ELSEVIER

Sphagnum re-introduction in degraded peatlands: The effects of aggregation, species identity and water table

Bjorn J.M. Robroek[a,b,*], Jasper van Ruijven[a], Matthijs G.C. Schouten[a,c],
Angela Breeuwer[a], Patrick H. Crushell[d], Frank Berendse[a], Juul Limpens[a]

[a]*Nature Conservation and Plant Ecology, Wageningen University, The Netherlands*
[b]*School of Geography, Faculty of Environment, University of Leeds, UK*
[c]*National Forest Service of the Netherlands, the Netherlands*
[d]*Department of Zoology, Ecology and Plant Science, University College Cork, Ireland*

Abstract

In European peatlands which have been drained and cut-over in the past, re-vegetation often stagnates after the return of a species-poor *Sphagnum* community. Re-introduction of currently absent species may be a useful tool to restore a typical, and more diverse, *Sphagnum* vegetation and may ultimately improve the functioning of peatland ecosystems, regarding atmospheric carbon sequestration. Yet, the factors controlling the success of re-introduction are unclear. In Ireland and Estonia, we transplanted small and large aggregates of three *Sphagnum* species into existing vegetation. We recorded changes in cover over a 3-year period, at two water levels (−5 and −20 cm).

Performance of transplanted aggregates of *Sphagnum* was highly species specific. Hummock species profited at low water tables, whereas hollow species profited at high water tables. But our results indicate that performance and establishment of species was also promoted by increased aggregate size. This mechanism (positive self-association) has earlier been seen in other ecosystems, but our results are the first to show this mechanism in peatlands. Our results do not agree with present management, which is aimed at retaining water on the surface of peat remnants in order to restore a functional and diverse *Sphagnum* community. More than the water table, aggregate size of the reintroduced species is crucial for species performance, and ultimately for successful peatland restoration.

Zusammenfassung

In den europäischen Mooren, die in der Vergangenheit trockengelegt und gemäht wurden, stagniert die Wiederbesiedlung häufig nach der Rückkehr zu einer artenarmen *Sphagnum*-Gesellschaft. Die Wiederansiedlung von bisher abwesenden Arten kann ein sinnvolles Werkzeug sein, um eine typische und diversere *Sphagnum*-Vegetation wiederherzustellen, und könnte letztendlich die Funktionsfähigkeit von Moorökosystemen in Hinsicht auf die Festlegung von atmosphärischem Kohlenstoffdioxid verbessern. Dennoch sind die Faktoren, die den Erfolg einer Wiederansiedlung bestimmen, bisher unklar. In Irland und Estland verpflanzten wir kleine und große Aggregate von drei *Sphagnum*-Arten in existierende Vegetation. Wir nahmen die Veränderungen im Deckungsgrad über eine Zeit von

*Corresponding author. Current address: Utrecht University, Department of Biology, Institute of Environmental Biology, Section of Landscape Ecology, P.O. Box 800.84, 3508 TB Utrecht, The Netherlands. Tel.: +31 302536852; fax: +31 302518366.
E-mail address: b.j.m.robroek@uu.nl (B.J.M. Robroek).

drei Jahren bei zwei verschiedenen Wasserständen (−5 und −20 cm) auf. Die Performanz war bei den verpflanzten Arten in hohem Maße artspezifisch. Hügelarten profitierten von geringen Wasserständen während Arten der Senken von hohen Wasserständen profitierten. Aber unsere Ergebnisse zeigten auch, dass die Performanz und die Etablierung der Arten durch eine zunehmende Größe der Aggregate verbessert wurde. Dieser Mechanismus (positive Selbstassoziation) wurde bereits bei anderen Ökosystemen festgestellt, aber unsere Ergebnisse sind die ersten, die das auch für Moore zeigen. Unsere Ergebnisse stimmen nicht mit dem derzeitigen Management überein, das darauf abzielt, Wasser auf der Oberfläche von Torfüberresten zurückzuhalten, um eine funktionierende und diverse Sphagnum-Gesellschaft wiederherzustellen. Die Größe der Aggregate der wiedereingeführten Arten ist von größerer Bedeutung für die Performanz als der Wasserstand, und damit für eine erfolgreiche Wiederherstellung von Mooren.
© 2009 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

Introduction

About 3% of the Earth's land surface is covered with peatlands. The largest portion of these peatlands is found at high latitudes in the Northern hemisphere. Vast areas of peatlands, however, have been damaged due to peat extraction or drainage (Joosten 1997). This degradation of peatlands has reduced plant diversity (e.g. Laine, Vasander, & Laiho 1995). In addition, many peatland ecosystems have now turned from carbon sinks into sources for atmospheric carbon (e.g. Waddington, Rotenberg, & Warren 2001). Thus, restoring damaged peatlands is a major issue in nature conservation (for a general overview see, Rochefort & Lode 2006). In Western-Europe, several restoration projects involve retaining rain water on the surface of the peatland remnants, in order to re-initiate the growth of *Sphagnum* mosses and other peat producing species (Schouwenaars 1993; Smolders, Tomassen, Van Mullekom, Lamers & Roelofs 2003). Several of these restored peatlands do now have an extensive plant cover, but many *Sphagnum* species characteristic of undamaged peatlands are absent and re-establishment of the *Sphagnum* acrotelm (i.e. the carbon sequestering layer) has stagnated at a pioneer phase (Money 1995) dominated by *Sphagnum* species typical of wet conditions (species such as *Sphagnum cuspidatum* and *S. fallax*). In no case has a complete species community re-established (Joosten 1995; Vasander et al. 2003), partly because of the high nutrient inputs (Limpens, Tomassen, & Berendse 2003), which favour fast growing species.

Experiments with *Sphagnum* mosses and brown mosses have shown that it is possible for transplanted species to persist and even expand in an existing vegetation (Gunnarsson & Söderström 2007; Kooijman & Bakker 1995; Mälson & Rydin 2007; Smolders et al. 2003), thereby ruling out unsuitable environmental conditions as the sole explanation for the absence of a highly diverse *Sphagnum* community. Since competition between *Sphagnum* species can be severe, it may be very hard for individual diaspores to establish in existing vegetation (Rydin 1997; Sundberg & Rydin 2002). Gunnarsson and Söderström (2007) have shown that regionally rare *Sphagnum* species in Sweden were limited by dispersal. Moreover, in countries with only scattered bog remnants, the absence of some species may be due to dispersal limitation. Campbell, Rochefort, and Lavoie (2003), however, exclude dispersal limitations as an explanation but indicate that establishment failure may be much more important. The above suggests that, although dispersal may play a role, the absence of some *Sphagnum* species is probably caused by establishment limitations. Re-introduction of *Sphagnum* target species may be crucial to restore *Sphagnum* diversity and to accelerate the re-establishment of a natural vegetation in damaged, species-poor peatlands. However, it is unclear which factors are important for successful re-introduction of *Sphagnum* species into existing vegetation. The success of transplanting target species may, for example, strongly depend on the distance to the water table, because it may affect the competitive ability of transplanted *Sphagnum* aggregates (Mulligan & Gignac 2002). Earlier, we hypothesised that the aggregate size of the monospecific *Sphagnum* community may be important for species to create their own hydrological defined niche (Robroek, Limpens, Breeuwer, Crushell, & Schouten 2007). Larger volumes of isotropic peat material have been shown to create favourable hydro-logical conditions at the bogs' surface (Kellner & Halldin 2002), probably because capillary water supply in isotropic peat material is not hampered by the structural heterogeneity of the material. The size of the transplanted aggregates may be an important factor for the competitive strength of *Sphagnum* mosses and may determine the success of transplantation as a tool for restoration of a diverse and functional peat moss vegetation. Such benefits of aggregation, sometimes referred to as positive self-associations, have already been observed in primary forest remnants (Frelich, Calcote, Davis, & Pastor 1993), in grassland ecosystems

(Seabloom, Bjørnstad, Bolker, & Reichman 2005; Stoll & Prati 2001) and in bryophyte communities (Pedersen, Hanslin, & Bakken 2001), but evidence from peatlands is absent.

With this experiment we aim to elucidate the importance of aggregate size, species identity and water table on the success of field introduction of *Sphagnum* mosses. We expected larger aggregate size to favour the establishment of the transplanted mosses, irrespective of the water table, because increased aggregate size is assumed to have positive ramifications on the ability to create a hydrologically defined niche. Second, high water table would be especially beneficial for the persistence of hollow species. Low water tables, on the other hand, were expected to be most beneficial for the lawn and hummock species.

Methods

Site description and regional climate

Clara bog (665 ha; 53°19′N, 007°37′W) is an ombrotrophic raised bog located in the Irish midlands. Mean annual temperature is ca. 9 °C and mean annual precipitation is about 804 mm, as measured during the period 1981–1990 at the Birr weather station. Mean May–September precipitation is 324 mm, and rainfall is more or less constant over the months (Met Éireann). Männikjärve bog (320 ha; 58°52′21 N, 26°14′56 E), an ombrotrophic bog belonging to the Endla mire complex, is situated in Central Estonia. Mean annual temperature is ca. 5 °C and mean annual precipitation is 675 mm. Mean May–September precipitation is about 329 mm. Rainfall is heaviest during summer and lightest in spring (Estonian Meteorological and Hydrological Institute).

Plant communities in Estonia and Ireland were similar. *Sphagnum magellanicum* Brid. was the most abundant peat moss species at both sites. *S. cuspidatum*, *S. rubellum* and *S. fuscum* occurred in both sites. Both bogs, thus, may act as reference sites to explore the potential of re-introduction as a restoration tool for peatlands with a degraded *Sphagnum* community. In both sites, *Rhynchospora alba*, *Andromeda polifolia*, *Oxycoccus palustris* and *Menyanthes trifoliata* were the most important vascular plants. In Männikjärve bog, *Scheuzeria palustris* was encountered in the hollows, while in Clara bog *Narthecium ossifragum* was regularly found. Characteristic vascular plant species of the lawns and hummocks were *A. polifolia*, *Eriophorum vaginatum*, *Calluna vulgaris* and *Erica tetralix*. Occasionally, *Pinus sylvestris* seedlings, *Rubus chamaemorus*, *Ledum palustre* and *Chamaedaphne calyculata* were encountered in Estonia.

Experimental design

In June 2003, we transplanted cores of three *Sphagnum* species, i.e., *S. cuspidatum* Ehrh. ex Hoffm., *S. rubellum* Wilson and *S. fuscum* (Schimp.) H. Klinggr., into an existing vegetation of *S. magellanicum* at a high and a low water table (ca. −5 and −20 cm, respectively). The latter species has a wide geographic distribution and a relatively wide range of habitats along the water table, and is often dominating in deteriorated peatlands (pers. obs.). All cores were taken from adjacent monospecific *Sphagnum* stands, and sparse vascular plant cover was clipped flush to the *Sphagnum*. At both water tables, the transplants were randomly assigned to one of the replicated blocks (five in Ireland, and six in Estonia), which were approximately 25 m apart from each other. In every block, we randomly transplanted *Sphagnum* species in two aggregate sizes: one large aggregate (ca. 150 cm^2; diameter 14 cm, depth 20 cm) and four small aggregates (ca. 37.5 cm^2; diameter 7 cm, depth 20 cm).

Earlier research has shown that vascular plants can have a positive effect on *Sphagnum* growth and reduce water loss of the *Sphagnum* layer (Heijmans, Arp, & Berendse 2001). Nevertheless, they may also cause a shading effect. In order to eliminate the effects of vascular plants, and differences therein between plots, all vascular plants over an area of ca. 625 cm^2 were clipped flush to the *Sphagnum* vegetation. Clipping was repeated every May and September. As a control the effects of clipping on the height increment and the wetness quotient (see below) of the *S. magellanicum* matrix were examined in separate plots close to the transplantation experiment in Estonia. To do so, we compared clipped plots with control (non-clipped) plots ($n = 6$). Clipping the vascular plant vegetation did not affect the *Sphagnum* height increment (ANOVA; $P > 0.05$), and did not affect the wetness quotient of the *Sphagnum* vegetation.

Measurements

Sphagnum performance

Height increment of the *S. magellanicum* matrix was measured using a modified cranked wire method (Clymo 1970; Limpens, Berendse, & Klees 2003). Cranked wires were calibrated at the beginning of every growing season (early May) and increment of the *Sphagnum* vegetation was noted at the end of each effective growing season (late September). Since calculating *Sphagnum* growth over the winter period can be problematic, due to compaction or displacement by frost and snow (Sonesson et al. 2002), we only used summer period data.

Expansion of the transplanted species was assessed using cover change throughout the experiment. Every September a digital photograph of the transplanted *Sphagnum* aggregates was taken. A reference frame was included in the photograph. Cover of each species was analysed using an image processing program (ImageJ 1 .33u; National Institutes of Health, USA). Covers of the four small aggregates were averaged before analysis.

At harvest, samples (2 cm deep, including capitula) were taken from the large transplants and the surrounding *S. magellanicum* matrix. Size of the samples varied between 5.6 and 52.0 cm^2, depending on the size of the patch at harvest. Samples were as large as possible to improve the reliability of the water content of these samples. Generally, the small transplants were too small to take a sample from. All samples were put in plastic 'zip-lock' bags after which fresh weight was measured. Thereafter, all samples were put in paper bags and pre-dried at room temperature. Finally, they were transported to the Netherlands, after which they were dried at 70 °C for at least 72 h. We defined water content as the fresh weight dry weight ratio (fw dw^{-1}), and we will further refer to it as the wetness quotient. Although, capitulum wetness quotients (WQ) were only measured once (at the end of the experiment), we suppose that the difference in WQ between the aggregates and the matrix (WQ$_{aggregate}$−WQ$_{matrix}$) gives a good estimate of the ability of the aggregate to create its own optimal micro-hydrological conditions.

Water tables and precipitation

At the experimental plots in Ireland, water tables were measured monthly in 30 dip-wells. It was made sure that these wells covered the experimental site, and were equally divided over the blocks and water tables. At the experimental plots in Estonia, water tables were measured in 26 dip-wells, but only in May and September. Hence, water tables were measured monthly in a permanent well which was in the vicinity (< 50 m) of the experimental site. These data were extrapolated to our measurements. Because Männikjärve bog was frozen during the winter months, we could only calculate mean water tables in the period in which the bog surface was not frozen (May–September). Consequently, water table comparisons between Clara bog and Männikjärve bog cover these months only. Summer water tables differed significantly between the two water-level treatments in both bogs each year ($P \leq 0.05$; Fig. 1A). No differences in water table between the two sites were observed in 2004, but in 2005 both water levels in Männikjärve bog were slightly lower than in Clara bog. In 2006, only the low water table was lower in Männikjärve (Fig. 1A).

Although mean summer precipitation was comparable between the two sites, mean annual precipitation in Estonia was about 200 mm less than in Ireland. Precipitation data for five subsequent days that preceded the sampling for the wetness quotients were estimated from data found at the websites of the Irish (Met Éireann) and Estonian (EMHI) meteorological institutes for Dublin and Tartu, respectively (Fig. 1B).

Statistical analyses

All data were tested for normality and equality of variance prior to analysis. Only the *S. fuscum* cover change, failed to meet the assumptions of homogeneity of variances, even after ln-transformation. Nevertheless,
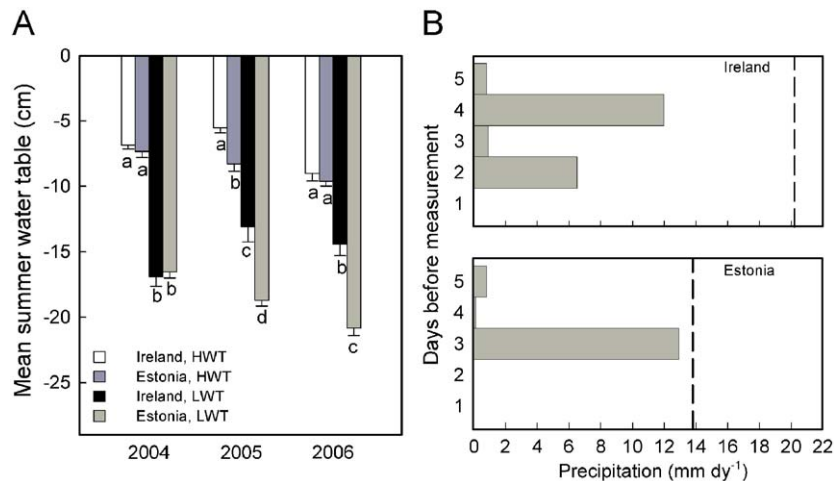
Fig. 1. (A) Mean annual summer water table depths (cm ± SEM) for each year at Clara bog (Ireland; $n = 30$) and Männikjärve bog (Estonia; $n = 26$) at high water table (HWT) and low water table (LWT) regimes. Different letters indicate significant differences (ANOVA; $P \leq 0.05$), within years. (B) Daily precipitation preceding final measurements at Clara bog (Ireland) and Männikjärve bog (Estonia). Dotted lines indicate total precipitation (mm) over the 5-day period preceding wetness quotient measurements.

we continued our analysis because analysis of variance (ANOVA) appears not to be highly influenced if this assumption is violated in balanced ANOVA designs (Cottingham, Lennon, & Brown 2005; Heath 1995). All statistical analyses were performed in the SPSS 14 statistical package for Windows.

Expansion or reduction of the transplanted aggregates, expressed as relative aggregate size (i.e. % of initial aggregate size), was tested with repeated measures (RM-) ANOVA, with site, species, water table and aggregate size as fixed factors. Initially, block, nested within site, was included as a random factor, but it was omitted from the analysis as block effects were not significant. Because of the large amount of significant interactions with species identity (see Appendix A), additional RM-ANOVA's were performed separately for the individual species. In case of violation of the assumption of homosphericity (Maulchy's test of Sphericity), we used the Huyn–Feldt epsilon to adjust the degrees of freedom (Potvin, Lechowicz, & Tardif 1990).

To see if the aggregate size of the transplanted species has an effect on the micro-hydrology of the aggregate at the time of harvest, we calculated the difference between the wetness quotient of the transplants and that of the surrounding matrix ($WQ_{aggregate} - WQ_{matrix}$).

Per site, we used the full ANOVA model with species and water table as fixed factors and aggregate size at harvest as a covariate. As species identity and aggregate size turned out to be correlated (i.e. aggregate size at harvest of one species was generally lower than the aggregate size at harvest of another species), type III sums of squares (SS) could not be used (Van Ruijven, De Deyn, & Berendse 2003). Instead, we used sequential (type I) SS in the ANOVA, in which species identity and water table were included before aggregate size. In this way, potential contributions of a species effect to the relationship between aggregate size and wetness quotient was avoided.

Results

In Männikjärve bog the height increment of the existing *S. magellanicum* vegetation was relatively low
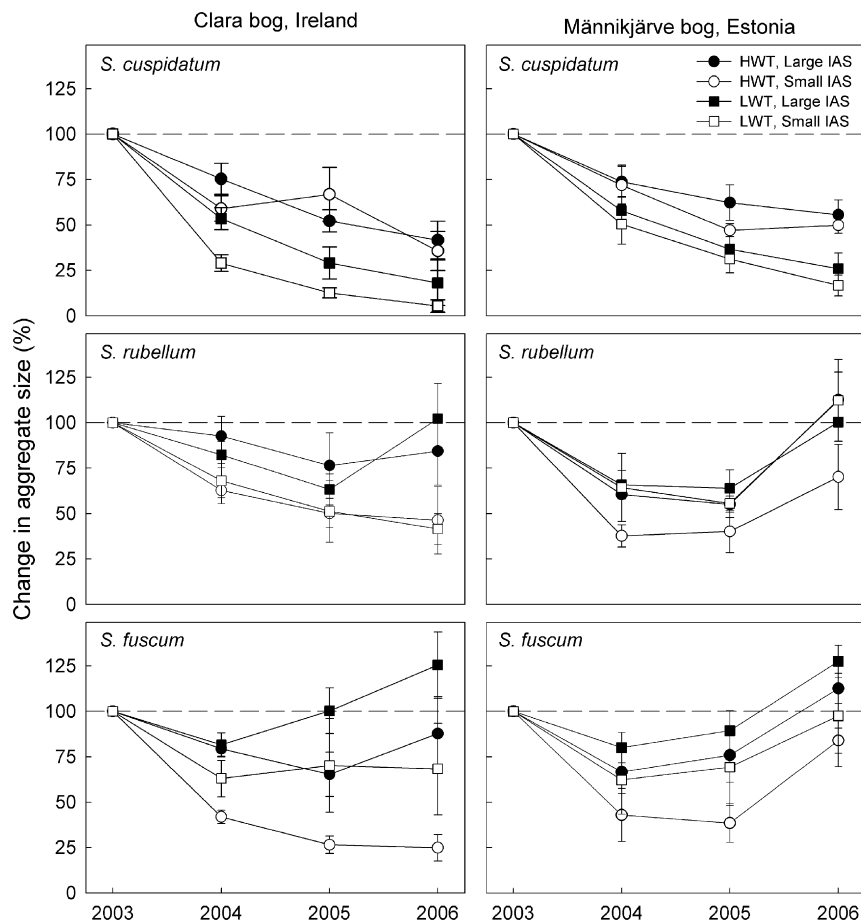
Fig. 2. Relative aggregate size ($\pm$SEM) over three subsequent years of *S. cuspidatum*, *S. rubellum* and *S. fuscum* grown at different water tables and different initial aggregate sizes. HWT = high water table, LWT = low water table, IAS = initial aggregate size. $n = 5$ for Clara bog, $n = 6$ for Männikjärve bog. For statistics (see Tables 1 and 2).

compared to Clara bog ($F_{1, 185} = 15$, $P \leq 0.001$; data not shown). Overall, the change in aggregate size differed between species (see Appendix A) throughout the experimental period, and larger aggregates performed better than smaller aggregates (see Appendix A). Yet, the difference in performance of the different initial aggregate sizes (IAS) varied between years (see Appendix A). Moreover, the difference between large and small aggregates evolved over the experiment (Fig. 2). In addition, we found developing interspecific differences in aggregate size (see Appendix A). These changes in aggregate size were also affected by water table (three-way interaction; see Appendix A). The cover of *S. cuspidatum* continued to decrease at low water table, whereas the decline appeared to level off after 2 years at high water table (Fig. 2). Except for the small aggregates in Clara bog, the cover of *S. rubellum* and *S. fuscum* increased after an initial decrease (year × IAS interactions for *S. rubellum* and *S. fuscum*; Table 1 and Fig. 2). Although no significant interactions were found between site and initial aggregate size, the recovery of *S. rubellum* and *S. fuscum* after the initial decrease appeared to be lower in Clara bog, particularly for the small aggregates (Table 1 and Fig. 2). For *S. cuspidatum*, low water table

resulted in a larger decrease compared to high water table in the first year, after which this difference was maintained, resulting in a lower cover after 3 years (Tables 1, 2 and Fig. 2).

After 3 years (i.e. at harvest), the relative decrease in *S. cuspidatum* aggregate size was similar for both initial aggregate sizes (Table 2 and Fig. 2). In contrast, initial aggregate size significantly affected change in cover (i.e. relative aggregate size) of the other two species (Table 2 and Fig. 2). This may have been caused by the apparent lower initial decrease and the subsequent stronger recovery in larger-sized aggregates (Fig. 2). Expansion of the hummock species *S. fuscum* after 3 years was promoted by low water tables, whereas low water tables hampered *S. cuspidatum* (Table 2 and Fig. 2).

In Clara bog, we did not find any effect of species, water table or aggregate size on the difference in wetness quotient between the transplanted aggregate and the surrounding *S. magellanicum* vegetation (Fig. 3). In Männikjärve bog, however, we found a strong positive effect of increased aggregate size ($F_{1, 26} = 90$, $P \leq 0.001$). *S. cuspidatum* wetness quotient was generally lower than that of the surrounding matrix, whereas that of *S. fuscum* was higher (Fig. 3). *S. rubellum* wetness quotient

Table 1. Between and within subject effects of RM-ANOVA $F_{df, df-error}$ and *P*-values to test the effects of site, water table (WT) and initial aggregate size (IAS) on the cover change over 3 subsequent years of three *Sphagnum* mosses that were transplanted in a *Sphagnum magellanicum* matrix.

Source	*S. cuspidatum*		*S. rubellum*		*S. fuscum*	
	$F_{1, 36}$	*P*	$F_{1, 36}$	*P*	$F_{1, 36}$	*P*
Between subjects						
Site	2.5	0.13	0.0	0.85	1.1	0.31
Water table (WT)	25.6	**≤0.01**	0.9	0.35	7.0	**≤0.05**
Initial aggregate size (IAS)	2.7	0.11	8.9	**≤0.01**	13.6	**≤0.001**
Site × WT	0.4	0.53	1.1	0.31	0.5	0.48
Site × IAS	0.1	0.80	1.4	0.25	0.6	0.43
WT × IAS	0.5	0.49	1.1	0.31	0.3	0.62
Site × WT × IAS	0.5	0.47	0.7	0.39	0.0	0.92
MS$_{error}$	702.5		1290.8		2031.5	
Source	*S. cuspidatum*		*S. rubellum*		*S. fuscum*	
	$F_{1, 108}$	*P*	$F_{1, 93}$	*P*	$F_{1, 108}$	*P*
Within subjects						
Year	267.4	**≤0.001**	30.3	**≤0.001**	24.9	**≤0.001**
Year × site	2.1	0.11	9.4	**≤0.001**	4.4	**≤0.05**
Year × WT	14.3	**≤0.001**	0.5	0.69	4.0	**≤0.01**
Year × IAS	2.0	0.12	3.7	**≤0.05**	7.1	**≤0.001**
Year × site × WT	1.8	0.16	0.4	0.71	1.1	0.36
Year × site × IAS	2.0	0.12	1.1	0.33	0.9	0.43
Year × WT × IAS	0.3	0.79	0.4	0.75	0.2	0.88
Year × site × WT × IAS	1.8	0.16	2.0	0.13	0.1	0.96
MS$_{error}$	148.8		605.5		541.3	

MS$_{error}$ = mean square of the error term. Values in bold indicate significant *P*-values (RM-ANOVA; $P < 0.05$).

Table 2. Mean square values, $F_{\text{df, df-error}}$-values and P-values for the effects of site, water table (WT) and initial aggregate size (IAS) on the aggregate size at harvest for three *Sphagnum* species.

Source	*S. cuspidatum*		*S. rubellum*		*S. fuscum*	
	$F_{1, 36}$	P	$F_{1, 36}$	P	$F_{1, 36}$	P
Intercept	546.4	**≤0.001**	7.2	**≤0.01**	2.2	0.15
Site	4.0	**≤0.05**	6.2	**≤0.05**	5.6	**≤0.05**
Water table (WT)	24.5	**≤0.001**	0.8	0.39	5.1	**≤0.05**
Initial aggregate size (IAS)	2.0	0.16	7.1	**≤0.05**	13.6	**≤0.001**
Site × WT	0.2	0.70	0.1	0.73	1.2	0.28
Site × IAS	0.0	0.88	1.9	0.17	1.6	0.22
WT × IAS	0.2	0.66	0.4	0.52	0.0	0.93
Site × WT × IAS	0.0	0.89	2.5	0.12	0.0	0.89
MS$_{\text{error}}$	379.1		1609.3		2031.5	

MS$_{\text{error}}$ = mean square of the error term. Values in bold indicate significant P-values (ANOVA; $P < 0.05$).
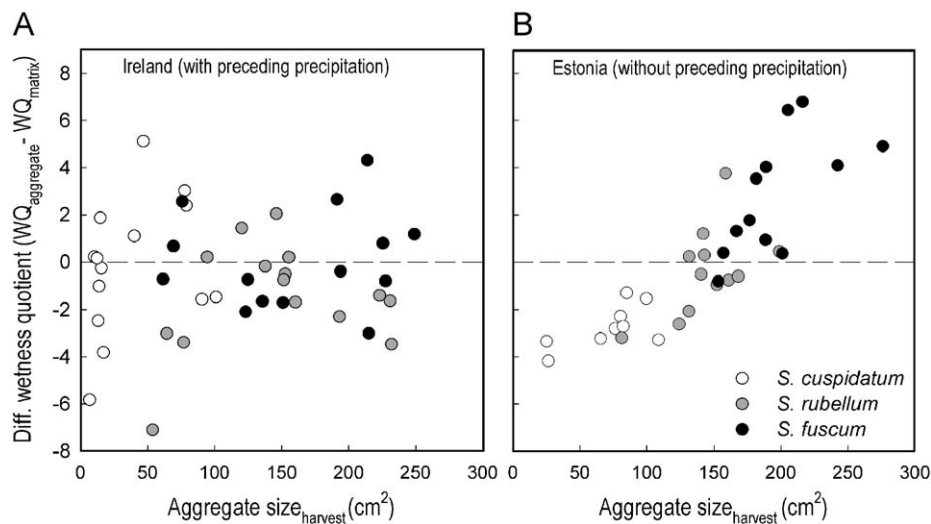
Fig. 3. The relationship between aggregate size of the large patches and the difference in wetness quotient (WQ) between the transplanted aggregate and its surrounding matrix at harvest in (A) Ireland, and (B) Estonia. Data are shown for *S. cuspidatum*, *S. rubellum* and *S. fuscum*. For precipitation data, see Fig. 1B.

was lower in some cases and higher in others. The difference in wetness quotient between the transplants and their surrounding matrix was positively related to aggregate size, but only in the case of a preceding period of low precipitation (Figs. 1B and 3).

Discussion

Interspecific differences in persistence: the role of aggregation, species and water table

Aggregate size of the transplanted species plays an important role in the survival of the hummock species *S. fuscum* and *S. rubellum*, but not in the survival of the hollow species *S. cuspidatum*. The competitive strength of the latter species seems to be relatively poor,

presumably due to its inferior water-holding capacity and inferior ability to transport water from the phreatic water table to its capitula (Clymo & Hayward 1982), and as such aggregate size, at the values we used, had no effect. For the other two species aggregate size did matter. One explanation could be that small aggregates decrease faster in cover, because their area: perimeter ratio is small compared to that of large aggregates. This means that the decline of smaller aggregates is relatively larger than that of larger aggregates, at similar absolute decline. A better explanation may be that large aggregates are superior in creating their own micro-hydrology. Consequently, the persistence of large aggregates of *Sphagnum* mosses may be greater because of better hydrological circumstances. The wetness quotient of *Sphagnum* mosses can be influenced by factors such as the water-holding capacity, and the ability to transport water from the water table to their

capitula by capillary rise (Clymo 1973; Hayward & Clymo 1983). Earlier we suggested that increased size may increase the ability of *Sphagnum* mosses to maintain a wetness quotient which is optimal for its performance (Robroek et al. 2007). That may also explain why Smolders et al. (2003) did not find an initial decrease after transplantation of *S. magellanicum* and *S. rubellum* into a matrix of *S. cuspidatum*. The aggregates they used were relatively large ($\approx 500 \, cm^2$) compared to the transplants used by Rydin (1993) ($\approx 30 \, cm^2$) and in our experiment (≈ 37.5 and $150 \, cm^2$), and as a result may have been able to create their own micro-environment. Our data from Estonia confirm the hypothesis that increased aggregate size enables species to control their own hydrology to a larger extent, since the difference in wetness quotient between the transplants and the surrounding vegetation was positively correlated to aggregate size (Fig. 3), irrespective of the water table. In Ireland, however, we did not find such a correlation. This can be explained because apart from water-holding capacity, and the ability to transport water from the water table to the capitula, precipitation also plays a role in the water supply of the *Sphagnum* vegetation. Precipitation patterns in the 5 days preceding our measurements did differ between the two sites. In Clara bog, precipitation over the 5 days preceding the measurements was more continuous and cumulative precipitation was slightly higher. The higher precipitation frequency in Clara bog may have diminished differences in wetness quotient between the transplants and the matrix. Although we only have wetness quotient measurements from one specific day, we believe our results provide evidence that in periods of drought, aggregate size becomes an important factor for species to maintain hydrological conditions which are advantageous for their performance. Yet, more elaborate measurements on the effects of aggregate size on the micro-hydrology (including evaporation) of transplants throughout the year would be needed to support this conclusion.

At harvest, we found interspecific differences in the response to water table depth; it did not affect the cover change of *S. rubellum*, but it affected *S. cuspidatum* and *S. fuscum*. This contradicts the results presented by Rydin (1993), who did not find a correlation between mean water table and the change in area of the species he transplanted. This difference, however, may have been caused by the different species identities in these experiments. In our experiment, *S. cuspidatum* cover declined most at low water tables, whereas low water table was advantageous for *S. fuscum* (Fig. 2). Regarding the natural position of these species along the water table gradient in raised bogs, these effects of water table seem obvious. Especially for species which occur far from the water table, competitive strength increases with increasing water table depth.

The initial decline in cover of all transplanted *Sphagnum* species, as seen in our experiment (Fig. 2), was also observed by Rydin (1993), who transplanted *S. fuscum* into hollow vegetation. Experimental handling and variation in weather conditions between years were ruled out to be causing this decline (Rydin 1993). Our results, however, indicate that different annual water tables are also unlikely since they did not differ much between years (Fig. 1). An alternative explanation is that transplanted aggregates always decrease initially since the existing vegetation has a strong initial competitive advantage, compared to the transplanted species, which may have been collected from a habitat with a different micro-environment. After the initial decrease, all aggregates of *S. rubellum* and *S. fuscum*, except for the small ones in Clara bog, recovered after 1–2 years, resulting in interspecific differences in cover after 3 years. The difference in growth of the matrix vegetation at the two sites may be explained by differences in the annual amounts of precipitation and in the temporal distribution of this precipitation. As a result of reduced competition from the surrounding vegetation, the transplanted species in Männikjärve bog may have declined less. This could explain the differences in persistence of the transplants between Männikjärve bog and Clara bog. A large library exists on the importance of spatial contexts as a factor which determines plant community interactions (e.g. Rees, Grubb, & Kelly 1996; Thórhallsdóttir 1990). If a species is able to adapt to, and to persist in the new environment, it gains in competitive ability and may eventually increase in cover.

Our experiment focused only on the first 3 years after transplantation and as such the data have to be treated with some caution, regarding the success of transplantation on a longer term. Nevertheless, our study reveals increased aggregate size is important for *Sphagnum* species to create hydrological defined niches which may lead to a greater competitive ability, especially during drought. These results are parallel to studies in primary forest and grassland ecosystems, where aggregation was shown to positively affect self-associations of species (Frelich et al. 1993; Seabloom et al. 2005). Our study indicates that these positive self-associations also control *Sphagnum* autecology and, in periods of drought, may even be more important than water table and the ability of mosses to transport water from the phreatic water table to their capitula (i.e. capillary transport) for the moss species' hydrology.

Sphagnum re-introduction: implications for the peatland vegetation

Present management of peatlands is aimed at retaining water on the surface of peat remnants in order to

restore a diverse and functional *Sphagnum* vegetation. Practice, however, shows that these restoration measures do not always result in a typical bog community. The development of the *Sphagnum* vegetation often stagnates at a species-poor *Sphagnum* community (often dominated by species like *S. cuspidatum* and *S. fallax*). These communities are generally less effective in sequestering carbon (Gunnarsson 2005; Laine, Byrne, Kiely, & Tuittila 2007) and are shown to be more sensitive to environmental changes (Breeuwer et al. in press). Using transplantations may speed up the development of a diverse vegetation, which ultimately increases the potential of the peatland to act as a sink for carbon (Kivimäki, Yli-petäys, & Tuittila 2008).

Acknowledgements

Appendix A. Supporting material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.baae.2009.04.005.

References

Breeuwer, A., Robroek, B. J. M., Limpens, J., Heijmans, M. M. P. D., Schouten, M. G. C., & Berendse, F. (2008). Decreased summer water table depth affects peatland vegetation. *Basic and Applied Ecology*, doi:10.1016/j.baae.2008.05.005.

Campbell, D. R., Rochefort, L., & Lavoie, C. (2003). Determining the immigration potential of plants colonizing disturbed environments: The case of milled peatlands in Quebec. *Journal of Applied Ecology*, *40*, 78–91.

Clymo, R. S. (1970). The growth of *Sphagnum*: Methods of measurement. *Journal of Ecology*, *58*, 13–49.

Clymo, R. S. (1973). Growth of *Sphagnum*—Some effects of environment. *Journal of Ecology*, *61*, 849–869.

Clymo, R. S., & Hayward, P. M. (1982). The ecology of *Sphagnum*. In A. J. E. Smith (Ed.), *Bryophyte ecology* (pp. 229–289). London, UK: Chapman & Hall.

Cottingham, K. L., Lennon, J. T., & Brown, B. L. (2005). Knowing when to draw the line: Designing more informative ecological experiments. *Frontiers in Ecology and Environment*, *3*, 145–152.

Frelich, L. E., Calcote, R. R., Davis, M. B., & Pastor, J. (1993). Patch formation and maintenance in an old-growth Hemlock-hardwood forest. *Ecology*, *74*, 513–527.

Gunnarsson, U. (2005). Global patterns of *Sphagnum* productivity. *Journal of Bryology*, *27*, 269–279.

Gunnarsson, U., & Söderström, L. (2007). Can artificial introductions of diaspore fragments work as a conservation tool for maintaining populations of the rare peatmoss *Sphagnum angermanicum*? *Biological Conservation*, *135*, 450–458.

Hayward, P. M., & Clymo, R. S. (1983). The growth of *Sphagnum*: Experiments on, and simulation of, some effects of light flux and water-table depth. *Journal of Ecology*, *71*, 845–863.

Heath, D. (1995). *An introduction to experimental design and statistics for biology*. London: UCL Press Limited.

Heijmans, M. M. P. D., Arp, W. J., & Berendse, F. (2001). Effects of elevated CO_2 and vascular plants on evapotranspiration in bog vegetation. *Global Change Biology*, *7*, 817–827.

Joosten, H. (1997). European mires: A preliminary status report. *International Mire Conservation Group Members Newsletter*, *3*, 10–13.

Joosten, J. H. J. (1995). Time to regenerate: Long term perspectives of raised bog regeneration with special emphasis on palaeoecological studies. In B. D. Wheeler, S. C. Shaw, W. J. Fojt, & R. A. Robertson (Eds.), *Restoration of temperate wetlands* (pp. 379–404). Chichester, UK: Wiley.

Kellner, E., & Halldin, S. (2002). Water budget and surface-layer water storage in a *Sphagnum* bog in central Sweden. *Hydrological Processes*, *16*, 87–103.

Kivimäki, S. K., Yli-petäys, M., & Tuittila, E.-S. (2008). Carbon sink function of sedge and *Sphagnum* patches in a restored cut-away peatland: Increased functional diversity leads to higher production. *Journal of Applied Ecology*, *45*, 921–929.

Kooijman, A. M., & Bakker, C. (1995). Species replacement in the bryophyte layer in mires: The role of water type, nutrient supply and interspecific interactions. *Journal of Ecology*, *83*, 1–8.

Laine, A., Byrne, K. A., Kiely, G., & Tuittila, E.-S. (2007). Patterns in vegetation and CO_2 dynamics along a water level gradient in a lowland blanket bog. *Ecosystems*, *10*, 890–905.

Laine, J., Vasander, H., & Laiho, R. (1995). Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland. *Journal of Applied Ecology*, *32*, 785–802.

Limpens, J., Berendse, F., & Klees, H. (2003). N deposition affects N availability in interstitial water, growth of *Sphagnum* and invasion of vascular plants in bog vegetation. *New Phytologist*, *157*, 339–347.

Limpens, J., Tomassen, H. B. M., & Berendse, F. (2003). Expansion of *Sphagnum fallax* in bogs: Striking the balance

between N and P availability. *Journal of Bryology*, 25, 83–90.

Mälson, K., & Rydin, H. (2007). The regeneration capabilities of bryophytes for rich fen restoration. *Biological Conservation*, 135, 435–442.

Money, R. P. (1995). Re-establishment of a *Sphagnum* dominated flora on cut-over lowland raised bogs. In B. D. Wheeler, S. C. Shaw, W. J. Fojt, & R. A. Robertson (Eds.), *Restoration of temperate wetlands* (pp. 405–422). Chichester, UK: Wiley.

Mulligan, R. C., & Gignac, L. D. (2002). Bryophyte community structure in a boreal poor fen II: Interspecific competition among five mosses. *Canadian Journal of Botany*, 80, 330–339.

Pedersen, B., Hanslin, H. M., & Bakken, S. (2001). Testing for positive density-dependent performance in four bryophyte species. *Ecology*, 82, 70–88.

Potvin, C., Lechowicz, M. J., & Tardif, S. (1990). The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. *Ecology*, 71, 1389–1400.

Rees, M., Grubb, P. J., & Kelly, D. (1996). Quantifying the impact of competition and spatial heterogeneity on the structure and dynamics of a four-species guild of winter annuals. *American Naturalist*, 147, 1–32.

Robroek, B. J. M., Limpens, J., Breeuwer, A., Crushell, P. H., & Schouten, M. G. C. (2007). Interspecific competition between *Sphagnum* mosses at different water tables. *Functional Ecology*, 21, 805–812.

Rochefort, L., & Lode, E. (2006). Restoration of degraded Boreal peatlands. In R. K. Wieder, & D. H. Vitt (Eds.), *Boreal peatland ecosystems* (pp. 381–421). Berlin, Heidelberg: Springer.

Rydin, H. (1993). Interspecific competition between *Sphagnum* mosses on a raised bog. *Oikos*, 66, 413–423.

Rydin, H. (1997). Competition between *Sphagnum* species under controlled conditions. *Bryologist*, 100, 302–307.

Schouwenaars, J. M. (1993). Hydrological differences between bogs and bog-relicts and consequences for bog restoration. *Hydrobiologia*, 265, 217–224.

Seabloom, E. W., Bjørnstad, O. N., Bolker, B. M., & Reichman, O. J. (2005). Spatial signature of environmental heterogeneity, dispersal, and competition in successional grasslands. *Ecological Monographs*, 75, 199–214.

Smolders, A. J. P., Tomassen, H. B. M., Van Mullekom, M., Lamers, L. P. M., & Roelofs, J. G. M. (2003). Mechanisms involved in the re-establishment of *Sphagnum*-dominated vegetation in rewetted bog remnants. *Wetlands Ecology and Management*, 11, 403–415.

Sonesson, M., Carlsson, B. A., Callaghan, T. V., Halling, S., Björn, L. O., Bertgren, M., et al. (2002). Growth of two peat-forming mosses in subarctic mires: Species interactions and effects of simulated climate change. *Oikos*, 99, 151–160.

Stoll, P., & Prati, D. (2001). Intraspecific aggregation alters competitive interactions in experimental plant communities. *Ecology*, 82, 319–327.

Sundberg, S., & Rydin, H. (2002). Habitat requirements for establishment of *Sphagnum* from spores. *Journal of Ecology*, 90, 268–278.

Thórhallsdóttir, T. E. (1990). The dynamics of a grassland community: A simultaneous investigation of spatial and temporal heterogeneity. *Journal of Ecology*, 78, 884–908.

Van Ruijven, J., De Deyn, G. B., & Berendse, F. (2003). Diversity reduces invasibility in experimental plant communities: The role of plant species. *Ecology Letters*, 6, 910–918.

Vasander, H., Tuittila, E.-S., Lode, E., Lundin, L., Ilomets, M., Sallantaus, T., et al. (2003). Status and restoration of peatlands in northern Europe. *Wetlands Ecology and Management*, 11, 51–63.

Waddington, J. M., Rotenberg, P. A., & Warren, F. J. (2001). Peat CO_2 production in a natural and cutover peatland: Implications for restoration. *Biogeochemistry*, 54, 115–130.