

Recovery of *Sphagnum* mosses in donor sites after cutting: effects of species and some environmental factors

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SUMMARY

Spontaneous revegetation of extracted peatlands is a very slow and sporadic process and, therefore, *Sphagnum* fragments cut from donor sites are often used for restoration. In two bogs in central and north-east Estonia, we studied the recovery and growth of *Sphagnum fuscum*, *Sphagnum rubellum* and *Sphagnum medium* after cutting of donor sites, in comparison with natural bog sites. On average, the water table was 13.8–17.4 cm higher in spring than in autumn, in both natural and donor sites, and mostly higher in the latter by 1.2–8.1 cm. Shoot length increment, density and weight of capitula of *Sphagnum* mosses were lower in the donor sites than in natural bog sites. The cover of *Sphagnum* mosses reached 5–50 % over a period of 3–11 years after cutting, indicating much slower recovery than has been reported previously. Of the *Sphagnum* species studied, *S. fuscum* showed better recovery in the donor sites. As the weather was similar in the natural and donor sites and the water table was mostly higher in the donor sites, the growth of *Sphagnum* mosses is most probably impeded by the combination of interrupted capillary water rise and a more pronounced drought effect in the donor sites. To promote revegetation of donor sites, plant fragments should be cut from the uppermost <10 cm only, and not from the entire area but instead leaving uncut patches or stripes to enable faster spreading of plants. Because of the slow recovery of donor sites, cutting of *Sphagnum* fragments from natural bogs should be avoided, and sites bordering expanding peat extraction areas should be chosen in preference.

KEY WORDS: bog, peatland restoration, peatmoss, revegetation

INTRODUCTION

For centuries peatlands were seen as areas of low economic value, offering benefits only through peat extraction or drainage for agriculture and forestry. This explains why there was no legal requirement for their restoration after exploitation in the past, and peat extraction areas were simply abandoned after mining or milling ended. Their spontaneous revegetation is a very slow and sporadic process owing to their large area, deep drainage and lack of viable plant propagules, alongside variable and unfavourable growth conditions (Triisberg *et al.* 2013). Continual mineralisation of drained peat has placed extracted peatlands amongst the largest greenhouse gas sources in peat-mining countries (Salm *et al.* 2009, Joosten 2016). Our understanding of the value of natural mires and the need to restore drained and extracted peatlands has changed remarkably during the era of ecological restoration. Valuable ecological benefits, including CO₂ fixation and carbon storage in peat for thousands of years, place natural mires among the most valuable ecosystems in the world (Constanza *et al.* 1997). Therefore, there is nowadays consensus that, if local

conditions allow, extracted peatlands should be restored to re-establish vegetation with plant species that are typical for natural mires, especially *Sphagnum* mosses, leading to the resumption of mire functions including peat accumulation and carbon storage (Money & Wheeler 1999). For example, a study in Estonia revealed that the restoration of extracted peatlands towards re-paludification gives a much greater reduction of GHG emissions than afforestation, and the monetary value of reduced CO₂ emission covers the costs of restoration within a decade (Valgepea *et al.* 2021).

Attempts to restore extracted peatlands towards re-paludification started in West Europe and mostly involved rewetting and flooding (Eggelsmann 1988, Verhoven 2014). The Moss Layer Transfer Technique (MLTT) (Quinty & Rochefort 2003), developed in Canada, has shown the best results for re-establishing *Sphagnum* carpet on extracted peatlands. The MLTT involves cutting *Sphagnum* fragments from a donor site, spreading them on the prepared cutover surface, covering them with straw mulch, and ultimately closing drainage ditches. Revegetation by this method has been used with promising results in Canada (Gonzalez & Rochefort

2014, 2019; Rochefort & Andersen 2017) and in some peatland areas in northern Europe (Karofeld *et al.* 2016, 2020; Purre *et al.* 2020), where GHG emission was superseded by CO₂ fixation and carbon accumulation in peat after only a few years (Järveoja *et al.* 2016, Nugent *et al.* 2018). However, restoration employing the MLTT may be less successful than planned if some important steps or requirements are omitted (Salm *et al.* 2021).

It is recommended that *Sphagnum* fragments from the donor sites are cut from a depth of up to 10 cm because the regeneration potential of fragments decreases rapidly if they are taken from greater depth (Campeau & Rochefort 1996, Quilty & Rochefort 2003). Díaz & Silva (2012) recommend a harvesting depth of up to 12 cm to ensure the regeneration of *Sphagnum* mosses. Fragments harvested from depths of up to 30 cm are sometimes used (Silvan *et al.* 2017) although the regeneration associated with deeper harvesting has been much slower (Reinikainen *et al.* 2012, Silvan *et al.* 2012).

To avoid damage to natural bogs, the most suitable locations for collection of plant fragments (e.g. donor sites) are in areas adjacent to active peat extraction that were drained 1–2 years previously in preparation for expansion of the extraction site. Selection of suitable donor sites, harvesting methods and timing should all be considered with a view to minimising the adverse effect on the environment. Elling & Knighton (1984) stated that little is known about the recovery potential of disturbed areas after a *Sphagnum* harvest. More recently, Guêné-Nanchen *et al.* (2019) published a good overview of ecosystem recovery at donor sites on *Sphagnum* peatlands 1–17 years after harvesting of surface vegetation. Published results about the time needed for donor sites to recover after harvesting are very variable, ranging from fast recovery to decades being needed for revegetation. Krebs *et al.* (2018) reported a fast recovery of *Sphagnum* carpet with new capitula attaining 80 % cover one year after cutting, on both a peatland in Georgia and a *Sphagnum* farming field in Germany, so that cutting could be repeated after 1–2 years. Sobze *et al.* (2012) found that donor sites harvested to 10 cm depth regenerate on their own within 5 years, and that no active restoration is required to improve the recovery of *Sphagnum* species. According to Silvan *et al.* (2017), *Sphagnum* biomass harvesting to a depth of up to 30 cm will affect *Sphagnum* coverage and carbon sequestration for less than 5 years. A similar recovery time of *Sphagnum* carpet is derived by Benson *et al.* (2019). Based on long-term experience, Quilty *et al.* (2019) found that, when harvesting is done correctly, it takes 5–10 years for the *Sphagnum* layer to regenerate after

collection of diaspores. Recovery of *Sphagnum* carpet and carbon sequestration in the donor sites are also highly dependent on water availability and several other site-specific factors, and may sometimes take much longer and be difficult to predict. Elling & Knighton (1984) estimated that 20 years would be needed for 90 % recovery after *Sphagnum* harvest, and a 20-year harvest cycle would appear to maximise yields. A cycle of 30 years is suggested by Silvan *et al.* (2021). Donor sites also release greater amounts of greenhouse gases than adjacent natural bog sites (Murray *et al.* 2017) - in fact, twice as much CO₂ (Pacheco-Cancino *et al.* 2023). This provides additional motivation to understand and apply methods that lead to a faster recovery of donor sites.

To fulfil goals for the successful restoration of abandoned extracted peatlands, and for the recovery of donor sites, it is necessary to know the principles of *Sphagnum* recovery on donor sites after cutting, and to determine measures to evaluate its speed and success. This study aims to:

- 1) evaluate the growth recovery of *Sphagnum* mosses after cutting from the donor sites;
- 2) compare this with their growth in natural bog conditions; and
- 3) elucidate the main factors controlling *Sphagnum* growth and recovery in donor sites.

METHODS

Study sites

The study was conducted in natural and donor sites on Soosaare and Punasoo bogs. Fieldwork was undertaken during two growing seasons, from spring (April) to autumn (October) in 2021 and 2022. On both bogs, all measurements were made during the same week.

The natural site on Soosaare bog (12,671 ha, Central Estonia, 58.556367 °N, 25.888327 °E) was located in typical hollow-ridge bog with sparse *Pinus sylvestris* trees up to 2–4 m tall on the ridges and a ground layer dominated by *Andromeda polifolia*, *Calluna vulgaris*, *Eriophorum vaginatum* and *Oxycoccus palustris*. The moss layer is dominated by *Sphagnum fuscum* and *S. rubellum* on hummocks and *S. medium* in lawns. The donor site was located in a treeless area with similar vegetation, approximately 50 m distant from the natural site. In the donor site, plant fragments were cut with string trimmers from the topmost layer of the *Sphagnum* carpet (~ 10 cm thick) in late April 2012. Cutting was done selectively from about 20 hummock patches of

average diameter 3–5 m. During the next few days, the *Sphagnum* fragments were collected with rakes and used to restore a section of the Tässä milled peatland using the MLTT method (Karofeld *et al.* 2016, 2020). Cutting of *Sphagnum* fragments from a nearby area was also done in late summer 2017 and 2019, from about ten patches of diameter 10–20 m, using trimmers and a tractor mounted rotary shredder. The plant fragments were collected with rakes.

Natural and donor sites in Punasoo bog (699 ha, north-east Estonia, 59.217329 °N, 26.742475 °E) were located on the bog edge bordering an active peat extraction area. The vegetation was similar to that on Soosaare bog with a sparse *P. sylvestris* tree layer, ground layer dominated by *C. vulgaris*, *A. polifolia* and *E. vaginatum*, and *S. fuscum*, *S. rubellum* and *S. medium* in the moss layer. *Sphagnum* fragments were cut at the beginning of September 2018 for the restoration of Palasi milled peatland (Salm *et al.* 2021). The fragments were cut with a tractor-mounted rotary shredder from the topmost moss layer (10–15 cm thick) on three donor patches of diameter 40–60 m, and collected with a tractor bucket. The bog surface was relatively uniform and contained small lawn areas, which allowed cutting of fragments across the entire area of the three donor sites (total 0.45 ha). Because the cut fragments were collected using the tractor bucket, some were probably collected from slightly greater depths than the intended 10 cm in places. In October 2022, the total cover of vegetation on the donor sites at both bogs was estimated visually with an accuracy of 5 % and the most frequent plant and moss species were registered.

Meteorological data and water table depth

Mean air temperature and total precipitation data from the nearest meteorological station, for quarterly (three months) periods and for the growing season (April–October), were provided by the Estonian

Environment Agency. For Soosaare bog, data from Viljandi meteorological station (26 km distant) and for Punasoo bog, data from Tudu precipitation station (7.2 km distant) were used (Table 1). Precipitation was more variable, and differed between the two bogs to a greater extent, than mean air temperature. At each *Sphagnum* growth measurement patch, water table depth (WTD) below the vegetation surface was measured with a tapeline in perforated plastic tubes inserted into the peat to a depth of 0.75 m. Six measurements per site were done for each studied species in April and October 2021–2022, giving a total of 24 measurements per species per site.

Studied species and length increment of *Sphagnum*

Sphagnum fuscum, *S. medium* and *S. rubellum* are common species in natural bogs in the northern hemisphere, and also dominate our study bogs. Due to their relative tolerance to dry conditions and desiccation (Hájek & Beckett 2008), they are also recommended for use in restoration (Quinty & Rochefort 2003, Karofeld *et al.* 2020) and were the target species in this study. The length increments of *Sphagnum* shoots were measured in 2021–2022 according to the brush wires method of Rydin & Jeglum (2013). Wires ~15 cm in length with small brushes at their lower ends were inserted into pure patches of the studied *Sphagnum* species. Three brush wires were inserted to 5–7 cm depth into each of six patches at each site, giving 18 wires per species per site in total. The length of each wire initially protruding above the moss carpet was measured at the beginning of the growing season, in the second half of April; and the measurement was repeated at the end of the growing season in late October. Then, the shortening of wire length represents the shoot increment of the particular *Sphagnum* species. Wires with obvious signs of disturbance (e.g. trampling) and wires with increased length were discarded and replaced with new wires.

Table 1. Quarterly and growing-season (April–October) mean air temperature (Temp., °C) and precipitation (Prec., mm) at Viljandi meteorological station and Tudu precipitation station.

Year	March–May		June–August		September–November		Growing season	
	Temp.	Prec.	Temp.	Prec.	Temp.	Prec.	Temp.	Prec.
Viljandi meteorological station for Soosaare bog								
2021	3.8	157.5	18.5	177.8	6.8	188.9	9.7	574.2
2022	4.9	80.9	18.3	182.6	6.4	144.6	9.8	408.1
Tudu precipitation station for Punasoo bog								
2021	4.3	177.3	18.0	126.7	6.3	188.9	9.5	492.9
2022	4.0	83.7	17.3	171.4	5.7	182.7	9.0	437.8

Shoot density and capitula weight of *Sphagnum*

Samples ($n=6$ for each studied species) were collected from uniform *Sphagnum* patches adjacent to the length increment measurement points at the four (natural and donor) sites in late October 2022. The samples were extracted using a 5.8 cm diameter metal cylinder with a sharp saw-like lower edge, and were about 10 cm thick. *Sphagnum* shoots with capitula were counted, and the density of the *Sphagnum* carpet (number of shoots in 1 dm²) was calculated. To estimate the weight of the *Sphagnum* capitula, the topmost 1 cm of the sample was cut off, dried in a ventilated electric oven at 65 °C for 48 h, and weighed after cooling. Considering the number of weighed capitula, results were re-calculated to express all results as the weight of 100 capitula.

Statistical analysis

The effects of fixed factors (*Sphagnum* species, bog Soosaare/Punasoo, site natural/donor and year 2021/2022) on the length increment of *Sphagnum* mosses were analysed with a linear mixed effects model (LMM), where a patch was included as a random factor. For analysing the variation in spring and autumn water table depth, the previously described LMM, including an additional fixed factor, ‘season’, was used. In the case of response variables

measured in only one of the study years (density and weight of *Sphagnum* capitula), we used the linear model without the factors ‘year’ and ‘sampling point’. Models included main effects as well as up to three-way interactions of the fixed factors. Compliance with the model assumptions was checked from the residual plots. Mixed model analyses were performed with the ‘lmer’ function from the ‘lme4’ package of R version 4.3.2 (R Core Team 2023). Post-hoc comparisons of the group means, and interaction plots, were made with the ‘emmeans’ package. Linear relationships between the studied variables were analysed based on the Pearson correlation coefficients and visualised with the ‘ggpubr’ package. The level of significance $\alpha=0.05$ was used for interpreting the results of statistical tests.

RESULTS

Water table depth

The results of the mean WTD measurements in the natural and donor sites are shown in Figure 1. WTD depended significantly on year, season, site, bog, species, and their interactions. The site mean water table was higher in spring, after the snow melted, in

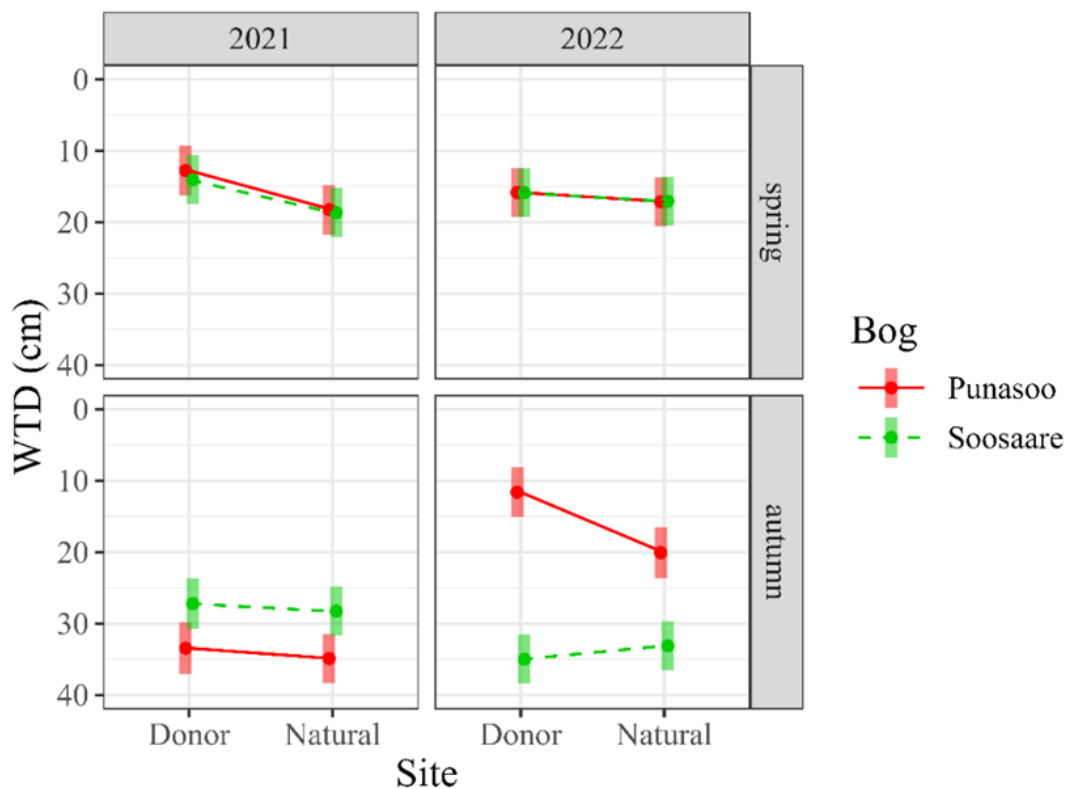


Figure 1. Spring and autumn water table depths (mean WTD in cm with 95 % confidence intervals) in donor and natural sites at Punasoo and Soosaare bogs, 2021–2022.

both natural and donor sites (by 13.8 ± 3.3 cm and 17.4 ± 4.3 cm, respectively) in 2021. Surprisingly, in Punasoo bog the WTD was slightly greater in autumn 2022 compared with spring, remaining non-significant in the natural site, while this difference was significant in the donor site ($p=0.018$). There was no significant difference in spring WTD between Soosaare and Punasoo bogs in either year, but in spring 2021 the WTD was significantly ($p=0.004$) deeper in natural sites than in donor sites. In autumn 2021, the water table was deeper in both Punasoo sites, whereas in autumn 2022 it was deeper in the Soosaare sites. In autumn 2022, WTD in Punasoo natural sites was significantly ($p=0.001$) deeper than

in the donor sites. Generally, the autumn water level changed less in Soosaare bog than in Punasoo bog.

Differences in WTD were more pronounced between the patches of different *Sphagnum* species. Following the natural positions of *Sphagnum* species on the bog microtopographical gradient, WTD in the natural and donor sites was mostly greatest under *S. fuscum*, least under *S. medium* and intermediate under *S. rubellum* patches (effect of species on WTD: $P < 0.001$). The water table was often deeper in natural than in donor sites, especially under *S. fuscum* and *S. rubellum* patches; on average by 4.6 ± 1.6 cm ($P=0.005$) and 5.9 ± 1.6 cm ($P < 0.001$), respectively (Figure 2). These differences were more distinct in

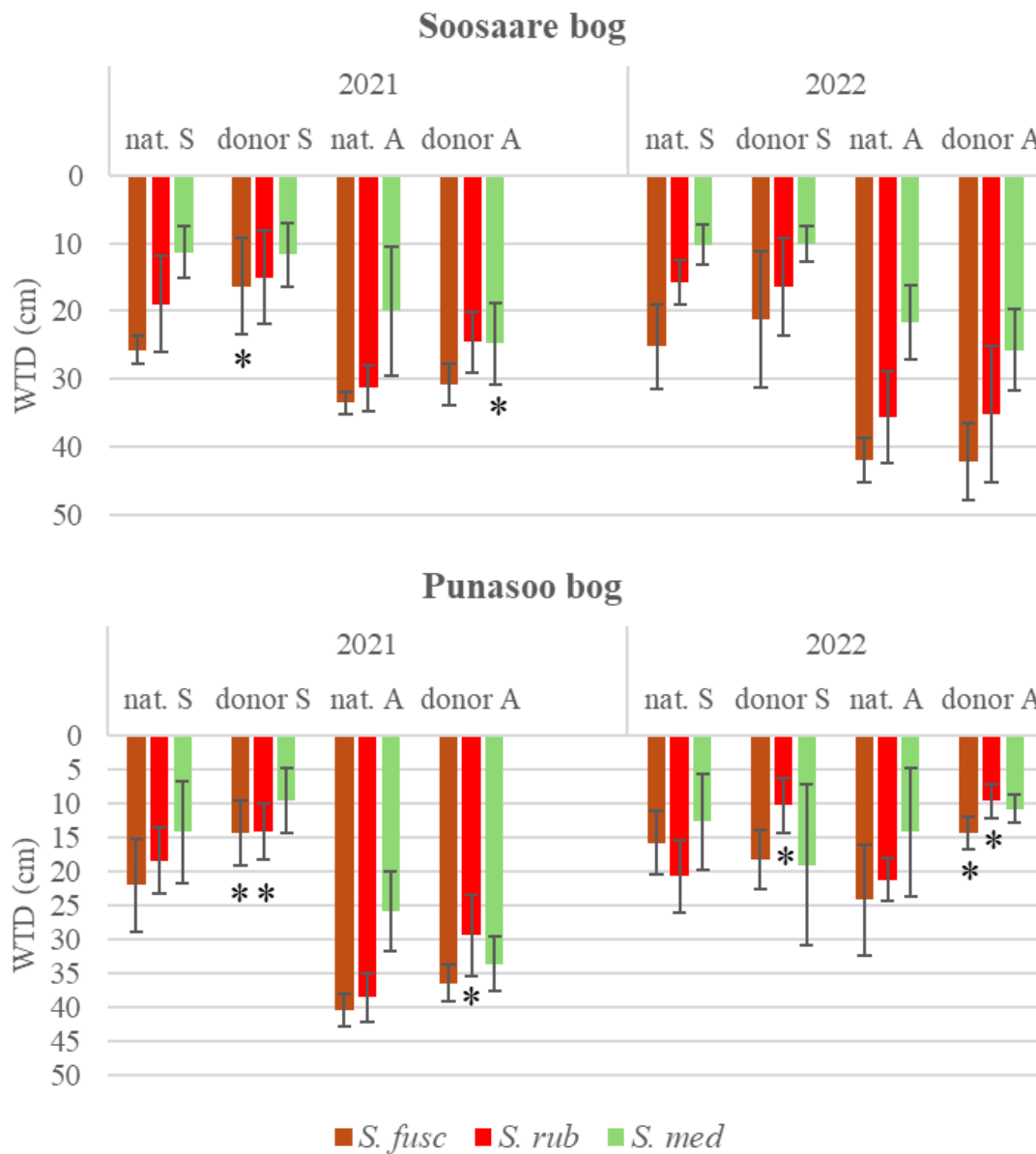


Figure 2. Water table depth (mean \pm SD, cm) under the patches of studied *Sphagnum* species natural and donor sites at Soosaare and Punasoo bogs in the spring (S) and autumn (A) seasons of 2021–2022. Significant differences between donor and natural sites in spring or autumn for a given species are indicated by asterisks.

Punasoo bog. Average WTD was slightly (2.1 ± 1.6 cm) greater in donor sites only under *S. medium*, and this difference was statistically significant ($P = 0.041$) only in Soosaare bog in autumn 2021.

Length increment of *Sphagnum*

The length increment of *Sphagnum* shoots was greater in natural sites than in donor sites on both bogs; by 13–42 % for *S. fuscum*, 41–61 % for *S. rubellum*, and 34–79 % for *S. medium* (Figure 3). The only exception was at the Punasoo donor site in 2022, when the increment of *S. medium* was 31 % greater than at the natural site. In the studied sites, the length increment of *Sphagnum* mosses was

significantly different ($p = 0.003$) between the two years, being higher in 2022 (Figure 4a). The effect of year did not differ between species, bogs (Soosaare/Punasoo) or sites (natural/donor). Shoot length increment was significantly ($p = 0.003$) affected by the interactions between ‘bog’, ‘site’ and ‘species’ (Table 2). The shoot increments of *Sphagnum* species differed between the different bogs, tending to be higher in natural sites. Shoot length increment of *S. fuscum* differed between natural and donor sites, but not significantly in either Punasoo or Soosaare bog. The increment of *S. rubellum* shoots was significantly higher in the natural site than in the donor site at Punasoo, and *S. medium* shoots showed

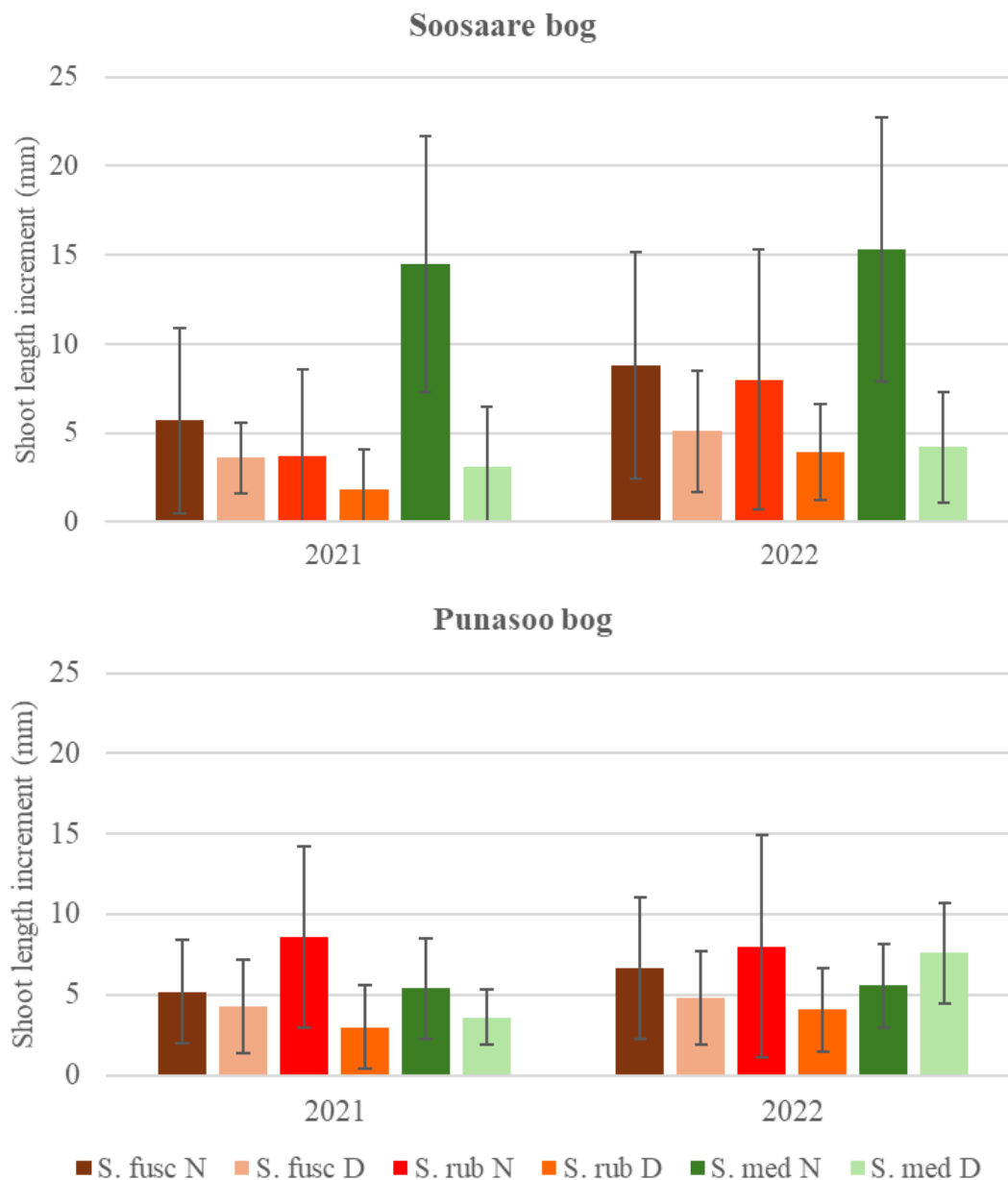


Figure 3. Shoot length increment (mean \pm SD, mm yr^{-1}) of three studied *Sphagnum* species in natural (N) and donor (D) sites at Soosaare and Punasoo bogs in 2021 and 2022.

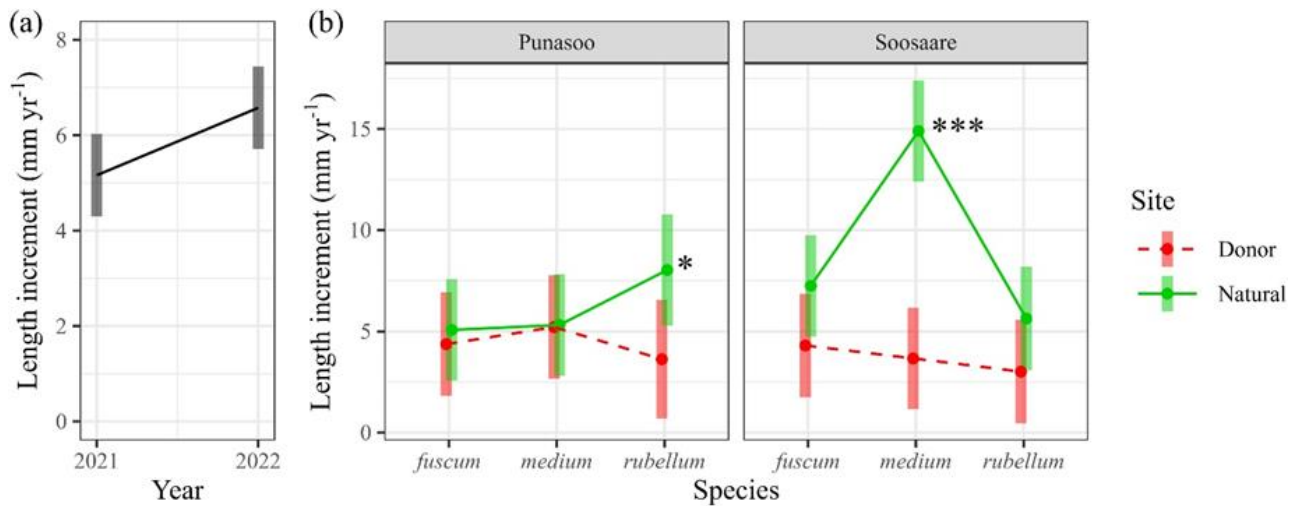


Figure 4. Difference in length increment (means with 95 % confidence intervals) of *Sphagnum* species between 2021 and 2022 (a) and *Sphagnum* species in natural and donor sites at Punasoo and Soosaare bogs (b). Significant differences between the sites are marked with asterisks (* $p < 0.05$, *** $p < 0.001$).

Table 2. Results of analyses of the effects of fixed factors on WTD and growth characteristics of *Sphagnum* mosses. Statistically significant p -values are shown in **bold** type.

Factors	Response variables			
	Water table depth	Length increment	Density	Capitula weight
Year	<0.001	0.003	-	-
Bog	0.001	0.115	0.928	0.059
Site	0.003	<0.001	<0.001	0.834
Season	<0.001	-	-	-
Species	<0.001	0.031	<0.001	<0.001
Year×Bog	<0.001	0.206	-	-
Year×Site	0.445	0.711	-	-
Year×Season	<0.001	-	-	-
Year×Species	0.616	0.934	-	-
Bog×Site	0.102	0.012	0.024	0.005
Bog×Season	<0.001	-	-	-
Bog×Species	0.018	0.014	0.500	0.802
Site×Season	0.566	-	-	-
Site×Species	0.001	0.105	0.011	0.628
Season×Species	0.150	-	-	-
Year×Bog×Site	0.068	0.082	-	-
Year×Bog×Season	<0.001	-	-	-
Year×Bog×Species	0.017	0.323	-	-
Year×Site×Season	0.024	-	-	-
Year×Site×Species	0.752	0.436	-	-
Year×Season×Species	0.405	-	-	-
Bog×Site×Season	0.047	-	-	-
Bog×Site×Species	0.421	0.003	0.366	0.062
Bog×Season×Species	0.758	-	-	-
Site×Season×Species	0.188	-	-	-

significantly higher length increment in the natural site than in the donor site at Soosaare (Figure 4b).

Length increment of the three *Sphagnum* species in the donor sites was significantly correlated with spring WTD ($p=0.036$; Figure 5). The increment of *S. rubellum* benefited significantly ($p=0.016$) from the deeper spring water table, regardless of site and bog, while the effect on the increment of the other

two species remained non-significant (Figure 6). Higher autumn water levels tended to favour shoot increment of all *Sphagnum* species in the donor sites, although the respective correlations were not significant. In natural sites, the autumn WTD showed a nearly significant ($p=0.094$) positive trend with the shoot length increment of *S. fuscum*, i.e. increment tended to increase at deeper water levels.

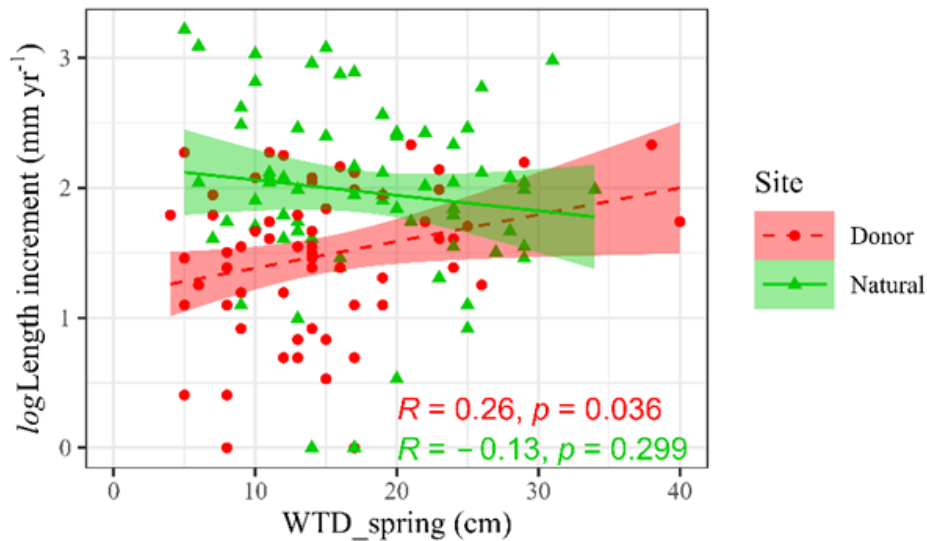


Figure 5. Relationship between length increment of *Sphagnum* shoots and spring water table depth (WTD) in natural and donor sites across both bogs and all species (linear trendlines with 95 % confidence bands).

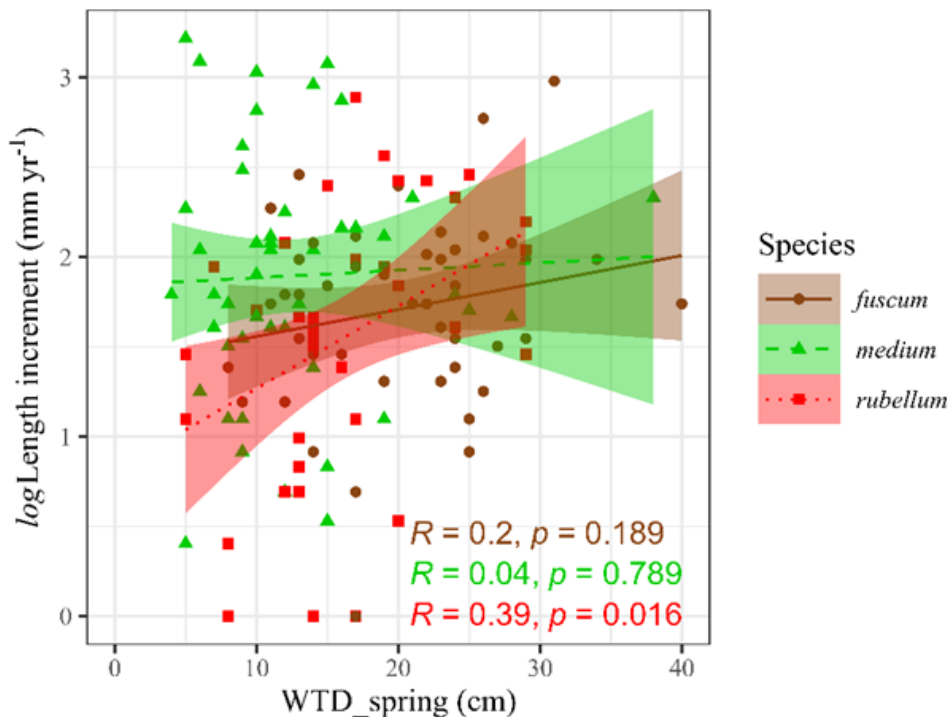


Figure 6. Relationship between the shoot length increment of *Sphagnum* species and spring water table depth (WTD) across both bogs and sites (linear trendlines with 95 % confidence bands).

Shoot density and capitula weight of *Sphagnum*

Interactions between ‘site’ and ‘bog’ had a significant effect on the shoot density of *Sphagnum* mosses ($p=0.024$; Figure 7a, Table 2). In Punasoo, the density of capitula was significantly lower ($p<0.001$) in the donor site; in Soosaare, this difference was insignificant. Interactions between ‘species’ and ‘site’ significantly affected the shoot densities of species ($p=0.011$). The densities of *S. fuscum* and *S. rubellum* shoots were significantly lower in donor sites compared to natural sites, whereas the density of *S. medium* shoots was almost

the same in both (Figure 7b).

The weight of *Sphagnum* capitula differed significantly ($p<0.001$) between studied species regardless of bogs and sites, being highest for *S. medium* and lowest for *S. rubellum* (Figure 8a). The weight of the capitula was significantly affected by the interaction between ‘bog’ and ‘site’ ($p=0.005$). *Sphagnum* capitula in the Soosaare donor site weighed significantly more ($p=0.0013$) than those in the Punasoo donor site, whereas the weights of capitula in natural sites were almost equal (Figure 8b).

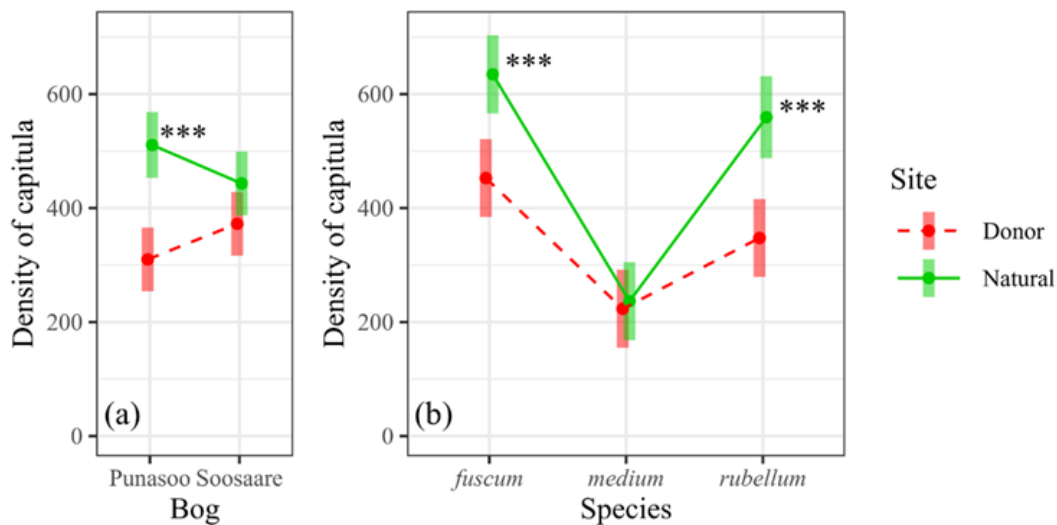


Figure 7. Differences in the density of *Sphagnum* capitula (means with 95 % confidence intervals) in natural and donor sites at Punasoo and Soosaare bogs (a) and between the species (b). Significant differences between the sites are marked with asterisks (***) ($p < 0.001$).

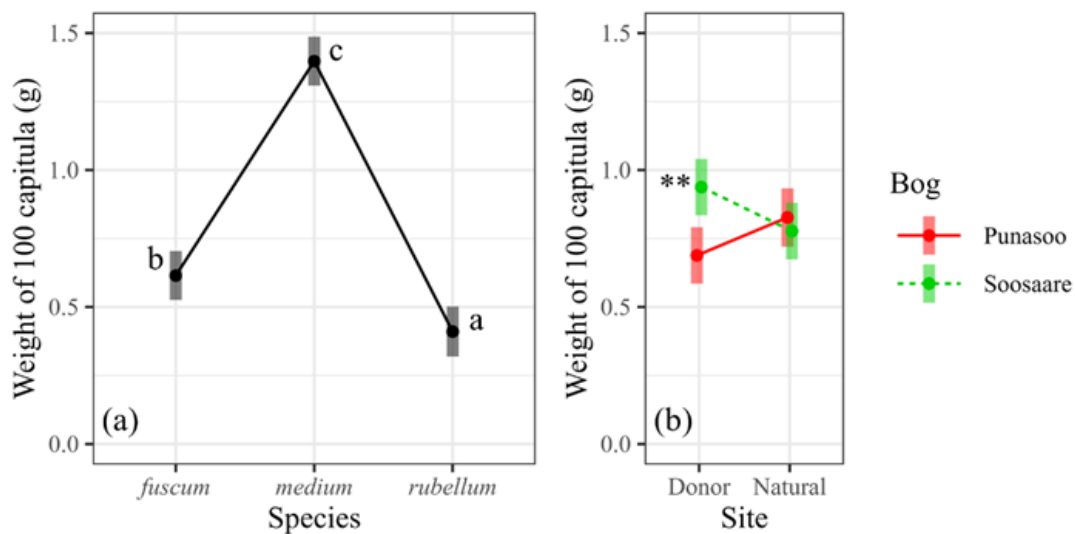


Figure 8. Differences of *Sphagnum* capitula weights (means with 95 % confidence intervals) according to species (a), bogs and sites (b). Significant differences between the species are indicated by lowercase letters, and between the bogs by asterisks (** $p < 0.01$).

The capitula weights of two species - *S. medium* and *S. fuscum* - were significantly correlated with autumn water table depth in the donor sites ($p=0.021$ and $p=0.044$, respectively, Figure 9), the capitula being heavier when autumn water table was deeper. Although the capitula of *S. medium* in natural sites weighed less when autumn water table was deeper, this relationship was not significant. *S. rubellum* did not show any significant responses to autumn WTD in either natural or donor sites.

Plant cover

In October 2022, total plant cover varied between 60 % and 80 % in the Soosaare donor site, and

between 50 % and 80 % in the Punasoo donor site; and was dominated by vascular plants. The most common species were *C. vulgaris*, dominating as pure patches in drier places, and *Rhynchospora alba* which was the dominant species in depressions. In addition, *E. vaginatum*, *A. polifolia*, *Rubus chamaemorus* and small saplings of *P. sylvestris* were present (Figure 10). The cover of viable *Sphagnum* patches was evaluated at 40–50 % in the Soosaare donor site, but only up to 5 % in the Punasoo donor sites. Most patches were formed by *S. rubellum* and *S. fuscum*, followed by *S. medium*. Especially in the Punasoo donor site, there were necrotic areas of cut *Sphagnum* mosses.

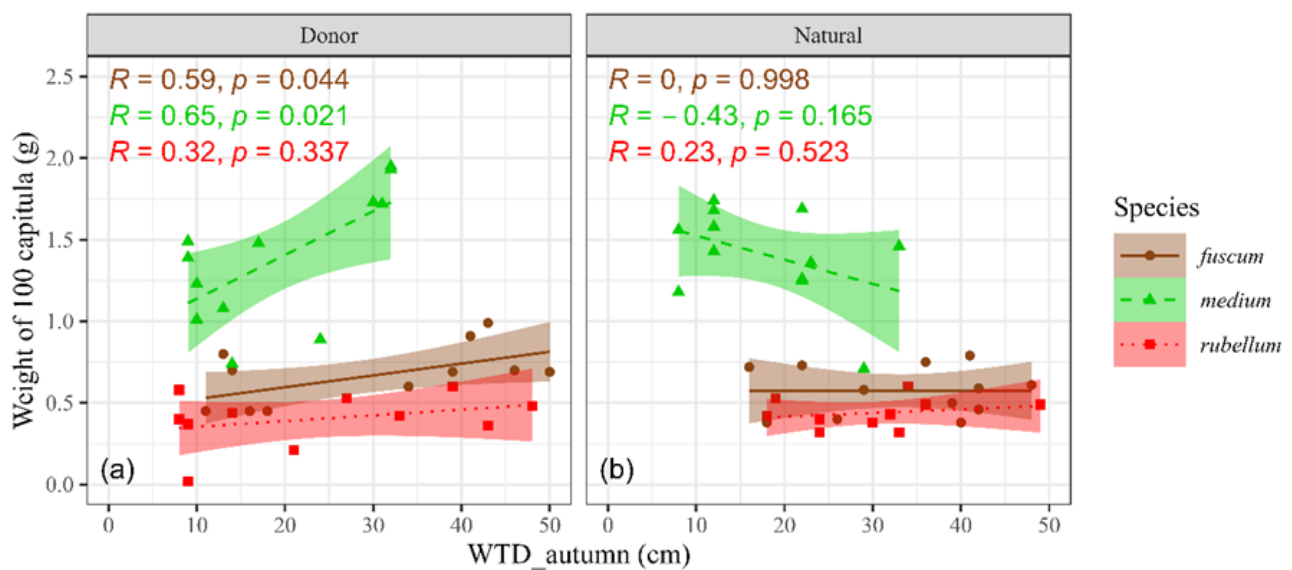


Figure 9. Relationship between capitula weights of *Sphagnum* species and autumn water table depth (WTD) in the donor (a) and natural (b) sites (linear trendlines with 95 % confidence bands).



Figure 10. General views of the donor sites on Soosaare bog (left) and Punasoo bog (right) in October 2022.

DISCUSSION

In our donor sites, 3–11 years after cutting, the total plant cover reached 50–80 % but cover of *Sphagnum* mosses was more variable, from only 5 % up to 50 %. Thus, their recovery seems to be slower than has been reported from some earlier studies (Sobze *et al.* 2012, Silvan *et al.* 2017, Krebs *et al.* 2018). Slow recovery of *Sphagnum* mosses reduces carbon sequestration and can benefit invasive species like *Campylopus introflexus* on bare peat surfaces (Samson *et al.* 2024). Thus, finding methods to speed up the recovery of vegetation is important. Revegetation of donor sites differs from that in post-mined sites, where the bare peat left at the surface after peat milling can be thousands of years old without any viable diaspores, so the re-establishment of vegetation depends entirely on dispersal from the outside. In our donor sites, it was mostly only the topmost peat layer ~10 cm thick that was removed, leaving behind many viable plant fragments and propagules. Thus, vegetation recovery may emerge from several sources including viable patches of uncut plants, surviving roots and other vegetative parts, cut plant fragments dropped during the collection, accumulated diaspores, and natural spreading of seeds and spores from the adjacent natural bog.

Sphagnum mosses are known for their ability to start growing even from small fragments, but this decreases rapidly with depth below 10 cm (Quinty & Rochefort 2003). Therefore, *Sphagnum* mosses growing in the donor sites most probably started from uncut patches and dropped fragments or spores, rather than from cut shoots. *Sphagnum* mosses are generally considered not to be dispersal-limited since their spores can be carried over thousands of kilometres (Sundberg 2013). Still, *Sphagnum* mosses in stable growth conditions rarely form sporophytes, *Sphagnum* carpet in bogs is considered unfavourable for germination of *Sphagnum* spores, and establishment is also impeded by insufficient phosphate (Sundberg & Rydin 2002). However, spores buried deeper in the peat can remain viable for several decades and germinate after disturbance or a change in growth conditions (Grandin & Rydin 1998, Mälson *et al.* 2010). Such disturbance occurs after cutting of plant fragments from the donor sites. After germination, favourable stable water levels and light conditions are needed for *Sphagnum* growth. According to our measurements, the length increment of *Sphagnum* mosses was smaller in donor sites than in natural sites. Length increments measured in natural sites at Punasoo and Soosaare were slightly smaller than those measured previously

in Estonian natural bogs, whereas the increments in donor sites were comparable to those in restored extracted peatland (Karofeld *et al.* 2020). WTD in the donor sites was mostly even higher than in natural sites and within the optimal range for *Sphagnum* mosses; and because of their close proximity, the natural and donor sites experienced similar rainfall regularity and amounts. Therefore, the differences in growth could be caused by difficulties with the capillary rise of water. In the donor sites, the uppermost parts of the *Sphagnum* shoots were cut off and, as the water level dropped to 30–40 cm depth in summer, the connection between *Sphagnum* moss offshoots and the water table was interrupted. Thus, as has been shown in other studies, *Sphagnum* mosses in donor sites are more dependent on precipitation regularity and more vulnerable to droughts and insufficient moisture content than in natural bogs (Jassey & Signarbieux 2019). The difference in length increment was smallest for *S. fuscum*. This species has been found to be less affected by water deficit than other *Sphagnum* species owing to its smaller leaf pores and smaller pore spaces between the (more densely packed) leaves having better capillary water uptake (McCarter & Price 2014, Bengtsson *et al.* 2021). Koronatova *et al.* (2022) also found that the traits most sensitive to weather were length increment and density, and that *S. fuscum* was less sensitive to weather. Greater length increment in 2022 could have been caused by more-regular rainfall events in June–July, while longer dry periods may have suppressed *Sphagnum* growth.

The growth of *Sphagnum* mosses is largely controlled by the moisture content of their capitula, which is maintained by the combination of capillary uptake of water and precipitation. Unlike vascular plants, *Sphagnum* mosses lack a complex water distribution system, and their water movement takes place mostly via the capillary system, which depends on hydraulic connectivity with the stable water table and storage. Van de Koot *et al.* (2024) showed that shoot density is an important determinant of water storage capacity for *Sphagnum* mosses and that higher densities hold larger quantities of water per unit of biomass, which increases resilience to desiccation. Thus, in drier habitats, colonies that are more dense might have an advantage. Insufficient and irregular rainfall, combined with diminished capillary connection, could be the main reason for insufficient *Sphagnum* capitula moisture content, resulting in lower photosynthesis (Robroek *et al.* 2009, Strack & Price 2009) and shoot growth, as shown also by our results. Even short desiccation periods can stop *Sphagnum* growth for several weeks



(Hájek & Vicheroová 2014, Nijp *et al.* 2014, Radu & Duval 2018), but even small amounts of precipitation can initiate their productivity again (Strack & Price 2009, Adkinson & Humphreys 2011). Therefore, it is not the amount of rainfall during a certain period that is important, but rather the regularity of rainfall and the absence of drought periods. This is especially important in late spring and summer, because more regular rainfall and high humidity are common in autumn.

The smaller density of *Sphagnum* carpet in the donor sites, especially in Punasoo bog which was cut several years later, shows that the mosses have not yet recovered after cutting. Smaller density constrains *Sphagnum* growth and competitive ability by increasing water loss and reducing capillary water transport (Rydin 1995). The weight of *Sphagnum* capitula in all sites studied here was much smaller than measured in other natural bogs and restored extracted peatlands (Karofeld *et al.* 2020). This may be caused by the co-effects of insufficient capillary uprise and insufficiently regular precipitation. The water table measurements, done only at the beginning and at the end of the growing season, do not give a comprehensive overview of the moisture conditions in summer when the growth of plants, especially *Sphagnum* mosses, could be limited by moisture deficit and dryness. This could explain the contradictory effects of spring and autumn water table depths on the growth of different *Sphagnum* species. Still, the proximity of natural and donor sites allows us to assume that the recovery and growth of *Sphagnum* mosses is influenced not only by differences in water table level, but also by a combination of different factors. For example, in the donor sites, the acrotelm is thinner, reducing its ability to stabilise moisture conditions so droughts and floods become more frequent, and this can impede the growth of *Sphagnum* mosses (Kim *et al.* 2021). Schouwenaars & Gosen (2007) also showed that a thin (5–15 cm thick) *Sphagnum* layer is most vulnerable to water stress.

The germination of diaspores in the donor sites could be influenced since favourable moisture conditions are even more essential for bryophyte spore germination than for seeds of vascular plants (Thomas 1995). However, little is known about the effect of dry/wet cycles on the spore germination of *Sphagnum* mosses. Fan *et al.* (2023) showed that an increase in dry/wet cycling frequency restricts the germination of *Sphagnum* spores and it is, therefore, necessary to ensure a high stable water level for *Sphagnum* establishment after disturbance. Chirino *et al.* (2006) also showed that the establishment of moss carpets from *Sphagnum* fragments is strongly

affected by climatic conditions, especially in the first year. Unfortunately, it was impossible to distinguish between patches cut in different years in the Soosaare donor site to study the effect of time on the re-establishment of *Sphagnum* mosses. It was also not possible to extend the study period because of the new drainage ditches dug close to the Soosaare donor site.

In the donor sites, vascular plant species with several dispersal strategies can gain an advantage and may suppress the recovery of *Sphagnum* mosses. One of the most common vascular plants on donor sites, *C. vulgaris*, does not spread vegetatively but may start to grow from uncut patches and from wind-carried seeds. Seeds can remain viable for several years (Huopalainen *et al.* 1998) and sprout under changed growth conditions with minimal competition between species, as occurring in the donor sites. A dense mat of *C. vulgaris* can hamper the sprouting of newly-arrived diaspores, including spores of *Sphagnum* mosses. Wind-pollinated *E. vaginatum* is an early-arriving pioneer species in extracted peatlands and in the donor sites (Lavoie *et al.* 2005, Triisberg *et al.* 2013, Kozlov *et al.* 2016). Once established, tussocks of *E. vaginatum* can increase their cover rapidly by seeding from established plants (Salonen *et al.* 1992) and may cause variable growth conditions for other bog species (Tuittila *et al.* 2000, Groeneveld & Rochefort 2002); although their influence on establishing *Sphagnum* mosses is not completely clear (Lavoie *et al.* 2005).

Rhynchospora alba in the donor sites could start from rhizomes or tillers, and by the germination of seeds accumulated over several years. Seeds of *R. alba* are relatively heavy, and their dispersal distance by wind is small, but they may be carried farther to donor sites downslope from the natural bog area by water (Masing 1955). These seeds can stay viable and sprout even better on bare peat surfaces than when buried in *Sphagnum* carpet (Hirata & Tsuyuzaki 2016). In natural bogs, *R. alba* grows in wet lawns and hollow margins, and a higher water table in the donor sites could favour its sprouting (Shiple & Parent 1991, Nishimura & Tsuyuzaki 2014). Clumps of drought-tolerant *R. alba* (Egawa & Tsuyuzaki 2015) develop persistent seedbanks and increase coverage fast by short-distance spreading, as in the overgrowing of mud-bottom hollows (Karofeld *et al.* 2015). The presence of vascular plants may create a more favourable microclimate and promote *Sphagnum* length increment until vascular plants reach a higher density, when the cover and biomass of *Sphagnum* will start to decrease owing to increased shade and competition (Malmer *et al.* 2003, Pouliot *et al.* 2011).

The weather could have manifold effects on the revegetation of donor sites. Warm, dry summers promote flowering and seed production in plants, whereas seed transport is reduced by lack of rain and inundation. Changed moisture, light and temperature conditions in donor sites can play an important role in breaking the dormancy of seeds, providing a signal for massive emergence. Climate warming and projected increase in summer droughts put northern peatlands under pressure through gradual drying and extreme weather events (Swindles *et al.* 2019, Köster *et al.* 2023). It is likely that such pressure will be even more pronounced in the donor sites, with their thinner acrotelm and interrupted capillary water rise. Vascular plants with roots can derive a constant water supply even from a relatively deep water table, whereas recovery of *Sphagnum* mosses with interrupted capillary rise is more dependent on rainfall. Kim *et al.* (2021) showed that rapid water table fluctuation (which occurs in donor sites) inhibited the growth of *Sphagnum* mosses and even reduced the extent of *Sphagnum*-covered areas, largely because of fungal proliferation.

Slow recovery and growth of *Sphagnum* mosses in the studied donor sites may be caused by the aggravated capillary water uprise amplifying the effect of irregular rain. *S. fuscum* showed the best growth results on restoration sites in our earlier studies (Karofeld *et al.* 2016, 2020), and recovered better in our donor sites. This species has also been found to have a growth advantage in boreal regions from climate warming (Bengtsson *et al.* 2021). Therefore, this species could be recommended for cutting from donor sites for revegetation of abandoned extracted peatlands. To promote vegetation recovery on donor sites, plant fragments should be cut no deeper than 10 cm and from only part of the entire donor area, leaving some uncut patches or stripes to promote faster recolonisation by plants. Still, because of the slow vegetation recovery, cutting of *Sphagnum* fragments from natural bogs should be avoided, and areas bordering active peat extraction should be preferred as donor sites.

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AUTHOR CONTRIBUTIONS

EK designed the study methods and fieldwork, made the field and laboratory measurements, carried out preliminary data analysis and was the lead author of this manuscript. AT performed statistical data analysis and results visualisation and participated in writing. KV participated in fieldwork, interpretation of results and writing, identified bryophyte species, and prepared data for the analyses. All authors participated in revision of the manuscript after peer review.

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