The Bryologist 105(1), pp. 96–103

Response of Peatland Mosses to Burial by Wind-dispersed Peat

PATRICK FAUBERT AND LINE ROCHEFORT
Centre d'Études Nordiques and Département de phytologie, Université Laval, Québec, G1K 7P4 Canada; e-mail: line.rochefort@plg.ulaval.ca

Abstract. *When abandoned peatlands undergo restoration following the extraction of peat moss, newly reintroduced diaspores may be buried by particles eroded from the stripped peat (decomposed) or from adjacent extraction activities. This study examined, in the greenhouse, the tolerance of six species of peat mosses to burial by peat. One of the experiments consisted of depositing predetermined thicknesses (0, 10, and 30 mm) of peat onto partially established mats of* Sphagnum *species and true mosses. A second experiment evaluated the effect of a wider range of burial depths (maximum set at 40 mm) on* Sphagnum fuscum*. After ten weeks of burial, the expansion of the established mosses buried under 10 mm of peat was slowed down but not arrested.* Dicranella cerviculata *is the only species that did not tolerate being buried. The mosses showed three types of final responses to burial: neutral, in which the increases and decreases in cover were not significantly different between the tested and the control depths (for* Sphagnum fuscum *buried under 5 mm and* Sphagnum fallax *buried under 10 mm); negative, in which the decrease in cover was significant at the depth tested (for* Sphagnum fuscum, Sphagnum magellanicum, Polytrichum strictum, *and* Dicranella cerviculata *buried under 10 mm or more, and for* Sphagnum fallax *and* Sphagnum capillifolium *buried under 30 mm of peat); and positive, in which the increase in cover was significant at the depth tested (for* Sphagnum capillifolium *buried under 10 mm of peat). After burial, mosses emerged by means of an innovation or a continuity of the stem of the initial individual for the* Sphagnum *species, and by means of an innovation growing out of the apex of buried individuals in the case of* Polytrichum strictum*. It appears that restoration efforts may be futile in cases where diaspores and newly established mats are likely to be buried at depths exceeding 10 mm.*

In North America, researchers in the field of peatland ecosystem restoration agree that a primary goal is to reestablish a vegetation cover dominated by *Sphagnum* or brown mosses, depending on the type of residual peat moss present at the restoration site (Rochefort 2000). Restoration also aims to reestablish the hydrological regime that characterizes natural peatlands. If these objectives are achieved, the ecosystem will more likely return to a peat-accumulating system. Restoration is carried out by means of three major interventions in the field where the peat was previously extracted (stripped bare following extraction): i) active reintroduction of moss diaspores, ii) application of a protective mulch covering the reintroduced diaspores, and iii) blockage of old drainage canals to raise the water table level close to the surface (Rochefort 2000).

In previously exploited peatlands, or peatlands undergoing restoration, erosion of peat by wind can be observed (Campbell et al. 2001; McNeil et al. 2000). During the extraction of horticultural peat, the peat deposit matrix is broken up to a depth of three to 10 cm so that it may dry and be harvested by giant vacuum harvesters. This activity results in a surface composed of loosened and aerated particles, which are more susceptible to erosion. Particles of peat, thus separated from the main deposit, can be lifted and dispersed by the wind. Vacuum harvesting also plays a major part in the dispersal of peat particles. Extraction activities involve regular harrowing between peat harvesting operations. Harrowing helps in the harvesting process by aerating the peat substrate. This aeration of the substrate is another factor likely to increase erosion of the peat.

These dispersed peat particles can have an impact on restoration, since the eroded particles are often deposited on adjacent lands, and particularly on sites undergoing restoration. In this way, the peat particles bury the reintroduced moss diaspores, and may potentially interfere with restoration efforts. This burial has an effect on certain factors essential to the growth of mosses. For example, light is considerably limited, which influences moss growth (Hayward & Clymo 1983) and the regeneration or development of diaspores (Clymo & Duckett 1986), and also interferes with photosynthesis (Tuittila 2000). On the other hand, shallow burial could act, at the microclimate level, as a protective cover when dry conditions prevail. A dry,

0007-2745/02/96–103$0.95/0

hot microclimate can have significant negative effects on the growth of mosses (Sagot & Rochefort 1996).

The general objective of this study, carried out in the greenhouse, was to examine the tolerance of peatland mosses to burial by peat. The first experiment evaluated the effect of three burial depths on six species of mosses, including four *Sphagnum* mosses and two true mosses, to determine whether the responses differed from one species to the next. The second experiment assessed the effect of a larger range of burial depths on one species of *Sphagnum* moss that has been very successful in establishing itself after introduction onto areas of stripped peat.

Material and Methods

The effect of applying peat onto pre-established moss mats in the greenhouse was studied in seedling trays (52 cm × 26 cm) by adding uniform thicknesses of sifted peat to simulate the different burial depths. The two experiments described below were carried out simultaneously in the same greenhouse over a 21-wk. period, from December 20, 1999 to May 14, 2000.

Burial experiment on six moss species.—The experimental set-up was factorial in complete randomized block design with repeated measures. It included eight blocks, and three factors that were species, burial depth, and time. The experiment consisted of three burial depths, resulting in a total of 18 treatments: six species × three burial depths. Four species of *Sphagnum* and two true mosses were subjected to burial: *Sphagnum fuscum* (Schimp.) Klinggr., *Sphagnum capillifolium* (Ehrh.) Hedw., *Sphagnum magellanicum* Brid., *Sphagnum fallax* (Klinggr.) Klinggr., *Polytrichum strictum* Brid., and *Dicranella cerviculata* (Hedw.) Schimp. These *Sphagnum* species were chosen because they are the most common species found in natural peatlands (Anderson et al. 1995; Gignac 1994). They are also frequently used in restoration activities (Campeau & Rochefort 1996; Ferland & Rochefort 1997; Rochefort 2000). *Polytrichum strictum* was chosen because it is a nearly omnipresent species in peatlands and in reintroduced diaspores. It is believed to assist in the establishment of *Sphagnum* species when they are reintroduced onto bare peat surfaces (Grosvernier et al. 1995). *Dicranella cerviculata* was selected because it frequently colonizes abandoned surfaces after peat extraction (L. Rochefort, pers. obs.) in places where the substrate is stable.

The mats of reintroduced shoot fragments were buried under thicknesses of 0, 10, and 30 mm of peat. The 10-mm thickness was chosen because it may actually assist in the survival and growth of mosses by providing nutrients and protecting them from desiccation. The maximum thickness of 30 mm was chosen because it was likely to prevent the growth and survival of the mosses. Nevertheless, it is known that certain *Polytrichum* species can emerge after being buried by up to 70 mm of sand (Birse et al. 1957; Martínez & Maun 1999).

Burial experiment on Sphagnum fuscum.—This experiment tested a wider range of burial depths on *Sphagnum fuscum*, the species with the greatest success rate for establishment following introduction onto areas of stripped peat (Chirino & Rochefort 2000). Burial depths of 0, 5, 10, 20, 30, and 40 mm in thickness were tested using a complete randomized block design comprising eight blocks. These burial depths allowed us to obtain a gradient of responses and to determine the maximum tolerance of the species.

Experimental Procedure

Collection of moss diaspores.—In the autumn of 1999, the diaspores of four *Sphagnum* species were collected in a peatland near St-Charles-de-Bellechasse (46°46′ N; 70°58′ W), from the five top centimeters near the surface. This collected layer can contained shoot apices, capitula, fragments, or spores of the mosses. This collection level (between 0 and 10 cm) is the layer with the greatest potential for containing regenerating diaspores (Campeau & Rochefort 1996). Diaspores of the two species of true mosses were collected in the abandoned sections of a peatland still being exploited at Saint-Henri-de-Lévis (46°42′ N; 71°03′ W). During collection, the mosses were placed in plastic bags and then stored in a refrigerator at an average temperature of 4°C for a maximum period of eight weeks. *Polytrichum strictum* and *Dicranella cerviculata* were collected in the field with the peat to which they were attached. *Polytrichum strictum* was separated from this peat using scissors, to conserve only the green parts of the stems, which were then rinsed. *Dicranella cerviculata* was separated from the peat using a scalpel, leaving only five mm of peat on the moss. These fragments were then rubbed by hand to eliminate clumps.

Preparation of trays.—The *Sphagnum* peat used in the experiments was fibric with a decomposition level of two on the von Post scale. A basal layer of peat about 1.5 cm thick served as the growing substrate. The peat was moistened with deionized water, then levelled and compressed. Clumps were broken up to make the peat as homogeneous as possible. The mosses were placed uniformly on the peat on December 20, 1999. The mosses had to adhere well to the peat to allow sufficient contact with the substrate. After the mosses were introduced, an agrotextile cloth was placed on the surface of the trays to create a protective microclimate for the beginning of the growth period. To prevent undesirable etiolation, the covering was taken off after 31 d.

The density of diaspores reintroduced into the growing trays corresponded to a ratio of 1:6, that is, the equivalent of a one m^2 area of vegetation collected in the field spread over six m^2 of surface area. This ratio was considered to be high compared to the 1:10 or 1:15 ratio normally used during restoration (Rochefort 2000). Nevertheless, this ratio was used in order to obtain an initial area of vegetation abundant enough to allow the experiment to be carried out in the greenhouse. Before reintroducing the moss material in the trays, it was cleaned of any vascular plant material collected along with the mosses. Finally, the diaspores from all the moss species were chopped coarsely to simulate the type of handling practiced in the field during restoration activities and to facilitate uniform reintroduction.

Watering and fertilization.—For the first 14 wk., the watering frequency was twice a wk. After 14 wk., the frequency was increased to three times a week due to a higher evaporation rate caused by the higher maximum temperatures of the spring time. Each tray received about 0.57 liter of solution at each watering period. The mosses were watered with a modified Rudolph nutrient solution (Campeau & Rochefort 1996; Rudolph et al. 1988). A light fertilization was needed as direct tap water cannot be used for watering because of its high calcium content detrimental to *Sphagnum* moss growth. Thus deionized water was supplemented with a nutrient solution. Details concerning the protocol, composition, and concentrations in this solution are found in Appendix 1. The concentrations of certain elements in the solution were modified according to the growth stages of the mosses. The concentration of NH_4NO_3 was set at 1.65 ml liter^{-1} at the beginning of the experiment to promote the onset of growth, and then decreased to 0.25 ml liter^{-1} after 24 d. After seven weeks, the concentrations of all the elements in the solution were reduced by a factor of four. The purpose of this reduction was to create conditions similar to those found in the field.

Burial method.—Burial with peat was carried out after 11 wk. of moss growth. The objective was to obtain a cover for the mat of reintroduced diaspores in the trays of 25 to 35% for the *Sphagnum* species and five to 15% for the true mosses, before adding the peat. These percentages of moss cover were representative of the levels of cover obtained after two to four years of restoration in the field (L. Rochefort, pers. obs.). The peat was deposited by adding successive layers five mm thick, depending on the desired burial depth. The peat used to make up these layers was of the same type used for the substrate. It had been previously sifted through a screen with openings of 4.75 mm so as not to exceed the burial depth of five mm and to represent the size of particles likely to be eroded by the wind (Campbell et al. 2001). The quantity of peat required to make up the 5-mm layer had been determined by dry weight, following six trials with peat flattened between two Plexiglas panels. The burial was carried out using a system that ensured a uniform deposition of peat particles on the newly established mosses.

Greenhouse conditions.—The photoperiod was set at 16 hr of light per day, and was composed of natural light supplemented with 400-watt sodium bulbs during periods of low sunlight. The light flux (PAR) varied between 730 μmol m^{-2} sec^{-1} for a sunny day (no artificial lighting), to a minimum of 145 μmol m^{-2} sec^{-1} for a cloudy day where a permanently installed shade covered the roof of the greenhouse due to warm springtime conditions. Data gathering cells were located at the centre of the greenhouse and measured the temperature and relative humidity every 30 min. The minimum and maximum averages for 15-d periods were calculated. The maximum average temperature and relative humidity increased after the first 10 wk. They varied between 21 and 24°C and 90 and 97% during the first 10 wk., and between 26 and 28°C and 98 and 100%, respectively, for the rest of the experiment. The average minimum temperatures remained stable throughout the experiment, and varied between 14 and 16°C. The average minimum relative humidities decreased after the first 14 wk. They varied between 66 and 73% during the first 14 wk., and between 53 and 64% for the rest of the experiment. A fogging system was used after the 11th week from 10:00 to 16:00 until the end of the experiments. It operated at 10-minute intervals for a duration of 1.5 min.

Variables Measured

For both experiments, percent cover was measured after eight weeks of growth without burial, and 2, 5, 8, and 10 wk. after burial with peat. The cover was evaluated by visual estimation, omitting the first two cm at the edge of the tray, in order to avoid any ''edge'' effect. Cover was estimated to the closest 1% under covers of 25% and to the nearest 5% for above. The percent cover estimated at different intervals after burial was compared to the cover estimated after eight weeks of growth without burial, to determine the increase or decrease in area occupied by the mosses.

TABLE 1. Expected and actual thickness of peat burial depths at the end of the experiments.

Expected burial depths (mm)	Actual burial depths (Average (mm) ± standard deviation)	*n*
5	6.1 ± 0.9	16
10	11.1 ± 1.5	112
20	21.8 ± 1.5	16
30	29.3 ± 1.8	112
40	38.7 ± 1.8	16

For both experiments, qualitative descriptions of the regeneration of buried fragments were carried out one week prior to taking the final cover estimates for the control and maximum depths. For the experiment on the six different species, the regeneration phenomena were described for a sample of 30.2 cm^2 taken in a tray representative of the treatment. For the experiment with *Sphagnum fuscum*, the descriptions were made using two samples per tray.

At the end of the two experiments, the actual thicknesses of the burial depths were measured at two places in each tray. Differences between the expected and actual thicknesses were minimal (Table 1). These slight differences indicated that the method of burial used was effective.

Statistical Analyses

Data were analyzed using analysis of variance with *a posteriori* protected LSD tests, using the GLM procedure of the SAS software (SAS Institute Inc. 1996). A first analysis of variance comparing the percentages of cover after eight weeks of growth without burial was carried out in order to verify the initial homogeneity of the trays between treatments. A repeated measure analysis of variance was then carried out on the values of increased or decreased cover calculated between the eighth week of growth without burial and the tenth week after burial. The values of the increased or decreased cover were transformed [log (x + 100)] before analysis. Differences between the treatments were considered significant with a likelihood of Type I error of 0.05.

Tray Conditions Before Burial

For both experiments, no significant difference could be detected between the groups of trays that received the different burial treatments. For the experiment on the six different species, *Sphagnum magellanicum* showed a slightly higher cover than the other *Sphagnum* species, and the cover of *Dicranella cerviculata* was significantly higher than that of *Polytrichum strictum* (protected LSD test, $p \leq 0.05$; Fig. 1). The higher cover of *Sphagnum magellanicum* and *Dicranella cerviculata* was considered minimal. For the experiment with *Sphagnum fuscum*, there was no significant difference in cover between the trays.

Results

Burial experiment on six moss species.—The four species of *Sphagnum* tested showed some tolerance to burial by peat, but this tolerance varied

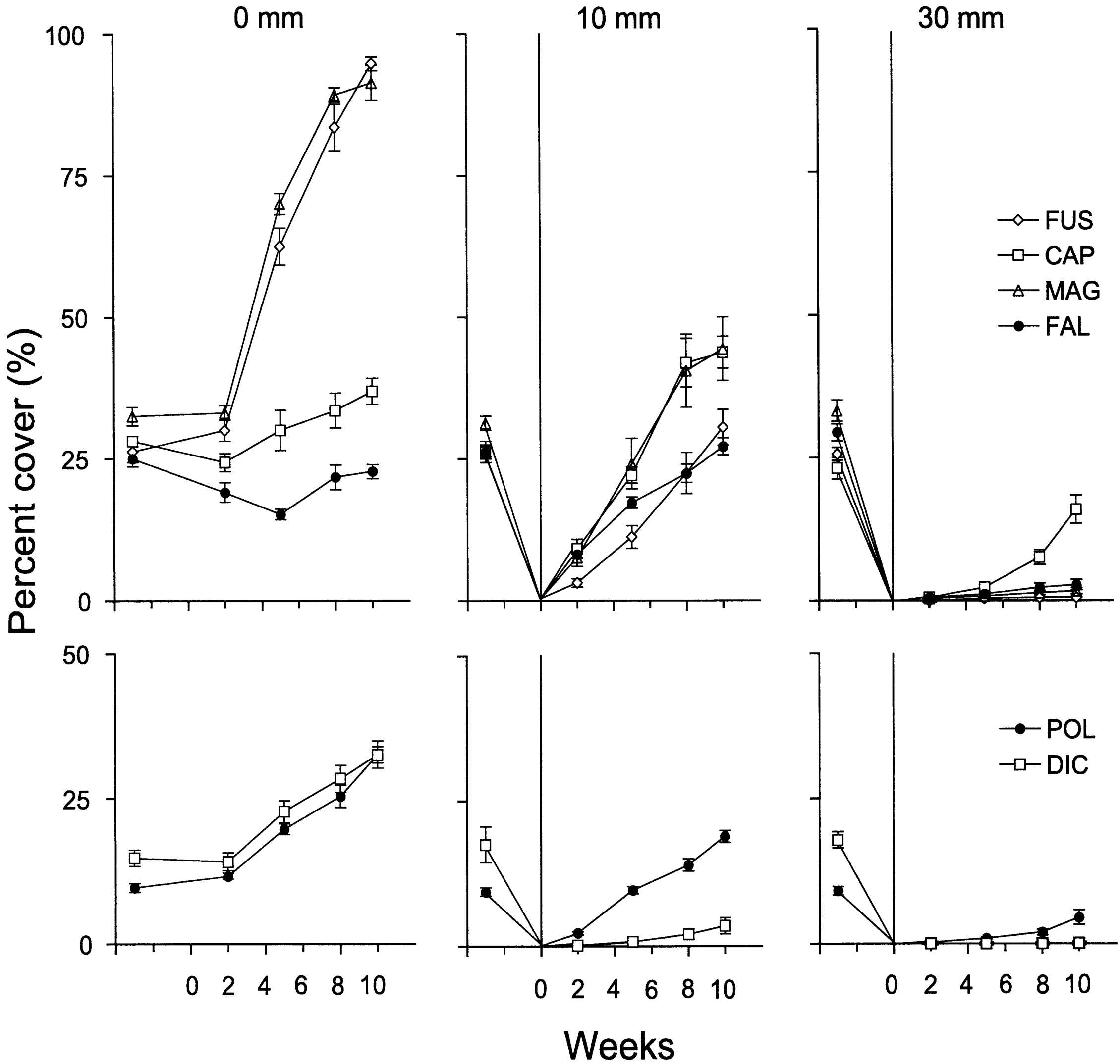

FIGURE 1. Responses of four *Sphagnum* species and two true moss species to burial by peat. The mean percent cover (± standard error) was evaluated after eight weeks of growth without burial (established mat) and 2, 5, 8, and 10 wk. after the application of peat ($n = 8$). The vertical line at week 0 indicates the time when the peat was applied. FUS, *Sphagnum fuscum*; CAP, *S. capillifolium*; MAG, *S. magellanicum*; FAL, *S. fallax*; POL, *Polytrichum strictum*; DIC, *Dicranella cerviculata*.

depending on the species and the burial depth (Fig. 1 and Table 2). Under 10 mm of peat, the final cover of the four species reached 25 to 50%, that is, 0 to 25% higher than before burial, which indicated some tolerance to burial at this depth (Fig. 1). *Sphagnum magellanicum* and *S. capillifolium* showed increases in cover when buried under 10 mm of peat that were significantly higher than *S. fuscum* and *S. fallax* (protected LSD test, $p \leq 0.05$). Burial slowed down development of the mat in *S. fuscum* and *S. magellanicum,* since the final cover attained under 10 mm of peat was 64% and 42% lower, respectively than that of the control. For *S. fallax*, development of the mat did not slow down under 10 mm of peat, since the increase in cover in the presence or absence of burial was not significantly different (protected LSD test, $p \geq 0.05$). For *S. capillifolium,* mat development under 10 mm of peat was higher in the absence of burial (protected LSD test, $p = 0.0201$). Almost all the *Sphagnum* species tested showed no regrowth in cover at a burial depth of 30 mm. *Sphagnum capillifolium,* with a final cover of 16%, nevertheless stood out from the other species and was by far the species that showed the greatest regrowth.

The two species of true moss showed different changes in percent cover after burial (Fig. 1 and Table 2). Under 10 mm of peat, *Polytrichum stric-*

TABLE 2. Repeated-measures ANOVA of increases and decreases in percent cover (log transformed data (x + 100)), obtained between the eighth week of growth without burial and the tenth week after burial, for six moss species. All factors were significant at $P = 0.0001$.

Source	Degrees of freedom	Mean square	F
Effects of main experimental unit			
Block	7	0.0113	
Species	5	0.0664	26.4
Burial depth	2	1.31	522
Species*Burial depth	10	0.0943	37.6
Error (Block*Species*Burial depth)	119		
Effects of repeated measures (experimental sub-units)			
Time	3 (1)[a]	0.166	747.8
Time*Species	15 (5)	0.00851	38.5
Time*Burial depth	6 (2)	0.024	108.5
Time*Species*Burial depth	30 (10)	0.00508	22.9
Error	378 (126)		

[a] The degrees of freedom in parentheses have been Box corrected.

tum regrew to its initial percent cover and even slightly more, whereas the cover of *Dicranella cerviculata* decreased. The tolerance of *Polytrichum strictum*, with a final percent cover of 19%, was clearly superior to that of *Dicranella cerviculata* which, with a final cover of 4%, did not tolerate this burial depth. Burial under 30 mm of peat had a considerable negative effect, since the cover of both species decreased. *Polytrichum strictum* showed a final cover of only 5%, whereas *Dicranella cerviculata* barely emerged with a final cover of almost zero (0.06%). Considering the similar responses of these two species when they were not buried, it can be stated that the burial had more pronounced negative effects on *Dicranella cerviculata*.

Burial experiment on Sphagnum fuscum.—The wider range of burial depths tested on *S. fuscum* show that the limit tolerated by this species is fixed at a thickness of 10 mm (Fig. 2). For example, at depths of five and 10 mm, *S. fuscum* showed a final cover of 93 and 31%, respectively whereas for depths of 20 mm and over, the cover was almost zero.

Regeneration of fragments following burial.—The four *Sphagnum* species showed differences in color between the initial individuals and the innovations. Specifically, the innovations were more green irregardless of the color of the initial individual. Furthermore, the innovations grew out of different parts of the buried initial individual. An emergent capitulum grew from the continuity of the stem of the initial individual. An interval with no branching, but with a few cauline leaves, was present on the buried part (Fig. 3A). An emergent innovation grew from the buried capitulum of the initial individual. The capitulum of the innovation was separated from the initial capitulum by an interval with no branching (Fig. 3B). This interval had a few cauline leaves in *S. magellanicum*, but there was none present in *S. capillifolium*. An emergent innovation also grew from the stem, immediately adjacent to a branch fascicle (Fig. 3C). In the samples of *S. fuscum*, the innovations in the process of emerging had no capitula at their extremities and were rather pointed in shape.

The emergent innovations from the buried diaspores of *Polytrichum strictum* grew from the stem apex of the initial individual (Fig. 4A). In some cases, emergent innovation seemed to have been favored by the bend created on the reintroduced fragments in response to geotropism (Fig. 4B). However, all emergent innovations possessed an interval without leaves before emerging from the peat regardless of their origin, and the buried parts were always more pale in color than the initial individuals. Finally, no emergence was observed in the sample of *Dicranella cerviculata* buried under 30 mm of peat.

DISCUSSION

Burial with peat.—The expansion of the established mosses in all species was slowed down but not arrested by burial. For most species, the time required to re-establish was longer when the burial depth was increased. This reaction is similar to that found in a study of the burial of mosses with sand, in which the time to re-establish for some species was longer at greater burial depths (Birse et al. 1957). Moreover, most species tolerated being buried under 10 mm of peat, with the exception of *Dicranella cerviculata* that did not tolerate any burial depth.

The moss species showed different final responses to being buried by peat. Their final responses can be compared to the three responses, as proposed by Martínez and Maun (1999), for dune

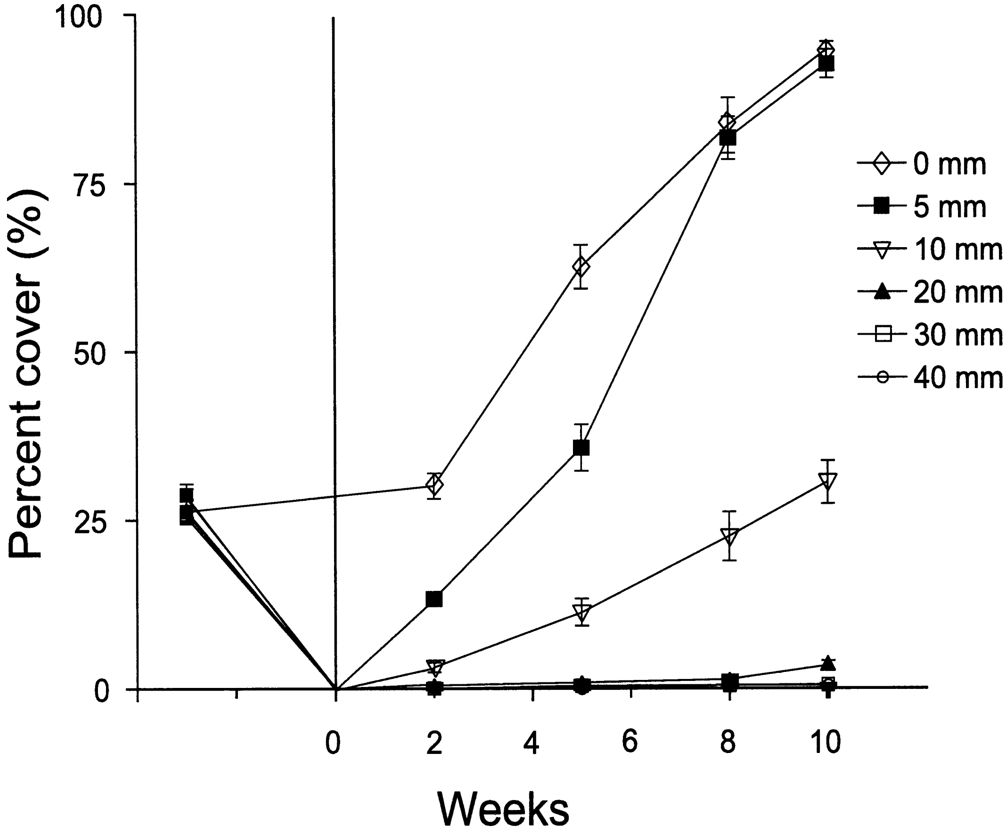

FIGURE 2. Response of *Sphagnum fuscum* to burial by peat. The mean percent cover (± standard error) was evaluated after eight weeks of growth without burial (established mat) and 2, 5, 8, and 10 weeks. after the application of peat (n = 8). The vertical line at week 0 indicates the time when the peat was applied.

mosses buried by sand 1) a neutral final response, in which the increase or decrease in cover between the eighth week of growth without burial and the tenth week after burial was not significantly different between the levels tested and the control, 2) a negative final response (inhibition) in which the decrease in cover was significant at the level tested, and 3) a positive final response (stimulation) in which the increase in cover was significant at the level tested. According to these strategies, *Sphagnum fuscum* and *S. fallax* showed a neutral final response under five and 10 mm of peat, respectively. In addition, *S. fuscum*, *S. magellanicum*, *Polytrichum strictum*, and *Dicranella cerviculata* under

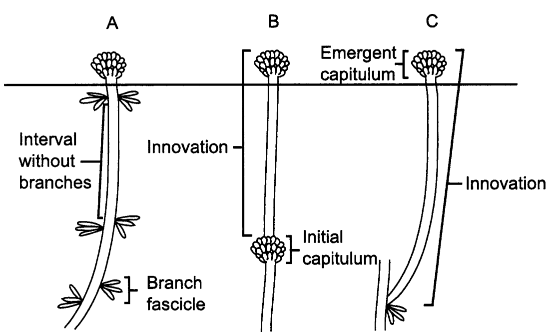

FIGURE 3. Regeneration of *Sphagnum* individuals following burial—A. Emergent capitulum arising from the continuity of the stem of the initial individual—B. Emergent innovation growing from the buried capitulum of the initial individual—C. Emergent innovation growing from the stem, immediately adjacent to a branch fascicle.

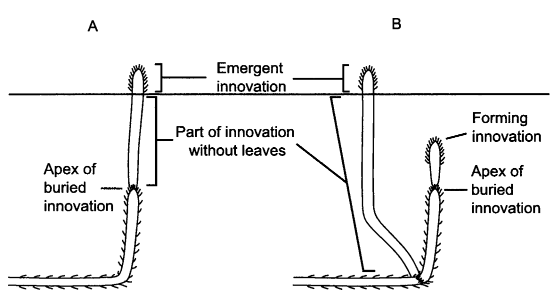

FIGURE 4. Regeneration of *Polytrichum strictum* shoots following burial—A. Emergent innovation growing from the stem apex of the initial individual—B. Emergent innovation growing from the bend of the reintroduced fragment in response to geotropism. An innovation can be forming as well at the apex of the same fragment.

10 mm of peat or more, as well as *S. fallax* and *S. capillifolium* under 30 mm, showed negative final responses. *Sphagnum capillifolium* showed a positive final response under 10 mm of peat. This positive final response led us to conclude that the 10-mm burial depth stimulated the growth of *S. capillifolium* in the greenhouse. The positive and neutral final responses may be explained by the loose structure of the moss mat in *S. capillifolium* and *S. fallax* reintroduced in the greenhouse. This loose structure allowed the deposited peat to percolate downwards between the capitula. This percolation favoured the growth of *S. capillifolium* and *S. fallax* by permitting more light to penetrate.

Regeneration of newly established moss following burial.—The descriptions of the regeneration of buried *Sphagnum* individuals resemble those described in a study by Clymo and Duckett (1986), in which the authors observed the regeneration of *Sphagnum* species from the *Sphagnum* and *Cuspidata* sections, common to our study. For example, the authors observed differences in color between the innovations and the initial individuals in the regrowth phase. On the other hand, Clymo and Duckett (1986) observed that regeneration in the *Cuspidata* section came from the branch, whereas in the *Sphagnum* section, regeneration took place on the stem (immediately adjacent to a branch fascicle), phenomena that were not observed in our study. However, these descriptions resemble those observed in a study by Rochefort et al. (1995) in which the regeneration of species in the *Sphagnum*, *Acutifolia*, and *Cuspidata* sections was studied. The authors observed that almost all parts of a *Sphagnum* plant had some regenerative power. Regeneration in the *Acutifolia* section took place from the capitulum, and in all the sections studied, the best regeneration were obtained from the stem (immediately adjacent to a branch fascicle), which corresponds to observations made for *S. capillifolium* in the present study.

Implications for the restoration of abandoned peatlands.—Although this study was performed in the greenhouse, certain conclusions can be drawn about the effects of burial by peat on diaspores reintroduced during peatland restoration and newly established mosses. First, restoration efforts would be futile in abandoned peatlands where the likelihood of burial by peat is high, since burial by over 10 mm of peat was not tolerated in the greenhouse under optimal moisture and nutrient regimes. Other experiments under field conditions with longer reestablishment times and greater burial depths (e.g., 50, 75, and 100 mm) would help to determine the burial limit that could potentially be tolerated in the field. However, if growth conditions for mosses are suitable, shallow burial (less than 10 mm) might be tolerated in the field. This tolerance would be accompanied by a longer than normal time for the reestablishment of diaspores (pers. obs.). Tolerances might also be greater for *Sphagnum capillifolium* and *S. fallax*, that did not show negative final responses under 10 mm of peat. In the field, the species that has showed the greatest establishment success after being introduced onto bare substrates was *Sphagnum fuscum* (Campeau & Rochefort 1996; Chirino & Rochefort 2000). In abandoned peatlands where the likelihood of burial by peat is almost zero, it would be better to use *Sphagnum fuscum* to ensure successful establishment. However, in abandoned peatlands where slight burial is likely to occur, restoration strategies should opt for the reintroduction of a mat of *Sphagnum* in which *S. capillifolium* is present with *S. fuscum*. *Sphagnum fallax* showed a low establishment success if it is reintroduced with species of *Sphagnum* from the *Acutifolia* section (Chirino & Rochefort 2000), and should not be reintroduced with these two species. Finally, restoration strategies should also consider the spatial conditions that may lead to burial by peat, such as the positioning of sectors to be restored with respect to sediment sources and the wind. Such spatial conditions would allow for the identification of locations with a high probability of burial.

Acknowledgments

We wish to thank Daniel Campbell, who provided us with practical advice throughout the experiments, as well as Suzanne Campeau, who provided valuable help during the statistical analyses. We also thank members of the Peatland Ecology Research Group (PERG) who revised the manuscript. Finally, we thank Simon Boudreau, Stéphane Dupuis and Ève Richelieu, who helped perform some of the experimental procedures.

Literature Cited

Anderson, D. S., R. B. Davis & J. A. Janssens. 1995. Relationships of bryophytes and lichens to environmental gradients in Maine peatlands. Vegetatio 120: 147–159.

Birse, E. M., S. Y. Landsberg & C. H. Gimingham. 1957. The effects of burial by sand on dune mosses. Transactions of the British Bryological Society 3: 285–301.

Campbell, D. R., C. Lavoie & L. Rochefort. 2002. Wind erosion and surface stability in abandoned milled peatlands. Canadian Journal of Soil Science (in press).

Campeau, S. & L. Rochefort. 1996. *Sphagnum* regeneration on bare peat surfaces: field and greenhouse experiments. Journal of Applied Ecology 33: 599–608.

Chirino, C. C. & L. Rochefort. 2000. Comportement des sphaignes en phase d'établissement dans une tourbière résiduelle/Establishment response of four *Sphagnum* species on cutover peatland, pp. 694–698. *In* L. Rochefort & J. Y. Daigle (eds.), Sustaining our Peatlands, Proceedings of the 11th International Peat Congress, August 6–12th, 2000, Québec city, Canada.

CLYMO, R. S. & J. G. DUCKETT. 1986. Regeneration of *Sphagnum*. New Phytologist 102: 589–614.

FERLAND, C. & L. ROCHEFORT. 1997. Restoration techniques for *Sphagnum*-dominated peatlands. Canadian Journal of Botany 75: 1110–1118.

GIGNAC, L. D. 1994. Peatland species preferences: an overview of our current knowledge base. Wetlands 14: 216–222.

GROSVERNIER, P., Y. MATTHEY & A. BUTTLER. 1995. Microclimate and physical properties of peat: new clues to the understanding of bog restoration processes, pp. 435–450. *In* B. D. Wheeler, S. C. Shaw, W. J. Fojt & R. A. Robertson (eds.), Restoration of Temperate Wetlands. John Wiley & Sons, Chichester.

HAYWARD, P. M. & R. S. CLYMO. 1983. The growth of *Sphagnum*: experiments on, and simulation of, some effects of light flux and water-table depth. Journal of Ecology 71: 845–863.

MARTÍNEZ, M. L. & M. A. MAUN. 1999. Responses of dune mosses to experimental burial by sand under natural and greenhouse conditions. Plant Ecology 145: 209–219.

MCNEIL, P., J. M. WADDINGTON, C. LAVOIE, J. S. PRICE & L. ROCHEFORT. 2000. Contemporary and long-term peat oxidation rates in a post-vacuum harvested peatland, pp. 732–741. *In* L. Rochefort & J. Y. Daigle (eds.), Sustaining our Peatlands, Proceedings of the 11th International Peat Congress, August 6–12th, 2000, Québec city, Canada.

ROCHEFORT, L. 2000. *Sphagnum*–A keystone genus in habitat restoration. THE BRYOLOGIST 103: 503–508.

———, R. GAUTHIER & D. LEQUÉRÉ. 1995. *Sphagnum* regeneration - Toward an optimisation of bog restoration, pp. 423–434. *In* B. D. Wheeler, S. C. Shaw, W. J. Fojt and R. A. Robertson (eds.), Restoration of Temperate Wetlands. John Wiley & Sons, Chichester.

RUDOLPH, H., M. KIRCHHOFF & S. GLIESMANN. 1988. *Sphagnum* culture techniques, pp. 25–34. *In* J. M. Glime (ed.), Methods in Bryology, Proceedings of the Bryological Methods Workshop, Mainz. Hattori Botanical Laboratory, Nichinan.

SAGOT, C. & L. ROCHEFORT. 1996. Tolérance des sphaignes à la dessiccation. Cryptogamie: bryologie, lichenologie 17: 171–183.

SAS INSTITUTE INC. 1989–1996. SAS Release 6.12 ed. SAS Institute Inc., Cary, NC.

TUITTILA, E. S. 2000. Restoring vegetation and carbon dynamics in a cut-away peatland. 38 p. Ph.D. dissertation, Publications in Botany from the University of Helsinki, No 30, Helsinki.

ms. submitted June 20, 2001; accepted Sept. 21, 2001.

APPENDIX 1. Protocol of the Rudolph Solution. The nutrient solution used was a modified version (S. Campeau, pers. comm.) of the solution described by Rudolph et al. (1988) and Campeau and Rochefort (1996). The base solutions were concentrated to reduce volumes for transport. In addition, the quantities of iron and micronutrients were increased compared to the solution described in Rudolph et al. (1988) and Campeau and Rochefort (1996), and the micronutrients came from a commercial product.

Formula	Concentration of stock solution ($g\ L^{-1}$)	Volume of stock solution used for watering (mL stock solution L^{-1})
$(NH_4)_2SO_4$	12	0.25
$MgSO_4 \cdot 7H_2O$	20	0.25
$CaSO_4 \cdot 2H_2O$	5	0.5
$CaCl_2 \cdot 2H_2O$	4	0.25
KH_2PO_4	12	0.25
KNO_3	4	0.25
NH_4NO_3	5	0.25
NaOH	8.8	0.25
$FeCl_3 \cdot 6H_2O$	2	0.25
EDTA	2.76	–
HNO_3	240 mL to 1N + 760 mL of water	0.25
Plant Products	1.5*	1

* Concentration of trace elements in Plant Products: Plant-Prod Chelated micronutrient mix–Plant Products Co. Ltd., 314 Orenda Road, Brampton, Ontario, Canada, L6T 1G1. Guaranteed analysis: Micronutrients chelated with EDTA: Fe: 5%; Mn: 2%; Zn: 0.4%; Cu: 0.1% EDTA (minimum): 42%. Micronutrients chelated with DTPA: Fe: 2%; Boron (actual): 1.3%; Mo (actual): 0.06%; DTPA (minimum): 13%.