

INFLUENCE OF DIFFERENT BRYOPHYTE CARPETS ON VASCULAR PLANT ESTABLISHMENT AROUND POOLS IN RESTORED PEATLANDS

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ABSTRACT

Vascular plants associated to natural peatland pools do not spontaneously colonize edges of man-made pools in restored peatlands and have proven to be recalcitrant to the usual restoration techniques. The goal of this study was to evaluate the effect of the species used as a seedbed (*Cladopodiella fluitans*, *Sphagnum cuspidatum*, or *Sphagnum magellanicum*) and its developmental stage (established carpet or newly reintroduced fragments) on establishment success in the field of the seeds of four vascular species: *Carex limosa*, *Carex magellanica*, *Carex oligosperma*, and *Scheuchzeria palustris*. The germination rate was measured after one season and growth after two seasons. Seedbed composition and developmental stage had no effect on *Carex*, whereas the germination of *S. palustris* was higher on *S. cuspidatum*. Growth of vascular plants was slightly improved on *S. magellanicum* carpets and was lower on seedbeds of *C. fluitans*. Our results lead us to recommend seeding at the same time as bryophyte fragments are spread and fostering introduction of *Sphagnum* mosses, preferably to *C. fluitans*, around artificial pool edges. Copyright © 2013 John Wiley & Sons, Ltd.

KEYWORDS: seed germination; substrate conditions; Cyperaceae; biodiversity; plant nursery; pools; peatland

INTRODUCTION

Worldwide, wetlands have been degraded and lost through severe anthropogenic disturbances such as drainage, conversion to agriculture, and urbanization (Lappalainen, 1996; Moore, 2002; Federal, Provincial and Territorial Governments of Canada, 2010; Alphan, 2012; Miettinen *et al.*, 2013). Recently, the need for improved restoration practices for these ecosystems has arisen. The long-term goal of restoring peatlands using the moss layer transfer technique is to restore the most unique function of these wetlands: accumulating carbon in the form of partially decomposed organic matter (Rochefort, 2000). Yet this technique produces homogeneous restored peatlands, devoid of the pools recognized as hotspots of natural peatland biodiversity (Fontaine *et al.*, 2007). Some specialized *Carex* and *Scheuchzeriaceae* are among the plants that form communities associated with *Sphagnum* mosses and other bryophytes established near pools and contribute to the species richness of these types of habitats. However, these vascular plants do not spontaneously reestablish near ponds created even 10 years after their restoration (Mazerolle *et al.*, 2006) and have also proved to be recalcitrant to the moss layer transfer technique (Poulin *et al.*, 2011). This approach that is 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). Yet a past trial for restoring pool margins using the moss layer transfer approach has proved to be successful for *Sphagnum* mosses only, as vascular plants were still scarce in experimental plots. Even after three growing seasons, herbaceous species typical of pool edges covered less than 5% (Poulin *et al.*, 2011).

Landry *et al.* (2012) demonstrated in greenhouse that the vascular plants typical of pool edges can be reintroduced as seeds but that each species has a particular ecological niche, especially in terms of the species composing the seedbed and water level. Despite significant progress in understanding the ecology of species associated with natural pools, the introduction of seeds around the edges of artificial pools in restored peatlands still presents major logistical challenges, particularly in terms of the timing compatible with seeding. A main question in fact remains: should seeds be planted when moss diaspores are introduced, or several years after restoration, on carpets that are well established?

Broadcasting seeds when moss diaspores are spread would not only simplify restoration logistics but would also have the advantage of casting seeds on a greater area of bare peat substrate. Indeed, bare peat can be more favorable to seed germination of certain plants than within well-established moss carpets (Kotorova & Leps, 1999; Roth *et al.*, 1999; Bullock, 2000; Poschlod & Biewer, 2005). However, the shade caused by the straw mulch essential for the survival of bryophyte diaspores (Price *et al.*, 1998) has been shown to hinder seed germination (Jurik *et al.*, 1994). Sowing seeds on a well-established bryophyte carpet several years after restoration has the advantage of reducing susceptibility to erosion by waves and frost heaving, which

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can inhibit seed germination and seedling growth. In microcosms under greenhouse conditions, Landry *et al.* (2012) observed a higher rate of germination and growth for certain typical pool-edge species on well-established moss carpets than on bare peat, at water levels close to the surface, as is the case in a natural environment. However, the growth pattern of *Sphagnum* mosses differs among species, each forming a carpet with its own attributes. Consequently, the type of bryophytes used as seedbeds is likely to affect the number of microsites favorable to seeds, whether at the seed or seedling stage (Hörnberg *et al.*, 1997; Gunnarsson & Rydin, 1998; Rydin *et al.*, 2006).

This study evaluates the influence of seedbed type on the establishment of four herbaceous species recalcitrant to the moss layer transfer technique: *Carex limosa*, *Carex magellanica*, *Carex oligosperma*, and *Scheuchzeria palustris*. More specifically, we verified (i) whether recalcitrant herbaceous species establish better on a bryophyte cover forming a well-established rather than fragmented carpet and (ii) whether the bryophyte species used as a seedbed has an influence. We tested two *Sphagnum* species (*S. cuspidatum* and *S. magellanicum*) as well as one liverwort (*Cladopodiella fluitans*), which are bryophytes commonly found around pools and known to be part of specific association with vascular species of interest (Fontaine *et al.*, 2007). Our hypothesis was that germination and growth of these four recalcitrant vascular plant species would be better on well-established carpets than on seedbeds at an earlier developmental stage, as the straw mulch needed to successfully establish newly introduced moss fragments may intercept light. We also expected that seedling germination and growth would be greatest on carpets of *S. cuspidatum*, as this species produces loose carpets (Joosten, 1995) that allow seeds to have more contact with adjacent substrate, contrary to dense *C. fluitans* carpets, a liverwort species commonly found around pools in peatlands of eastern Canada (Gauthier, 1980).

MATERIALS AND METHODS

The experiment was conducted in an ombrotrophic peatland located in Shippagan, in the northeastern part of the Acadian Peninsula, in New Brunswick, Canada (47°40'N, 64°43'O), where the climate was characterized by relatively cool temperature (average temperature 4–5°C) and humid conditions (1110–1 mm average annual precipitation; Environment Canada, 2013). Peat had been harvested by the manual block-cut method, leaving a topography characterized by alternating baulks and trenches, the latter with a more humid microclimate. The experiment was conducted within such trenches.

A factorial experiment in a randomized complete block design was set up to test the effect of the species used as a seedbed and its developmental stage on the germination and establishment of four herbaceous species: *C. limosa*, *C. magellanica*, *C. oligosperma*, and *S. palustris*. Three bryophyte species that naturally form colonies around pool edges, *C. fluitans*, *S. cuspidatum*, and *S. magellanicum*, were established

in monospecific colonies at two stages of development, either as a carpet grown over a 3-year period or in fragments spread 1 month earlier to seed introduction. These six types of seedbeds were replicated six times. Each was set up on a minimum area of 1 m² in six trenches (blocks) from which spontaneously established vegetation had been removed. Well-established carpets had a 100% cover and thickness of about 1 cm (*C. fluitans*), 3 cm (*S. cuspidatum*), and 10 cm (*S. magellanicum*). Fragments covered about 50% of the peat surface after introduction at a ratio of 1 m² per 10 m² for both *Sphagnum* species, and 1 m² per 4 m² for *C. fluitans*, a species that needs higher ratios according to its low propagation speed. A protective layer of straw was applied on the bryophyte fragments at a ratio of 1000 kg/ha, 30% of the ratio recommended by Rochefort *et al.* (2003) for restoring drier zones of ombrotrophic peatlands following peat harvesting by vacuum extraction. Less straw was indeed needed as a water-level control device maintained the water table level near the peat surface (mean ± SD: 8.2 ± 5 cm) throughout the growing season. The straw covered about 75% of newly spread fragments experimental units, and 0% of well-established carpets units, as it decomposed quickly after restoration. A net was fastened over each seedbed to prevent plant or straw movement under flooding conditions, especially during fall and spring time. The *Sphagnum* used for seedbeds were collected from the natural part of the Shippagan peatland, and *C. fluitans* was collected at the St-Charles-de-Bellechasse peatland (Quebec, 46°46'N, 71°00'O), shortly before transfer.

On 1 June 2010, cylinders were installed as retaining structures for the seeds of the herbaceous species. 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. Beds were weeded prior to planting seeds. Each seedbed held four cylinders, and 100 seeds of one of the four herbaceous species were planted in each cylinder (1 cylinder = 1 experimental unit) under the straw mulch, which was lifted up and replaced carefully. The mature infructescences of the four herbaceous species were collected between 30 August and 15 September 2009, near natural pools of several peatlands in Eastern Canada. Seeds of each species from different collecting areas were mixed together. Prior to planting, seeds were stratified on humid sand at 4°C for 3 months then submitted to a viability test using tetrazolium (Grabe, 1970).

The number of seedlings was counted at the end of the first growing season (14 August 2010), in order to determine the germination rate of the herbaceous species in the field. The length of 15 randomly chosen plants per cylinder was measured at the end of the second growing season (2 August 2011), to estimate annual growth.

Each species grown from seed was submitted to statistical analysis individually, and two variables were analyzed: germination and growth. Variables were analyzed using a

Table I. Comparison of seed viability and germination rates in the field by species

Herbaceous species	Viability (%)	Germination (% ± SE)
<i>Carex limosa</i>	37	14 ± 3
<i>Carex magellanica</i>	21	22 ± 3
<i>Carex oligosperma</i>	33	<1
<i>Scheuchzeria palustris</i>	59	22 ± 3

two-way ANOVA in a complete block design for the following treatments: bryophyte species and seedbed developmental stage. Statistical analyses of germination were conducted using the SAS GLM procedure (version 9.2, ©2010, SAS, Cary, NC, USA), while growth analyses were conducted using the same software's MIXED procedure, given the variability of the data and the limited number of samples per experimental unit. Significance level was established at $p < 0.05$. Data were also tested for homogeneity of variance and residual normality, and log-transformed when necessary. In the case of a significant interaction effect, differences between treatments were determined using the least squares means procedure, whereas in the presence of a significant interaction between the two factors, we used the SLICE option of the least squares means to determine the levels of the first factor in order to test the second, so as to define the differences between each treatment.

RESULTS

The germination rates observed in the field were generally inferior to the viability measured by the tetrazolium test on a batch of 100 seeds (Table I), with the exception of *C. magellanica*, for which germination in the field was equivalent to the viability measured. The germination of *C. oligosperma* was particularly low, and for this reason, it was impossible to evaluate the effect of seedbed type on its germination and growth. After one growing season, the germination rates of *C. limosa* and *C. magellanica* had not been influenced by the species used as a seedbed, nor by the developmental stage (Table II). The germination of *S. palustris* was higher on *S. cuspidatum* seedbeds (mean ± SE: 22 ± 3%), regardless of developmental stage, than on seedbeds composed of the other two bryophyte species (12 ± 3% for *C. fluitans* and 13 ± 3% for *S. magellanica*; Figure 1).

The well-established carpets of *S. magellanica* significantly favored growth for the three vascular species studied (Table III; Figure 2). *S. cuspidatum* fragments also promoted plant growth but to a lesser extent than full *S. magellanica* carpets. On the other hand, seedbeds of *C. fluitans*, particularly the treatment forming a closed carpet, were less favorable to the growth of the young seedling and this was the case for all species. In general, a lower growth rate was observed for carpets, compared to fragments, for seedbeds of *C. fluitans* and *S. cuspidatum* (with the exception of *S. palustris* on *C. fluitans* seedbed, which resulted in similar growth independent of the developmental stage). The inverse tendency, for example, increased growth on carpets rather than fragments, was observed for seedbeds of *S. magellanica*, for all herbaceous species tested.

DISCUSSION

Beside *C. oligosperma*, which did not germinate in the field, the establishment of the three other herbaceous species recalcitrant to the moss layer transfer technique was not influenced by the developmental stage of the seedbeds. Contrary to our hypothesis, the presence of straw on recently introduced carpets did not reduce germination, although 75% of the experimental unit area was covered by straw. This is somewhat surprising, as *Carex* seeds are known to be affected by insufficient light exposure (Jurik *et al.*, 1994; Schütz & Rave, 1999; Kettenring *et al.*, 2006), particularly in the case of small seeds, which require more light to germinate (van Tooren & Pons, 1988). In former restoration experiments, a straw density of 3000 kg/ha has been shown to reduce by 70% the amount of photosynthetic active radiation reaching the mosses fragments (Groeneveld *et al.*, 2007). In our study, straw mulch probably did not interfere with sunlight to a critical degree for seed germination as we spread a thinner cover (30%) than is generally recommended for the moss layer transfer technique.

The species used as a seedbed did not influence establishment of Cyperaceae, whereas germination was higher for Scheuchzeriaceae on seedbeds of *Sphagnum cuspidatum*. Large-seeded species, such as *S. palustris*, generally produce seedlings with shorter roots than small-seeded species such as *C. magellanica* and *C. limosa*, making them more vulnerable to desiccation or to the instability of deeper loose structure

Table II. Two-way ANOVA in a randomized complete block design was used to evaluate the effect of the bryophyte species used as a seedbed and the developmental stage of the latter on the germination (for the first year of growth) for three species of herbaceous plants

Variation source	d.f.	<i>Carex limosa</i>		<i>Carex magellanica</i>		<i>Scheuchzeria palustris</i>	
		<i>F</i>	<i>P > F</i>	<i>F</i>	<i>P > F</i>	<i>F</i>	<i>P > F</i>
Block	5	0.42	0.8336	1.50	0.2260	4.91	0.0036
Bryophyte species	2	0.48	0.6274	2.23	0.1296	9.79	0.0009
Developmental stage	1	0.28	0.6013	0.23	0.6327	1.13	0.2997
Species * Stage	2	1.11	0.3471	0.06	0.9432	2.79	0.0829
Error	24						
Total	35						

Values in bold indicate significant differences, $p < 0.05$.

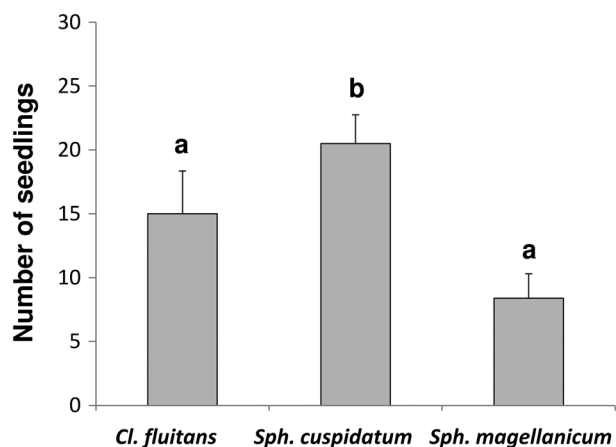


Figure 1. Germination of *Scheuchzeria palustris* on seedbeds of *Cladopodiella fluitans*, *Sphagnum cuspidatum*, or *Sphagnum magellanicum* ($n=6$). Letters indicate significant differences between treatments ($p=0.05$). Error bars represent the standard error of the mean. For each seedbed, results from plots with well-established carpet and from plot with bryophyte fragments were pooled together as this treatment (restoration stage) did not have a significant effect on germination. This figure is available in colour online at wileyonlinelibrary.com/journal/ldr.

(Campbell *et al.*, 2002). *S. palustris* germination was shown to be favored simply by a water level closer to the surface, regardless of the substrate type (Landry *et al.*, 2012), but the experiment by Landry *et al.* (2012) used thinner carpet of *Sphagnum magellanicum* (2–3 cm), which may explain discrepancies with our study. *C. fluitans* seedbeds are difficult for large seeds to penetrate and can limit root expansion (Chambers & MacMahon, 1994; Landry *et al.*, 2012), which may have hindered germination of *S. palustris*. Germination of *Carex* was not influenced by the bryophyte species used as a seedbed, despite that carpet structure and thickness are known to influence the evaporation rate within the carpet as well as the number of microsites favorable to seed germination (Hörnberg *et al.*, 1997; Gunnarsson & Rydin, 1998; Rice *et al.*, 2001; Rydin *et al.*, 2006). However, it is possible that the high water level (8 ± 5 cm) maintained under the soil surface throughout the growing season attenuated the effect of granulometric differences between the surface types (Keddy & Constabel, 1986).

Seed viability was low (under 25%), especially for *Carex* species. Germination rates were about 40% of viability, except for *Carex magellanica* for which seed germination was similar than viability. *C. oligosperma* has barely germinated at all despite seed viability of 33%. This may be due to improper stratification for this particular species, which has been shown difficult to germinate in other experimental work as well (Landry *et al.*, 2012).

Seedbeds of *S. magellanicum*, particularly well-established carpets, fostered elongation in the three species tested. The microclimate in this very thick carpet (sometimes almost 10 cm thick), along with diminished winds and very high relative humidity, may have reduced seedling water loss through transpiration, thereby having a facilitating effect. In addition, previous studies have shown that the mortality risk of seedlings to winter frost is lower in a bryophyte carpet (Keizer *et al.*, 1985; Groeneveld *et al.*, 2007).

In general, seedling growth was inferior on seedbeds of *C. fluitans*, particularly on well-established carpets, probably because their high-density hinders root penetration (Chambers & MacMahon, 1994), making this factor particularly influential. *Sphagnum* mosses seem more successful than liverworts at preventing desiccation of young plants (Rice *et al.*, 2001).

IMPLICATIONS FOR RESTORATION

While seeds introduction at different seedbed restoration stages had little effect on germination rate, it did influence plant growth to a degree. However, in the context of introducing vascular plants associated with pools to increase biodiversity of restored sites, the successful establishment of a species is more important than its growth rate. Thus, to facilitate restoration activities, seeds of vascular species can be introduced simultaneously with bryophytes along the edges of artificial pools, with a straw cover half as thick as generally recommended for the moss layer transfer technique (Rochefort *et al.*, 2003). In addition to facilitating restoration activities, planting seeds at the first stage of restoration offers other advantages: the species introduced have a better chance of persisting in the ecosystem (Simmers &

Table III. Two-way ANOVA in a randomized complete block design was used to evaluate the effect of the bryophyte species used as a seedbed and the developmental stage of the latter on elongation achieved by seeds (for the second year of growth) of three species of herbaceous plants

Transformation	d.f.	<i>Carex limosa</i>		<i>Carex magellanica</i>		<i>Scheuchzeria palustris</i>	
		log		—		log	
Variation source		<i>F</i>	<i>P</i> > <i>F</i>	<i>F</i>	<i>P</i> > <i>F</i>	<i>F</i>	<i>P</i> > <i>F</i>
Block	5	12.61	≤0.0001	7.29	≤0.0001	6.21	≤0.0001
Bryophyte species	2	47.91	≤0.0001	110.05	≤0.0001	40.74	≤0.0001
Developmental stage	1	1.66	0.1983	13.62	0.0003	5.53	0.0195
Species * Stage	2	27.48	≤0.0001	21.12	≤0.0001	60.18	≤0.0001
Error	24						
Total	35						

Values in bold indicate significant differences, $p < 0.05$.

— no transformation required; log, transformation $\log(x+1)$.

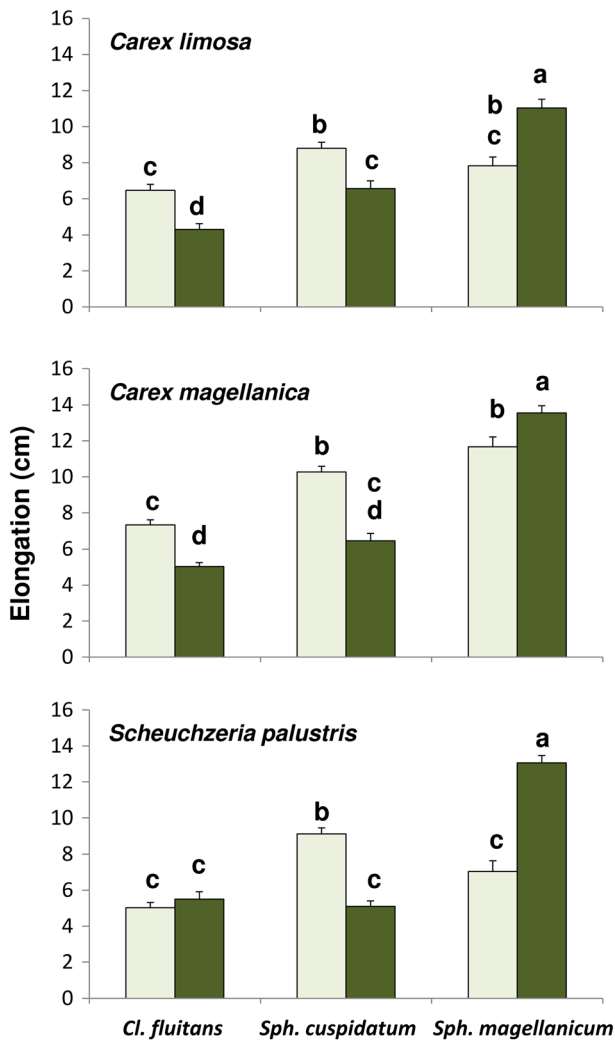


Figure 2. Seedling elongation (cm) of three recalcitrant herbaceous species ($n=6$) established on seedbeds of *Cladopodiella fluitans*, *Sphagnum cuspidatum*, or *Sphagnum magellanicum* at two seedbed developmental stages (recently restored and at a fragment stage in light green; well-established and forming continuous carpets in dark green). Letters indicate significant differences between treatments ($p=0.05$). Error bars represent the standard error of the mean. This figure is available in colour online at wileyonlinelibrary.com/journal/ldr.

Galatowitsch, 2010) because invasion by other species is usually reduced (Iannone *et al.*, 2011), and the seeds of re-introduced species would benefit from the nutrients supplied by the decomposing straw (Sottocornola *et al.*, 2007). With regard to the bryophyte species introduced as seedbeds, *Sphagnum* mosses seem the preferable choice, as they favor both germination and growth of the different vascular species tested. Carpets of *C. fluitans* should not be completely ruled out particularly for species such as *Utricularia cornuta*, strongly associated with them in a natural environment (Fontaine *et al.*, 2007). Our approach could be adapted to enhance restoration of other wetland types. Seed introduction has been used and suggested for restoring wetlands (Budelsky & Galatowitsch, 1999; Zedler, 2000). Defining the optimal time frame and substrate type should increase restoration success of saline wetlands (Morzaria-Luna & Zedler, 2007; Ma *et al.*, 2012; Domínguez-Beisiegel *et al.*, 2013), freshwater

marshes (Baldwin & Derico, 1999; Neff & Baldwin, 2005; Soons, 2006), and peatlands throughout the world. It remains that the applicability of restoration knowledge will depend on land user acceptance, especially in emergent or undeveloped countries (Nabahungu & Visser, 2013).

CONCLUSION

Our study showed that seed addition can be used to restore vascular plant communities around pool edges in restored peatlands. Despite low germination rates, seedlings of *C. limosa*, *C. magellanica*, and *S. palustris* were able to establish on all tested seedbeds, although *S. cuspidatum* best favored seedling establishment of *S. palustris* compared to the seedbeds composed of *S. magellanicum* and *C. fluitans*. The developmental stage of the seedbeds (established carpet or newly reintroduced fragments) did not influence seed germination, which may facilitate restoration efforts. Indeed, despite the presence of straw mulch atop *Sphagnum* or *Cladopodiella* fragments, seeds could be added along edges of man-made pool at initial restoration phase without additional delay. Well-established carpets of *S. magellanicum* may be favored as it fostered the growth of the three vascular species, which succeeded to germinate. Seedbed of *C. fluitans* should be used only when associated vascular plants such as *U. cornuta* are targeted, as it hampered seedling growth.

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