Impact of seedbed and water level on the establishment of plant species associated with bog pools

IMPLICATIONS FOR RESTORATION

Tommy Landry, Line Rochefort, and Monique Poulin

Downloaded from by guest on October 9, 2026. Copyright 2012

ABSTRACT

Our study found that a water level close to the surface and a seedbed composed of bare peat or a *Sphagnum* carpet favored the germination of vascular species associated with pools in peatlands. A greenhouse experiment was conducted to study the impact of seedbed and water level on the germination and growth of 7 plant species associated with pools: *Carex limosa* L., *C. magellanica* Lam. ssp. irrigua (Wahlenb.) Hultén, *C. oligosperma* Michx., *C. pauciflora* Lightf., and *Rhynchospora alba* (L.) Vahl from the Cyperaceae family as well as *Drosera intermedia* Hayne (Droseraceae) and *Scheuchzeria palustris* L. (Scheuchzeriaceae). The 3 seedbeds tested were 1) bare peat; 2) a carpet of *Sphagnum cuspidatum* Ehrh. ex Hoffm. and *S. fallax* (Klinggr.) Klinggr. (Sphagnaceae); and 3) a carpet of *Cladopodiella fluitans* (Nees) H. Buch (Cephaloziaceae), common bryophytes along pool edges. Seedbeds were combined with 2 water levels (0 and 10 cm below the soil surface) in a complete factorial block design. Germination periods were generally longer when seeds were submitted to drier conditions and placed on *C. fluitans* carpets. Conditions favoring biomass production were more variable among species. These results will facilitate the identification of the best ecological conditions for successful establishment of pool edge species in the context of restoration projects, thereby increasing biodiversity and ecological value of restored peatlands.

Landry T, Rochefort L, Poulin M. 2012. Impact of seedbed and water level on the establishment of plant species associated with bog pools: implications for restoration. Native Plants Journal 13(3):205–215.

KEY WORDS

seed germination, pool margin, *Carex*, peat stability, seed viability, bryophyte, green house experiment

NOMENCLATURE

Plants: USDA NRCS (2012)
Bryophytes: Faubert (2007)

CONVERSIONS

1 mm = 0.04 in
1 cm = 0.4 in
(°C x 1.8) + 32 = °F

Pools are an important component of peatlands because they contribute to landscape heterogeneity as well as to floristic and faunal diversity (van Duinen and others 2003; Verberk and others 2006; Fontaine and others 2007). Nevertheless, pool creation is often ignored when peatlands are restored using the well-established moss transfer technique (Rochefort and others 2003) on industrial peat fields. This method creates a relatively flat topography and favors uniform vegetation typical of lawns. Creating pools in restored peatlands would increase site biodiversity, but plants must be actively introduced as pool edge species do not recolonize spontaneously (Mazerolle and others 2006; Fontaine and others 2007).

The restoration of pool vegetation communities has been examined in several studies. For bryophytes, Poulin and others (2011) successfully introduced *Sphagnum* species associated with hollows and pools using the moss transfer technique, which consists of collecting a thin layer of vegetation from a nearby undisturbed bog and spreading plant fragments over an area of cut-over peatland that is 10 times larger than the collection site (Rochefort and others 2003). Starting as dispersed fragments, the percentage cover of *Sphagnum* along created pools tripled during the first year following introduction to reach as high as 60% for some species. The restoration of a carpet of *Cladopodiella fluitans* (Nees) H. Buch (Cephaloziaceae), a liverwort associated with pools, is also possible by introducing fragments and covering them with straw mulch (Poulin and other 2011). Successful establishment of a moss carpet following the moss layer transfer technique, however, does not stimulate the spontaneous return of pool vascular species, even though a certain amount of propagules are transferred with the moss fragments (Poulin and others 2011). For these species, it appears that we cannot rely on the rhizomes, roots, or plant fragments occurring in the donor sites, probably because density is too low or because underground structures deeper than the harvested layer are needed.

Re-establishing pool edge communities by seed introduction is an interesting alternative. Seed introduction can increase the genetic diversity and thereafter the resilience of the restored site with better adapted plants (Linhart and Grant 1996; Montalvo and others 1997; Luck and others 2003; Falk and others 2006); however, seeding requires knowledge of the specific germination and establishment conditions needed by each species. Germination of many wetland plants is significantly affected by light exposure, temperature, hydrology, and substrate (Kotowski and others 2001; Kellogg and others 2003). Substrate type may be a particularly important factor to consider for successful restoration of pool edges, as natural peatlands are generally covered by carpets of *Sphagnum* and the liverwort *C. fluitans* (Fontaine and others 2007), whereas the substrate dominating restoration sites is bare, decomposed peat. For created pools in restored peatlands, the influence of substrate type on seed germination may vary with distance from the water edge due to changes in water conditions along the slope. Substrate type (hereafter referred to as "seedbed") should thus be studied in synergy with water level for germination of vascular plants associated with peatland pools.

Seed introduction in a moss carpet may facilitate germination. On one hand, a moss carpet is a microhabitat that traps seeds and prevents them from being washed away. On the other hand, moss could limit seed germination by blocking light (Clymo and Hayward 1982; Robroeck and others 2009), which is essential to many wetland species for germination (Baskin and Baskin 1998; Schültz 2000; Campbell and Rochefort 2003; Kettenring and others 2006). Bryophytes may also compete with plants emerging from their carpet (Hörnberg and others 1997; Rydin and others 2006). Yet, compact carpets of *C. fluitans* could restrain seeds near the surface, minimizing competition and increasing light access compared with *Sphagnum* carpets. The fine particles of a bare peat substrate may easily bury seeds, reducing germination (Campbell and Rochefort 2003). A high water level could exacerbate peat instability through frost heaving (Groeneveld and Rochefort 2005). Generally, however, a high water level lessens the effect of the seedbed, improving germination on less favorable or coarser substrates (Keddy and Constabel 1986; Coops and van der Velde 1995; Baskin and Baskin 1998; Kellogg and others 2003). Water level also has a direct impact on seed imbibition, a factor strongly associated with germination rates (Harper and Benton 1966).

The effect of substrate type and water level has not yet been investigated in synergy for the specific context of peatland plant communities typical of pool edges, despite the well-known importance of these two factors for the germination of wetland plants. In this study, the authors aimed to identify the optimal seedbed and hydrology for the germination of vascular plants typical of pool edges and humid depressions in peatlands. Our specific objective was to determine the influence of 3 types of seedbed as well as 2 water levels (0 and –10 cm) on the germination and growth of 7 vascular plant species commonly found at pool edges in peatlands.

MATERIALS AND METHODS

Experimental Design

A greenhouse experiment was initiated in March 2008. The experimental design included 3 seedbeds (bare peat; a carpet of *Sphagnum cuspidatum* Ehrh. ex Hoffm. and *S. fallax* (Klinggr.) Klinggr. [Sphagnaceae]; or a carpet of the liverwort *Cladopodiella fluitans*, a common bryophyte along pool edges) and 2 water levels (at the surface [0 cm] and 10 cm below the surface) with 6 replicates in a completely randomized block design (36 experimental units). Each experimental unit consisted of a mesocosm (rigid plastic container 70 cm in length, 40 cm wide, and 50 cm deep).

Downloaded from by guest on October 9, 2026. Copyright 2012

Seed Collection, Treatment, and Viability

We selected 7 species identified as being highly associated with pool edges in natural peatlands but absent from restored sites (Fontaine and others 2007). These species were *Carex limosa* L., *C. magellanica* Lam. ssp. *irrigua* (Wahlenb.) Hultén, *C. oligosperma* Michx., *C. pauciflora* Lightf., and *Rhynchospora alba* (L.) Vahl from the Cyperaceae family as well as *Drosera intermedia* Hayne (Droseraceae) and *Scheuchzeria palustris* L. (Scheuchzeriaceae). Mature infructescences were collected from the edges of pools in natural peatlands in Quebec and New Brunswick (between 5 August and 15 September 2007). In the laboratory, infructescences were air-dried for 3 mo. Seeds and perigynium were manually separated from the floral stalk and vegetative debris. We use "seeds" in reference to both fruits (perigynium from *Carex*) and real seeds (*D. intermedia, R. alba,* and *S. palustris*). An air column separator was used to clean the seeds for species with a seed diameter >2 mm. The species *D. intermedia* and *R. alba* were cleaned manually, as their seeds are too small for processing through the machine. For each species, seeds from different locations were composited to prevent provenance from biasing the treatments. Seeds were stratified between wet filter papers at 4 °C for 4 mo. A subsample of seeds was then used for evaluating their viability using the tetrazolium test (TZ) (Grabe 1970), with 4 replicates of 25 seeds, except for *C. magellanica*, which was replicated only 3 times. Seeds were soaked for one night in distilled water at room temperature. Their envelope was incised and they were then soaked in a tetrazolium solution at 1% for one night at 30 °C.

Seedbed Establishment

Each mesocosm was fitted with a water level control system consisting of an internal horizontal drain (a uniformly perforated pipe covered with geotextile) connected through the side of the container to an external vertical pipe that was adjustable to retain variable water quantities as necessary. Mesocosms were then filled to a depth of 33 cm with fibric peat (H4 from Von Post scale; Parent 2001) and watered with distilled water until the peat was completely wet. Afterward, the mesocosms were drained and the peat surface was leveled. To create the *Sphagnum* seedbeds, a carpet 2 to 3 cm deep was grown on peat base using fragments from the section Cuspidata (mainly composed of *S. cuspidatum* and *S. fallax*, collected near pools of a natural peatland in Saint-Charles-de-Bellechasse, Quebec (lat 46°46′N, long 71°00′W) during September 2007. To establish *C. fluitans* seedbeds, we placed complete, dense carpets (collected from the same location at the same time as described above) onto the peat base in appropriate mesocosms. All *in situ* carpets were chosen for uniform cover (particularly for *C. fluitans*), as well as for absence of algae, necrosis, and vascular plants, and were stored in plastic containers at –4 °C until use.

Water level was maintained at 5 cm below the surface for the 4-mo period of carpet establishment (from March to June 2008). During this period, the mesocosms were weeded regularly and an average temperature of 21.5 ± 0.4/16.0 ± 0.5 °C (day/night) with a relative humidity of 68.2 ± 2.4/71.1 ± 3.8% (day/night) was maintained. Natural light was supplemented by artificial light (400 W sodium lights) to maintain a photoperiod of 16 h with an average intensity of 35 mol/m^2/day (PAR). The modified Rudolph solution was used for watering the mesocosms during establishment to rapidly obtain a uniform *Sphagnum* carpet (Faubert and Rochefort 2002a,b, among others: 12 g/l of NH_4SO_4; 5 g/l of NH_4NO_3; 2.76 g/l of HNO_3). All of the mesocosms were randomized after 1.5 mo to limit the potential impact of a light or air draft gradient on seedbed establishment.

After the seedbed establishment period and one week prior to introducing vascular plant seeds, mesocosm water level was adjusted to 0 and 10 cm below the surface to represent wet and dry conditions found near pools of natural peatlands. During the rest of the experiment, we measured water level 3 times per wk and applied rainwater as required to maintain appropriate levels. In practice, the water level was maintained on average at –3.9 ± 0.25 cm for the wet treatment and –16.8 ± 0.47 cm for the dry treatment. Throughout all phases of the experiment, water was added by hand with a sprinkler held approximately 30 cm above each container.

Germination and Growth

We inserted 8 polypropylene pots (bottoms removed; Twin-Pak™, 500 ml, diameter 107 mm) vertically into the peat substrate of each mesocosm to a depth of 3 cm, leaving 7 cm of the pot above the surface. Pots were easily inserted without disturbing the substrate. They served as barriers to segregate seeds from different species within each mesocosm. Into each pot, we placed 100 stratified seeds of one of the 7 tested species on top of the selected seedbeds (the eighth, a control pot, was not seeded). We counted germinants 3 times per week for the first 6 wk and then once per week until the end of the experiment (91 d). A seed was considered to have germinated when the seedcoat was broken and first cotyledons or leaves were visible. For *D. intermedia*, a seed was considered to have germinated when the first leaf had completely developed, as it was difficult to distinguish from the seedbed at younger stages. Special attention was given to ensure that no seeds were left on the wall of the pots after watering. The first 5 plants to germinate were allowed to grow for monitoring purposes, but subsequent plants were removed using tweezers. Seedling growth was evaluated every month by measuring the length from the collar to the tip of the longest leaf. Aboveground biomass was collected after 3 mo of growth, dried at 70 °C for 48 h, and weighed to the closest 0.001 g using an electronic scale (Sartorius MC1 Laboratory LC 620 P). Average temperature was 23.5 ± 1.3 °C/18.8 ± 1.2 °C (day/night) and relative humidity was 67.0 ± 4.1%/75.4 ± 7.3% (day/night).

Downloaded from by guest on October 9, 2026. Copyright 2012

Statistical Analyses

Germination and aboveground biomass data were analyzed with a two-way ANOVA for a completely randomized block design using the SAS GLM procedure (version 9.3.1, SAS Institute). The significance level was established as $p = 0.05$. Data were tested for variance homogeneity and normal distribution of residuals. For those effects found to be significant, the difference among treatments was determined using the LSMEANS procedure. When an interaction was significant, the option SLICE was used in conjunction with LSMEANS.

Each species was analyzed separately. Because *D. intermedia* and *R. alba* appeared spontaneously in our control pots, we adjusted the germination totals of these 2 species by subtracting the number of germinants in the control pots from the number of germinants in the pots where they had been introduced. The germination number for *D. intermedia* was based on the genus *Drosera*, as it was impossible to distinguish between species at this early stage of development.

RESULTS

Germination and Aboveground Biomass

Viability as assessed with TZ was relatively low for certain species (Table 1) and directly influenced the observed germination (Figure 1). In general, germination increased with a water level close to the surface and a seedbed of *Sphagnum* (Figure 1). The combination of these treatments generally produced the highest number of seedlings in the shortest period of time (Figure 2). The longest germination periods often coincided with drier treatments on a denser seedbed (*C. fluitans*), where the seeds were more exposed and less well-anchored in the seedbed. In general, biomass production was favored by species-specific conditions. The members of the genus *Carex* had a higher rate of production on *Sphagnum* seedbed, while *D. intermedia* showed a better growth rate with drier treatments and *Cladopodiella* seedbed (Figure 1). *Rhynchospora alba* showed the highest biomass production on *Cladopodiella* and *Sphagnum* seedbed when water levels were kept close to the surface. Finally, the growth of *S. palustris* was favored simply by a water level closer to the surface for all seedbed treatments. A more detailed analysis of these results by species is presented in the following section.

Carex limosa

Seed viability of *C. limosa* was low (20 ± 2%; Table 1); this species also had the lowest germination (6.6% average). On a *Cladopodiella* seedbed, germination was 1.9 to 1.7 times lower, and occurred more slowly, than on bare peat or *Sphagnum* seedbeds (Figure 1; Table 2). A higher water level increased *C. limosa* germination by 1.4 times, and germination occurred more rapidly, regardless of seedbed (Figure 2). *Carex limosa* produced the most aboveground biomass on a *Sphagnum* seedbed, less on bare peat, and the least on a *Cladopodiella* seedbed. Water level did not affect biomass production (Table 2).

Carex magellanica

The average germination of *C. magellanica* was 18%, only half of the seed viability (32 ± 6%). Germination was most successful on bare peat for the drier treatment, while *Sphagnum* and bare peat resulted in the highest germination under wetter conditions (Figure 1; Table 2). The effect of water level was more pronounced for *Cladopodiella* and *Sphagnum* seedbeds, where the germination was 2 to 2.5 times higher for the wetter treatment. Conditions that produced the highest germination also favored the fastest germination (Spha-0, Peat-0, Peat-10; Figure 2). Biomass production was 1.5 times higher on the *Sphagnum* and bare peat seedbeds than on *Cladopodiella* seedbed (Figure 1; Table 2).

Carex oligosperma

Although seed viability was 37 ± 2.5% (Table 2), no germination occurred on any of the treatments.

Carex pauciflora

While seed viability of *C. pauciflora* was moderate (30 ± 6%), germination was low (9.6% on average; Table 1). Germination was 1.4 times higher for the wetter treatment than for the drier (Figure 1; Table 2). *Cladopodiella* seedbed was not conducive to germination, with germination 2.2 and 2.4 times lower than for the *Sphagnum* and bare peat seedbeds (Figure 1; Table 2). Among *Carex* species, *C. pauciflora* showed a less pronounced difference in time required for germination among the various treatments; most treatments allowed for the majority of seeds to germinate in less than 35 d (Figure 2). Biomass production was not affected by water level, paralleling findings

TABLE 1

Average viability (± standard deviation) of seeds used for a germination and growth experiment for 7 species of plants associated with pool edges.

Species	Average viability (%)
Carex limosa	20 (±2)
Carex magellanica	32 (±6)
Carex oligosperma	37 (±3)
Carex pauciflora	30 (±6)
Drosera intermedia	49 (±5)
Rhynchospora alba	73 (±3)
Scheuchzeria palustris	57 (±3)

Note: Viability was estimated by a tetrazolium test (groups of 25 seeds with 4 replicates, except for *C. magellanica*, which had 3 replicates).

Downloaded from by guest on October 9, 2026. Copyright 2012

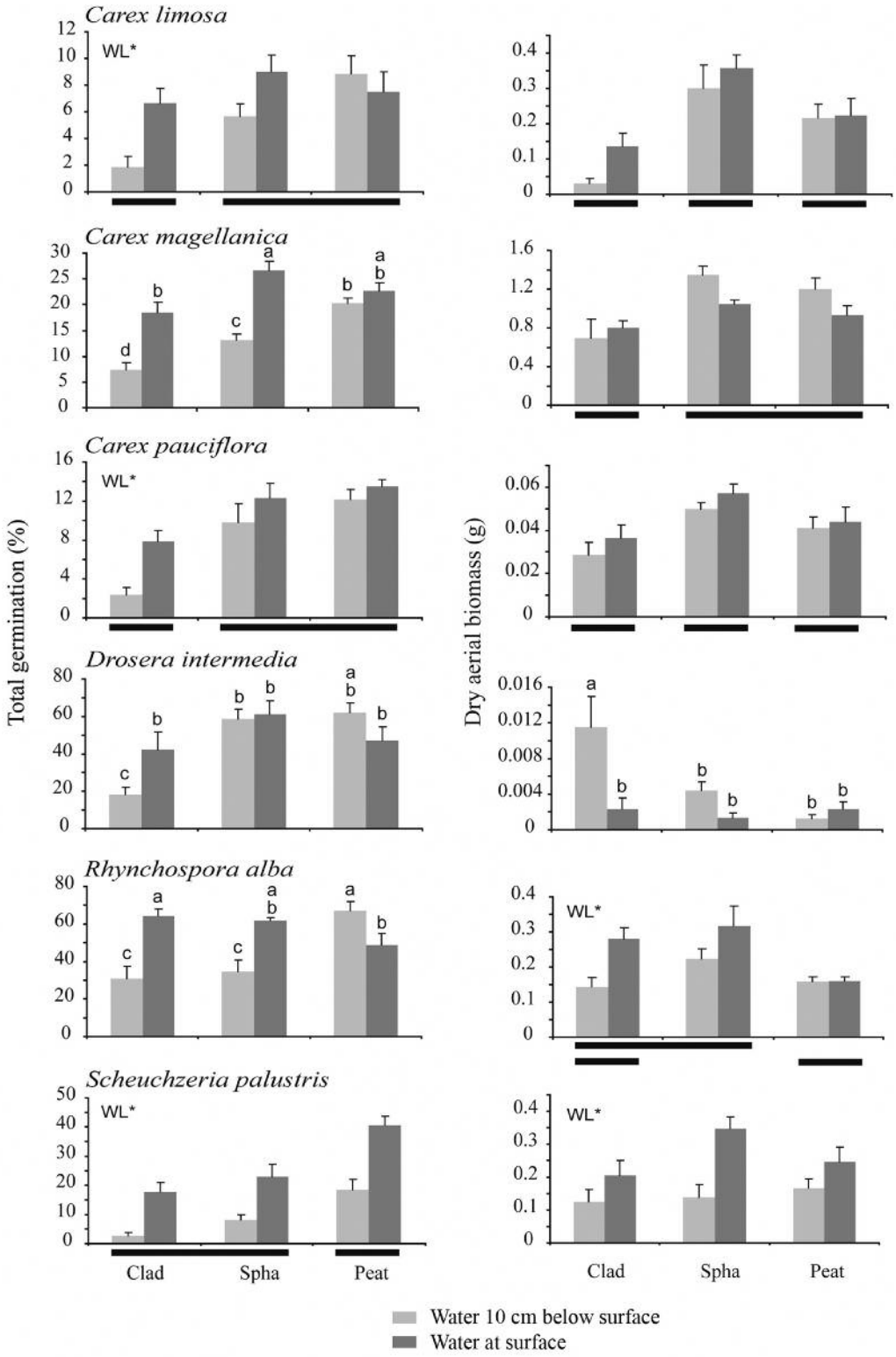


Figure 1. Germination and aboveground biomass production for 3 seedbed types (Clad: *Cladopodiella fluitans*, Spha: *Sphagnum*, Peat: bare peat); 2 water levels (pale gray: water 10 cm below the surface; dark gray: water at surface); and 6 species associated with pool edges in peatlands. Six replicates were used for each species. Error bars represent the standard error. Letters indicate significant differences in the case of significant interaction among the 2 factors ($p \leq 0.05$). When no significant interaction was detected, we illustrated the effect of principal factors by horizontal bars (for seedbeds) or by an asterisk (*) for water level. When significant, a water level close to the surface (0 cm) was always giving higher germination or growth rates than a lower water level (–10 cm). Note that scales differ among species.

Downloaded from by guest on October 9, 2026. Copyright 2012

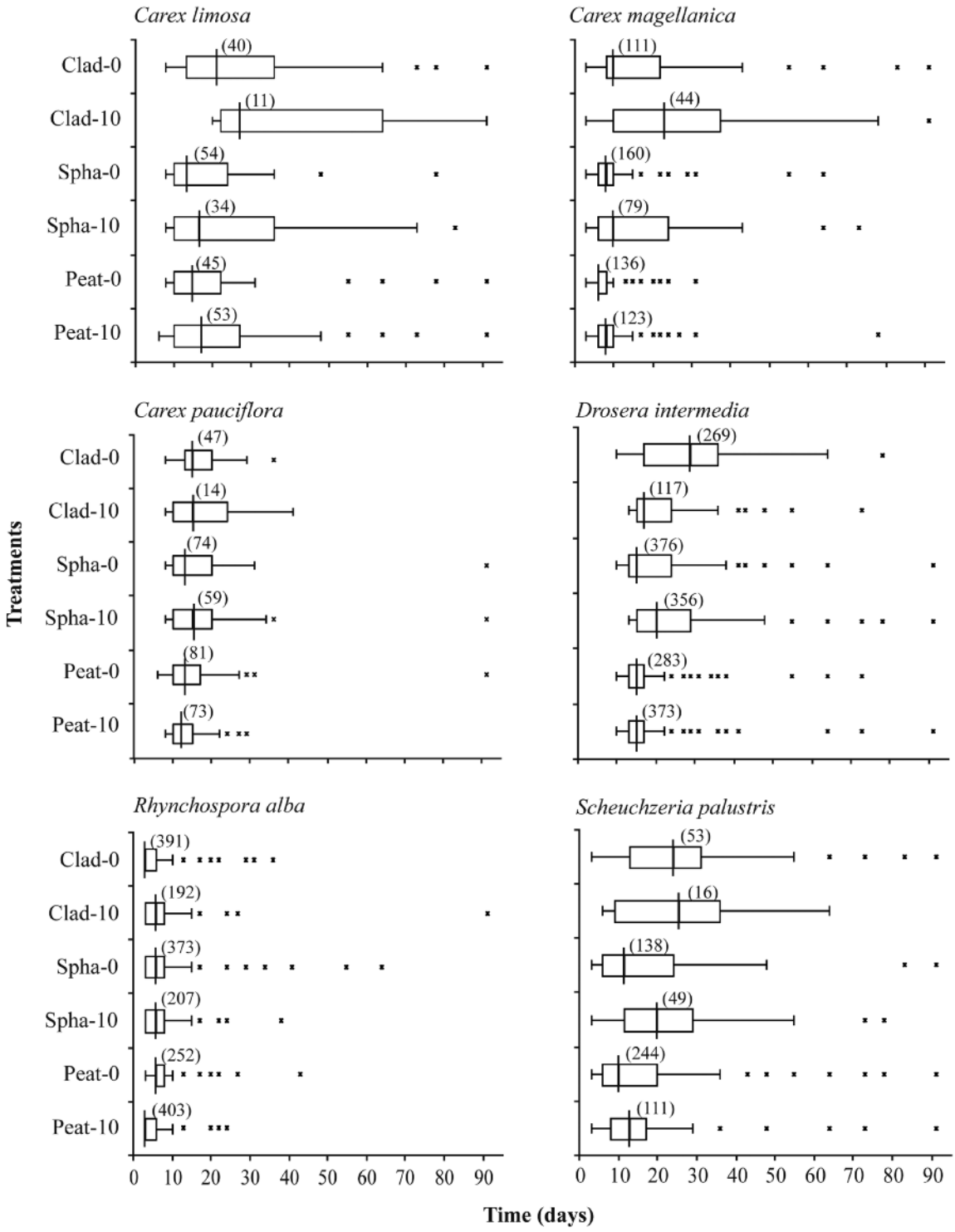


Figure 2. The distribution of seed germination over time for the 6 species associated with pool edges in peatlands. Seedbed treatments were: 1) Clad = *Cladopodiella fluitans*, 2) Spha = *Sphagnum*, 3) Peat = bare peat; and water level treatments were 1) 0 = water at surface and 2) 10 = 10 cm below the surface. The number in parentheses represents the total count of seedlings for the 6 replicates. Boxes represent 25% to 75% of the germination, while lines represent the beginning and end of the germination period, except for extreme values (*). The long vertical line in the box represents the median (50%). Shown values were not corrected for seeds that might have been contained in the seedbeds (germination found on control plots). No statistical analysis was conducted on these data.

Downloaded from by guest on October 9, 2026. Copyright 2012

for other *Carex*. Highest biomass production was obtained on a *Sphagnum* carpet and lowest on a *Cladopodiella* carpet, as with *C. limosa* (Figure 1; Table 2).

Drosera intermedia

Seed viability (49 ± 5%) and germination for *D. intermedia* were relatively high (48% on average; Table 1). Germination was reduced on only the dry treatments of *Cladopodiella* carpets (Figure 1; Table 2), where germination was approximately 3.3 times lower than on dry treatments of *Sphagnum* or bare peat seedbeds. The germination period was shorter on peat. Water level had a strong influence on the length of germination periods for only the *Cladopodiella* carpet, where the drier treatment (Clad-10) accelerated germination (Figure 2). The seedbed influenced biomass production for only the drier treatments, with the *Cladopodiella* seedbed producing 3 and 6 times more biomass than *Sphagnum* and peat seedbeds, respectively (Figure 1; Table 2). For wetter treatments, seedbeds contributed to no significant difference. In brief, growth responses showed inverse results to germination responses.

Rhynchospora alba

Germination of *R. alba* was high (on average 51%). Yet, for drier treatments, germination was 2 times higher on bare peat than on *Cladopodiella* or *Sphagnum* seedbeds (Figure 1; Table 2). Dry peat produced results similar to wet *Cladopodiella* and *Sphagnum* seedbeds. *Rhynchospora alba* also had the fastest germination of any species, less than 15 d across all treatments (Figure 2). The wet treatment allowed aboveground biomass production 1.3 times higher than was obtained for dry treatments (Figure 1; Table 2). Highest growth rates were observed for wet treatments of bryophyte seedbeds.

Scheuchzeria palustris

While *S. palustris* showed a high seed viability (57 ± 3%; Table 1), its germination success was moderate (on average 18%) in comparison with other species. Germination for wet treatments was 3 times higher than for dry treatments (Figure 1; Table 2), and 2 and 3 times greater on bare peat than on the *Sphagnum* and *Cladopodiella* seedbeds, respectively. Bare peat also allowed for faster germination than did the other 2 seedbeds. Although water level did not affect the duration of the germination period (Figure 2), it did influence biomass production, which was twice as high for the wetter treatments (Figure 1; Table 2).

DISCUSSION

Germination

For most species tested in this study, germination was higher when the water level was closer to the surface. Additionally, a high water level attenuated the effect of the seedbed for most species. Keddy and Constabel (1986) obtained similar results in their study of lake shoreline plants. They found that a water level close to the surface favored germination and diminished the effect of a particle-size gradient in the seedbed, especially for small seeds. Indeed, the proximity of water to the seedbed surface facilitated the imbibition of seeds. Germination is thus higher when water tension is lower or when the seed is buried, which improves the contact with the seedbed and protects the seed from evaporation (Harper and Benton 1966).

In our experiment, fine peat particles were able to partially bury seeds and improve seed contact with soil water, which may have facilitated their imbibition and seedling survival. A *Sphagnum* carpet is also permeable for seeds and can maintain a microclimate favorable for germination (Hörnberg and others 1997; Rydin and others 2006). Conversely, a *Cladopodiella* carpet keeps the seeds on the surface, reducing their imbibition. The leaves and stems of this particular liverwort form a tight and stable carpet that only the smallest seeds can penetrate to benefit from a more favorable microclimate. Indeed, our study showed that the species with the smallest seeds (*D. intermedia, R. alba*) had the highest germination on the liverwort carpet.

Reduced light due to seed burial did not seem to affect the species studied. The best germination was observed on bare peat and *Sphagnum* seedbeds (Figure 1; Figure 2). And yet, it is known that light exposure is particularly important for many wetland species (Baskin and Baskin 1998; Schültz 2000; Kotowski and others 2001; Campbell and Rochefort 2003; Kettenring and others 2006). In peat, light is transmitted below the first few millimeters only (Campbell and Rochefort 2003) whereas a *Sphagnum* carpet allows light to penetrate up to 2 cm, depending on the species (Robroeck and others 2009). In our experiment, the 2 seedbeds probably allowed for good light exposure, as the peat substrate was highly compact and *Sphagnum* density was low.

Continued dormancy of seeds could be the cause of low germination for *C. oligosperma*, although the seeds were shown to be viable (Table 1). Campbell and Rochefort (2003) were able to stimulate *C. oligosperma* seeds to germinate by incubating them in peat for 54 wk at 4 °C, but in a preliminary study, scarification of the achene's integument and a cold stratification of 20 wk at 4 °C did not result in germination. *Carex oligosperma* may require a longer cold stratification than other *Carex* species, or simply removing the perigynium may improve its germination, as has been shown for *C. nebrascensis* (Hoag and others 2001).

Aboveground biomass

Carex species accumulated more aboveground biomass on *Sphagnum* carpets without demonstrating a pronounced difference in response to water level. Only *C. magellanica* had higher biomass accumulation on bare peat. All of the bryophyte seedbeds in this experiment had an underlying peat substrate. The *Sphagnum* carpet's microclimate and relative protection

Downloaded from by guest on October 9, 2026. Copyright 2012

TABLE 2

Effect of seedbeds and water level on the germination and biomass production of 6 species associated with pool edges.

Carex limosa		**Germination**		**Biomass**	
Source	**df**	**F**	**p**	**F**	**p**
Block	5	0.2	0.967	0.8	0.548
Water	1	4.8	**0.039**	2.0	0.167
Seedbed	2	5.21	**0.013**	12.3	<**0.001**
Water x seedbed	2	3.2	0.059	0.5	0.622
Error	25				
Total	35				

Carex magellanica		**Germination**		**Biomass**	
Source	**df**	**F**	**p**	**F**	**p**
Block	5	0.5	0.783	1.7	0.183
Water	1	51.9	<0.001	3.2	0.085
Seedbed	2	17.8	<0.001	9.4	<**0.001**
Water x seedbed	2	7.4	**0.003**	2.2	0.130
Error	25				
Total	35				

Carex pauciflora		**Germination**		**Biomass**	
Source	**df**	**F**	**p**	**F**	**p**
Block	5	0.7	0.619	3.2	0.023
Water	1	9.1	**0.006**	2.8	0.106
Seedbed	2	20.6	<**0.001**	11.2	<**0.001**
Water x seedbed	2	1.4	0.256	0.2	0.813
Error	25				
Total	35				

Drosera intermedia		**Germination**		**Biomass**	
Source	**df**	**F**	**p**	**F**	**p**
Block	5	0.8	0.596	1.0	0.431
Water	1	0.5	0.502	8.1	0.009
Seedbed	2	11.0	<0.001	5.6	0.010
Water x seedbed	2	4.1	**0.028**	5.1	**0.014**
Error	25				
Total	35				

Rhynchospora alba		**Germination**		**Biomass**	
Source	**df**	**F**	**p**	**F**	**p**
Block	5	2.0	0.113	0.7	0.625
Water	1	12.7	0.002	8.7	**0.007**
Seedbed	2	2.9	0.073	6.0	**0.007**
Water x seedbed	2	17.3	<**0.001**	2.4	0.115
Error	25				
Total	35				

Scheuchzeria palustris		**Germination**		**Biomass**	
Source	**df**	**F**	**p**	**F**	**p**
Block	5	0.9	0.505	1.1	0.398
Water	1	48.5	<**0.001**	14.7	<**0.001**
Seedbed	2	21.6	<**0.001**	2.0	0.154
Water x seedbed	2	0.9	0.403	1.6	0.2276
Error	25				
Total	35				

Notes: Six replicates were used for each species. A two-way ANOVA for a completely randomized block design was used for evaluations. The *p* values in bold indicate significant differences.

Downloaded from by guest on October 9, 2026. Copyright 2012

from erosion during watering probably favored the establishment of seedlings more so than other mesocosms with only bare peat. The porous nature of the *Sphagnum* carpet allowed better root development, as seeds sometimes have difficulty establishing on smooth or compact surfaces (Sheldon 1974; Chambers and MacMahon 1994). As root penetration rate is directly associated with seedling establishment success (Campbell and Rochefort 2003), seedbed permeability could have favored greater biomass accumulation for *Carex* introduced on *Sphagnum* carpets. Water level did not affect the growth of the 3 *Carex* species, a result supported by the literature (Visser and others 2000; Weltzin and others 2000).

The dry liverwort carpet treatment clearly favored much higher aboveground biomass accumulation for *D. intermedia*. After germination, successful establishment depends on the ability to grow quickly and to avoid competition with other plants. Many carnivorous plants are known to be shade-intolerant (Brewer 1998; Schnell 2002; Ellison 2006), and the small size of *Drosera* seedlings makes them more vulnerable to burial by unstable peat particles or competing plants (Brewer 1999). During the experiment, visual observations of *Cladopodiella* at the lowest water level showed that liverwort growth slowed and plants yellowed, probably due to conditions drier than those found in its natural habitat (Thum 1986; Bragazza and Gerdol 1996). Because competition with *Cladopodiella* stems was reduced, *D. intermedia* seedlings were able to grow more rapidly.

Rhynchospora alba produced more aboveground biomass on wet treatments of *Sphagnum* and *Cladopodiella* carpets. In its natural setting, *R. alba* grows along the edges of pools in carpets of *Sphagnum* or *C. fluitans* (Backéus 1985; Ohlson and Malmer 1990; authors' personal observations), and where the water table is high (Weltzin and others 2000; Gignac and others 2004). This species also prefers open locations where there is little competition (Ohlson and Malmer 1990).

Scheuchzeria palustris accumulated more biomass when the water level was high, regardless of the seedbed. In its natural habitat, this species grows in *Sphagnum* carpets and on muddy bottoms (Backéus 1985), as well as on floating *Sphagnum* carpets surrounding pools (Tallis and Birks 1965). This species seems to tolerate a range of seedbed conditions, even those that are more instable, which may explain the lack of seedbed effect in our study. Weltzin and others (2000) did not observe differences in aboveground biomass in *S. palustris* when adjusting the water level in peatland mesocosms to conditions similar to those we tested. However, our observations correspond to the *in situ* distribution of this species, which is often in the wettest areas of the peatlands (Tallis and Birks 1965; Bragazza and Gerdol 1996; Soro and others 1999).

Implications for Restoration

Seedbeds in our study differed from the substrate that is prevalent soon after peatland restoration using the moss layer transfer technique. In restored peatlands, the lower initial density of the *Sphagnum* carpet and the use of straw could influence the germination and establishment of seedlings by modifying the relative light and humidity in the seedbeds, as well as other components. Pool edges may therefore be restored following a two-step procedure: first, generating a full *Sphagnum* or *C. fluitans* carpet and thereafter introducing seeds for vascular plant establishment. In our study, peat was not detrimental to seed germination and even proved to be as favorable as *Sphagnum* substrate for the germination of most species; but in practice, bare peat at a pool edge may be susceptible to frost heaving and erosion. A *Sphagnum* carpet may act as a seed trap, retaining seeds above the water edge in pools and protecting them from frost heaving, which is a phenomenon observed with other moss carpets (Mallik and others 1984; van Tooren 1988; Kikvidze 1993; Groeneveld and others 2007).

The results of our study show that for *Carex* species in particular, wet *Sphagnum* carpets are the preferred seedbed, favoring both germination and growth. Also, while *D. intermedia* and *R. alba* could be introduced on either *Sphagnum* or *C. fluitans*, the latter should be favored. Indeed, *C. fluitans* is strongly associated with pools in natural peatlands (Fontaine and others 2007), and it apparently increases biodiversity because other uncommon species, such as *Utricularia cornuta* Michx. (Lentibulariaceae), seem to grow in strict association with it. Because this type of seedbed may be inefficient in retaining seeds on a slope, an artificial structure such as phytoplankton net fencing should be installed to trap seeds at the appropriate distance from the water's edge. The preference shown by *S. palustris* for a high water table as well as its presence on loose, floating *Sphagnum* carpets in pools and in the wettest parts of the peatland (Tallis and Birks 1965; Bragazza and Gerdol 1996) indicate that this species would be suitable for introduction in flooded areas or on artificial floating carpets on pool edges. Substrate stability could be a problem though so *Sphagnum* carpets should be favored over bare peat, and seeds may be trapped in artificial structures as well. Since species such as *C. pauciflora* and *S. palustris* germinate over an extended period of time, introduction should be timed to avoid early spring flooding or drought periods typical of midsummer.

ACKNOWLEDGMENTS

The authors thank Sébastien Nadeau, Jérémy Détrée, Mathieu Frégeau, Josée Landry, Mylène Marchand-Roy, and Isabelle Casaubon for their help during fieldwork, as well as Claudia Saint-Arnaud for her advice and logistical support. We are grateful to Stéphanie Boudreau for her statistical advice and to M Graf and K Grislis for English revision. This study was supported by NSERC's Industrial Research Chair in Peatland Management, the Ministry for Natural Resources of New Brunswick, and members of the Canadian Sphagnum and Peat

Downloaded from by guest on October 9, 2026. Copyright 2012

Moss Association. We also thank Les Tourbes Nirom Peat Moss Inc, La Mousse acadienne (1979) ltée, Sun Gro Horticulture Inc, as well as the Duchesnay Touristique Station for allowing access to their property for material collection. We thank the team of technicians in the greenhouse, particularly Carole Martinez and Claudette Roy of Université Laval. This research was funded by a scholarship from the Natural Sciences and Engineering Research Council of Canada to Tommy Landry for Master of Science studies.

REFERENCES

Backéus I. 1985. Aboveground production and growth dynamics of vascular bog plants in central Sweden. Acta Phytogeographica Suecica 74:1–98.

Baskin CC, Baskin JM. 1998. Seeds: ecology, biogeography and evolution of dormancy and germination. San Diego (CA): Academic Press. 666 p.

Bragazza L, Gerdol R. 1996. Response surfaces of plant species along water-table depth and pH gradients in a poor mire on the southern Alps (Italy). Annales Botanici Fennici 33:11–20.

Brewer JS. 1998. Effects of competition and litter on a carnivorous plant, *Drosera capillaris* (Droseraceae). American Journal of Botany 85:1592–1596.

Brewer JS. 1999. Effects of fire, competition and soil disturbances on regeneration of a carnivorous plant (*Drosera capillaris*). American Midland Naturalist 141:28–42.

Campbell DR, Rochefort L. 2003. Germination and seedling growth of bog plants in relation to the recolonization of milled peatlands. Plant Ecology 169:71–84.

Chambers JC, MacMahon JA. 1994. A day in a life of a seed: movements and fates of seeds and their implication for natural and managed systems. Annual Review of Ecology and Systematics 25:263–292.

Clymo RS, Hayward PM. 1982. The ecology of *Sphagnum*. In: Smith AJE, editor. Bryophyte ecology. London: Chapman and Hall. p 229-289.

Coops H, van der Velde G. 1995. Seed dispersal, germination and seedling growth of six helophyte species in relation to water-level zonation. Freshwater Biology 34:13–20.

Ellison AM. 2006. Nutrient limitation and stoichiometry of carnivorous plants. Plant Biology 8:740–747.

Falk DA, Richards CM, Montalvo AM, Knapp EE. 2006. Population and ecological genetics in restoration ecology. In: Falk DA, Palmer MA, Zedler JB, editors. Foundations of restoration ecology: the science and practice of ecological restoration (The science and practice of ecological restoration series). Washington (DC): Island Press. p 14–41.

Faubert J. 2007. Catalogue des bryophytes du Québec et du Labrador. Quebec (Qc): Herbier Louis-Marie, Provencheria 30. 138 p.

Faubert P, Rochefort L. 2002a. Response of peatland mosses to burial by wind-dispersed peat. Bryologist 105:96–103.

Faubert P, Rochefort L. 2002b. Erratum to 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 and Peat 2: art. 6. URL: http://www.mires-and-peat.net/map02/map_02_06.pdf (accessed 18 May 2012).

Gignac LD, Gauthier R, Rochefort L, Bubier J. 2004. Distribution and habitat niches of 37 peatland Cyperaceae species across a broad geographic range in Canada. Canadian Journal of Botany 82:1292–1313.

Grabe DF. 1970. Tetrazolium testing handbook for agricultural seeds. Washington (DC): Association of Official Seeds Analysts. Contribution 29. 62 p.

Groeneveld E, Rochefort L. 2005. *Polytrichum strictum* as a solution to frost heaving in disturbed ecosystems: a case study with milled peatlands. Restoration Ecology 13:74–82.

Groeneveld E, Massé A, Rochefort L. 2007. *Polytrichum strictum* as a nurse-plant in peatland restoration. Restoration Ecology 15:709–719.

Harper JL, Benton RA. 1966. The behaviour of seeds in soil: II. The germination of seeds on the surface of a water supplying substrate. Journal of Ecology 54:151–166.

Hoag JC, Dumroese RK, Sellers ME. 2001. Perigynium removal and cold, moist stratification improve germination of *Carex nebrascensis* (Nebraska sedge). Native Plants Journal 2:63-66.

Hörnberg G, Ohlson M, Zackrisson O. 1997. Influence of bryophytes and microrelief conditions on *Picea abies* seed regeneration patterns in boreal old-growth swamp forests. Canadian Journal of Forest Research 27:1015-1023.

Keddy PA, Constabel P. 1986. Germination of ten shoreline plants in relation to seed size, soil particle size and water level: an experimental study. Journal of Ecology 74:133–141.

Kellogg CH, Bridgham SD, Leicht SA. 2003. Effects of water level, shade and time on germination and growth of freshwater marsh plants along a simulated successional gradient. Journal of Ecology 91:274–282.

Kettenring KM, Gardner G, Galatowitsch SM. 2006. Effect of light on seed germination of eight wetland *Carex* species. Annals of Botany 98:869–874.

Kikvidze Z. 1993. Plant species association in alpine-subnival vegetation patches in the Central Caucasus. Journal of Vegetation Science 4:270–302.

Kotowski W, van Andel, J, van Diggelen R, Hogendorf J. 2001. Responses of fen plant species to groundwater level and light intensity. Plant Ecology 155:147–156.

Linhart YB, Grant MC. 1996. Evolutionary significance of local genetic differentiation in plants. Annual Review of Ecology & Systematics 27:237–77.

Luck GW, Daily GC, Ehrlich PR. 2003. Population diversity and ecosystem services. Trends in Ecology & Evolution 18:331–336.

Mallik AU, Hobbs RJ, Legg CJ. 1984. Seed dynamics in *Calluna-Arctostaphyllos* in north-easterm Scotland. Journal of Ecology 72:855–871.

Mazerolle MJ, Poulin M, Lavoie C, Rochefort L, Desrochers A, Drolet B. 2006. Animals and vegetation patterns in natural and man-made bog pools: implications for restoration. Freshwater Biology 51:333–350.

Montalvo AM, Williams SL, Rice KJ, and 6 others. 1997. Restoration biology: a population biology perspective. Restoration Ecology 5:277–290.

Ohlson M, Malmer N. 1990. Total nutrient accumulation and seasonal variation in resource allocation in the bog plant *Rhynchospora alba*. Oikos 58:100–108.

Parent LE. 2001. Classification, pédogénèse et degradation des sols. In: Rochefort L, Payette S, coordinators and editors. Écologie des tourbières du Québec-Labrador. Québec (Qc): Les Presses de l'Université Laval. p 241–255.

Poulin M, Fontaine N, Rochefort L. 2011. Restoration of pool margin communities in cutover peatlands. Aquatic Botany 94:107–111.

Robroeck BJM, Schouten MGC, Limpens J, Berendse F, Poorter H. 2009.

Downloaded from by guest on October 9, 2026. Copyright 2012

Interactive effects of water table and precipitation on net CO_2 assimilation of three co-occurring *Sphagnum* mosses differing in distribution above the water table. Global Change Biology 15:680–691.

Rochefort L, Quinty F, Campeau S, Johnson K, Malterer T. 2003. North American approach to the restoration of *Sphagnum* dominated peatlands. Wetlands Ecology and Management 11:3–20.

Rydin H, Gunnarsson U, Sundberg S. 2006. The role of *Sphagnum* in peatland development and persistence. In: Wieder RK, Vitt DH, coordinators and editors. Ecological studies, Vol. 188. Boreal peatland ecosystems. Berlin: Springer. p 47–65.

SAS Institute. 1999–2001. SAS Proprietary Software. Release 8.02. Cary (NC): SAS Institute.

Schnell DE. 2002. Carnivorous plants of the United States and Canada. Portland (OR): Timber Press. 468 p.

Schültz W. 2000. Ecology of seed dormancy and germination in sedges (*Carex*). Perspectives in Plant Ecology, Evolution and Systematics 3:67–89.

Sheldon JC. 1974. The behaviour of seeds in soil: III. The influence of seed morphology and the behaviour of seedlings on the establishment of plants from surface-lying seeds. Journal of Ecology 62:47–66.

Soro A, Sunberg S, Rydin H. 1999. Species diversity, niche metrics and species associations in harvested and undisturbed bogs. Journal of Vegetation Science 10:549–560.

Tallis JH, Birks HJB. 1965. The past and present distribution of *Scheuchzeria palustris* L. in Europe. Journal of Ecology 53:287–298.

Thum M. 1986. Segregation of habitat and prey in two sympatric carnivorous plant species, *Drosera rotundifolia* and *Drosera intermedia*. Oecologia 70:601–605.

[USDA NRCS] USDA Natural Resources Conservation Service. 2012. The PLANTS database. URL: http://plants.usda.gov (accessed 2 Mar 2012). Greensboro (NC): National Plant Data Team.

van Duinen GJA, Brock AMT, Kuper JT, and 6 others. 2003. Do restoration measures rehabilitate fauna diversity in raised bogs? A comparative study on aquatic macroinvertebrates. Wetlands Ecology and Management 11:447–459.

van Tooren BF. 1988. The fate of seeds after dispersal in chalk grassland: the role of the bryophyte layer. Oikos 53:41–48.

Verberk WCEP, van Duinen GA, Brock AMT, and 5 others. 2006. Importance of landscape heterogeneity for the conservation of aquatic macroinvertebrate diversity in bog landscapes. Journal for Nature Conservation 14:78–90.

Visser EJW, Bogemann GM, Van de Steeg HM, Pierik R, Blom CWPM. 2000. Flooding tolerance of *Carex* species in relation to field distribution and aeranchyma formation. New Phytologist 148:93–103.

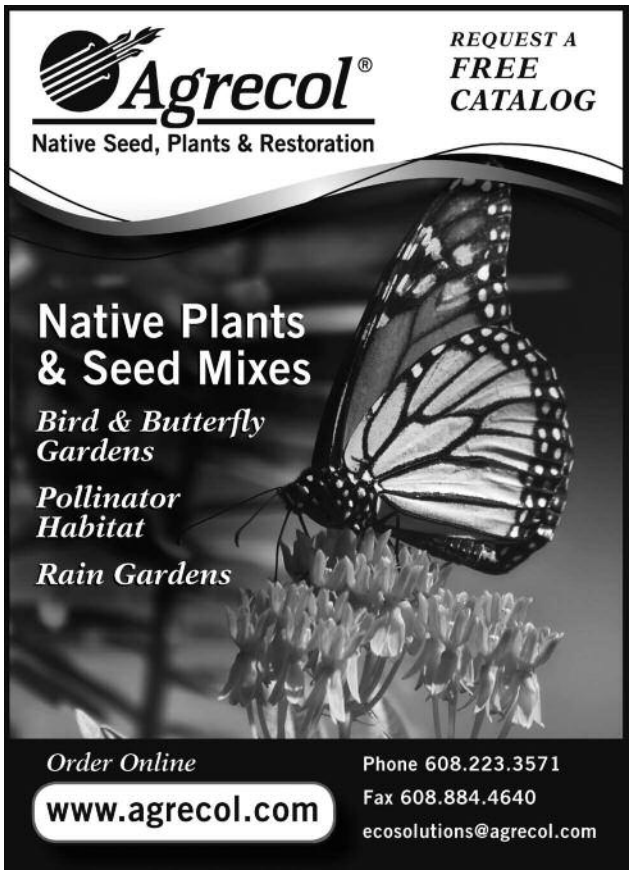
Weltzin JF, Pastor J, Harth C, Bridgham SD, Updegraff K, Chapin CT. 2000. Response of bog and fen plant communities to warming and water-table manipulations. Ecology 81:3464–3478.

Downloaded from by guest on October 9, 2026. Copyright 2012

AUTHOR INFORMATION

Tommy Landry
Biologist
Genivar Inc
300–3450, Gene H Kruger, bureau 300
Trois-Rivières (Québec) G9M 4M3 Canada
tommy.landry.2@ulaval.ca

Line Rochefort
Professor
line.rochefort@fsaa.ulaval.ca

Monique Poulin
Professor
monique.poulin@fsaa.ulaval.ca

Peatland Ecology Research Group and Centre d'études nordiques
Département de phytologie, 2425, rue de l'Agriculture, Université Laval
Ville de Québec, Québec G1V 0A6 Canada