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Sphagnum regeneration on bare peat surfaces: field and greenhouse experiments

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Summary

1. The re-establishment of *Sphagnum* mosses on bare peat surfaces is one of the main challenges faced in the restoration of post-harvested peatlands. One suggested approach to ensure moss recolonization is to use fragments of *Sphagnum* plants collected from a natural area as diaspores. The regeneration and recolonization potential of fragments of different species of *Sphagnum* were tested on bare peat, both in the field and in a greenhouse. We examined how diaspore size, density and depth of origin influence recolonization and re-establishment success. The greenhouse experiment also tested the impact of water level on *Sphagnum* regeneration and recolonization.

2. Field and laboratory experiments showed that only the surface layer (0–10 cm) of a peat profile contained enough viable material to be of practical use as a source of diaspores.

3. Small (0·5-cm), medium (1-cm) or large (2-cm) diaspores had similar recolonization success. Obtaining a precise and even size of fragments will not, therefore, be an important aspect to consider when scaling up to the quantities needed for restoring large surfaces.

4. Greenhouse experiments showed that water level in the peat column greatly influences the recolonization success of *Sphagnum* diaspores. Most species reacted positively to wetter conditions, with the notable exception of *S. fuscum*.

5. A density of 450 *Sphagnum* plants per m^2 resulted in some *Sphagnum* species covering up to 50% of the peat surface in 3 months and 100% in 6 months, when the water table was close to the peat surface in the greenhouse experiment. *Sphagnum* cover reached 5–10% after 3 months in the drier treatments of the greenhouse experiment and was generally comparable to the results obtained in the field after one season of growth under shade cloth.

6. Improving the humidity conditions offered to diaspores is by far the most promising approach to reduce the quantity of diaspores needed to re-establish a significant moss cover rapidly on a post-harvested surface. The selection of appropriate species and densities according to the dryness of the surface to be restored are two other elements to consider in minimizing the amount of source material needed for restoration.

Key-words: bog, humidity, mire, plant re-introduction, restoration.

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Introduction

With 12% of its territory covered by peatlands (Zoltai 1988), Canada currently accounts for about two-thirds of North-America's peat production (Keys 1992). Canadian peat production is mainly aimed at the horticultural market, although in recent years the harvesting of peat for other industrial uses, such as the production of *Sphagnum*-based absorbent board, has increased in importance (Keys 1992).

Most of Canada's peatlands are fens or northern bogs underlain by permafrost and, thus, are unsuitable for peat harvesting. Hence, the southern ombrotrophic peatlands are the ones under greater pressure of exploitation since they contain the type of peat sought by the industry and are close to roads, markets and manpower. In recent years, when the value of

wetlands and peatlands as natural systems has become more appreciated, there has been growing pressure on the peat industry for better environmental integration of its activities. These environmental concerns include the fate of sites after harvesting has ceased (Keys 1992).

Peat can be harvested at the same site for periods varying from a few years to several decades but, once the harvesting reaches peat layers which are too decomposed for the intended use, the surface is abandoned. Unfortunately, post-harvested bogs do not usually revert to functional peatland ecosystems (L. Rochefort & F. Quinty, personal observations of 30 abandoned sites in eastern Canada). This situation is also common in Manitoba and Alberta (D.H. Vitt, personal communication). Many abandoned surfaces remain almost devoid of vegetation even 10 years after harvesting stops. Others are colonized by ericaceous shrubs or cotton-grass (*Eriophorum* sp.), without noticeable recolonization by the *Sphagnum* mosses that are normally a key component of bog ecosystems. A minority of abandoned sites show the re-establishment of both the vascular and bryophyte flora typical of peatlands. These observations suggest that, while the re-establishment of peatland vegetation on a bare peat surface is possible, active steps have to be taken to encourage and speed up return of the functions of a peatland ecosystem.

The recolonization of bare peat surfaces by *Sphagnum* mosses is one of the main challenges in the restoration of post-harvested peatlands. New *Sphagnum* plants can be produced either starting from spores or by vegetative reproduction (Cronberg 1991). Little is known of the factors which control spore production and germination in *Sphagnum* and it is generally believed that, in nature, the importance of spore production in the development and maintenance of a *Sphagnum* colony is small in comparison with the role played by vegetative mechanisms (Cronberg 1991). In the field, dichotomous division of *Sphagnum* capitula to produce two individuals is often observed. New *Sphagnum* individuals can also be produced from plant fragments that do not initially include the capitulum (Baker & Boatman 1985; Poschlod & Pfadenhauer 1989; Rochefort, Gauthier & Lequéré 1995). A promising method for restoring the moss layer on a post-harvested surface is thus to use *Sphagnum* fragments as units of dispersal here termed diaspores (Elling & Knighton 1984; Poschlod & Pfadenhauer 1989). Preliminary field work conducted in 1992 showed that a number of fragments introduced by hand on bare peat at mid-summer were still alive the following year, and that this restoration technique has a good potential for success (Rochefort *et al.* 1995).

This approach requires collection of a certain quantity of plants from unharvested peatlands near the area of restoration. Elling & Knighton (1984) showed that areas of bog that were stripped of their live *Sphagnum* layer will revegetate to *Sphagnum* within *c.* 5 years, although the total recovery of the *Sphagnum* biomass could take as much as 20 years. Collecting *Sphagnum* from a natural area for restoration purposes thus has a long-term, although likely reversible, impact. To reduce this impact, optimal use of the collected material is necessary.

This study examines the success of diaspore reintroduction on bare peat. A series of concurrent field, laboratory and greenhouse experiments was performed in 1993 to answer the following questions.

1. How deep in the peat column can *Sphagnum* diaspores be collected for restoration purposes?
2. What is the optimal density of diaspores for recolonization of bare peat surfaces?
3. What is the optimal size of *Sphagnum* diaspores for recolonization?
4. Does regeneration success and the ability to recolonize bare peat surfaces vary between species?
5. How does water level in the peat column influence diaspore regeneration and recolonization success, and what are the optimal conditions for recolonization?

Answers to these questions will help in developing reintroduction strategies that would ensure an optimal recolonization of a post-harvested surface with the minimum amount of *Sphagnum* collected from natural areas.

Methods

The field experiments were conducted during the 1993 growing season at the Sainte-Marguerite-Marie peatland, in the Lac Saint-Jean region, Québec (48°47′N, 72°10′W). Greenhouse and laboratory regeneration trials were performed during the summer and autumn of 1993 at Laval University, Québec City.

Lac Saint-Jean is located in the Low Boreal Wetland region of Canada (National Wetlands Working Group 1986). Total precipitation for the Sainte-Marguerite-Marie area is 906 mm $year^{-1}$, with a mean July and January temperature of +17°C and −17°C, respectively. The Sainte-Marguerite-Marie peatland extends to 4315 ha and comprises a mixture of bog and poor fen areas. The moss layer of the ombrotrophic (bog) areas is dominated by *Sphagnum fuscum*, *S. angustifolium*, *S. magellanicum* and *S. capillifolium* (*sensu lato*), while *S. fallax* and *S. papillosum* are abundant in the minerotrophic (poor fen) areas. The taxonomy follows Anderson (1990). A portion of the central, ombrotrophic part of the peatland is exploited for the production of *Sphagnum* absorbent board using a block-cutting technique. A smaller portion of the ombrotrophic area is also harvested for horticultural peat using the vacuum method.

Field re-introduction trials were conducted at four sites of the block-cut area, where harvesting operations ceased in 1990 and 1991. Rewetting of the post-harvested area was achieved by blocking the drainage ditches with small peat dams (5 m thick) that were

made in the spring of 1992 and 1993 using a bulldozer. In the spring of 1993, the rewetted area was found to be waterlogged with some shallow pools at the surface. In the summer, however, no standing water remained at the surface except in the blocked drainage ditches or after heavy rains. The distance from the water table to the peat surface in the post-harvested area was generally greater than in a natural area nearby, except in the spring and sometimes late autumn (Fig. 1). The surface of the experimental site was fibric-mesic peat. Water and peat chemistry values observed on the rewetted site were similar to those of the natural area, with the exception of some enrichment with nitrogen (NH_4-N and NO_3-N: Wind-Mulder, Rochefort & Vitt, in press).

The six species used in the field, greenhouse, and laboratory regeneration and recolonization trials were collected by hand in peatlands near the experimental surfaces. The variables that were measured to compare *Sphagnum* re-establishment between the different species and treatments are regeneration success (i.e. the final number of capitula obtained) and recolonization success (i.e. the visually estimated percentage of the bare peat covered by live *Sphagnum* capitula). To be counted, a capitulum needed to have at least four or five branches arranged in a rosette-like fashion.

EXPERIMENT ON THE DEPTH OF COLLECTION OF *SPHAGNUM* DIASPORES

Four peat cores (17 cm diameter, 30 cm long) were collected in monospecific patches of *S. angustifolium*, *S. magellanicum* and *S. fuscum*. Each core was cut into three sections, corresponding to layers 0–10, 10–20 and 20–30 cm below the peat surface. Each section was weighed and homogenized by hand. A subsample corresponding to one-tenth of the fresh weight was kept and brought back to the laboratory for regeneration trials, and for the determination of a conversion factor between the fresh weight and the mass of the material after drying at 70 °C for 48 h.

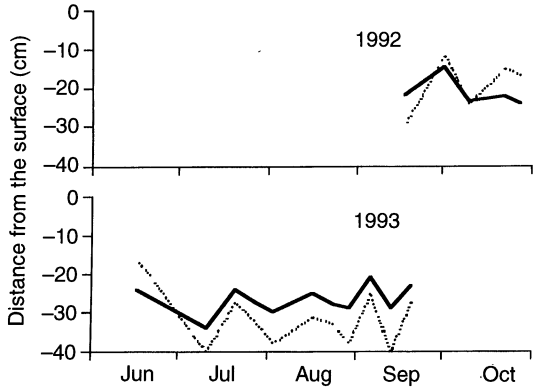

Fig. 1. Water table fluctuations in the post-harvested rewetted area (..... means over nine dip wells) and the adjacent undrained natural area (— means over four dip wells) of the Sainte-Marguerite-Marie bog. The surface is defined as the bare peat substrate in the post-harvested area and the surface of the *Sphagnum* carpet surrounding the water well in the natural area.

In the field, four blocks of three plots (2 × 2 m) were delimited on the rewetted post-harvest surface. Each plot was further divided into four subplots (1 × 1 m). The field experiment was organized as a split-plot in a completely randomized block design, with the three levels of the 'Species' factor randomized to the main plot units of each block and the three levels of the 'Depth in the peat column' factor randomized to the subplot units of each main plot. The fourth subplot did not receive any material and was used as a control.

The homogenized peat material was spread by hand at the beginning of June 1993. Each main plot was delimited by a wooden frame which supported a plastic shade cloth (Agrinet, 40% shade, Les Industries Harnois Inc., Joliette, Québec) of the type used for tree nurseries. The shade cloth was placed *c.* 10 cm above the surface and descended to the peat on all sides of the plot. These shading devices help diaspore survival and establishment by reducing the desiccating effect of wind and solar radiation (Bastien 1996). In October 1993, the number of capitula was counted in four quadrats (25 × 25 cm) within each subplot. The *Sphagnum* cover for the same quadrats was estimated visually.

Laboratory regeneration trials consisted in taking three small samples (mean and standard deviation = 22 ± 3 g, fresh mass) of material from each core and layer, and placing each sample in a covered Petri dish. Each dish received 10 ml of a nutrient solution at the beginning and at midpoint through the trial. The content of this solution (μM) was as follows: Na^+, 55; K^+, 32; NH_4^+, 73; Ca^{2+}, 22; Mg^{2+}, 22; Fe^{3+}, 2; Cl^-, 20; NO_3^-, 100; SO_4^{2-}, 58; PO_4^{3-}, 22. This nutrient solution was modified from that of Rudolph, Kirchhoff & Gliesmann (1988) by reducing the concentration of NH_4 by 18 μM. The Petri dishes were randomly placed on a laboratory bench fronting a south-facing window. Artificial light supplemented natural light from 06·00 to 20·00 h each day. Distilled water was added to the dishes when necessary to prevent desiccation of the material. Ten weeks after the beginning of the regeneration trial, the number of capitula present in each dish was counted.

GREENHOUSE EXPERIMENT ON SPECIES, WATER LEVEL AND SIZE OF DIASPORES

Fifty-four rigid plastic containers (51 × 33 × 30 cm deep) were filled with horticultural peat wetted with distilled water. At the front of each container a small chamber (4 × 2 × 30 cm deep) was separated from the main section by a plastic screen. This screen allowed water movement between the peat-filled container and the front chamber which was free of peat. A series of 1-cm holes along the outside wall of the small chamber

allowed drainage of excess water. If the water level became too low (because of evaporation) distilled water was added to the small chamber to re-establish the desired level in the main container. The containers were organized in three blocks of 18, to account for possible light and ventilation gradients in the greenhouse.

The greenhouse experiment was organized as a split-plot in a completely randomized block design, with the 'Species' and 'Water level' factors ($6 \times 3 = 18$ combinations) randomized to the main plot units and the 'Size of diaspores' factor randomized to the subplot units. The three water levels tested were 5, 15 and 25 cm below the peat surface. The six species tested were *S. fuscum*, *S. capillifolium*, *S. magellanicum*, *S. papillosum*, *S. angustifolium* and *S. fallax*. The peat surface in each container was divided into three parts which received diaspores of the same species, but cut to a different length (0·5, 1 and 2 cm). Twenty-five *Sphagnum* plants (10 cm long) were used in each of the three sections of a container, which corresponds to a density of about 450 *Sphagnum* plants per m^2. Therefore, while the number of *Sphagnum* plants (and, by extension, of capitula) was the same (450) in the different treatments, the total number of fragments was 2250, 4500 or 9000 in the 2-, 1- and 0·5-cm treatments respectively.

The experiment began in early August 1993 and continued for 6 months. The greenhouse was subjected to natural light only from the beginning of the experiment to mid-September. From mid-September to the end of the experiment in February 1994, 400 W sodium lamps supplemented the natural light from 06.00 to 20.00 h each day. Temperature in the greenhouse fluctuated between 15 °C and 25 °C. Relative humidity varied between 40 and 80%.

The containers were watered three times a week with a diluted nutrient solution, for a total weekly addition of 3·5 L of liquid, which corresponds to the average weekly precipitation in the Sainte-Marguerite-Marie area between May and October (22 mm). The watering solution was a fivefold dilution of the nutrient solution described earlier. This dilution level was chosen to adjust the concentration of nitrogen in the solution to the level recorded on average in the rain water of the Lac Saint-Jean region.

The number of capitula in each section of the containers was counted after 3 months. The percentage of peat surface covered by live *Sphagnum* capitula was estimated after 3 and 6 months.

FIELD EXPERIMENT ON THE EFFECT OF SPECIES, DENSITY AND SIZE OF DIASPORES

This field experiment was organized as a split-plot in a completely randomized block design, with 'Species' randomized to the main plot units, and 'Density' and 'Size of diaspores' randomized to the subplot units. Four blocks of five plots (5×2 m) were delimited on the rewetted post-harvest surface. *Sphagnum* plants (10 cm long) of four species were used in this experiment: *S. magellanicum*, *S. fuscum*, *S. angustifolium* and *S. capillifolium*. One species was allocated to each plot of each block. The fifth plot received a mixture of all four species in equal quantities to determine whether *Sphagnum* plants benefit from being re-introduced in multispecies plots rather than in single-species ones.

Each main plot was further divided into eight subplots. The six combinations of the three densities (150, 300 and 450 *Sphagnum* plants per m^2, and two sizes of diaspores (1 and 2 cm) were randomized to the subplot units. The two remaining subplots did not receive any material and were used as controls. As in the greenhouse experiments, the total number of fragments in the 1-cm diaspore treatments was twice the number in the 2-cm diaspore ones of the same density, while the initial numbers of capitula were equal.

Plant material was spread by hand at the beginning of June 1993. Each main plot was covered with a plastic shade cloth as in the first experiment. In October 1993, the number of capitula was counted in four quadrats (25×25 cm) within each subplot. The percentage of the peat surface covered by live *Sphagnum* capitula was estimated visually in the same quadrats.

STATISTICAL ANALYSES

All statistical analyses were performed using the GLM procedure of SAS (SAS Institute Inc. 1988). A Tukey's test (Sokal & Rohlf 1981) was used to locate differences between treatment means once treatment effects were found significant according to the appropriate analysis of variance model for each experiment. When the analysis of variance showed a significant interaction between treatments, multiple comparisons were limited to comparing the means of one factor within each level of the other factor. The data for number of capitula were square-root transformed [$\sqrt{(x+0{\cdot}5)}$] prior to analysis to reduce heterogeneity of variances. Data for the percentage of the peat area covered by capitula were analysed untransformed. The level of significance for testing treatment effects and for multiple comparisons between treatment means was set at $P = 0{\cdot}05$.

Results

EXPERIMENT ON THE DEPTH OF COLLECTION OF *SPHAGNUM* DIASPORES

For both the field and laboratory regeneration trials, the number of capitula produced from material originating in the 0–10-cm layer was generally significantly greater ($P < 0{\cdot}05$) than the number produced from deeper material of the same species (Fig. 2). The only exception was *Sphagnum magellanicum* where the

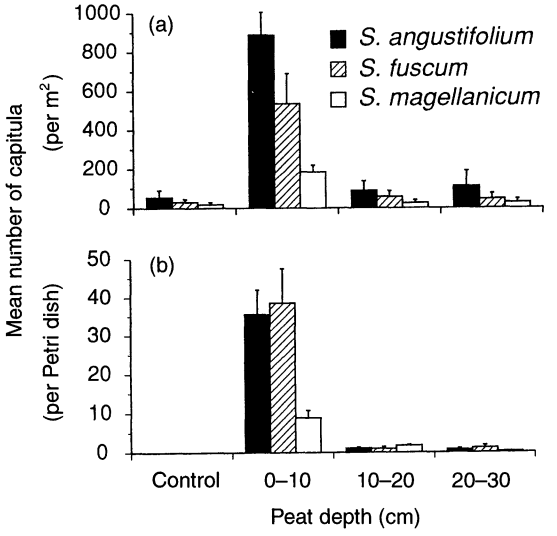

Fig. 2. Regeneration potential of peat material originating from layers situated at different depths below the surface. Capitula counts were performed (a) after one growing season (June–October) in the field and (b) after 10 weeks in the laboratory. Half-I-bars represent standard error of the mean. Results of the ANOVAS on square-root transformed data are as follows: (a) species, $P = 0{\cdot}0231$; depth, $P = 0{\cdot}0001$; interaction species × depth, $P = 0{\cdot}0015$. (b) Species, $P = 0{\cdot}0106$; depth, $P = 0{\cdot}0001$; interaction species × depth, $P = 0{\cdot}0004$.

difference between the 0–10-cm layer and the 10–20-cm layer was not significant. These discrepancies in the effect of depth in the different species explains the significant interaction between the two factors that was observed in both field and laboratory trials.

Within the 0–10-cm layer, the number of capitula recorded for *S. magellanicum* was significantly smaller than the number recorded for *S. fuscum* and *S. angustifolium* for both field and laboratory trials (Fig. 2). Field data showed no significant differences between the plots receiving no diaspores (control plots) and plots receiving material from the 10–20- or the 20–30-cm layers for any of the three species (Fig. 2a).

For the field trials, the mean number of capitula ($\pm$SE) per g dry mass of initial material for the 0–10-cm layer, was 26 ± 4 for *S. angustifolium*, 19 ± 7 for *S. fuscum* and 4 ± 1 for *S. magellanicum* after subtraction of the mean number of capitula observed for the plots receiving no diaspores. The mean values for the 10–20- and 20–30-cm layers varied between 0 and 0·8 capitula per g dry mass. The number of capitula obtained per g dry mass for the surface layer in the Petri dish trials were much larger than the field values: 81 ± 18 for *S. angustifolium*, 128 ± 34 for *S. fuscum* and 22 ± 6 for *S. magellanicum*. The mean values for the 10–20- and 20–30-cm layers were also higher for the Petri dish trials than for the field trials and varied between 0·3 and 4·4 capitula per g dry mass.

GREENHOUSE EXPERIMENT ON SPECIES, WATER LEVEL AND SIZE OF DIASPORES

The analysis of variance comparing the number of capitula recorded after 3 months for each treatment showed significant two–way interactions between species and water level, between water level and size of diaspores, and between species and size of diaspores. The first interaction is explained by the tendency to observe more capitula per m^2 at high water level than at low water level for most species except *S. fuscum* (Fig. 3). The second and third interactions are explained by the tendency to observe more capitula per m^2 in the 0·5 cm diaspore treatments at high water level, but not at low water level for most, though not all, species (Fig. 3).

Most but not all species reacted to higher water levels by an increase in the fraction of the peat substrate covered by capitula (Fig. 4). Indeed, the analysis of variance on the cover data showed a significant interaction between species and water level at both 3 and 6 months after the beginning of the experiment. In contrast to capitulum counts, neither the size of diaspores, nor any of the interactions involving the size of diaspores, had a significant effect on the fraction of the substrate covered by capitula.

Six months after the beginning of the experiment, *S. fuscum* was the only species for which no significant differences in cover could be detected between the three water levels according to the Tukey multiple comparison test (minimum significant difference = 17·6% cover). In all other cases, the fraction of cover recorded for each water level was significantly different from the two others. The multiple comparison test showed no significant differences in cover between the different species when the water level was low. At high and medium water level, however, several species differed significantly from one or more of the others, but *S. fuscum* was the only species with a cover significantly different from the cover of all five other species.

For all species and water levels, the number of capitula recorded after 3 months largely exceeded the number of plants (and, by extension, of capitula) that were initially introduced (Fig. 3). Even in *S. fuscum*, the species with the lowest regeneration success, the number of capitula recorded per m^2 nearly doubled during the initial 3-month period.

FIELD EXPERIMENT ON THE EFFECT OF SPECIES, DENSITY AND SIZE OF DIASPORES

After one field season, the fractional cover and the number of capitula recorded in the different field treatments varied significantly between species and between densities, with no significant interaction between the two factors (Fig. 5). *Sphagnum angustifolium* and *S. fuscum* were the two species that showed the best regeneration success on bare peat in the field (Fig. 5a). Their recolonization success also tended to be higher than that of *S. capillifolium* and *S. magellanicum* (Fig. 5b).

Neither the size of diaspores, nor any of the interactions involving size of diaspores, had a significant

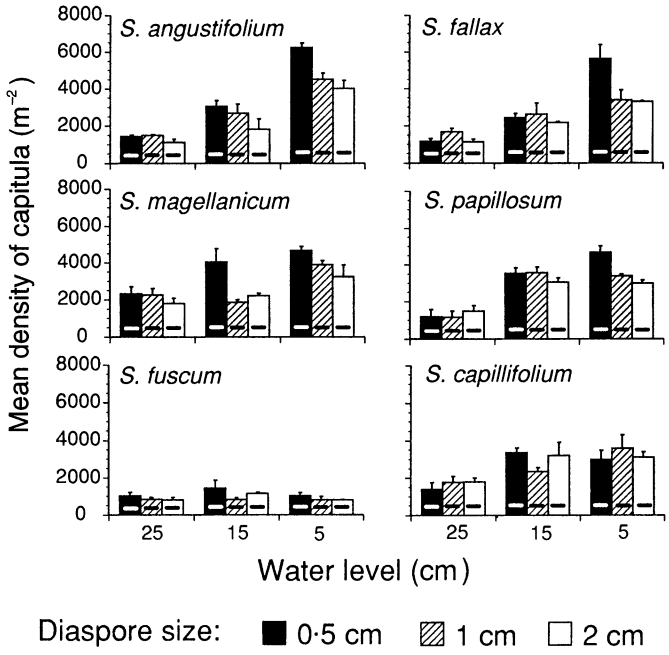

Fig. 3. Effect of species, size of diaspores and water level recorded as depth below peat surface, on the regeneration of *Sphagnum* after 3 months in the greenhouse. The white and black markers indicate the initial number of plants re-introduced. Half-I-bars represent standard error of the mean. Results of the ANOVA on square-root transformed data are as follows: species, $P = 0{\cdot}0001$; water level, $P = 0{\cdot}0001$; size of diaspores, $P = 0{\cdot}0001$. Two–way interactions: (1) species × level, $P = 0{\cdot}0001$; (2) species × size, $P = 0{\cdot}0474$; (3) level × size, $P = 0{\cdot}0024$. Three–way interaction: $P = 0{\cdot}1239$.

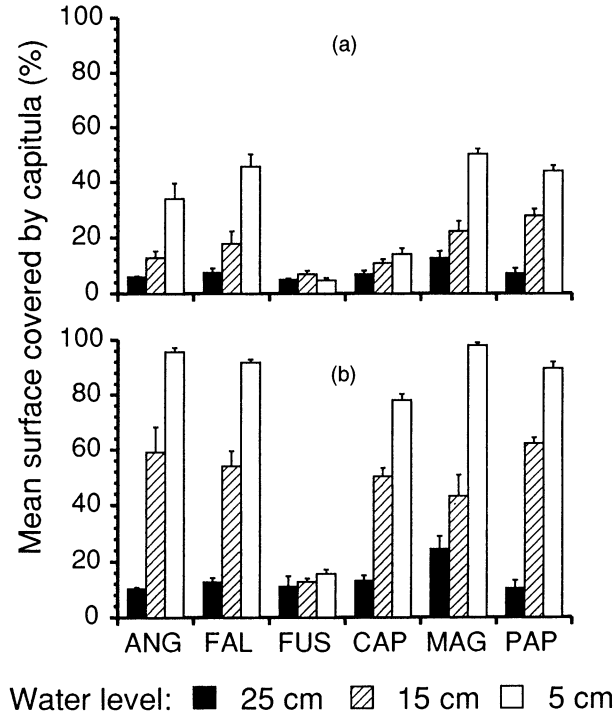

Fig. 4. Recolonization success recorded as depth below peat surfaces of different *Sphagnum* species in the greenhouse in relation to water level (a) after 3 months and (b) after 6 months. The following abbreviations are used: ANG = *S. angustifolium*; FAL = *S. fallax*; FUS = *S. fuscum*; CAP = *S. capillifolium*; MAG = *S. magellanicum*; PAP = *S. papillosum*. Half-I-bars represent the standard error of the mean. Results of the ANOVAS on non-transformed data are as follows: (a) species, $P = 0{\cdot}0001$; water level, $P = 0{\cdot}0001$; size of diaspores, $P = 0{\cdot}11$. Two–way interactions: species × level: $P = 0{\cdot}0001$; species × size, $P = 0{\cdot}85$; level × size: $P = 0{\cdot}36$. Three–way interaction: $P = 0{\cdot}13$. (b) Species: $P = 0{\cdot}0001$; water level: $P = 0{\cdot}0001$; size of diaspores: $P = 0{\cdot}28$. Two–way interactions: species × level, $P = 0{\cdot}0001$; species × size, $P = 0{\cdot}48$; level × size, $P = 0{\cdot}84$. Three–way interaction: $P = 0{\cdot}45$. Minimum significant differences according to the Tukey test are (a) 10·7 and (b) 17·6.

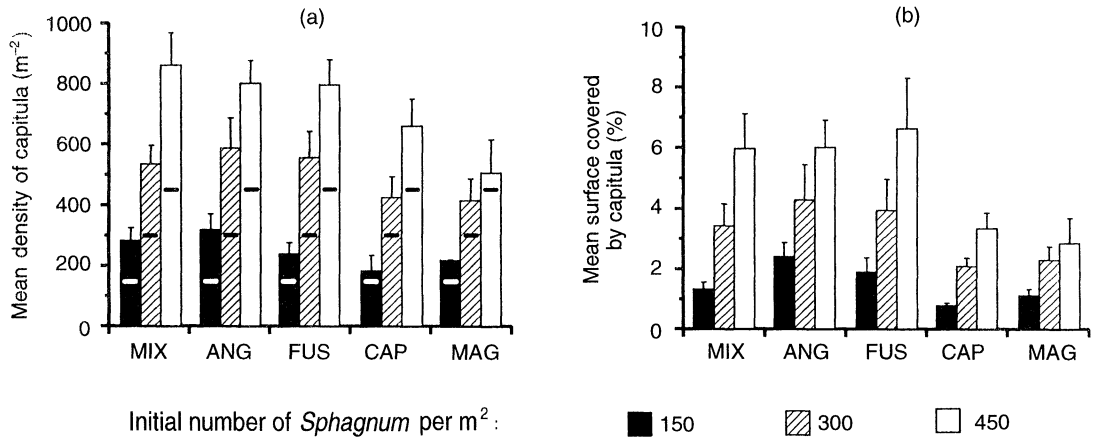

Fig. 5. Regeneration and recolonization success of different *Sphagnum* species after one growing season (June–October) in the field, recorded as (a) density and (b) cover. The white and black markers indicate the initial number of plants re-introduced. The four last species abbreviations are as in Fig. 4. MIX represents a mixture of plants of the four species. Half-I-bars represent standard error of the mean. Results of the ANOVAS on (a) square-root transformed data and (b) non-transformed data are as follow: (a) species, $P = 0{\cdot}007$; density, $P = 0{\cdot}0001$; size of diaspores, $P = 0{\cdot}0393$. Two–way interaction: species × density, $P = 0{\cdot}39$; species × size, $P = 0{\cdot}53$; size × density, $P = 0{\cdot}80$. Three–way interaction: $P = 0{\cdot}73$. (b) Species: $P = 0{\cdot}0144$, density, $P = 0{\cdot}0001$; size of diaspores, $P = 0{\cdot}33$. Two–way interaction: species × density, $P = 0{\cdot}28$; species × size, $P = 0{\cdot}98$; size × density, $P = 0{\cdot}66$. Three–way interaction: $P = 0{\cdot}65$.

effect on the number of capitula or on the fractional cover recorded after one field season. As in the greenhouse trials, the number of capitula recorded at the end of the experiment (corrected for the values observed in the control plots) always exceeded the initial number of plants introduced (Fig. 5).

Discussion

ORIGIN OF DIASPORES

Both our laboratory and field results showed that the most succesful regeneration was from plant material taken from the 0–10-cm layer. Because slices from this layer already contained capitula, it is to be expected that the plots receiving the surface material would also contain more capitula at the end of the regeneration trials. However, the Petri dish trials showed numerous new plants in excess of the initial capitula for the 0–10-cm layer, while the other layers showed only a few new shoots. It was difficult in the field to separate new shoots from initial capitula, and we do not have an exact count of the number of capitula introduced initially in the 0–10-cm layer plots to compare with the final count. Approximate calculations based on an estimated density of capitula in the field for a 17-cm diameter disc for each species, suggest that more capitula could be found after one field season in the plots treated with material from the 0–10-cm layer than the number originally introduced for *Sphagnum angustifolium*, but possibly not for the other species. The significantly lower number of capitula recorded for *S. magellanicum* at the end of the experiment in comparison with the other species may, in part, be due to the fact that a smaller number of capitula were originally introduced for this species whose capitula are larger than those of *S. fuscum* and *S. angustifolium*.

In the laboratory, Clymo & Duckett (1986) obtained regeneration of *Sphagnum* from slices of peat cores originating from at least 30 cm below the surface. Even though some regeneration of material of deeper origin was also observed in our study, results suggest that there is little to gain, from a practical point of view, by collecting material below 10 cm. In certain species, the layer from which viable diaspores could effectively be obtained might even be less than 10 cm deep. Furthermore, mixing surface material with deeper peat may hinder regeneration because live diaspores from the surface layer risk being buried under dead material. Collecting the surface material alone might also help moss recovery at the collection site, since it increases the chances of live *Sphagnum* fragments being left behind to act as diaspores on these sites (Elling & Knighton 1984).

The number of capitula per gram of dry material obtained in Petri dishes was much larger than the number obtained in the field, because of the difficult conditions for *Sphagnum* regeneration in the field setting. Despite this, there is a remarkable agreement in the conclusions that can be reached from the two types of experiment (Fig. 2). Petri dish trials are thus a convenient and rapid method of testing the regeneration potential of *Sphagnum* diaspores and of investigating the factors that affect regeneration. Moreover, the general similarity in fractional cover obtained in the field and in the greenhouse at low water levels validates the use of greenhouse trials for studying *Sphagnum* regeneration and recolonization on bare peat. However, differences in species performance in the two situations raise interesting questions regarding

species requirements. *Sphagnum fuscum*, in particular, performs poorly in the greenhouse while being one of the best perfoming species in the field. It is possible that even the low-water-level greenhouse treatment, with its tri-weekly watering frequency, is still too wet for *S. fuscum*.

SIZE OF DIASPORES

Both greenhouse and field results showed that the size of diaspores had no influence on the recolonization success of *Sphagnum*. Part of the explanation may be that fragments are not limited to the production of only one new capitulum. The higher number of capitula observed after 3 months in some of the small diaspore treatments with high water table were not associated with a higher percentage of the peat surface covered by capitula, and did not result in better recolonization 3 months later. Therefore, it is concluded that, under a given set of conditions, *Sphagnum* plants have a more or less fixed recolonization success, whether the plants are cut into small or large fragments. From a practical point of view, this means that obtaining a precise and even fragment size is not an important part of the prescription for scaling up the preparation of *Sphagnum* diaspores to the quantities needed for restoring large surfaces.

DENSITY

In the field conditions prevailing now, results indicated that densities higher than 450 plants per m^2 are needed to re-establish a *Sphagnum* carpet effectively within one growing season. The effect of density on recolonization and regeneration success in the field was more or less additive for the range of densities tested. In other words, the number of capitula and the percentage of cover obtained at 450 plants per m^2 roughly tripled the corresponding values obtained at 150 plants per m^2 (Fig. 5). The percentage of cover obtained with the highest density was *c.* 5%. If this additive trend is extrapolated to higher densities, we can calculate that densities 5–10 times higher than 450 plants per m^2 would be needed to obtain a 25–50% ground cover within one field season. A density of 450 plants per m^2 is equivalent to spreading 1 m^2 of moss (10 cm deep) from a natural area on 50–100 m^2 of post-harvested surface, depending on species. A 5- to 10-fold increase would mean collecting material from 1 m^2 of material from the natural area for each 5–20 m^2 of surface in restoration. However, it is possible that once a certain threshold density is reached, density effects become multiplicative instead of additive because of a mutual positive sheltering effect of the new regenerating capitula. If so, densities needed to obtain a 25–50% ground cover would be lower than those calculated from the additive model. This hypothesis remains to be tested.

SPECIES

Our results show that different *Sphagnum* species differ markedly in their reaction to changes in the humidity conditions of the substrate. For most species, a high water table in the greenhouse resulted in better regeneration and recolonization success. A remarkable exception is *S. fuscum*, a species that otherwise seemed to do well in the drier field conditions. Other field and laboratory observations (S. Campeau, unpublished data) suggest that *S. fuscum* regeneration is limited when the fragments are covered by water.

The species to be re-introduced must therefore be selected having regard to the humidity of the surface to be restored. For example, if the humidity conditions of the bare peat substrate are high, species other than *S. fuscum* will produce better recolonization with smaller quantities of material collected from a natural area. Conversely, *S. fuscum* and *S. angustifolium* are appropriate choices for drier sites, even though higher densities may be required to achieve a satisfactory cover in these cases.

Sphagnum fuscum is a hummock-forming species, and is generally found at drier locations along the hummock to hollow gradient than *S. angustifolium* (Andrus 1986). In natural conditions, hummock formers have been shown to be able to maintain a higher water content than hollow species, because of their higher ability to transport water (Rydin 1993). As the photosynthesis of *Sphagnum* species is reduced at low water content (Rydin 1993), it seems reasonable to assume that *S. fuscum* should withstand drier field conditions better than *S. angustifolium*. On the other hand, while there seems to be no evidence of any general difference in desiccation tolerance between hummock and hollow species (Rydin 1993), Sagot & Rochefort (in press) showed that *S. fuscum* was less tolerant to desiccation than *S. magellanicum* and *S. fallax* (a species very similar to *S. angustifolium*). The present results showed that *S. fuscum* and *S. angustifolium* had similar recolonization success in the field after one season. Thus, both water-transport ability and desiccation tolerance seem to play a role in determining the ability of a given *Sphagnum* species to re-establish from fragments in the field.

WATER LEVEL

The striking difference in recolonization success between high and low water table in the greenhouse shows that improving the humidity conditions of the substrate is by far the most promising approach to reducing the quantity of source material needed for restoration purposes. Starting from fragments distributed at a density of 450 plants per m^2, a continuous *Sphagnum* ground cover was obtained in less than 6 months with a high water table. In contrast, *Sphagnum* cover in the drier treatments of the greenhouse experi-

ment reached only 5–10% after 3 months and generally compared more closely to the results obtained in the field.

The humidity of the substrate can be increased by raising the water table of the area undergoing restoration. This, however, may be difficult to achieve in the field, especially toward the end of the summer (Schouwenaars 1988). In any case, it is possible that the uppermost layers of the peat surface and the associated diaspores would still tend to dry up on warm summer days despite a high water table. The experimental high water level in the greenhouse was also associated with an increased fungal and algal colonization in some of containers. It is not known if a high water table would have a similar impact in the field, or if this situation is restricted to the more unnatural conditions offered by the greenhouse environment.

An alternative approach to improve the humidity conditions available to diaspores may be achieved by preventing desiccation of the peat surface by wind and solar radiation, i.e. either with a mechanical barrier or by surface irrigation (Bastien 1996). Salonen (1992) showed that the protection offered by plant covers improved vascular plant recolonization of a bare peat surface. The author attributed this effect, in part, to the improved moisture and temperature conditions at the soil–air interface in the covered plots. In our study, a 40% shade cloth was used to protect the re-introduced diaspores from desiccation. Other mechanical barriers might prove more effective and reduce the need to increase diaspore densities. A third method of encouraging the re-establishment of diaspores would be to time diaspore re-introduction to coincide with the period at which humidity conditions of the substrate are at their best, i.e. in late autumn or immediately after snow melt.

Further work is needed to assess which of these methods, or which combination of methods, will be most effective at improving the humidity conditions of the peat substrate to promote rapid *Sphagnum* recolonization. These methods, in combination with an appropriate selection of species and densities, could significantly enhance the effective re-establishment of *Sphagnum* on a post-harvested surface and thereby minimize disturbance to natural areas that are used as sources of diaspores. Longer-term field work is also needed to monitor the health of the re-introduced *Sphagnum* diaspores and to assess the capacity of a re-established moss carpet to maintain itself.

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