



Ericaceae stabilize peat and foster *Sphagnum majus* establishment at pool margins in restored peatlands

Virginie Laberge, Line Rochefort, Monique Poulin *

Peatland Ecology Research Group & Centre d'études nordiques, Pavillon Paul-Comtois, Université Laval, 2425 rue de l'Agriculture, Québec G1V 0A6, Canada



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ABSTRACT

Pools are recognized as biodiversity hotspots in natural peatlands, thus creating pools would increase the ecological value of restored peatlands. However, the peaty margins of artificial pools are unstable, as frost heave creates much surface erosion restricting establishment of vascular plant seedlings. This study evaluates the ability of heather shrubs (*Ericaceae*) to stabilize created pool margins in restored peatlands. *Andromeda polifolia* var. *latifolia* and *Vaccinium macrocarpon* plants were introduced to form a sparse cover (<25%) at pool margins. *Sphagnum majus* fragments were spread simultaneously between the shrubs over half the surface at a density of 50% in ground cover, and seeds of herbaceous plants typical of pool margins were sown at two distances from the low-water mark (0.5 and 3.5 m). We examined the impact of *Ericaceae* on (1) frost heave intensity, (2) *S. majus* establishment and (3) herbaceous species establishment. Treatments using ericaceous shrubs or *Sphagnum*, both alone or in combination, all reduced frost heave by about 50%. After one year, it also increased survival of *S. majus* (four-fold) on the wettest soil along the banks. However, at a greater distance from the water (2 and 3.5 m), the *Sphagnum* cover was not influenced by the presence of *Ericaceae*. Establishment and growth of herbaceous plants grown from seeds were not influenced by the presence of *Ericaceae*. This study demonstrates the potential of *Ericaceae* for stabilizing the peat substrate close to the water line and improving survival of *S. majus* introduced at the immediate edge of created pools.

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1. Introduction

The creation of artificial pools is an emerging technique for restoring peatland after peat extraction, particularly because it increases their ecological value (Fontaine et al., 2007). However, the peat substrate at the margins of created pools is wetter than elsewhere in the peatland rendering the substrate more unstable and complicates restoration. Frost heave is one mechanism contributing to peat instability particularly in early spring and late fall, and it compromises the survival of newly-introduced vegetation by uprooting the young seedlings (Luoto and Seppälä, 2000). Amplified in proximity to pools, this phenomenon represents a critical factor impeding the restoration success of these ecotones. In cutover peatlands, reintroducing a vegetation cover, such as one dominated by *Polytrichum* mosses (Groeneveld et al., 2007) or *Eriophorum* sedges (Marcoux, 2000), makes it possible to control frost heaving of the peat. We think that peatland shrubs could also be used for stabilization, with the further advantage of providing an anchor structure

for *Sphagnum* and favoring their establishment. Previous studies on ericaceous shrubs in peatlands had focused on their capacity to improve microclimate and its positive effect on *Sphagnum* establishment (Farrick and Price, 2009; McNeil & Waddington, 2003; Crum, 1992) as well as on their structural role for favoring *Sphagnum* growth (Malmer et al., 1994; Pouliot et al., 2011). However, to our knowledge, no study has documented the role of ericaceous shrubs for controlling frost heave in peatlands.

This study assesses the impact of an ericaceous cover composed of glaucous-leaved bog rosemary (*Andromeda polifolia* var. *latifolia* Aiton) and large cranberry (*Vaccinium macrocarpon* Aiton) on the stability of peat surrounding created pools in restored peatlands. These two species of the *Ericaceae* family are associated with wet depressions, and have morphological characteristics (aerial architecture and root biomass) that are likely to foster aggregation of peat at pool margins, as it does in other environments (Reubens et al., 2007), although this hypothesis needs to be explored. More specifically, we tested whether ericaceous shrubs could reduce the formation of ice needles and consequently favor establishment of six species of semi-aquatic plants associated with peatland pools. We hypothesized that an ericaceous cover would reduce frost-induced heaving of peat, much like other types of vegetation cover. We also expected that *Sphagnum majus* introduced as fragments would form a denser cover beneath the *Ericaceae*, due to the

* Corresponding author. Tel.: +1 418 656 2131x13035; fax: +1 418 656 7856.

E-mail addresses: virginie.laberge@gmail.com (V. Laberge), line.rochefort@fsaa.ulaval.ca (L. Rochefort), monique.poulin@fsaa.ulaval.ca (M. Poulin).

structural support provided by these shrubs. *S. majus*, a moss species associated with wet depressions and commonly found at pool margins in natural peatlands, is growing in trenches of an abandoned block-cut extracted peatland nearby the study site and therefore presents a good establishment potential when introduced at early stages of restoration. Finally, we hypothesized that the presence of an ericaceous cover would improve establishment of vascular plants reintroduced as seeds, a technique recommended for increasing plant diversity at pool margins (Landry et al., 2012). The presence of a plant cover is in fact likely to modify the microclimate at the soil surface (Breshears et al., 1998; Farrick and Price, 2009; Pouliot et al., 2011) and provide young herbaceous seedlings with the specific light and humidity conditions they require to germinate and grow. The targeted herbaceous species are associated with natural bog pools of eastern Canada but do not establish easily in restored peatlands when introduced as plant fragments (Poulin et al., 2011). For some of them, seed germination and early growth behavior on seedbeds of different species composition and humidity conditions have been tested in a greenhouse experiment (Landry et al., 2012) and in a field experiment on wet trenches used as a proxy for pool edges (Laberge et al., unpublished results). The current study investigates their establishment potential at early stages of restoration when seeds are actively introduced at pool margins in a real restoration context.

2. Materials and methods

2.1. Description of the study site

The experiment was carried out in an ombrotrophic peatland located near Inkerman Ferry, in the north-eastern part of the Acadian Peninsula in New Brunswick, Eastern Canada ($47^{\circ}42'N$, $64^{\circ}49'W$). The climate is typical of the Atlantic Northeast region, characterized by relatively cool temperatures (average temperature $4.5^{\circ}C$) as well as humidity (1058.6 mm average annual precipitation) (Environment Canada, 2011). The number of days with maximal temperature $<0^{\circ}C$ is around 90 while the number of growing degree days is 1678 (Environment Canada, 2011). A small 8 ha section of the peatland had been vacuum-harvested for horticultural purposes during decades and then closed to production in early 90s, leaving behind a layer of peat up to 4 m thick. Vacuum harvesting implies intense drainage for drying peat and leaves extensive surfaces of residual peat deposit, devoid of any vegetation and seed bank (Salonen, 1987). Almost 20 years after the abandonment of peat extraction activities at the study site, vegetation was still scarce. The residual surfaces mainly remained as bare peat, beside few tussocks of *Eriophorum vaginatum* and sparse and young *Betula papyrifera* (both considered as invasive species in peatlands). In 2008, the 8 ha surface was restored by the moss layer transfer technique (Quinty and Rochefort, 2003). This approach developed in North America consists in transferring the upper vegetation layer from a natural donor site (i.e. the first 5–10 cm) over a 10–15 times larger area in a residual peatland (Rochefort & Lode, 2006). This layer contains *Sphagnum* fragments and plant propagules such as fruits, seeds, rhizomes, and roots, and usually leads to the recovery of typical plant communities found in natural bogs (Rochefort et al., 2013). Along the traditional restoration of these large surfaces, six artificial pools were created, and a 5 m zone around them was left bare for setting up this experiment, which took place two years later.

2.2. Description of the pools

The created pools are rectangular in shape, with a depth of 1.5 m and an area of 130 m². Each has one gently sloping side that forms

an angle of less than 10° and covers an area of approximately 40 m² (8 m by 5 m). The combination of both steep and gentle sloping sides ease mechanized operations and should optimize biodiversity (Quinty & Rochefort, 2003). The gentle slope was composed of peat only and no vegetation was present on surfaces used for the current experiments, especially after peat reprofiling. Water content and apparent density of the peat were measured in the summer of 2010 along the slope gradient at two distances from the low-water mark of the pools. Peat water content was higher at 0.5 m from the low-water mark ($70 \pm 1\%$) than at a distance of 3.5 m ($50 \pm 1\%$). Apparent peat density was significantly lower near the low-water mark ($0.092 \pm 0.01 \text{ g/cm}^3$) than at a distance of 3.5 m ($0.114 \pm 0.01 \text{ g/cm}^3$).

2.3. Experimental design and treatments

A split-split block experiment was set up on the gently sloping bank of each of the six pools to test the effect of an ericaceous cover on the stability of the substrate as well as on the growth of *Sphagnum* and the vascular plants introduced as seeds. The ericaceous cover was established in main plots of 20 m² and the *Sphagnum* cover in subplots of 10 m² under the *Ericaceae*. Sub-subplots of 1 m² were marked out at three distances from the low-water mark (0.5 m, 2 m and 3.5 m). All sub-subplots were used to study peat frost heave, and those closest and farthest from the low-water mark were used to study vascular plant establishment. In August 2009, *Andromeda polifolia* var. *latifolia* (25–35 cm) and *Vaccinium macrocarpon* (15–35 cm) plants were collected in the natural, portion of an adjacent peatland and transplanted uniformly on one-half of the gently sloping bank of each pool (20 m²), so as to form a cover of about 25%, a shrub density commonly found around natural peatland pools (Mazerolle et al., 2006) (main plots determined randomly). Several weeks after planting the *Ericaceae*, *S. majus* collected from former drainage ditch of an adjacent abandoned peatland (upper 10 cm) was spread over the surface of half the main plots to cover 50% of the ground (subplots with and without *Sphagnum* determined randomly). A protective layer of straw (3000 kg/ha or 300 g/m²; covering about 90% of experimental units) was spread over the *Sphagnum*, both on the subplots with *Sphagnum* alone and those also planted with *Ericaceae*. A net was then spread over the entire area of the gently sloping pool banks, to prevent plant or straw displacement when water level fluctuated. Finally, metal rods (diameter = 1 cm, length = 2.5 m) were inserted 2 m deep into the peat, to serve as stable points of reference for measuring frost heave. One pair of rods was inserted per subplot, and a nylon line was firmly tied between each pair, at about 20 cm above the experimental units (EU) surface. This design was repeated for each pool (Fig. 1).

In the spring of the following year (2010), the sub-subplots of 1 m² that were at 0.5 and 3.5 m from the low-water mark were stocked with seeds of the six following vascular plants: *Carex oligosperma* Michaux, *C. pauciflora* Lightfoot, *C. magellanica* subsp. *irrigua* (Wahlenberg) Hiitonen, *Eriophorum virginicum* L., *Rhynchospora alba* (L.) Vahl, and *Scheuchzeria palustris* L. The term seed is being used for seed-like fruits such as achene as well as for real seeds (in follicles of *Scheuchzeria*). Six cylinders were installed in each sub-subplot to serve as retaining structures for seeds. The cylinders, 18 cm in diameter, constructed from a strip of perforated plastic (20 cm high) and covered with a fine mesh screen (mesh <1 mm), were inserted 10 cm deep in the peat of each seedbed. Their purpose was to prevent seed dispersal while allowing light, water and wind to freely pass through, thus having a minimal impact on microclimate inside of them. In early June, seeds of each vascular plant species were sown in the cylinders, 100 seeds of the same species per cylinder, in the EU situated at 3.5 m from the low-water

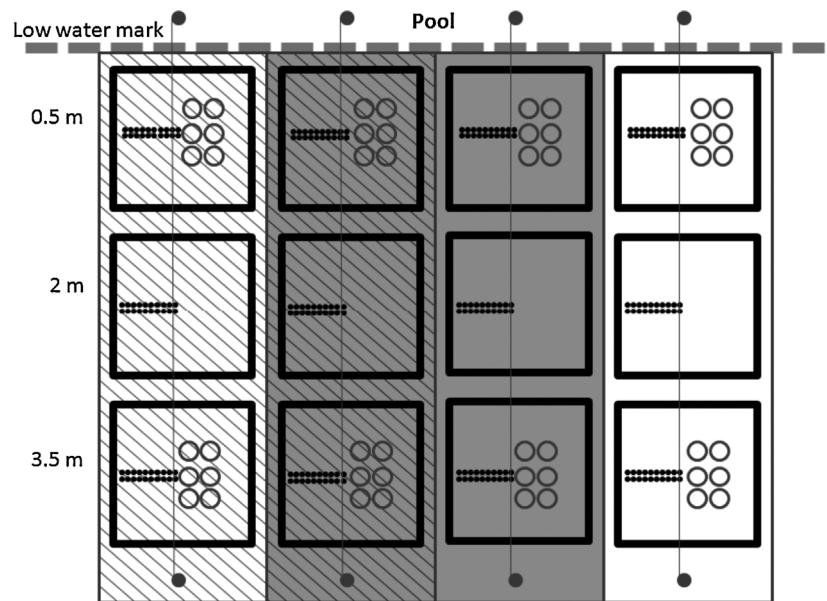


Fig. 1. Illustration of treatments set up near created pools, in which cross-hatched areas represent ericaceous cover (in main random plots of 20 m²) and shaded areas represent *Sphagnum* cover (in random subplots of 10 m²). Black squares represent experimental unit (EU), each measuring 1 m², situated at three distances from the pool (fixed factor in sub-subplots), within which six cylinders were placed as stocking structures for seeds and equipment to measure frost heave (20 wooden dowel rods per EU). The transversal lines along each type of cover represent the reference line used to measure frost heave. No seeds were introduced at a distance of 2 m from the low-water mark.

mark. Another series of seeds was sown three weeks later in the EU closest to that mark, at 0.5 m, at the time when the water level has lowered enough to allow sowing (Fig. 1). To obtain the seeds, mature infructescences of each species had been collected near natural pools in several eastern Canadian peatlands. These seeds were stratified on moist sand at 4 °C for three months, then tested for viability with 1% tetrazolium solution (Grabe, 1970). Seeds were first soaked in deionized water at room temperature for 12 h and then in the tetrazolium solution at 30 °C for an additional 12 h. For *Cyperaceae* species, the perigyne and/or pericarp of the fruit was cut in half to ensure embryo coloration whereas for *Scheuchzeria palustris*, only the seed tegument was cut off.

The water table level for each pool was measured at regular intervals throughout the 2010 growing season in three wells inserted at different distances from the low-water mark, along the sloped gradient (0.5 m, 2 m and 3.5 m). On average, the water table levels were at respectively 2 ± 10, 22 ± 11 and 40 ± 10 cm below the surface.

2.4. Data collection

Frost heave data was collected in the fall of 2010, one year after the *Ericaceae* and *Sphagnum* mosses were introduced. Wooden dowel rods (diameter 3 mm, length: 15 cm) were used to estimate vertical displacement of peat following episodes of frost heave. For each treatment, 20 of these dowels had been previously inserted (August 2010) under the nylon line extended between the fixed pairs of metal rods, 10 cm into the peat in two rows 5 cm apart, with 5 cm between each dowel (Fig. 1). At the time of insertion, the distance between the nylon line and the tip of each dowel was measured. This distance was remeasured in early November of the same year, at the onset of fall frost for that region. The method described here is similar to that used by Groeneveld and Rochefort (2005), and based on that used by Decker and Ronningen (1957).

For each EU where *Sphagnum majus* had been introduced, *Sphagnum* cover was evaluated after one year (August 13, 2010), based on two quadrats 25 cm by 25 cm per EU of 1 m². Only living *capitula* were considered and dry ones were omitted from cover estimates.

Finally, the number of seedlings was counted at the end of the growing season (August 13, 2010, i.e. 10 weeks after sowing) to determine the germination rate of the six herbaceous species. The elongation of 15 randomly selected plants per cylinder was then measured, to estimate annual elongation.

2.5. Statistical analyses

Vertical displacement of the wooden dowel rods was the sole variable analyzed to measure frost heave. Data were summarized as means for each of the 12 experimental conditions (three distances from the low-water mark, the presence/absence of *Ericaceae* and the presence/absence of *Sphagnum*; 1440 samples in total). A three-way ANOVA split-split-block design was used, in which the main factor "Ericaceae" was randomly distributed, like the sub-factor "Sphagnum", whereas the "distance from the low-water mark", considered as a sub-sub-factor, was fixed.

To evaluate *Sphagnum* establishment in each of the plant communities, the percent cover variable was analyzed. Data were summarized as means for each of the six experimental conditions (three distances from the low-water mark, the presence/absence of *Ericaceae*; 72 samples in total). A two-way ANOVA split-split-block design was used, with the main factor "Ericaceae" randomly distributed, whereas the "distance from the low-water mark" was considered as a fixed sub-factor.

In order to track the effect of *Ericaceae* on establishment of vascular plants, each species planted was treated individually in statistical analyses, and two variables were considered: germination and elongation. Data were summarized as means for each variable and each of the eight experimental conditions (two distances from the low-water mark, the presence/absence of *Ericaceae* and the presence/absence of *Sphagnum*; 720 samples in total). Variables were analyzed using three-way ANOVA split-split-block design, but for which the fixed sub-sub-factor "distance from the low-water mark" had only two levels (0.5 m and 3.5 m).

All statistical analyses were performed using the MIXED procedure of SAS software (version 9.2, SAS, Cary, NC, USA, ©2010), given the variability of data and limited number of samples per

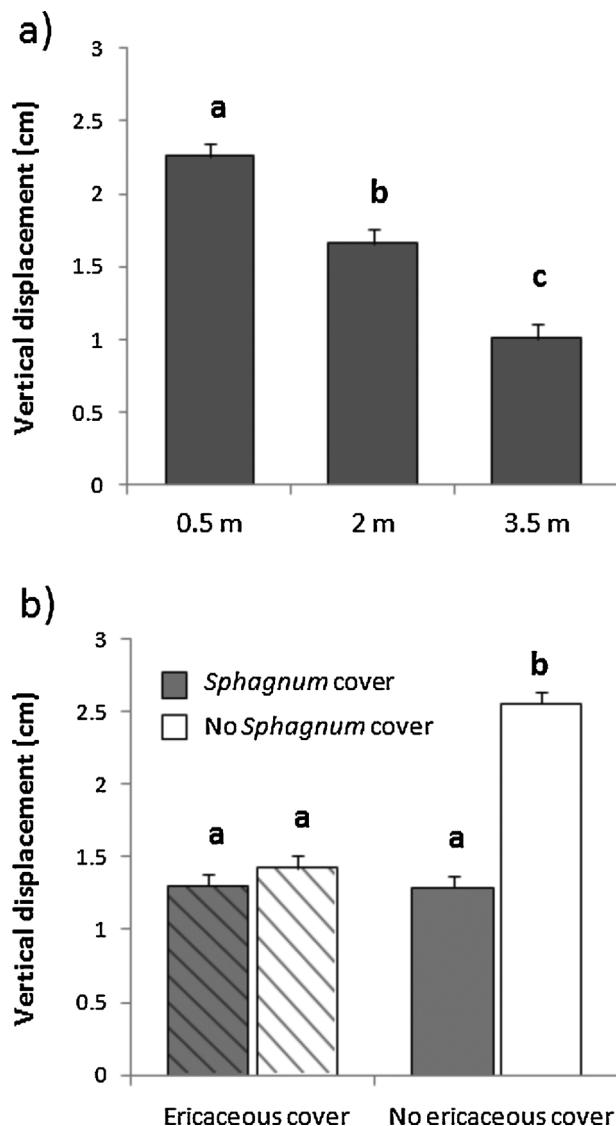


Fig. 2. Intensity of frost heave as evaluated by vertical displacement of wooden dowel rods (cm) in peat, according to (a) three distances from the low-water mark (0.5 m, 2 m and 3.5 m) and (b) presence of an ericaceous cover and a *Sphagnum* cover ($n=6$). Letters indicate significant differences between treatments ($p<0.05$). Error bars represent standard error of the mean.

experimental unit. Significance level was set at $p<0.05$. Data were also tested for homogeneity of variance and normality of residuals. Where required, data were transformed (square root or \log_{10} transformation). In the case of a significant effect, differences between treatments were determined using the LSMEANS procedure, while in the presence of a significant interaction between two factors, the SLICE option of LSMEANS was used to establish the level of the first factor in order to test the second.

3. Results

3.1. Ericaceae cover on peat stabilization

There were ten nights with frost events between the first frosts (mid-October 2010) and the time when heave measurements were made (early November 2010). Measurements of frost heave indicate that the amplitude of vertical displacement by peat diminished significantly with distance from the low-water mark of the pools ($F=14.0$, $p<0.0001$; Fig. 2a). Heave was 1.3 and 2.8 times stronger

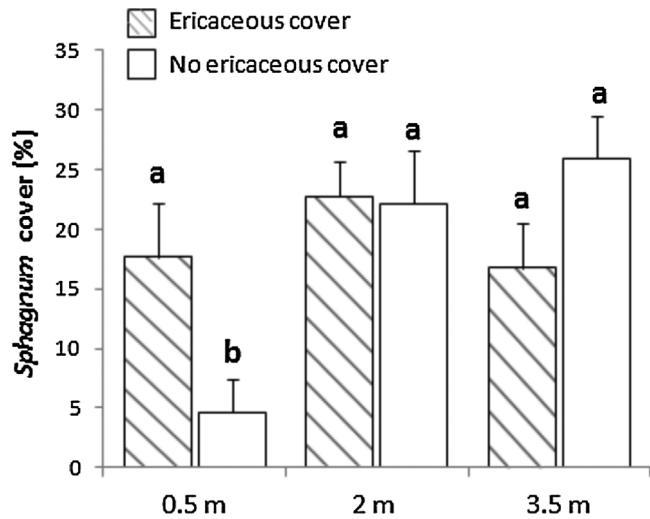


Fig. 3. Final percent cover of *Sphagnum majus* (%) as a function of distance from the low-water mark (0.5 m, 2 m and 3.5 m) and presence of an ericaceous cover ($n=6$). Letters indicate significant differences between treatments ($p<0.05$). Error bars represent standard error of the mean.

near this mark than at a distance of 2 m and 3.5 m, respectively. The amplitude of frost heave under ericaceous cover (1.3 ± 0.1 cm with *Sphagnum* and 1.4 ± 0.1 cm without *Sphagnum*) was similar to that observed when only *Sphagnum* was present (1.3 ± 0.1 cm; $F=9.9$, $p_{\text{interaction}}=0.01$). Moreover, the presence of a vegetation cover of any kind was able to control the amplitude of peat frost heave twice as well (52% less displacement) than control treatments with no cover (Fig. 2b).

3.2. Ericaceae cover on *Sphagnum* growth

After one growing season, the presence of Ericaceae fostered the survival of *Sphagnum* only in the low-water mark zone, closest to the water ($F=4.6$, $p_{\text{interaction}}<0.05$; Fig. 3). At this location, the *S. majus* cover was almost four times more dense under shrubs than with no protection. Elsewhere, the presence of Ericaceae did not influence establishment success of *Sphagnum* ($F=0.23$, $p=0.65$).

3.3. Establishment of herbaceous species

Germination rates observed in the field were generally inferior to the viability measured by tetrazolium tests on a batch of 100 seeds (Table 1), except for *C. magellanica*, for which germination in the field was higher than tested lab viability. Germination of *C. oligosperma* was particularly weak, and consequently it was impossible to evaluate the effect of different treatment combinations on its germination and elongation.

Table 1

Viability of seeds used for an experiment to evaluate establishment of six species associated with pool margins, estimated by tetrazolium testing of a batch of 100 seeds per species, as well as germination rate evaluated after their introduction around created pools in restored peatlands (data represent average germination rates from the experiment presented in Figs. 4 and 5).

Herbaceous species	Viability (%)	Germination (% \pm SE)
<i>Carex magellanica</i> (Car mag)	21	29 ± 4
<i>C. oligosperma</i> (Car oli)	33	<1
<i>C. pauciflora</i> (Car pau)	13	9 ± 2
<i>Eriophorum virginicum</i> (Eri vir)	29	21 ± 4
<i>Rhynchospora alba</i> (Rhy alb)	50	39 ± 6
<i>Scheuchzeria palustris</i> (Sch pal)	59	4 ± 1

Table 2

ANOVA in a split-split-block design was used to evaluate the effect of an ericaceous cover, a *Sphagnum* cover and the distance from the low-water mark (0.5 m, 2 m and 3.5 m) on the germination on seeds of herbaceous species sown at created pool margins ($n=6$). Values in bold indicate a significant difference, $p < 0.05$. Species names corresponding to the acronyms are indicated in Table 1.

Transformation	Variation sources	Germination									
		<i>Car mag</i>		<i>Car pau</i>		<i>Eri vir</i>		<i>Rhy alb</i>		<i>Sch pal</i>	
		F	$p > F$	F	$p > F$	F	$p > F$	F	$p > F$	F	$p > F$
Block		5									
Ericaceous cover	1	1.69	0.2507	2.28	0.1913	1.13	0.3367	0	0.96	0.02	0.8991
<i>Sphagnum</i> cover	1	0.23	0.6413	11.8	0.0064	15.33	0.0029	25.56	0.0005	6.87	0.0256
Ericaceous \times <i>Sphagnum</i>	1	0.75	0.4075	1.37	0.269	1.3	0.281	0.01	0.9421	0.79	0.3961
Distance	1	5.77	0.0262	3.05	0.1	3.11	0.0932	10.75	0.0038	93.43	<0.001
Ericaceous \times distance	1	0.75	0.3975	0.39	0.539	0.72	0.4069	0.47	0.4992	1.27	0.2733
<i>Sphagnum</i> \times distance	1	1.48	0.2378	0.19	0.6723	6.21	0.0216	6.27	0.021	4.19	0.0541
Ericaceous \times <i>Sphagnum</i> \times distance	1	2.77	0.1115	0.69	0.4193	0.52	0.4794	0.01	0.9058	0.16	0.6955
Error		35									
Total		47									

-: no transformation required; sqrt: square root transformation.

At the end of the growing season, the germination rates of the five herbaceous seedlings that could be evaluated during the experiment had not been influenced by a cover of Ericaceae (Table 2). However, each species was affected differently by the presence of *Sphagnum* and distance from the low-water mark.

Thus, *C. magellanica* germinated better at a greater distance from the low-water mark ($F=5.8$, $p=0.03$; Table 2), whereas the inverse tendency was observed in *Scheuchzeria palustris*, which germinated better near pools ($F=93.4$, $p < 0.0001$; Table 2; Fig. 4a and e). Germination rates of *C. pauciflora* were lower in the presence

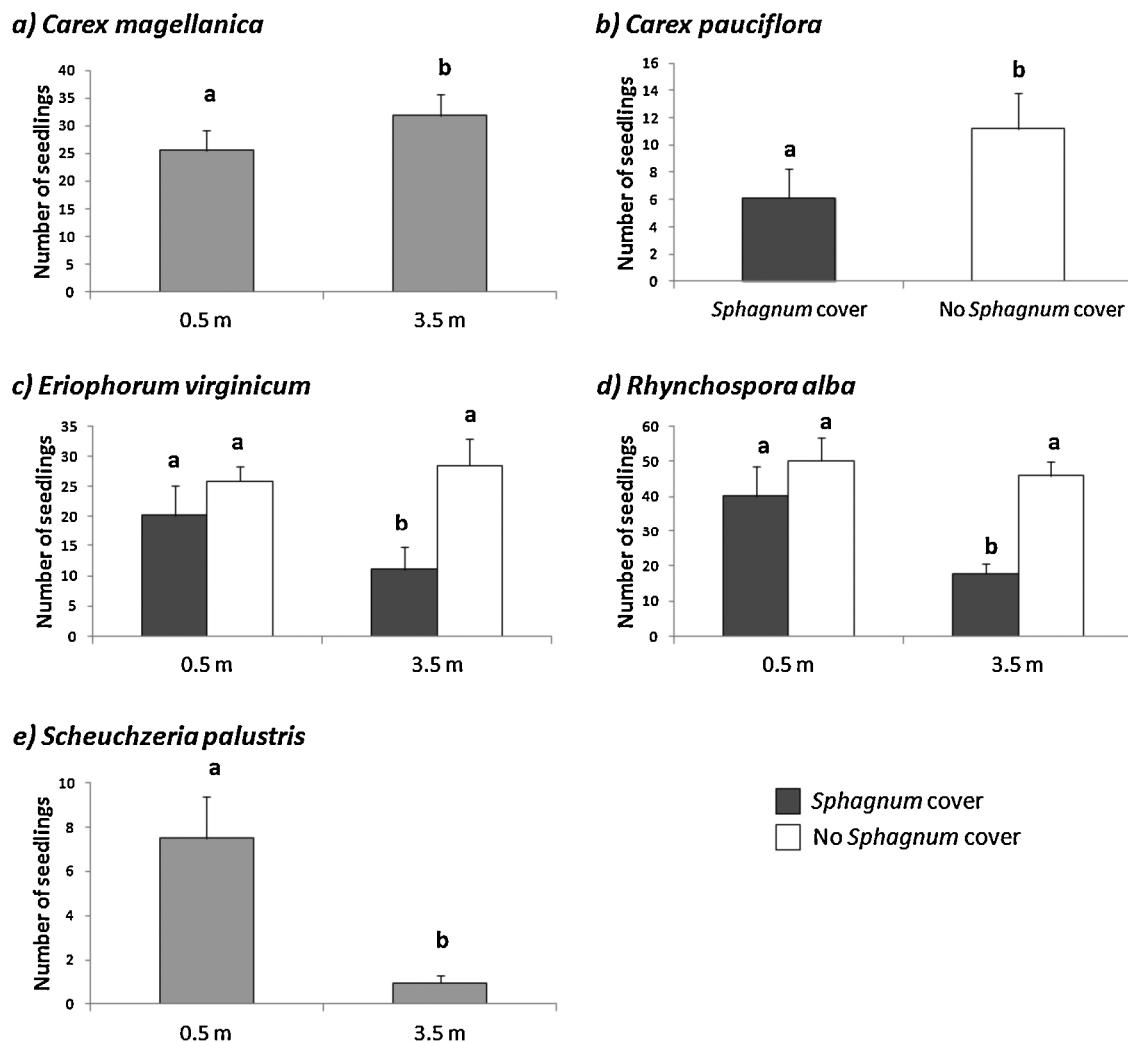


Fig. 4. Germination (number of seedlings) in five herbaceous species associated with pool margins at two distances from the low-water mark (0.5 m and 3.5 m) and in presence of a *Sphagnum* cover ($n=6$). Letters indicate significant differences between treatments ($p < 0.05$). Error bars represent standard error of the mean.

Table 3

ANOVA in a split-split-block design was used to evaluate the effect of an ericaceous cover, a *Sphagnum* cover and the distance from the low-water mark on the elongation of seedlings of herbaceous species introduced by seeds at created pool margins ($n=6$). Values in bold indicate a significant difference, $p < 0.05$. Species names corresponding to the acronyms are indicated in Table 1.

Transformation	Variation sources	Elongation (cm)							
		<i>Car mag</i> sqrt		<i>Car pau</i> sqrt		<i>Eri vir</i> log		<i>Rhy alb</i> –	
		df	F	p	F	p	F	p	F
Block		5							
Ericaceous cover	1		1.97	0.2193	2.83	0.1535	0.01	0.909	0
<i>Sphagnum</i> cover	1		48.46	<.0001	61.77	<.0001	2.02	0.186	20.14
Ericaceous × <i>Sphagnum</i>	1		2.26	0.1639	0.6	0.4592	0.15	0.7028	1.74
Distance	1		10.67	0.0039	1.61	0.2309	40.02	<.0001	25.63
Ericaceous × distance	1		0.12	0.7285	1.39	0.2638	0.13	0.7182	0.86
<i>Sphagnum</i> × distance	1		5.95	0.0242	10.7	0.0075	0.41	0.531	0.69
Ericaceous × <i>Sphagnum</i> × distance	1		1.26	0.2749	0.02	0.8985	0.72	0.4065	0.14
Error		35							
Total		47							

–: no transformation required; sqrt: square root transformation.

of *Sphagnum* ($F=11.8$, $p=0.006$; Table 2; Fig. 4b). The same effect was observed in *Eriophorum virginicum* and *Rhynchospora alba*, but only in the zone farthest from the pools, where germination was reduced by half in the presence of *Sphagnum* ($F=6.2$, $p_{\text{interaction}}=0.02$ for both; Table 2; Fig. 4c and d).

Given the low germination rate of *Scheuchzeria palustris*, elongation could not be evaluated for this species. Elongation of the

other four herbaceous species was not influenced by the presence of a cover of Ericaceae, paralleling findings on their germination (Table 3). Elongation of *E. virginicum* and *R. alba* was greatest near the low-water mark, regardless of cover type ($F=40.0$, $p < 0.0001$ for *E. virginicum* and $F=25.6$, $p < 0.0001$ for *R. alba*; Table 3; Fig. 5c and d). Elongation of *Carex* and *R. alba* benefitted from the presence of *Sphagnum*, an effect that was particularly pronounced in *Carex*

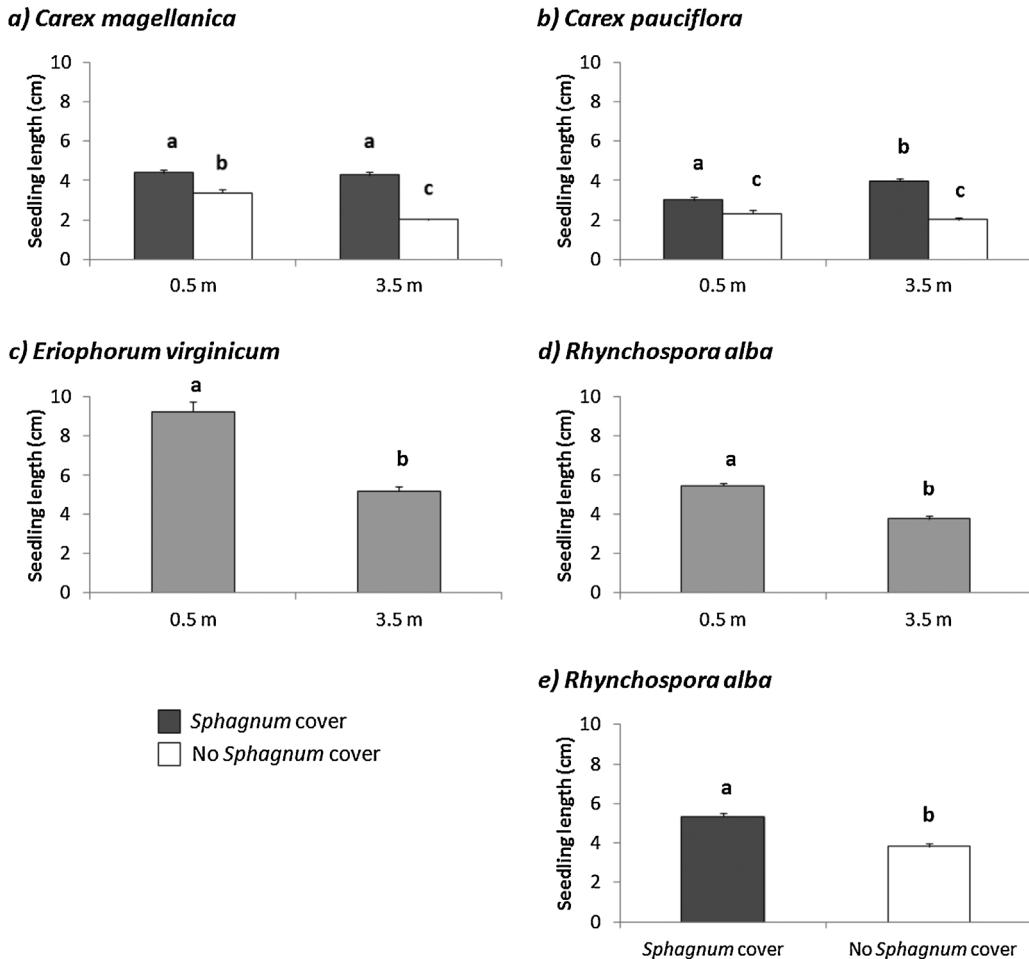


Fig. 5. Elongation of seedlings (cm) in four herbaceous species associated with pool margins at two distances from the low-water mark (0.5 m and 3.5 m) and in presence of a *Sphagnum* cover ($n=6$). Letters indicate significant differences between treatments ($p < 0.05$). Error bars represent standard error of the mean.

far from the pools where elongation was two times higher in the presence of *Sphagnum* as compared to when absent (Table 3; Fig. 5a, b and e).

4. Discussion

During episodes of ground frost, peat heaved more near pools' low-water mark, where the water content of the substrate was higher. The amplitude of frost heave (more than 2 cm) was not negligible, given that the thickness of *Sphagnum* carpets and the length of the herbaceous seedling roots were no longer than a few centimeters. Substrate heaving can be limited with a dense cover of vegetation (Decker and Ronningen, 1957) or straw mulch, which prevents the ground from freezing before sub-zero temperatures set in for the winter (Groeneveld and Rochefort, 2005; Kohnke and Werkhoven, 1963). However, the results obtained near pools in this experiment show that a sparse cover of *Ericaceae* (<25%) reduced heaving by 50%, just as effectively as a dense cover of *Sphagnum* fragments and straw.

S. majus established less well near the low-water mark in the absence of *Ericaceae*. Yet this was the location with ideal conditions for *Sphagnum* survival, with a water table level close to the surface throughout the growing season (<20 cm) and highest water content in peat (70%). Furthermore, *S. majus*, a species typical of the wettest depressions and floating carpets (Gauthier, 1980; Bragazza, 1997), grows well when submerged (Rochefort et al., 2002). Other factors may thus explain the poor survival rates of *Sphagnum*, such as, for example, mechanical disturbances caused by the significant fluctuations in pool water level which are greater at the young post-restoration stage than in natural peatlands. Furthermore, the usual flooding or waves generated on water bodies during episodes of high wind can displace straw and the not yet grounded moss carpet mostly composed of *Sphagnum* propagules. This mechanical movement causes erosion and covers *Sphagnum* mosses with fine peat particles (Kløve, 1998; Holden and Burt, 2002), thus impeding their regeneration after water lever has dropped (Faubert and Rochefort, 2002). As well, straw can stick to the substrate when the water level drops, thus losing its three-dimensional structure and thereby its protective effect on mosses (Rochefort and Lode, 2006). As a result, the mosses may have lacked adequate protection from the mulch. However, at the lowest elevation, the *Sphagnum* was four times more dense under the cover of *Ericaceae* than in their absence, which highlights the positive role of these shrubs. Emerged plants are recognized as protecting shorelines from erosion, since their above-ground parts reduce wave velocity and can intercept the sediment that remains on their persistent foliage, while their submerged parts hold soil in place (Coops et al., 1996) and prevent sediment from being stirred up (Carpenter and Lodge, 1986). We can therefore suppose that ericaceous shrubs introduced were able to mechanically protect the growing *Sphagnum* under the cover they provided, by stabilizing and aggregating the substrate. Entwined shrub branches may also have helped to hold straw in place while providing a vertical structure, thereby fostering *Sphagnum* growth during very dry periods (Pouliot et al., 2011). The results obtained at the two other distances from the pools support this hypothesis. At 2 m from the low-water mark, where treatments were subjected to flooding for a briefer period, *Ericaceae* had no impact on *Sphagnum* survival. *Ericaceae* treatments at the greatest distance from this mark, which were virtually unaffected by hydrodynamic erosion factors, seemed to negatively affect *Sphagnum*, although this tendency was not statistically significant. Their superficial roots probably increased water uptake close to the surface, which may have resulted in desiccation of the *Sphagnum*, as suggested by Tomassen et al. (2003).

Contrary to our initial hypothesis, the presence of *Ericaceae* had no positive effect on germination rate or growth of any of the

six herbaceous species tested. This finding differs from previous experiments with *Ericaceae* species, which indicated that hydric conditions were improved under their cover, and a higher level of relative humidity was observed (Pouliot et al., 2011), as well as lower water pressure in soil and an elevated water content in peat (Farrick and Price, 2009). Furthermore, shade created by the *Ericaceae* does not seem to have influenced germination or establishment of *Cyperaceae* or *Scheuchzeria palustris* seeds, species known to be sensitive to a decrease in the quality and intensity of sunlight (Jurik et al., 1994; Schütz and Rave, 1999; Kettenring et al., 2006a,b). It is probable that the planting density of the shrubs was too low to have had a real impact on the surface microclimate and light conditions.

On the other hand, each of the vascular species was affected differently by the presence of *Sphagnum* and distance from the low-water mark. Seedling germination was lower for *C. pauciflora* on *Sphagnum* carpets, an effect visible only in dry zones for *E. virginicum* and *R. alba*. These results contradict similar germination experiments in which the presence of mosses was more advantageous to seeds than bare soil (Richardson, 1958; Johnson and Thomas, 1978; Landry et al., 2012). However, in our experiment, bryophytes were covered with a layer of straw that was still well in place one year later. Although straw presence is essential for *Sphagnum* establishment in restored peatlands, its shade may have had a negative impact on seeds germination in this case (Kettenring et al., 2006a,b), particularly in zones where it remained intact, (such as in zones farther from pools, which were not subjected to flooding). The effect of straw might depend on substrate humidity level since other field trials conducted under conditions of water saturation showed that germination of the same vascular plants was not influenced by the developmental stage of the *Sphagnum* carpet and hence by the presence of straw (Laberge et al., unpublished results).

Once seeds established, *Sphagnum* in combination with straw had a positive influence on the elongation of most seedlings, an effect more evident for *Carex* in the drier zone. Modification of the microclimate by the presence of straw and *Sphagnum* fragments thus resulted in conditions favorable to seedling development in this zone, most likely by reducing wind and surface evaporation, and maintaining a higher, more stable level of relative humidity near the ground surface (Price et al., 1998). While elongation of *E. virginicum* was not influenced by *Sphagnum*, this species experienced the most significant elongation, reaching almost 10 cm of growth at the lowest elevation. The protection provided by *Sphagnum* and straw was thus superfluous for this cotton-grass species, considering its ability to establish on its own. The good regeneration capacity of *E. virginicum* along blocked ditches in a restored peatland has also been shown in a study conducted by Poulin et al. (2011).

5. Implications for restoration

Creating specific habitats like pools in restored peatlands presents particular challenges. The banks of created pools experience significant disturbances, particularly between the low- and high-water marks, where the moss layer transfer technique must be adapted accordingly. In this zone, a sparse cover of *Ericaceae* (<25%) composed of *Andromeda polifolia* var. *latifolia* and *Vaccinium macrocarpon* successfully controlled frost heave in fall, resolving the main problem inherent of newly created pools, which is substrate instability. The presence of *Ericaceae* also contributed to increase survival of *S. majus* in the shoreline zone most affected by water level fluctuations. We recommend using *Ericaceae* transplants as a technique to stabilize the margins of pools created in the context of restoration. However, it remains unclear whether an ericaceous cover improves microclimatic conditions in this setting,

since seed establishment was not influenced by shrub presence. As the germination rate of vascular species was rather low, it would be interesting to test the effect of an ericaceous cover and *Sphagnum* carpet on the survival and growth of vascular plants introduced as seedlings, rather than as seeds. Considering that our study was conducted over only one growing season, vascular seedling survival and growth remains to be evaluated through time. Our study however represents a sound preliminary study on the potential of the proposed approach for controlling frost heave and successfully restoring peatland pools.

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References

- Bragazza, L., 1997. *Sphagnum* niche diversification in two oligotrophic mires in the southern Alps of Italy. *Bryologist* 100, 507–515.
- Breshears, D.D., Nyhan, J.W., Heil, C.E., Wilcox, B.P., 1998. Effects of woody plants on microclimate in a semiarid woodland: Soil temperature and evaporation in canopy and intercanopy patches. *Int. J. Plant Sci.* 159, 1010–1017.
- Carpenter, S., Lodge, D., 1986. Effects of submersed macrophytes on ecosystem processes. *Aquat. Bot.* 26, 341–370.
- Coops, H., Geilen, N., Verheij, H.J., Boeters, R., van der Velde, G., 1996. Interactions between waves, bank erosion and emergent vegetation: an experimental study in a wave tank. *Aquat. Bot.* 53, 187–198.
- Crum, H., 1992. *A Focus on Peatlands and Peat Mosses*. The University of Michigan Press, Ann Arbor, pp. 306.
- Decker, A.M., Ronningen, T.S., 1957. Heaving in forage stands and in bare ground. *Agron. J.* 49, 412–415.
- Environment Canada, 2011. Canadian Climate Normals 1971–2000, <http://www.climate.weatheroffice.gc.ca/climate.normals/results.e.html> (10.04.11).
- Farrick, K.K., Price, J.S., 2009. Ericaceous shrubs on abandoned block-cut peatlands: implications for soil water availability and *Sphagnum* restoration. *Ecohydrology* 2, 530–540.
- Faubert, P., Rochefort, L., 2002. Response of peatland mosses to burial by wind-dispersed peat. *Bryologist* 105, 96–103.
- Fontaine, N., Poulin, M., Rochefort, L., 2007. Plant diversity associated with pools in natural and restored peatlands. *Mires Peat* 2, 34–56.
- Gauthier, R., 1980. La végétation des tourbières et les sphaignes du parc des Laurentides, Québec. Études écologiques 3. Université Laval, Québec.
- Grabe, D.F., 1970. *Tetrazolium Testing Handbook: For Agricultural Seeds*. Association of Official Seeds Analysts, North Brunswick.
- Groeneveld, E.V.G., Rochefort, L., 2005. *Polytrichum strictum* as a solution to frost heaving in disturbed ecosystems: a case study with milled peatlands. *Restor. Ecol.* 13, 74–82.
- Groeneveld, E.V.G., Masse, A., Rochefort, L., 2007. *Polytrichum strictum* as a nurse-plant in peatland restoration. *Restor. Ecol.* 15, 709–719.
- Holden, J., Burt, T.P., 2002. Infiltration, runoff and sediment production in blanket peat catchments: implications of field rainfall simulation experiments. *Hydro. Process.* 16, 2537–2557.
- Johnson, C., Thomas, A.G., 1978. Recruitment and survival of seedlings of a perennial *Hieracium* species in a patchy environment. *Can. J. Bot.* 56, 572–580.
- Jurik, T.W., Wang, S.C., Valk, A.G., 1994. Effects of sediment load on seedling emergence from wetland seed banks. *Wetlands* 14, 159–165.
- Kettenring, K.M., Gardner, G., Galatowitsch, S.M., 2006a. Effect of light on seed germination of eight wetland *Carex* species. *Ann. Bot.-London* 98, 869–874.
- Kettenring, K.M., Gardner, G., Galatowitsch, S.M., 2006b. Effect of light on seed germination of eight wetland *Carex* species. *Ann. Bot.* 98, 869–874.
- Kløve, B., 1998. Erosion and sediment delivery from peat mines. *Soil Till. Res.* 45, 199–216.
- Kohnke, H., Werkhoven, C.H., 1963. Soil temperature and soil freezing as affected by an organic mulch. *Soil Sci. Soc. Am. J.* 27, 13–17.
- Landry, T., Poulin, M., Rochefort, L., 2012. Impact of seedbed and water level on the establishment of plant species associated with bog pools: implication for restoration. *Native Plants J.* 13, 205–215.
- Luoto, M., Seppälä, M., 2000. Summit peats ('peat cakes') on the fells of Finnish Lapland: continental fragments of blanket mires? *Holocene* 10, 229–241.
- Malmer, N., Svensson, B., Wallén, B., 1994. Interactions between *Sphagnum* mosses and field layer vascular plants in the development of peat-forming systems. *Folia Geobot.* 29, 483–496.
- Marcoux, K., 2000. *Les invasions de linaigrette (*Eriophorum vaginatum* L.): aide ou frein à la restauration des tourbières?* Master Thesis. Université Laval, Quebec.
- Mazerolle, M.J., Poulin, M., Lavoie, C., Rochefort, L., Desrochers, A., Drolet, B., 2006. Animal and vegetation patterns in natural and man-made bog pools: implications for restoration. *Freshwater Biol.* 51, 333–350.
- McNeil, P., Waddington, J.M., 2003. Moisture controls on *Sphagnum* growth and CO₂ exchange on a cutover bog. *J. Appl. Ecol.* 40, 354–367.
- Poulin, M., Fontaine, N., Rochefort, L., 2011. Restoration of pool margin communities in cutover peatlands. *Aquat. Bot.* 94, 107–111.
- Pouliot, R., Rochefort, L., Karofeld, E., Mercier, C., 2011. Initiation of *Sphagnum* moss hummocks in bogs and the presence of vascular plants: is there a link? *Acta Oecol.* 37, 346–354.
- Price, J.S., Rochefort, L., Quinty, F., 1998. Energy and moisture considerations on cutover peatlands: surface microtopography, mulch cover and *Sphagnum* regeneration. *Ecol. Eng.* 10, 293–312.
- Quinty, F., Rochefort, L., 2003. *Guide de restauration des tourbières*, Deuxième édition. Association canadienne de la mousse de sphaigne. Ministère des Ressources naturelles du Nouveau-Brunswick, Quebec.
- Reubens, B., Poesen, J., Danjon, F., Geudens, G., Muys, B., 2007. The role of fine and coarse roots in shallow slope stability and soil erosion control with a focus on root system architecture: a review. *Trees* 21, 385–402.
- Richardson, J.A., 1958. The effects of temperature on the growth of plants on pit heaps. *J. Ecol.* 46, 537–546.
- Rochefort, L., Campeau, S., Bugnon, J.L., 2002. Does prolonged flooding prevent or enhance regeneration and growth of *Sphagnum*? *Aquat. Bot.* 74, 327–341.
- Rochefort, L., Lode, E., 2006. Restoration of degraded boreal peatlands. In: Wieder, R.K., Vitt, D.H., Rochefort, L., Lode, E. (Eds.), *Boreal Peatland Ecosystems Ecological Studies Series*, 188. Springer-Verlag, Berlin, pp. 381–423.
- Rochefort, L., Isselin-Nondedeu, F., Boudreau, S., Poulin, M., 2013. Comparing survey methods for monitoring vegetation change through time in a restored peatland. *Wetlands Ecol. Manag.* 21, 71–85.
- Salonen, V., 1987. Relationship between the seed rain and the establishment of vegetation in two areas abandoned after peat harvesting. *Holarctic Ecol.* 10, 171–174.
- Schütz, W., Rave, G., 1999. The effect of cold stratification and light on the seed germination of temperate sedges (*Carex*) from various habitats and implications for regenerative strategies. *Plant Ecol.* 144, 215–230.
- Tomassen, H.B.M., Smolders, A.J.P., Limpens, J., Lamers, L.P.M., Roelofs, J.G.M., 2003. Expansion of invasive species on ombrotrophic bogs: desiccation of high N deposition. *J. Appl. Ecol.* 41, 139–150.