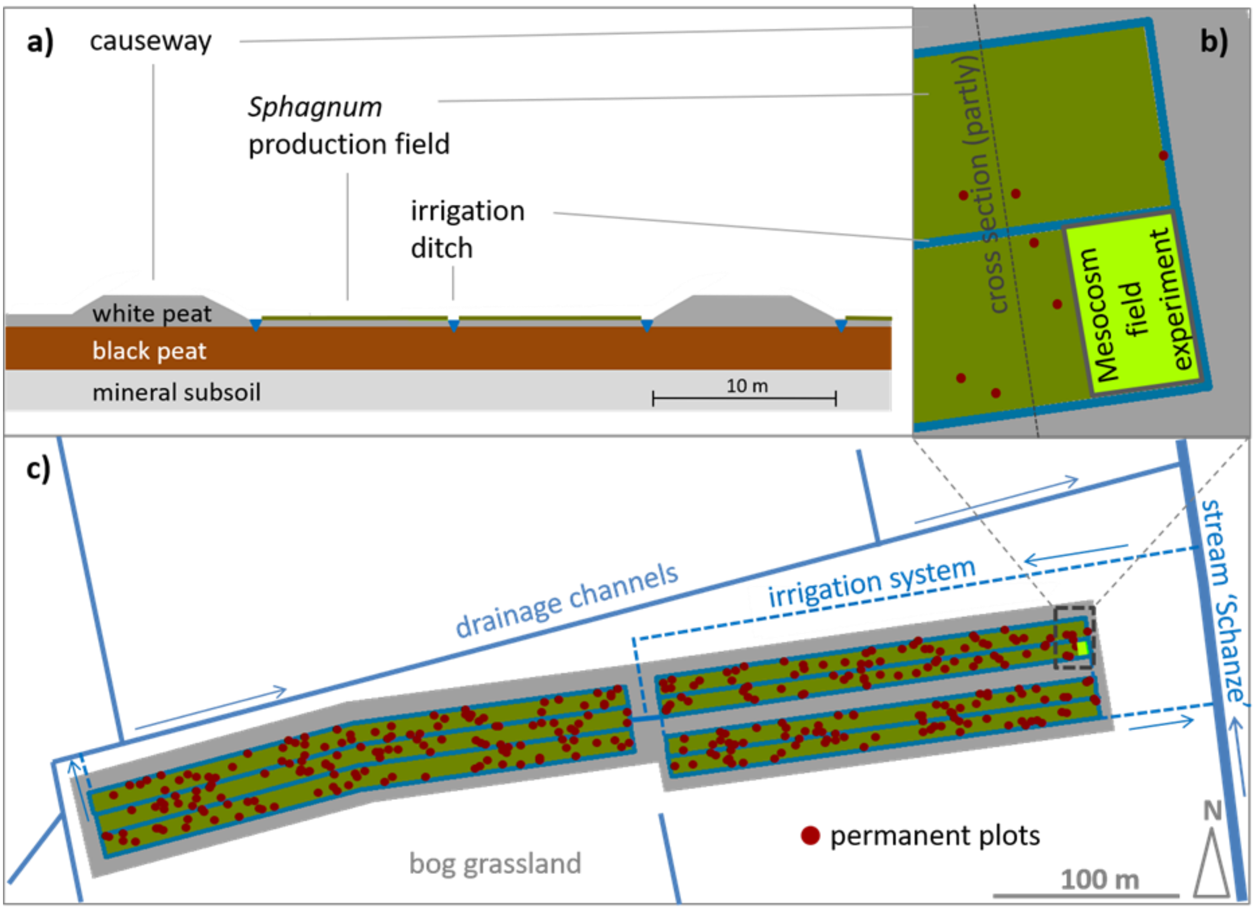

Figure 2. a) Cross section and c) plan of the *Sphagnum* paludiculture field experiments on former bog grassland at the Hankhauser Moor peatland; plus b) an enlarged plan of the mesocosm field experiment site. Red-brown dots mark permanent plots. For detailed information about the irrigation system see Brust *et al.* (2018).

drainage water from surrounding agricultural areas. To ensure continuously high water table even during summer droughts, an automatic water management system was installed (Brust *et al.* 2018). For more details about the installation, see Wichmann *et al.* (2017).

Site conditions

The study region is characterised by a warm-temperate climate. Annual precipitation was below the long-term average of 849 mm in both 2011 (822 mm) and 2012 (762 mm) (Figure 3; Brust *et al.* 2018). The period in spring 2011 when the *Sphagnum* paludiculture site was prepared was the driest part of the year (Figure 3). Because the surface peat had high saturated hydraulic conductivity (Roßkopf *et al.* 2016, Brust *et al.* 2018) and the distance to an irrigation ditch was nowhere more than 5 m, the water table level could be adjusted readily by the water management system even though height differences of the peat surface across the whole study area amounted to only 14 cm (differential GPS measurements two months after installation using Trimble TSC3, Trimble R6-Model2). Thus, the mean water table level ranged from 29 cm below to 12 cm above the peat surface over the entire study period (Figure 3a). The nutrient conditions were eutrophic. In addition to total nitrogen deposition of 20 kg ha^{-1} yr^{-1} (UBA 2016), the site received high nutrient inputs from the irrigation water, estimated at 0.7–2.4 kg ha^{-1} yr^{-1} of P, 13 kg ha^{-1} yr^{-1} of K and 3–9 kg ha^{-1} yr^{-1} of N (Temmink *et al.* 2017).

Mesocosm field experiment

About 30 m² of the field trial area was used for the mesocosm experiment (Figures 2b and 2c). Three fragment sizes of fresh *Sphagnum palustre* ('small': 0.5–1 cm; 'medium': 1–3 cm; 'large': 5–10 cm), prepared from 10–15 cm long moss stems collected from the upper part of a lawn, were spread manually on the bare peat at a rate of 800 g m^{-2} (dry mass equivalent approximately 130 g m^{-2}) which resulted in a mean initial vital moss cover of around 80 %. The fragments were: (1) not covered ('without straw');

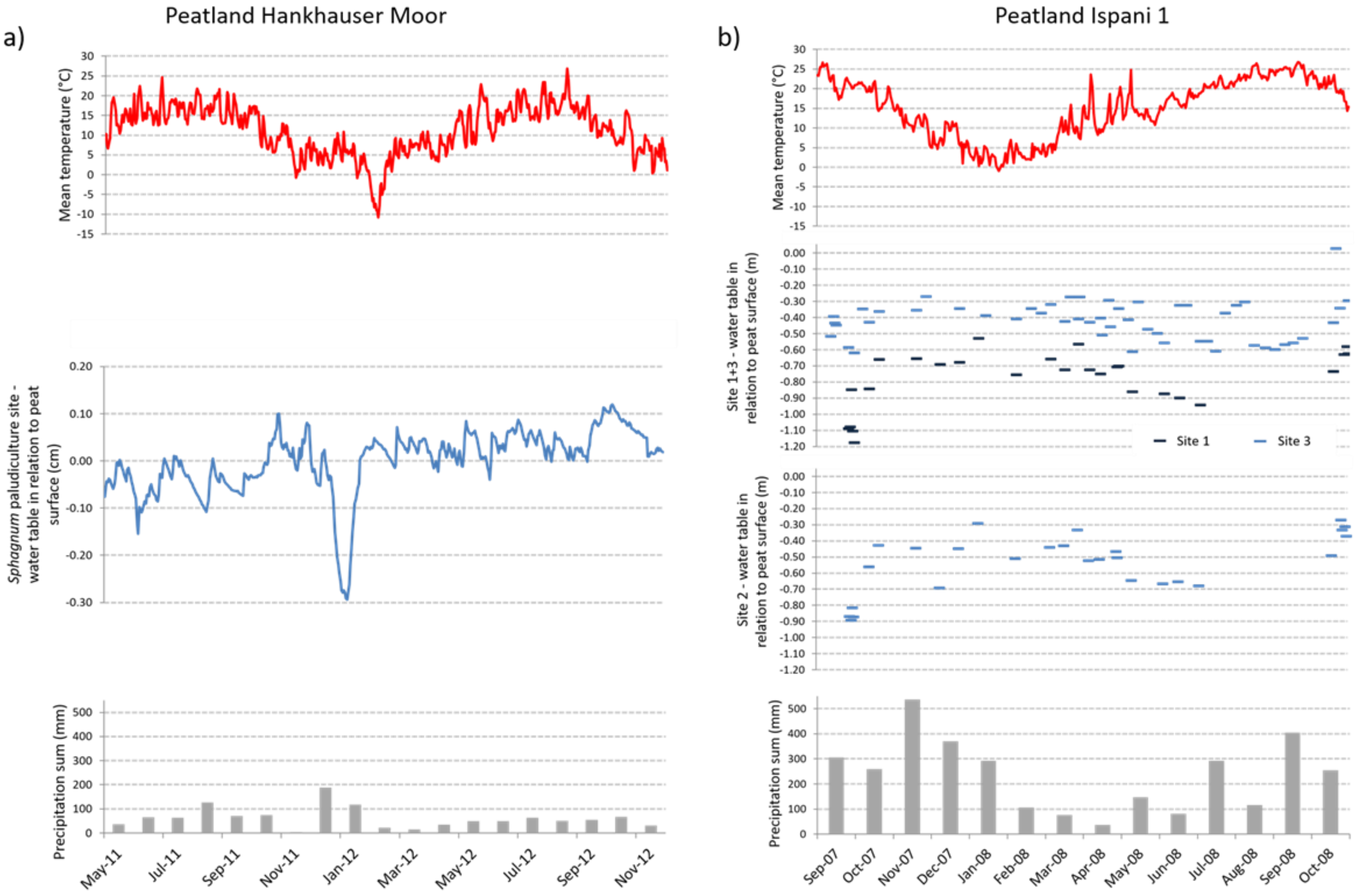

Figure 3. Mean air temperature (red line), water table level relative to peat surface (blue line or dashes) and precipitation (grey columns) for the study periods at a) Hankhauser Moor (Germany) and b) Ispani 1 (Georgia).

(2) covered with ‘loose straw’ at 300 g m^{-2} (mean cover 28 %); and (3) covered with a thin quilted ‘straw mat’ (Grünfix Strohfaschine) of density 250 g m^{-2} (mean cover 34 %). The treatments for different combinations of fragment size and straw cover (three replicates per treatment; $n = 27$) were applied in random order to 1 m × 1 m study plots (Figure A1 in the Appendix). Water table level was similar for all plots and corresponded to that for the large-scale experiment. Vascular plants were mowed manually, by cutting with scissors above the moss surface and removing the mowed material, at monthly intervals during the growing season. After twelve months the *Sphagnum* cover for each study plot was recorded on an area of 90 × 90 cm (whole plot excluding 10 cm edge) and the thickness of the *Sphagnum* lawn was measured at 20 points per plot.

Large-scale field experiment

To initiate the large-scale field trial, *Sphagnum* founder material was spread across a total area of 1.7 ha of (bare peat) production fields (application rate 78 m³ ha^{-1}) using an adapted snow groomer equipped with a manure spreader (Wichmann *et al.* 2017), resulting in a mean initial *Sphagnum* cover of 75 %. We tested *S. palustre* cut to two mean fragment sizes (‘chopped’: 0.2–1.1 cm; ‘non chopped’: 0.5–6.0 cm) and *S. papillosum* (‘chopped’ only). The donor sites were a reed harvesting area in The Netherlands for *S. palustre* and the *Sphagnum* paludiculture site in Ramsloh, Germany (see Gaudig *et al.* 2017) for *S. papillosum*. These materials contained 69 and 75 Vol. % of *S. palustre* and *S. papillosum*, respectively, along with other mosses and vascular plants (Table A1 in the Appendix). The moss fragments were then mulched with straw (Rochefort *et al.* 2003) providing an initial coverage of 45 ± 26 % (mean ± SD).

We monitored various factors in 310 randomly located 25 cm sampling squares (Figure 2c) immediately after installation and three times during each of the years 2011 and 2012. The factors were: water table level; cover of vascular plants; cover of visible total, vital and dry mosses for each *Sphagnum* species, open water, bare peat and litter including the applied straw using the scale of Londo (1976); and *Sphagnum* lawn thickness (at five points in each sampling square). Vascular plants growing on the *Sphagnum* production fields were mown regularly (6–8 times per year) with a single-axle motor mower (Wichmann *et al.* 2020). To accelerate *Sphagnum* establishment, gaps in the developing moss carpet were replenished in May 2012 by manually applying additional *Sphagnum* fragments (at 20 m³ ha^{-1}) to the production fields.

Mesocosm field experiment in Georgia

The field experiment in Georgia was conducted from September 2007 to October 2008 on the Ispani 1 peatland (41° 50.3' N, 41° 47.5' E, ~1 m a.s.l.), which is located in the Kolkheti Lowlands east of the settlement Kobuleti (South Kolkheti) and 0.5 km from the Black Sea (cf. Krebs *et al.* 2016; Figure 4). This bog comprises 500 ha of open peatland partly surrounded by alder forest (*Alnus glutinosa* ssp. *barbata*, cf. Krebs *et al.* 2018), and is highly degraded owing to peat extraction. From the 1920s until the 1980s, most of the top 2 m layer of peat was extracted (Joosten *et al.* 2003, Krebs *et al.* 2017). The less degraded northern part has been protected as part of the Kobuleti Protected Areas since 1996 and designated as a buffer zone for the UNESCO World Heritage Site ‘Colchic Rainforests and Wetlands’ since 2021. We installed our experiments on strongly degraded parts of the peatland.

Site conditions

The study region is characterised by its warm-temperate climate (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, which is similar to the total for our study period (Figure 3b). Air humidity is almost continuously high (70–83 %) and frost is rare, meaning that *Sphagnum* can grow for most of the year (Krebs *et al.* 2016).

The open part of Ispani 1 was recently characterised, especially to the north, by *Sphagnum* vegetation (*S. papillosum*, *S. rubellum*, *S. austinii* and *S. palustre*), and to the south by large degraded areas with *Pteridium aquilinum* and *Rubus* species growing amongst a network of drainage channels at spacings of 20–50 m.

Our experiment was installed at three locations on the degraded peatland where peat depth was 0.3–2.0 m and the surface peat was strongly decomposed (degree of humification H8–9 after von Post 1924), implying low saturated hydraulic conductivity. Water table levels ranged from 3 cm above to 118 cm below the peat surface, being lowest at Site 1/lowestWT (mean -78 cm) and highest at Site 3/lowWT (mean -42 cm; Figure 3b, Table 1). The pore water in the peat was subneutral to acidic, with low electric conductivity (EC), and potassium and phosphorus concentrations similar to those in intact bogs (Succow & Joosten 2001) (Table 1; Krebs *et al.* 2016). The nitrogen deposition rate was rather low at 5.4 kg ha^{-1} yr^{-1} (data for 2008 from EMEP 2015).

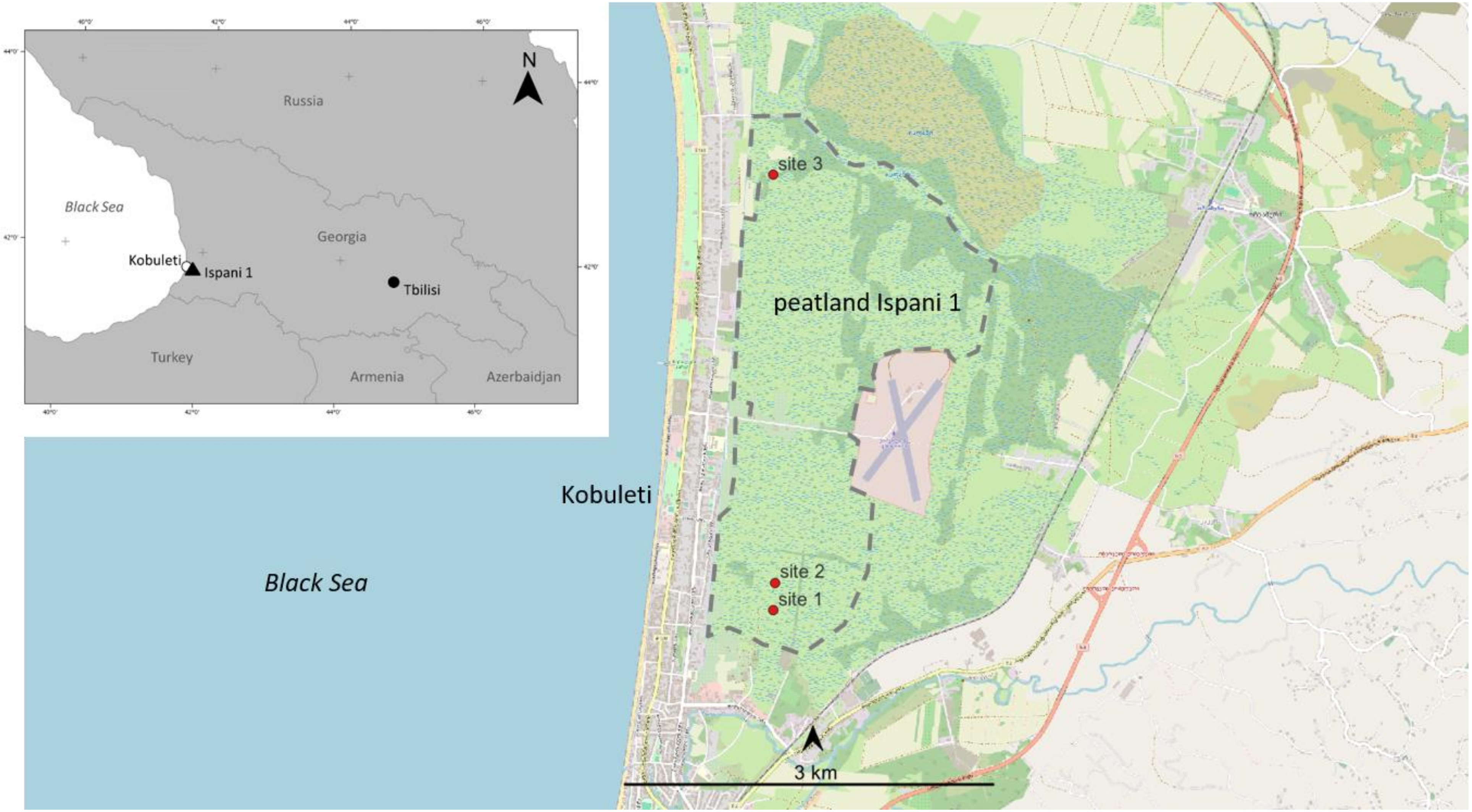

Figure 4. Locations of the study sites (red dots) on the Ispani 1 peatland (grey dashed line, ▲) in Georgia, and the nearby settlement Kobuleti (o) on the Black Sea coast. Detailed map based on OpenStreetMap contributors (2015b).

Table 1. Characteristics of the three experimental sites in the Ispani 1 peatland (Georgia): pH and EC of the peat pore water, phosphorus and potassium concentrations in surface peat (at depth ~ 5 cm), and the mean water table level relative to the peat surface ± standard error. The site conditions were measured at three points per site. T = number of times measurement were made during the study; N = total number of measurements per site during the period October 2007 to October 2008.

	Characteristic	pH	EC (μS cm^{-1})	N (mg g^{-1})	P (mg g^{-1})	K (mg g^{-1})	water table (cm below peat surface)
	T/N	4/12	3/9	1/3	1/3	1/3	24/72
Site	1/lowest water table	5.5 ± 0.5	44 ± 10	3.97 ± 1.63	0.08 ± 0.01	0.78 ± 0.02	78 ± 3.3
	2/lower water table	5.4 ± 0.7	49 ± 9	7.61 ± 1.96	0.05 ± 0.01	0.63 ± 0.01	54 ± 3.5
	3/low water table	8 ± 0.4	125 ± 26	22.73 ± 0.59	NA	0.10 ± 0.01	42 ± 1.7

Field experiment

To create similar starting conditions on an area of 10 × 10 m at each of the three sites, the vegetation and the uppermost 5 cm of peat were removed. Moss stems of *S. papillosum* and *S. palustre* about 10 cm long, with capitula, were collected from the surrounding peatland and immediately spread manually in fresh condition on 1.5 × 1.5 m study plots within the prepared bare peat areas at a rate of 1 kg m^{-2}, giving approximately 70 % coverage. No mulch or netting was applied. We established three replica plots per *Sphagnum* species at each of the three sites, i.e. six plots per site and 18 plots in total. After one year, the cover of living peat mosses was measured at three randomly distributed sampling squares (13.5 × 13.5 cm) per study plot. Every 2–3 months during the growing season, vascular plants were mown manually by cutting at the peat moss surface with scissors and removing the mowings.

Data analysis

We define a *Sphagnum* lawn as ‘established’ when vital *Sphagnum* cover reaches at least 90 %. Differences between treatments of several of the variables that were measured to evaluate the establishment of *Sphagnum* in the different experiments (e.g. cover of vital *Sphagnum*, *Sphagnum* lawn thickness, number of new *Sphagnum* shoots) were analysed using the non-parametric Kruskal-Wallis test and a multiple comparison test after Siegel & Castellan (1988).

For the large-scale *Sphagnum* paludiculture site on the Hankhauser Moor peatland we used principal correspondence analysis (PCA) as a multivariate statistical technique to assess the effects of different factors on *Sphagnum* establishment as indicated by the cover (%) of vital *Sphagnum* one year after installation (monitoring data from 310 plots; Šmilauer & Lepš 2014). We included the following variables: straw cover, vital and total *Sphagnum* cover (three months after installation), shortest distance to a ditch, water table level (mean of all measurements per plot), elevation above the lowest point on the peat surface, *Sphagnum* species (*S. palustre* or *S. papillosum*), initial fragment size, and cover of vascular plants one year after installation. To visualise the influence of these factors on the vital *Sphagnum* cover after 12 months, in the PCA biplot each study plot was assigned a symbol size based on the vital *Sphagnum* cover after 12 months. We applied PCA analysis using the prcomp R-function using standard scaling and centring.

For data exploration, computation and figure design we used the software package R (R Development Core Team 2009) and the packages ‘mgcv’ (Wood 2017), pgirmess (Giraudoux 2010), ‘vegan’ (Oksanen *et al.* 2020) and ‘stats’ (R Development Core Team 2009).

RESULTS

Glasshouse experiment on the effect of *Sphagnum* plant part

The top part (0–1 cm = capitulum) of *Sphagnum palustre* generated significantly more new shoots (Figure 5) than other parts. After six months’ growth, up to 22 (8 on average) new shoots had developed from the topmost centimetre whereas only one new shoot per centimetre (on average) had developed from fragments that originated below the capitulum.

Glasshouse experiment on the effect of initial size of *Sphagnum* founder material

On average, fragments larger than 0.5 cm and up to 10 cm developed 76 % cover of vital *Sphagnum* after four months’ growth (Figure 6a). The establishment of *S. papillosum* was slightly but not significantly

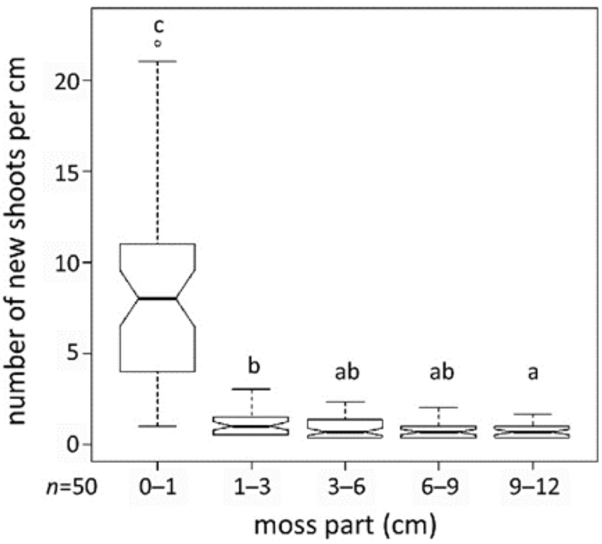

Figure 5. Number of new shoots (innovations and new capitula) per cm of moss stem produced by *Sphagnum palustre* fragments six months after installation, classified according to position along the original (12 cm) stem with Part 0–1cm = capitulum. Columns marked with different lowercase letters (a, b or c) differ significantly (Kruskal-Wallis $\chi^2 = 128.11$, $df = 4$, $P \leq 0.05$). For general explanations of the boxes see Figure 9. If the notches in the sides of two plots do not overlap this is ‘strong evidence’ (confidence interval roughly 95 %) that the two medians differ (Chambers *et al*. 1983).

less than that of *S. palustre* (Kruskal-Wallis $\chi^2 = 2.07$, $df = 1$, $P = 0.15$). In contrast, ‘tiny’ fragments (0.1–0.3 cm) showed significantly less development, with only 32 % cover of vital *Sphagnum* for *S. palustre* and 10 % for *S. papillosum* (Kruskal-Wallis $\chi^2 = 14.07$, $df = 3$, $P \leq 0.05$).

Glasshouse experiment on the effect of initial density of *Sphagnum* founder material

The *Sphagnum* lawn became established (at least 90 % cover of vital *Sphagnum*) during the investigation period only from an initial fragment cover of 80 %, independently of species; while 40 % initial fragment cover led to a mean vital *Sphagnum* cover after four months’ growth of 74 %, which was significantly lower (Kruskal-Wallis $\chi^2 = 17.68$, $df = 1$, $P \leq 0.05$; Figure 6b). There was no difference between the species (Kruskal-Wallis $\chi^2 = 0.054$, $df = 1$, $P = 0.82$).

Glasshouse experiment on the application method

After four months’ growth, the increase in thickness of the *Sphagnum* lawns grown from plugs was about 20 % greater than that of lawns grown from spread mosses (Figure 7). On the other hand, vital *Sphagnum* plants grown from spread mosses almost covered the whole of the plots whereas those developed from plugs covered less than 45 % of the plots. The mean increase in area covered by vital mosses over 113 days was 3.3 times for plugs and 3.7 times for spread mosses.

Mesocosm field experiments

Three months after installation of the mesocosm field experiment in Germany, the mean cover of vital *S. palustre* was 81 %. Whereas initial fragment size (‘small’: 0.5–1 cm, ‘medium’: 1–3 cm or ‘large’: 5–10 cm) had no effect on establishment (Kruskal-Wallis $\chi^2 = 2.17$, $df = 2$, $P = 0.34$), no straw cover led to significantly higher *Sphagnum* cover than covering with straw (Figure 8). After six months a *Sphagnum* lawn had established in almost all of the treatments (mean cover of vital *Sphagnum* ≥ 90 %, Kruskal-Wallis $\chi^2 = 1.73$, $df = 2$, $P = 0.42$). In the first six months after installation the development of lawn thickness differed between both the straw treatments and the initial fragment sizes (loose straw ≥ without straw ≥ straw mat, Kruskal-Wallis $\chi^2 = 7.88$, $df = 2$, $P \leq 0.05$; ‘large’ = ‘medium’ > ‘small’, Kruskal-Wallis $\chi^2 = 72.45$, $df = 2$, $P \leq 0.05$). After one year the mean cover of vital *Sphagnum* was 99 % and the mean lawn thickness was around 6 cm with maxima up to 13 cm, without any significant differences between treatments (cover of vital *Sphagnum*: Kruskal-Wallis $\chi^2 = 2.36$, $df = 2$, $P = 0.31$; lawn thickness: Kruskal-Wallis $\chi^2 = 8.49$, $df = 8$, $P = 0.39$; see Figure 8).

In the mesocosm field experiment in Georgia that investigated the effect of high precipitation combined with low water table, the cover of vital *Sphagnum* one year after installation differed between the three sites (Figure 9). The greatest mean cover (17 %) was recorded at site 2/lowerWT and the lowest mean value (6 %) at site 3/lowWT (Figure 9). Both *Sphagnum* species had the same vital cover after one year (Kruskal-Wallis $\chi^2 = 0.129$, $df = 1$, $P = 0.72$).

Large-scale field experiment in Germany

One year after installation of the large-scale *Sphagnum* paludiculture field experiment, the average cover of vital *Sphagnum palustre* originating from ‘non chopped’ mosses was 76 % with a mean lawn thickness of 3.6 cm, whereas using ‘chopped’ mosses of the same species led to 62 % cover and 2.7 cm lawn thickness. While the differences in cover were not significant, the lawn thickness increments were different (Figure 10). Significantly lower mean values of cover (33 %) and lawn thickness (1.3 cm) were recorded for the area where ‘chopped’ *S. papillosum* was applied (Figure 10).

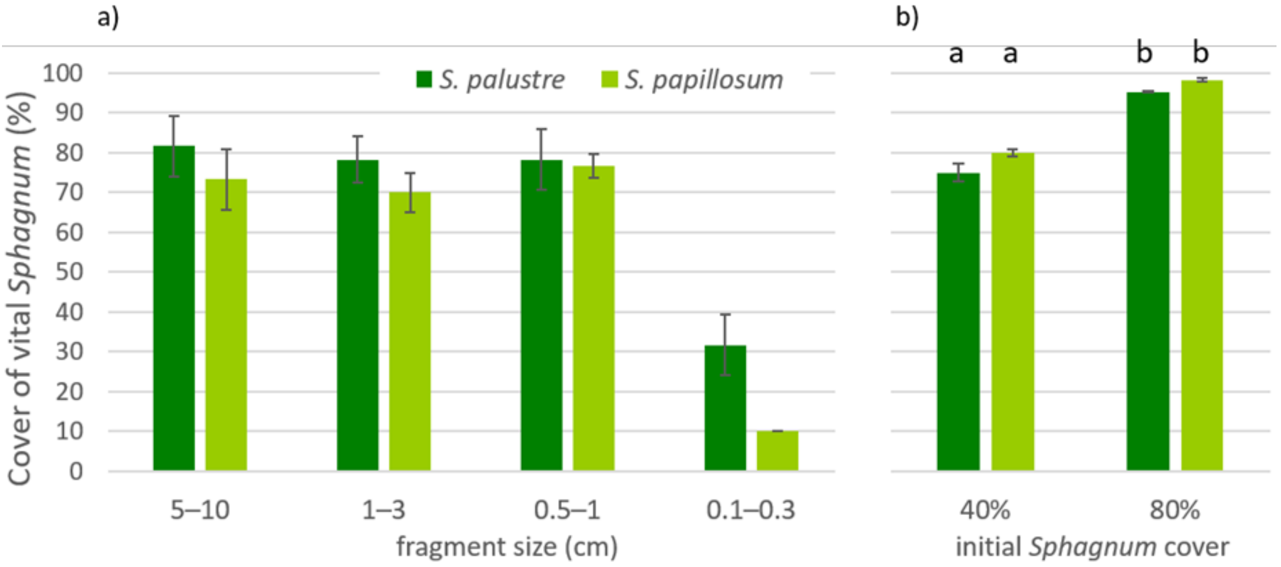

Figure 6. Mean cover ± SE (standard error) of vital *Sphagnum* (%) developed four months after installation, depending on *Sphagnum* species and a) initial fragment size ($n = 3$) or b) initial *Sphagnum* cover ($n = 6$). In a) there are significant differences in cover of vital *Sphagnum* between the fragment size 0.1–0.3 cm and the larger fragment sizes (Kruskal-Wallis $\chi^2 = 13.39$, $df = 1$, $P \leq 0.001$). In b), values with different lowercase letters differ significantly.

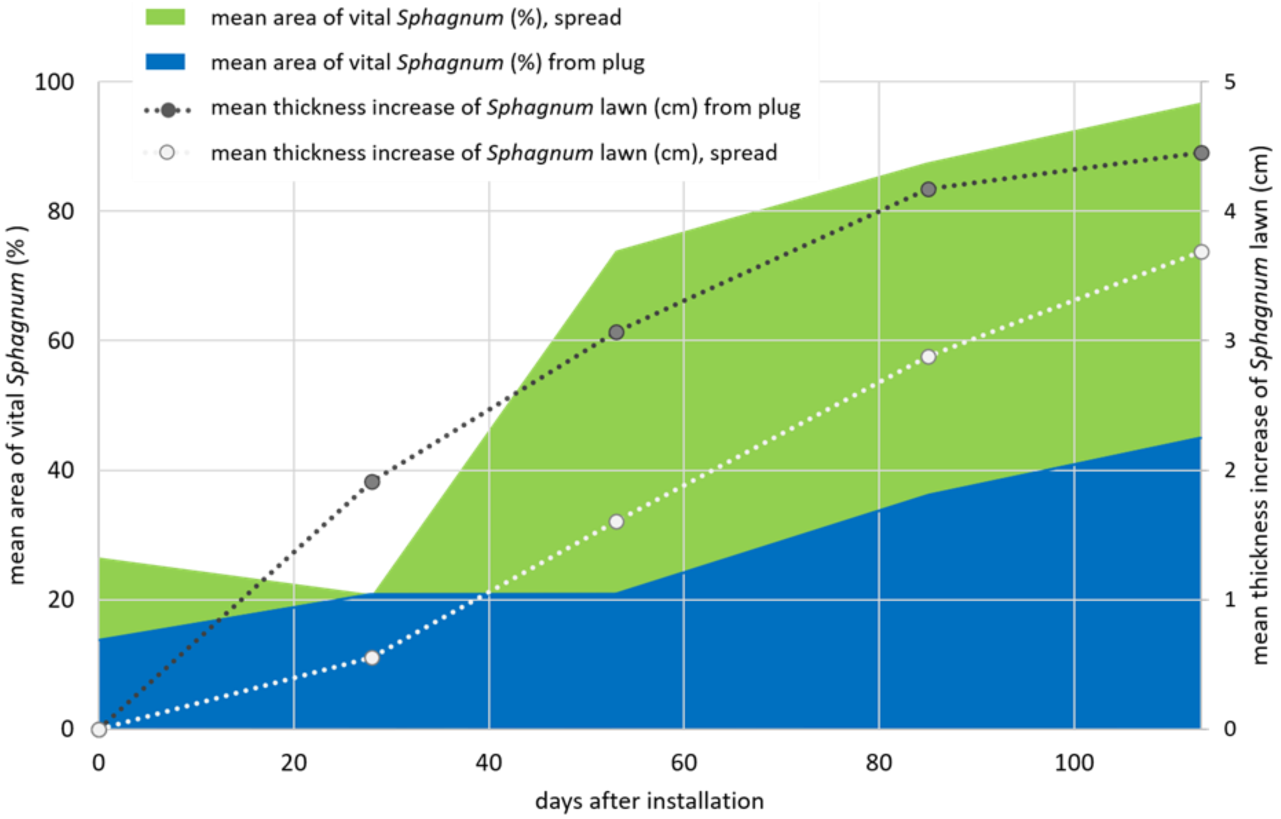

Figure 7. Development (over 113 days) of *Sphagnum* lawns grown from planted plugs and spread mosses ($n = 4$), in terms of mean area of vital *Sphagnum* (% of 367.5 cm^2 tray area) and mean increase in lawn thickness (cm).

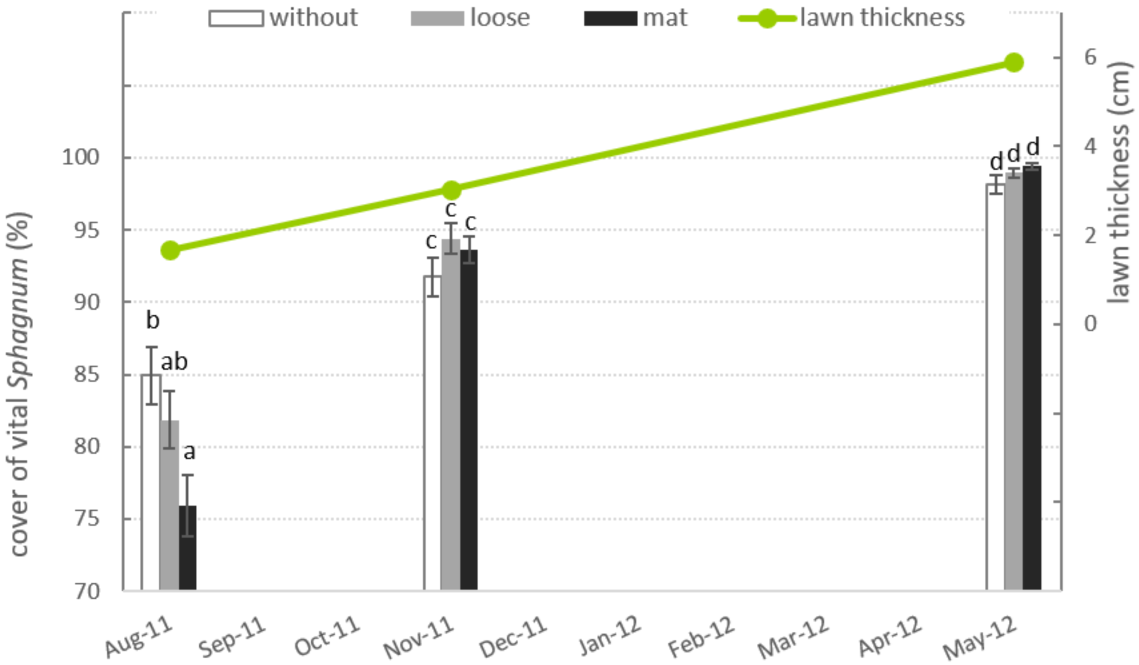

Figure 8. Development of mean cover ± SE (standard error) of vital *Sphagnum palustre* (%, averaged across all initial fragment sizes) in the mesocosm experiment on the Hankhauser Moor peatland (Germany), installed May 2011. The data are categorised according to straw coverage treatment (without straw, loose straw or straw mat; *n* = 27) and mean *Sphagnum* lawn thickness (all treatments, *n* = 405). Differences in the cover of vital *Sphagnum* (%) between the straw coverage treatments were analysed with the non-parametric Kruskal-Wallis test after Siegel & Castellan (1988) for each measurement event (3, 6 and 12 months after installation). The only significant differences between treatments were observed three months post-installation, as indicated by the lowercase letters.

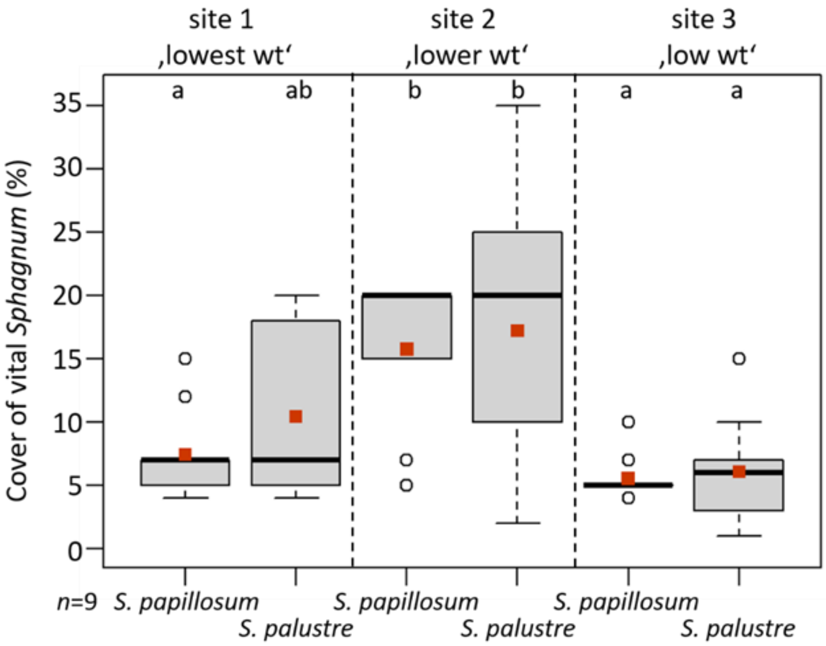

Figure 9. Cover of vital *Sphagnum* (%) one year after spreading of the *Sphagnum* founder material (*S. palustre* or *S. papillosum*, in autumn 2007) between the three investigated sites on the Ispani 1 peatland (Georgia). Each box shows the median (bold line), the mean (red point) and the upper and lower quartiles (creating the box and including 50 % of the data). The whiskers indicate the lowest and highest values within 1.5 interquartile range (IQR) of the lower and upper quartile, respectively; and the outliers (o) are the values outside these ranges. Treatments labelled with different lowercase letters differ significantly.

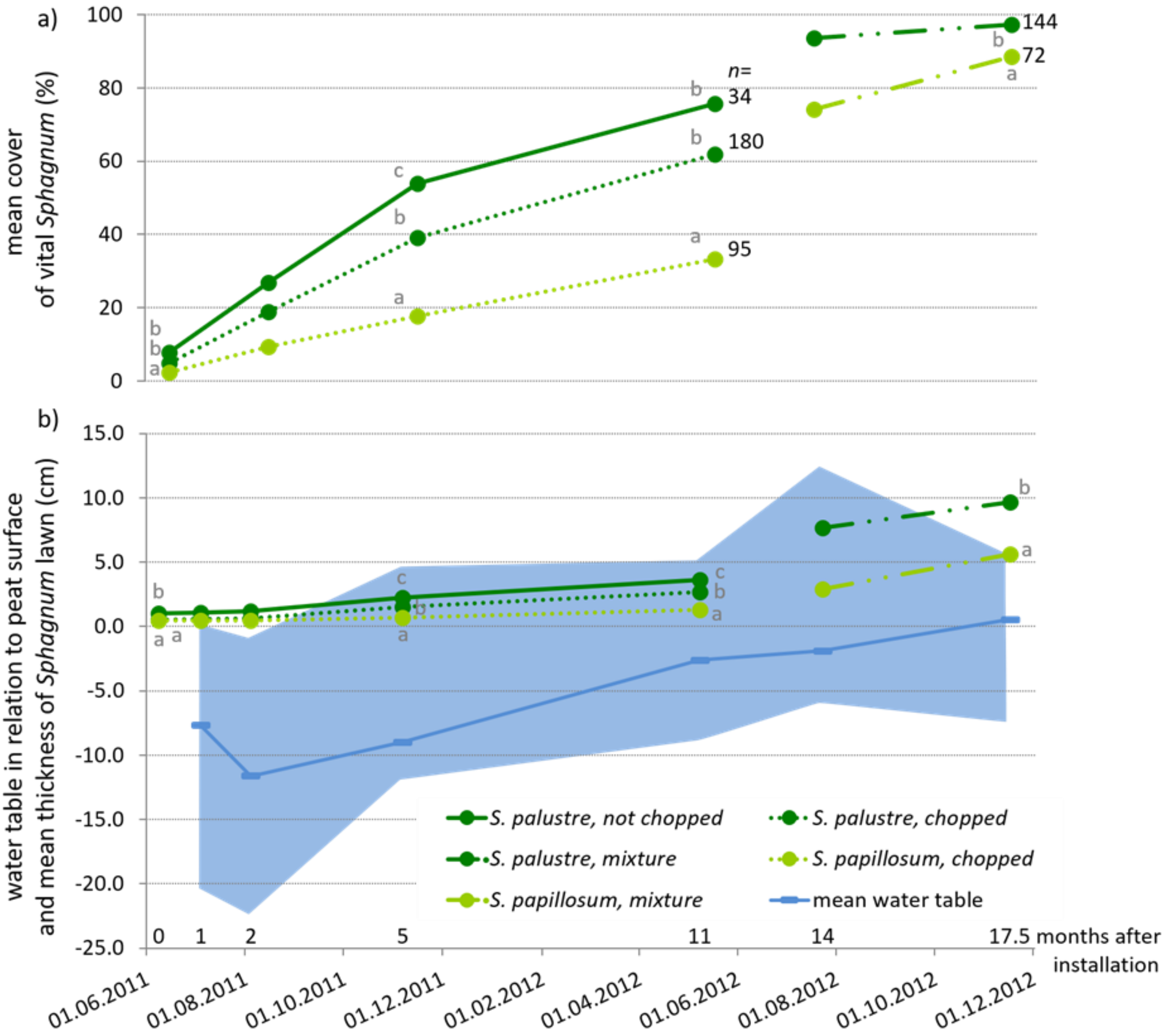

Figure 10. Development of *Sphagnum* lawns at the *Sphagnum* paludiculture site installed in May 2011 on former bog grassland at Hankhauser Moor (Germany). a) Mean cover of visible vital *Sphagnum* (%). b) Mean lawn thickness of the two *Sphagnum* species (*S. palustre* and *S. papillosum*) with different initial fragment sizes (green lines) and water table level relative to peat surface (blue line: mean value; light blue area: minimum–maximum range). The diagrams are interrupted in May 2012 when the *Sphagnum* fragments were replenished, resulting in a mixture of fragment sizes. The number of samples (*n*) for *Sphagnum* cover per treatment is shown in a); we made five measurements of lawn thickness per cover sample. The number of samples for water table measurements was 160 (July 2011) or 310 (all other measurement events). The significance of differences in vital *Sphagnum* cover between treatments (different combinations of *Sphagnum* species and initial fragment size) was tested at the outset, after six months and after one year; in a), values labelled with different lowercase letters differ significantly ($P \leq 0.05$). For details of the statistical analysis, see Table A2.

The mean cover of litter (mainly mowed material but also including the remains of applied straw) decreased continuously from 45 % one month after installation to 12 % after one year, then remained constant for the final six months of the experiment (Figure 11). From two months after installation, the average cover of vascular plants was stable (at 13 %) and dominated by *Juncus effusus* (11 %) until the end of the study period. The total cover of vascular plants was kept below 30 % by regular mowing.

The cover of vital peat mosses three months after site installation was identified as the best indicator for establishment success after one year (Figure 12), although total *Sphagnum* cover after three months was only slightly less reliable. At the ‘three months’ stage, 80 % of the *Sphagnum* was vital but total

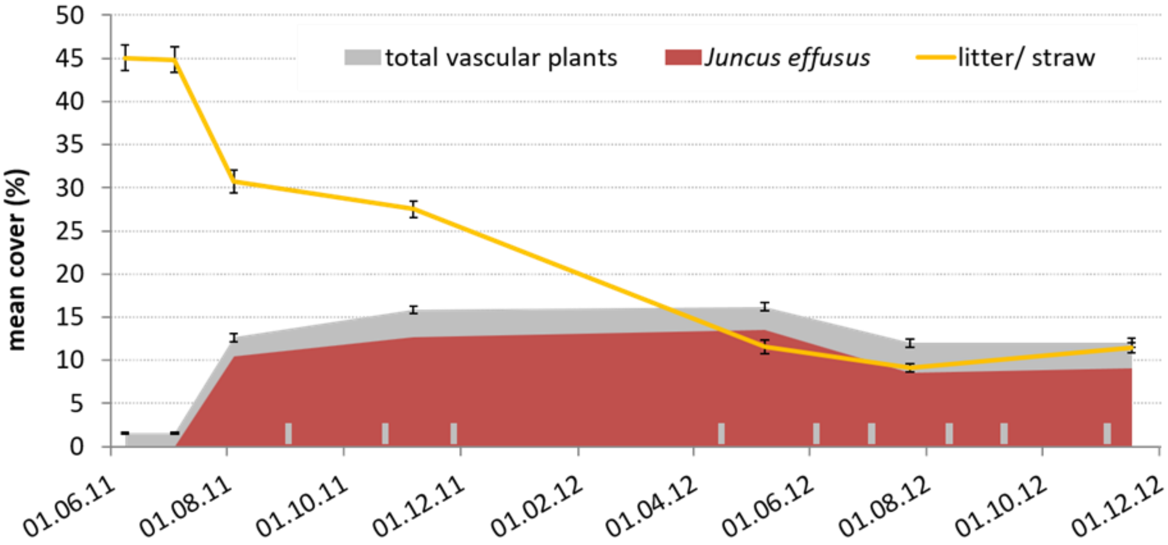

Figure 11. Development of mean cover ± SE (standard error) of (all) vascular plants (grey), *Juncus effusus* (red) and litter including straw and mowed material (yellow line) (%) at the *Sphagnum* paludiculture site on Hankhauser Moor (Germany) after its installation in May 2011. Standard errors are shown for mean cover of vascular plants and litter. The grey bars indicate mowing dates.

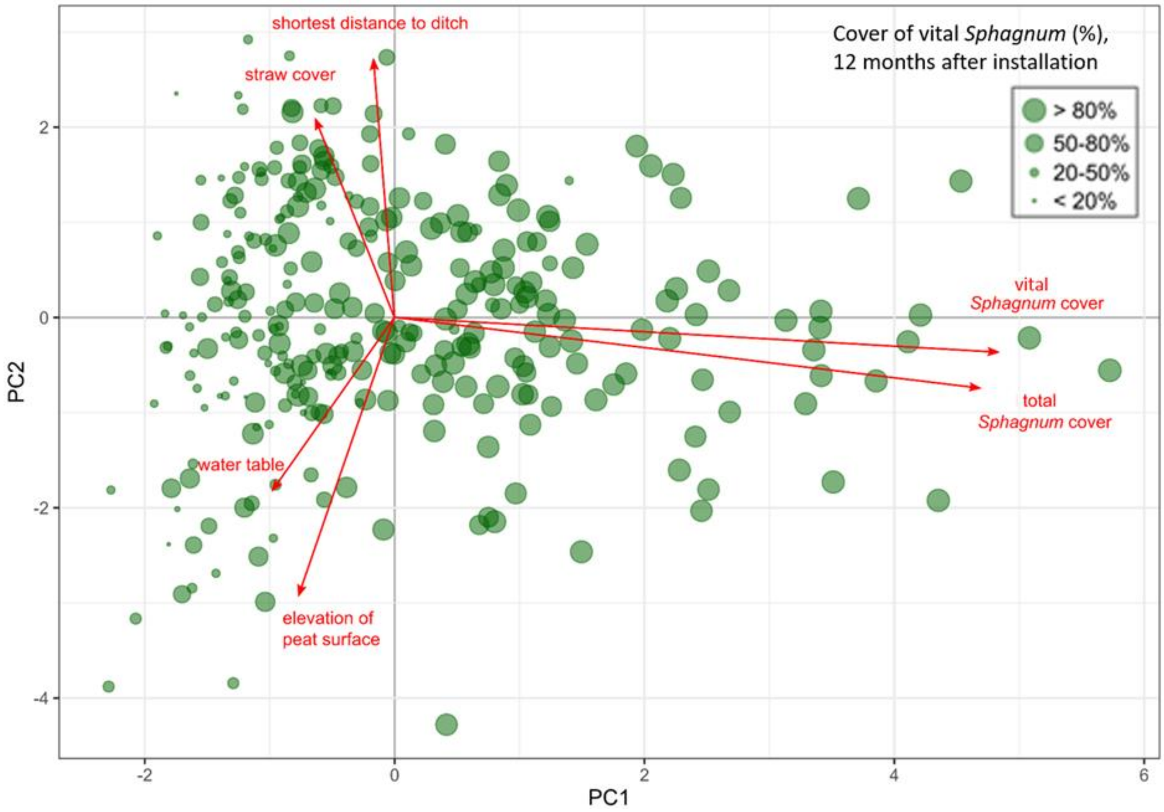

Figure 12. Principal component analysis (PCA) for mean cover of vital *Sphagnum* (%) one year after installation of the large-scale *Sphagnum* paludiculture site on the Hankhauser Moor peatland (data from 310 monitoring plots). Six factors for axis explanation are shown in red, namely: straw cover, vital and total *Sphagnum* cover recorded three months after installation, shortest distance to the ditch, water table depth (mean of measurements made on four occasions per plot), and elevation of peat surface. *Sphagnum* species (*S. palustre* or *S. papillosum*), initial fragment size of founder material, and cover of vascular plants one year after installation had no effect on Axis 1 or Axis 2 and are not displayed. Proportion of variance for Axis 1 = 0.34 and for Axis 2 = 0.26.

Sphagnum cover still differed significantly from vital *Sphagnum* cover (Kruskal Wallis $\chi^2 = 9.57$, $P \leq 0.01$). Other measured variables such as those relating to water supply (mean water table depth, distance from ditch, elevation of peat surface) and straw cover showed smaller effects on *Sphagnum* establishment within one year.

DISCUSSION

Water from below is needed

Because peat mosses are poikilohydric plants, a permanent external water supply is needed to support their growth. In our experiments, both in the glasshouse and at the Hankhauser Moor field site, we were able to maintain high water table and prevent surface flooding through very precise water management. In the field, water table depth ranged from 4 cm to 13 cm below the peat moss surface. For this reason, the shortest distance to the irrigation ditch and the elevation of the peat surface (as indicators for water supply) had only small effects on *Sphagnum* establishment.

In the Kolkheti Lowlands (Georgia), precipitation is very high and evenly distributed through time, with only 3.8 contiguous days without rain on average during the study period (Krebs *et al.* 2016). Although very high *Sphagnum* productivity can occur under these conditions (Krebs *et al.* 2016), establishment of a *Sphagnum* lawn was very slow with less than 20 % cover of vital *Sphagnum* one year after the start of the experiment (with 70 % initial coverage of founder material). It seems that (the high) precipitation was insufficient to compensate for water losses by evaporation and infiltration/seepage to greater depths or surrounding areas. On this basis and contrary to our expectation, we conclude that high precipitation in a wet warm-temperate climate cannot mitigate the adverse effects of deep water table on the establishment of *Sphagnum* fragments on bare (highly decomposed) peat. Therefore, water table close to the surface is necessary.

If high water table level cannot be ensured, the establishment of a new *Sphagnum* lawn could be accelerated by: a) a thick (residual) peat layer, preferably with high saturated hydraulic conductivity (Grobe *et al.* 2021); b) a straw mulch to improve microclimate (Rochefort *et al.* 2003); and c) vascular plants, although these should not intercept light beyond a threshold corresponding to 50 % reduction of photosynthetically active radiation (PAR) reaching the *Sphagnum* (cf. Clymo & Hayward 1982). If the surface peat layer has low hydraulic conductivity, short-term shallow flooding (up to 10 cm for one month; Rochefort *et al*. 2002) might improve water availability for the *Sphagnum* fragments although measures to prevent them from being washed away may be needed.

Use a high density of *Sphagnum* capitula as founder material

Diaz & Silva (2012) found that the top 3 cm of *S. magellanicum* creates most new shoots. We found that the top centimetre (capitulum) of *S. palustre* is the most regenerative part, and even the subcapitulum (the part directly below the capitulum) produces significantly fewer shoots. Indeed, the number of new shoots produced by fragments taken from different depths was in the same range from subcapitulum down to 12 cm depth. Both of these results indicate that the reduced regeneration of fragments with capitula (due to apical dominance) postulated by Clymo & Duckett (1986) is unlikely. Mosses with numerous capitula produced in bioreactors (Beike *et al.* 2015, Heck *et al.* 2021) are probably most suitable for fast establishment of a new *Sphagnum* lawn. To accelerate *Sphagnum* establishment, Campeau & Rochefort (1996) recommend moss fragment densities corresponding to 2,250–4,500 capitula m^{-2}. We found that 825–1,100 capitula m^{-2} (the ‘80 % treatment’ in the glasshouse) with high water table resulted in faster establishment. We conclude from this that, for fast establishment, stable high water table is more important than very high initial cover of *Sphagnum* fragments.

Our large-scale field experiment showed that, under conditions of stable high water table, the success of *Sphagnum* establishment (at least 90 % cover of vital *Sphagnum*) is determined mainly by the cover of vital mosses at a much earlier stage (average 20 % after three months). However, this correlation was not observed when water availability was suboptimal (Gaudig *et al*. 2017). Therefore, our hypothesis that higher initial *Sphagnum* cover leads to faster lawn establishment is valid for situations with constantly high water table. Additional *Sphagnum* founder material may be applied to replenish gaps in the developing *Sphagnum* lawn and accelerate its establishment.

Our results also showed that the fragment size of *Sphagnum palustre* founder material had no effect on the establishment of a new *Sphagnum* lawn when it exceeded 0.5 cm. This corresponds with results from Canada and Germany for several other *Sphagnum* species (Campeau & Rochefort 1996, Hölzel *et al.* 2022). Contrary to our hypothesis, establishment of lawns from *Sphagnum* fragments smaller than 0.3 cm was possible under glasshouse conditions but much slower, probably because the capitula were also chopped. In our large-scale experiment, lawns of *S. palustre* established faster from 'non chopped' mosses than from 'chopped' mosses. One reason for this difference may be the presence of fragments smaller than 0.3 cm (which establish slowest) in the chopped material. Additionally, the fragments were spread mechanically by an adapted snow groomer and then covered with straw, which involved driving across the fragments; 'non chopped' mosses may be more tolerant of this procedure.

No straw cover is necessary if water table is high

Rochefort *et al*. (2003) recommended that *Sphagnum* fragments should be covered with straw mulch to improve the microclimatic conditions for their growth on bare peat surfaces in eastern Canada. In our study at the large-scale *Sphagnum* paludiculture site in Germany, however, the effect of initial straw cover on *Sphagnum* establishment was negligible. Here, the mean straw cover was reduced to 31 % in just two months because the mulch was blown away by wind within a short period. In our mesocosm field experiment, the straw was fixed with a net to ensure longer-lasting coverage. Nonetheless, the establishment of *S. palustre* cover was faster without straw although it became similar after one year. Gaudig *et al.* (2017) found that straw cover < 40 % and thickness > 3 cm even impeded the establishment of *S. papillosum* lawns, most probably because of low water table and too much shading. In the present study, special attention was paid to improving microclimatic conditions for the mosses by ensuring a constant water supply. We can now conclude that straw mulch does not affect the speed of *Sphagnum* establishment in such situations (cf. Wichmann *et al*. 2020).

Because mowing of the large-scale field site started in August 2011, the straw/litter cover one year after installation (in May 2012) consisted mainly of vascular plant mowings, which were not removed. The site was mowed every 3–5 weeks during the growing season which meant that, in May 2012, the cover of both vascular plants (around 15 %) and litter (~ 12 %) was low. For a site with suboptimal water supply, Gaudig *et al.* (2017) found that litter cover (mean value 30 %) was the most relevant variable for successful *Sphagnum* establishment, and optimal at < 20 %. In the present study we did not find such a relationship, probably owing to the lower litter cover and better water supply. If a reduction of mowing frequency were to be necessary (e.g. for economic reasons) and this increased the amount of litter generated, the mowings may have to be removed if they shaded the mosses sufficiently to slow down their growth (cf. Clymo & Hayward 1982).

Spread the moss fragments

Spreading fragments resulted in a higher initial cover of vital mosses than planting plugs because the fragments were laid down across the peat surface enabling the whole length of vital stem to develop new *Sphagnum* plants. This is probably the main reason why, four months after installation, *Sphagnum* lawns that had developed from spread fragments almost covered the available growing area whereas lawns developed from plugs covered less than half that area. Therefore, spreading of moss fragments emerges from this study as the more efficient method for initiating a new *Sphagnum* paludiculture site. On the other hand, it is expected that plugs will perform better than fragments in situations with suboptimal water supply because they should be less vulnerable to desiccation (cf. Caporn *et al.* 2018, van de Koot *et al*. 2024), especially in windy areas where any protection from straw mulch will last only until the straw is blown away.

Although site conditions (water table, peat thickness, nutrient availability, etc.) and initial *Sphagnum* cover were similar in the two field experiments conducted in Germany, moss lawns became established much faster in the mesocosm than in the large-scale experiments. The difference may be due to mechanical stress on the mosses caused by driving tracked machinery over the production fields during installation and management of the large-scale experiment.

Other factors determining establishment success

In the glasshouse, establishment of the two tested *Sphagnum* species was similar except that 'tiny' (< 0.3 cm) *S. palustre* fragments established much faster than *S. papillosum* fragments of the same size. On the other hand, in the field experiment in Germany the cover of vital *Sphagnum* one year after application was higher for *S. palustre* than for *S. papillosum* even when the fragment sizes were similar. Possible reasons for the better performance of *S. palustre* are that it has a higher growing potential than *S. papillosum* (Krebs *et al.* 2016), a slightly higher initial fragment cover at the German site, and/or greater tolerance of eutrophic conditions (Daniels & Eddy 1985, Temmink *et al.* 2017, Gaudig *et al.* 2020). Further investigation is required to determine whether different *Sphagnum* species or groups (e.g. hummock, lawn or hollow species) might establish faster in particular microsites, e.g. on drier areas or in locations where the water table level fluctuates so the surface offers alternating dry and flooded conditions.

The vitality of the moss fragments used as founder material determines the speed of lawn establishment.

Fragments for initiating a *Sphagnum* paludiculture site should be applied as soon as possible after production (e.g. in a bioreactor; cf. Beike *et al.* 2015, Heck *et al.* 2021) or harvesting from the field, because their vitality decreases during storage (Prager *et al.* 2012). For instance, the mosses that we used to establish the large-scale field experiment in Germany were stored (for logistical reasons) outside in the shade for 1.5 months in spring, and this may have affected their vitality. To achieve immediate growth, the best time of year for the application of *Sphagnum* founder material may be the start of the growing season, provided an optimal water supply can be arranged. In locations where the hydrological conditions fluctuate, application during a rainy period (with lower evapotranspiration) that is not too late in the growing season is probably preferable.

Nutrients are essential for *Sphagnum* growth. In our experiments in Germany the conditions were nutrient-rich compared to natural *Sphagnum* habitats. This could promote the growth of vascular plants sufficiently for them to outcompete *Sphagnum* species. However, with regular mowing and a balanced nutrient stoichiometry, peat mosses established quickly; although in the long term, nutrient accumulation in the tissues of slow-growing *Sphagnum* species could become toxic (Käärmelahti *et al.* 2023). In contrast, *Sphagnum* establishment was slow under the nutrient-poor conditions of our field experiment on the Ispani 1 peatland in Georgia, mainly owing to low water table. A fertilisation experiment on the adjacent Ispani 2 peatland showed that, for the growth of *Sphagnum* lawns, high water table was more important than additional nutrient supply (Krebs & Gaudig 2005). Further investigations are required to determine the effect of unbalanced nutrient stoichiometry on the establishment of *Sphagnum* lawns in situations where the water supply is sufficient. Finally, future research should aim to develop a manual for *Sphagnum* paludiculture (and restoration) under different water, nutrient and (possibly) climate conditions, as well as to further identify suitable species for different site conditions.

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AUTHOR CONTRIBUTIONS

All authors developed the study idea with AP supervising setting-up of the glasshouse and mesocosm field experiments in Germany, MK designing and carrying out the field experiment in Georgia, and MK and GG being responsible for the large-scale *Sphagnum* paludiculture field trial in Germany. MK analysed the data and created the Figures and Tables. GG wrote the original draft and AP and MK critically revised the manuscript.

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Author for correspondence:
Dr Greta Gaudig, University of Greifswald, partner in the Greifswald Mire Centre, Institute of Botany and Landscape Ecology, Department of Peatland Science, Soldmannstrasse 15, D-17489 Greifswald, Germany
Tel: +49 3834 4204692; Email: gaudig@uni-greifswald.de

Appendix

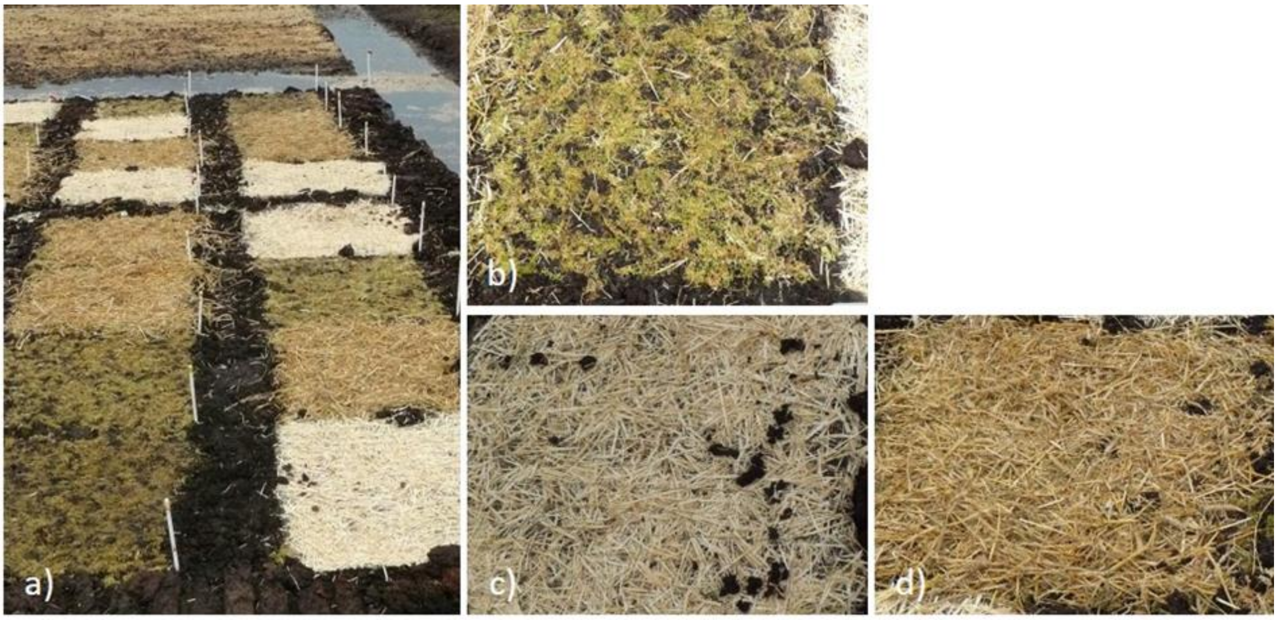

Figure A1. a) Overview of the mesocosm experiment on the Hankhauser Moor peatland immediately after installation; and plan views of the three coverage treatments: b) ‘without straw’, c) ‘loose straw’ and d) ‘straw mat’.

Table A1. Composition of the seeding material (in Vol. %) for the large-scale *Sphagnum* paludiculture site on the peatland 'Hankhauser Moor' (Germany), according to donor site.

	donor site	
Constituent	reed harvest area (The Netherlands)	*Sphagnum* paludiculture site (Ramsloh, Germany)
S. palustre	69	-
S. papillosum	-	75
S. fallax	16	< 1
S. magellanicum	-	2
Vascular plants and litter	14	20
Other mosses	2	< 1
Peat	-	1

Table A2. Kruskal-Wallis test results for Figure 10.

Variable	χ^2	Degrees of freedom	*P*
Cover of vital *Sphagnum*			
May 2011	34.37	2	≤ 0.001
Nov 2011	68.31	2	≤ 0.001 (p-value = 1.472e-15)
May 2012	58.38	2	≤ 0.001
Nov 2012	59.27	1	≤ 0.001 (p-value = 1.374e-14)
Thickness of *Sphagnum* lawn			
May 2011	101.37	2	≤ 0.001 (p-value < 2.2e-16)
Nov 2011	315.71	2	≤ 0.001 (p-value < 2.2e-16)
May 2012	243.20	2	≤ 0.001
Nov 2012	253.11	1	≤ 0.001 (p-value < 2.2e-16)