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# *Sphagnum* establishment on bare peat: The importance of climatic variability and *Sphagnum* species richness

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**Abstract**

**Question:** What is the relative ability of four species of *Sphagnum* (*S. fuscum, S. rubellum, S. magellanicum* and *S. angustifolium*) to establish on bare peat substratum in the field when re-introduced as single or multi-species re-introductions and in relation to interannual variations in climate?

**Location:** Continental southeastern Canada.

**Methods:** Diaspores (fragments) of four *Sphagnum* species alone or in combination were re-introduced onto residual peat surfaces and were monitored to follow the development of the moss carpet over four growing seasons. In order to compare results under a variety of climatic conditions, this whole experimental setting was repeated four times (trials), with a four-year follow-up for each trial.

**Conclusions:** The establishment rate of the moss carpet varied among years, in response to climatic variations between growing seasons. The relative success of different moss species and combinations of species, however, did not vary within or between trials. Thus, the species and combinations of species resulting in the highest short-term or long-term establishment rates remained the same for all trials, independent of the climatic conditions at the time of re-introduction. Our results showed no link between the number of species in the diaspore mixture and successful establishment of the moss carpet. Yet successful regeneration was clearly influenced by the identity of species chosen for re-introduction. *S. fuscum*, alone or in combination, was the species found to lead to the most extensive development of the moss carpet under the current test conditions.

**Keywords:** Bog; Cut-over peatland; Damaged mire; Ecological restoration; Multi-species carpet; Peatland; Plant re-introduction; Single-species carpet; *Sphagnum fuscum*.

**Abbreviations:** LSD = Least significant difference; LSMEANS = Least Square Means.

**Nomenclature:** Anderson (1990).

## Introduction

*Sphagnum* mosses are keystone species in ombrotrophic peat bogs in terms of ecosystem function (van Breemen 1995). Under favourable conditions, these mosses stimulate development of peatlands by decreasing pH levels and by maintaining a high water table. Accordingly, peat mosses need to be taken into account for successful repair of peatland ecosystems (Rochefort 2000). Understand *Sphagnum* establishment ecology on bare peat substratum is of interest for ecosystem restoration after fire, agriculture or peat extraction disturbances, and useful for designing *Sphagnum* farms in which renewable biomass in the form of *Sphagnum* fibers is produced.

Peatlands used for agriculture or for peat extraction and then abandoned are not readily recolonized by vegetation that is typical of peatland habitats (Salonen 1992; Money 1995; Rowlands & Feehan 2000; Lavoie et al. 2003, 2005; Poulin et al. 2005). Such exploitation transforms the soil surface and the soil profile to such an extent that the residual peatland hardly offers habitats suitable for the return of poikilohydric *Sphagnum* mosses (Price 1996, 1997; Price & Schlotzhauer 1999; Van Seters & Price 2001; Tomassen 2004; Groeneveld & Rochefort 2005). If one aims at re-establishing a peat-accumulating system within a human lifetime then intervention is needed (Rochefort 2000). Successful intervention to restore the growth of a *Sphagnum* carpet involves the active re-introduction of diaspores, together with techniques (i.e. blocking of drainage canals and use of a mulch cover) to improve hydrological conditions and protect the diaspores from desiccation (Wheeler & Shaw 1995; Rochefort et al. 2003; Tuittila et al. 2003; Blankenburg & Tonnis 2004). Similar interventions are also required for development of a *Sphagnum* culture system (Joosten 1998; Campeau & Rochefort 2002; Gaudig & Joosten 2002).

This study focuses on the establishment of *Sphagnum* species, singly or in mixtures, under a variety of climatic conditions at the time of re-introduction. To date, all experiments to evaluate the relative success of different *Sphagnum* species have been conducted using single-species treatments (Campeau & Rochefort 1996; Grosvernier et al. 1997; Buttler et al. 1998; Rochefort & Bastien 1998). Re-introduction of *Sphagnum* species in mixtures might, however, make a difference because the establishment rates of individual species are likely to be affected by the processes of competition or facilitation (Rydin 1993).

The specific aims of this study are to determine which species or combination of species of *Sphagnum* is most appropriate for successful establishment on residual peat surfaces. We hypothesized that: 1. Climatic conditions, particularly those during the re-introduction year, affect the long-term success of the introduced mosses and determine the relative success of moss species; 2. The presence of several *Sphagnum* species in the re-introduced material results in improved moss coverage in the long term in relation to interannual variations in climate; and 3. Including moss species typical of dry conditions in the dissemination material favours development of a moss carpet in cut-over peatlands following abandonment.

## Material and Methods

### *Study site*

The study was performed in the Lac-Saint-Jean region, Québec, Canada (48°47' N, 72°10' W). The average annual temperature (normal of 1961-1990) was 1.7 °C, with average January and July temperatures of –17.1 and 17.3 °C, respectively (Anon. 1992). Mean annual total precipitation was 906 mm (32% falling as snow).

The Sainte-Marguerite peatland is part of a 4315-ha bog-poor fen complex, classified as 'plateau bog' (Anon. 1997). This study took place in a cut-over sector of the peatland located on a large previously bog-species dominated area. This cut-over sector was drained and block-cut using heavy machinery for four years removing the upper 0.35 to 0.60 m. Drainage ditches were blocked in 1994 and residual peat thickness currently ranges from 1.2 to 1.8 m. The study was conducted 1995-2001.

### *Experiment*

Four species of *Sphagnum* were used in this: *S. fuscum*; *S. rubellum* (*S. capillifolium* s.l. in previous studies of the Peatland Ecology Research Group, PERG); *S. magellanicum*; and *S. angustifolium*. These species are representative of different microhabitats found along the hydrological gradient of natural peatlands in eastern Canada. Representative specimens are deposited in the Québec Faculté Agriculture herbarium (QFA).

Diaspores (any part of the moss or spore which can disperse and produce a new individual) of the four species of *Sphagnum,* alone or in combination, were spread onto residual peat substrates and the development of a moss carpet was monitored for four growing seasons. In order to compare results under a variety of climatic conditions (Hypothesis 1), the whole experiment (nine treatments with replicates) was repeated in four separate trials, with moss re-introductions made in spring 1995, 1996, 1997 and 1998 and then followed, in each case, for the next four years. Therefore, the term trial used throughout the text refers to a set of replicated treatments monitored for four growing seasons. Within each trial, the nine treatments were replicated five times (i.e. in five blocks dispersed over 25 ha) except for 1995 where treatments were replicated six times. Thus, there were a total of 189 sampling units, each monitored for four years (756 recordings).

Species number and the proportion of each species in the introduced material varied among the nine treatments as shown in Table 1. Four treatments consisted of single-species re-introductions while the other five treatments contained from two to four species of *Sphagnum* to evaluate the effect of the number of species in the mixture on the rate of establishment (Hypothesis 2). We also tested if the presence of species typical to relatively dry microhabitats (*S. fuscum* and *S. rubellum,* Section *Acutifolia*) favoured development of the moss carpet (Hypothesis 3).

The moss carpet coverage was estimated in each experimental plot in the fall, all four years from and including the re-introduction year (repeated measures design). Experimental plots were 30 $m^2$ in area. In order

**Table 1.** The proportion of *Sphagnum* species in the nine diaspore mixtures used for the experiment. Surface *Sphagnum* material collected on 2 $m^2$ surfaces of natural bogs were spread on experimental units of 30 $m^2$. For example, FR treatment includes: 1 $m^2$ of *S. fuscum* and 1 $m^2$ of *S. rubellum*.

| Treatments | Proportion of species on the total surface of reintroduced material | | | |
|---|---|---|---|---|
| Code | *S. fuscum* | *S. rubellum* | *S. magellanicum* | *S. angustifolium* |
| F | 1 | | | |
| R | | 1 | | |
| M | | | 1 | |
| A | | | | 1 |
| FR | 0.5 | 0.5 | | |
| FRA | 0.25 | 0.25 | | 0.5 |
| FRM | 0.25 | 0.25 | 0.5 | |
| MA | | | 0.5 | 0.5 |
| FRMA | 0.25 | 0.25 | 0.25 | 0.25 |

F = *S. fuscum*; R = *S. rubellum*; M= *S. magellanicum* ; A = *S. angustifolium* to increase heterogeneity of environmental substrate conditions, blocks were placed in a variety of peat surfaces such as shallow depressions protected by 50 cm high peat embankments (Price et al. 2002) or on flat or slightly concave surfaces.

*Sphagnum* diaspores were collected manually from natural sites using 0.5- and 1.0-m$^2$ quadrats. Quadrats were positioned to contain > 90% of a single *Sphagnum* species and then all mosses present within the quadrat were collected to a depth of 10 cm (Campeau & Rochefort 1996). Mosses were collected in plastic bags for transport and spread over the appropriate experimental plot by hand between 01.05 and 15.05 each re-introduction year (1995 to 1998). Even spread of individual stems was accomplished by prior disentangling of clumps. The spreading density ratio of 1:15 (collection: spreading surface area; Rochefort et al. 2003) was used, meaning that dissemination material collected from 2 m$^2$ of natural bog was spread over a 30-m$^2$ plot of bare peat. Treatments were assigned randomly to plots within each block. Immediately following re-introduction, plots were covered with oat straw mulch to protect diaspores from heat and desiccation (ca. 3000 kg/ha, i.e. 300 g/m$^2$ of dry loose straw). After two growing seasons, a second application of straw mulch was judged necessary: half the initial application was added (ca. 1500 kg/ha). A growing season in southern Québec usually extends from 01.05 to 30.09.

*Data*

*Sphagnum* establishment success was monitored each fall by visually estimating the percentage cover on 30 25 cm × 25 cm quadrats that were distributed systematically along transects within in each plot. Values for the 30 quadrats were averaged to provide a yearly cover value for each experimental plot. The percent cover of other mosses (mainly *Polytrichum strictum*), herbaceous plants and ericaceous shrubs were also estimated to document the general development of vegetation cover in the plots. (After six growing seasons the mean cover of shrubs and mosses other than *Sphagnum* were 15 and 5%, respectively, for the plots initiated in 1995.)

The humidity strongly affects establishment success of *Sphagnum* on restoration plots (Campeau et al. 2004). To control for a potential positioning effect of certain plots or blocks within more or less dry zones, the water content of the peat surface was determined in each of the 189 experimental sampling units on three sampling dates each of the years 1998, 1999 and 2000. Peat water content was estimated in surface peat retrieved with a cutter that sampled the upper 3 cm of soil over a 5-cm diameter area. Three sub-samples from within each experimental unit were mixed to provide one single sample representing each experimental unit. This sample was taken to the laboratory for drying and weighing. Water content of the peat was calculated in terms of volumetric soil moisture (cc water/cc peat). All 1998, 1999 and 2000 volumetric soil moisture values recorded from a single experimental unit were averaged and the final mean values used as a covariable in statistical analyses of *Sphagnum* establishment success.

Weather data at the Normandin governmental station, situated 24 km from the experimental site, were used to evaluate the influence of climate on development of the moss carpet. We used mean monthly temperature, total monthly precipitation and total number of days with precipitation to describe the climate in the experimental period.

In addition to recording the number of days with precipitation, we evaluated for each month the number of days with 'effective rain', i.e. days with measurable precipitation $\geq$ 2 mm. Indeed, this is the approximate quantity of rain absorbed by the mulch cover (Price et al. 1998). Finally, we calculated for each day the number of days since the last previous day of 'effective rain' (e.g. a day of rain received a value of 0 and a day for which the last rainfall took place two days before received a value of 2). From these data, we calculated the cumulative probability (in percent) that it had not rained within the past 3, 6, 9 or 12 days. This cumulative probability was only calculated for the 92-day period from 01.06 to 31.08, that is the time when a shortage of water is likely most critical for *Sphagnum* mosses. Indeed in the Lac-St-Jean-Region, the presence of ground frost often limits the penetration of snow melt and rain water in May. In September, shorter days and cooler temperatures limit evaporation while morning dew also provides a significant source of humidity to mosses.

The level of the water table was monitored regularly at the Sainte-Marguerite peatland between June and August of each year from 1995 to 1999. Water table data were recorded using a series of dip wells located a few meters apart along a transect running from the centre of a peat field to the edge of its blocked drainage ditch. Volumetric soil moisture samples were also taken along this series of wells on the same days, using the same technique as above. These water level and soil moisture values were recorded in order to describe yearly differences in moisture regime at the experimental site. These data are thus different from the volumetric moisture values measurements presented in the previous section and which were used to assess the relative levels of substrate humidity among experimental units (covariate).

*Statistical analysis*

Establishment success, estimated as percentage cover of the moss carpet, was compared between trials, treatments and age of the carpet by an analysis of covariance with repeated measures. The repeated measure was the age of the plot, i.e. 1, 2, 3 or 4 years and the covariable was the average volumetric soil moisture values for each experimental unit. The analysis was performed with the MIXED procedure of SAS (Anon. 1990).

The factor of block nested within trial (BLOCK (TRIAL)) was included as a random factor (RANDOM). Several types of covariance matrix structure were considered and the compound symmetry structure (TYPE = CA; Littell et al. 1996) was the one which minimized the Akaike Information Criterion and thus determined the most appropriate temporal structure for the experiment.

Cover data were log-transformed – log ($x$ +1) – before analyses in order to reduce heterogeneity of variances. *A priori* contrasts were utilised to compare treatments and test initial hypotheses, i.e. (1) single-species treatments were compared to multi-species treatments and (2) treatments containing hummock-forming species of the Section *Acutifolia* were compared to those without. In addition, LSD tests were used *post hoc* to determine differences between levels of a factor once the global analyses were shown to be significant (protected LSD test). This test was used for the main effects that were not involved in significant interactions. For the interactions, the overall effect of a factor within each level of the other factor needed to be significant (using option SLICE in LSMEANS) before proceeding with the protected LSD tests. Differences between treatments were considered statistically significant below the threshold probability of 0.05.

## Results

*Annual climatic conditions*

The 1995 field season was very dry, with only 17 days in the summer period of June to August with precipitation ≥ 2 mm (18.5%; Table 2). The 1995 season had the lowest number of days with effective rain in summer which was coupled with the highest mean temperature in summer for all the years of this study. In July and August 1995, the water table and especially the moisture content of the soil were very low (Table 2).

The second driest summer season in terms of total precipitation was 2000 (Table 2). The 2000 growing season had few days of effective rain and records showed a long period without effective rain (18 days). The 1997 field season was somewhat similar to 2000, with a very dry July in which we recorded the longest period in summer without rain, i.e. 22 days (Table 2). Both seasons had relatively cool springs.

The years 1998 and 1999 had warmer springs and more equitably distributed precipitation than 1995 and 2000. The years 1996 and 2001 were generally very wet,

**Table 2.** Summary of the major climatic and environmental characteristics for the study area 1995 - 2001. Normal represents averages 1961-1990.

| Variables | Normal | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 |
|---|---|---|---|---|---|---|---|---|
| **For the whole growing season (May-October)** | | | | | | | | |
| Average temperature (°C) | | | | | | | | |
| Spring (May) | 8.7 | 8.6 | 7.1 | 6.5 | 12.2 | 12.5 | 9.1 | 11.9 |
| Summer (June-August) | 15.7 | 16.8 | 16.2 | 15.7 | 16.1 | 16.4 | 14.7 | 16.2 |
| Fall (Sept.-October) | 7.5 | 8.1 | 8.0 | 7.6 | 8.3 | 8.7 | 7.1 | 9.0 |
| Total precipitation (mm) | | | | | | | | |
| Spring (May) | 77 | 133 | 67 | 78 | 89 | 43 | 74 | 39 |
| Summer (June-August) | 279 | 138 | 344 | 240 | 232 | 313 | 174 | 326 |
| Fall (Sept.-October) | 154 | 126 | 247 | 132 | 103 | 175 | 109 | 233 |
| Number of days with precipitation | - | 74 | 101 | 103 | 82 | 80 | 66 | 89 |
| **For the summer period (June-August)** | | | | | | | | |
| Number of days with precipitation | | | | | | | | |
| All rain events | - | 32 | 55 | 45 | 41 | 46 | 32 | 52 |
| Rain events ≥ 2 mm only | - | 17 | 30 | 23 | 26 | 33 | 23 | 31 |
| Longest period without rain ≥ 2 mm (days) | | 13 | 6 | 22 | 12 | 14 | 18 | 11 |
| Water table depth below surface (cm) | | | | | | | | |
| June average at control site | - | 29 | 44 | 34 | 37 | 32 | - | - |
| July average at control site | - | 60 | 26 | 56 | 50 | 24 | - | - |
| August average at control site | - | 66 | 34 | 73 | 65 | 33 | - | - |
| Surface peat volumetric moisture content (%) | | | | | | | | |
| June average at control site | - | 69 | 59 | 54 | 62 | 52 | - | - |
| July average at control site | - | 34 | 68 | 43 | 60 | 51 | - | - |
| August average at control site | - | 22 | 67 | 33 | 54 | 44 | - | - |

including the fall season. The maximum interval between rain events was only 6 days in 1996 and 11 days in 2001 (Table 2). As a result, the water table level and the water content of the soil were very high in 1996 and, most likely, almost as high in 2001 (Table 2 and C. Chirino pers. obs.).

*Main patterns of Sphagnum establishment*

Based on knowledge of different habitat preferences or tolerances of different *Sphagnum* species, we expected the relative success of species or mixtures to vary between trials and with time within each trial. Contrary to expectations, however, we found no significant three-way trial × mixture × age nor two-way trial × mixture or mixture × age interactions (Table 3). Therefore, the response of the different mixtures was consistent over the four trials, invariant of different climatic conditions. Also, the relative response of the different mixtures was consistent within each trial.

The significant trial × age interaction (Table 3) indicated that the moss carpet developed differently over time in the four trials, independent of mixture. The presence of only one single interaction greatly simplified the further analysis because the effect of climatic variation on the growth of the moss carpet (see below) could be meaningfully studied using the mean response of all mixtures for each age and trial. In addition, comparisons between treatments or mixtures could be carried out using all trials and years combined.

Contrary to expectations, the effect of the covariable soil moisture on *Sphagnum* cover was not significant in our experiment (Table 3). Nevertheless, this factor was kept in the statistical model as it removed some of the variability and improved the power of the analysis.

**Table 3.** Analysis of covariance for the effects of climate and species mixture on the establishment of a *Sphagnum* moss carpet on bare peat. Moss cover data were log-transformed ($\log_{10}(x + 1)$) prior to analysis. DF : Numerator degrees of freedom.

| Factors | DF | *p*-value |
|---|---|---|
| Average soil moisture (covariable) | 1 | 0.2738 |
| Trial (re-introduction year) | 3 | 0.0135 |
| Treatment (diaspore mixture) | 8 | ≤ 0.0001 |
| Trial × Treatment | 24 | 0.0862 |
| Age (number of growing seasons) | 3 | ≤ 0.0001 |
| Trial × Age | 9 | ≤ 0.0001 |
| Treatment × Age | 24 | 0.5298 |
| Trial * Treatment × Age | 72 | 0.5637 |
| Contrasts | | |
| Presence vs absence of hummock species in the mixture | 1 | ≤ 0.0001 |
| Single specie vs multi-species mixtures | 1 | 0.4182 |

*Climatic influence on Sphagnum establishment*

The effect of the interannual climatic variation on the development of *Sphagnum* carpets for each of the four trials are shown in Fig. 1, in which all treatments have been combined. In trials initiated during a dry year (e.g. 1995 and 1997), *Sphagnum* carpets developed slowly also the subsequent years when compared to other trials initiated during more favourable summers. Initial climatic conditions thus seemed to have a long-term effect on carpet development but did not alone determine cover in subsequent years. Indeed, the presence of a significant trial × age interaction revealed that the development of the moss carpet was not only influenced by the climatic conditions during the year of re-introduction, but also by the climatic conditions of subsequent growing seasons (Fig. 1a). For example,

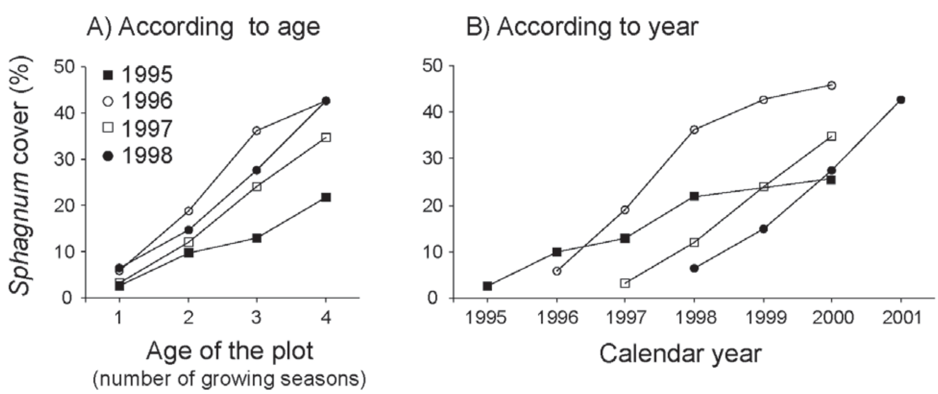


**Fig. 1.** Climate influence on *Sphagnum* establishment during the four trials. Cover averages presented here were calculated for the nine mixtures (retro-transformed averages obtained from the statistical analyses). **A.** *Sphagnum* cover development according to the carpet age (ages used during the statistical analysis only). **B.** *Sphagnum* carpet development according to calendar years. Fifth and sixth growth seasons were included for the 1995 and 1996 re-introduction trials. 1995 = 1995 reintroduction trial; 1996 = 1996 re-introduction trial; 1997 = 1997 re-introduction trial; 1998 = 1998 re-introduction trial.

moss cover observed at age 1 and 2 were not significantly different between the 1995 and 1997 trials (results from the protected LSD tests). At age 3 and 4 however, moss cover was significantly higher in the 1997 trial compared to the 1995 trial, likely due to favourable 1999 and 2000 growing seasons (Fig. 1b).

After four growing seasons, mean percent coverage was low for the 1995 re-introduction trial (22% cover, all treatments combined), intermediate for the 1997 trial (34% cover) and high for the 1998 and 1996 trials (43 and 45% cover, respectively).

Data for the fifth and sixth growing seasons were recorded for the earliest re-introduction trials but not included in the statistical analysis. Fig. 1b shows that the growth rate of the moss carpet slowed down after several years and suggested that after the initial years of establishment the effect of climatic conditions on carpet development progressively diminished. The level at which the coverage of the moss carpet stabilized, however, still appeared to be determined to a large part by initial climatic conditions, as exemplified by the relatively low level for the 1995 re-introduction in a dry year and the relatively high level for the 1996 re-introduction in a wet year.

*Effect of species number*

Contrary to our second hypothesis, no significant difference was detected between multi-species and single-species treatments (Table 3, Fig. 2). The percent coverage of the moss carpet with several species of *Sphagnum* in the re-introduction material was not higher than when species of mosses were re-introduced singly (Fig. 2c). Indeed, the mixture containing the highest number of diaspore species fell into the group of treatments showing the lowest performance, together with one single-species treatment (*S. magellanicum*) and one treatment containing two species (*S. magellanicum* and *S. angustifolium*; Fig. 2a, b). At the same time, the group with the highest mean percent coverage included both single-species and multi-species treatments (*S. fuscum*, *S. fuscum* and *S. rubellum*; Fig. 2b).

*Effect of species identity*

In support of our third hypothesis, inclusion of species adapted to dry conditions (*S. fuscum* and *S. rubellum*) in the dissemination material favoured the development of the moss carpet on residual peat surfaces (Table 3, Fig. 3). The single-species re-introduction of *S. fuscum* resulted in the highest mean percent cover compared to the other re-introduction combinations (Fig. 3a). According to the protected LSD tests the performance of *S. rubellum*, another hummock-forming species, was significantly lower, than that of *S. fuscum*. *S. rubellum* performance was similar to that of *S. angustifolium*, a species of the Section *Cuspidata* which is typical of dense lawn and humid depressions in bogs. The single-species re-introduction of *S. magellanicum* resulted in the lowest performance at every age with all trials combined (Fig. 3b). In addition, three of the four treatments including *S. magellanicum* fell into the group of treatments showing the lowest performance in our experiments (Fig. 3a, b). Hummock-lawn species thus tend to perform better during the establishment phase on bare peat than lawn-hollow species (Fig. 3c) when colonisation does not take place under permanently inundated conditions.


**Fig. 2.** Effect of the presence of more than one species on the development and establishment of *Sphagnum* carpet. Covers presented for each mixture and age were averaged over the four trials (retro transformed averages obtained from the statistical analyses). Results for each of the nine species mixtures (treatment codes F, R, FR, etc. as described in Table 1) are grouped on two separate plots according to absence (**A**) or presence (**B**) of more than one species in the mixture. Average cover for all single or multi-species treatments are presented in **C**.

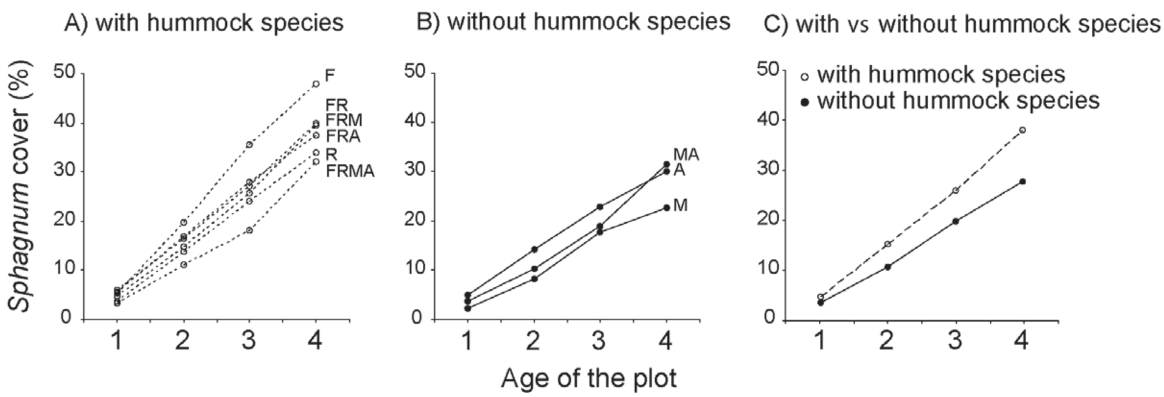


**Fig. 3.** Effect of the presence of *Sphagnum fuscum* and/or *S. rubellum* (hummocks species) on the development and establishment of *Sphagnum* carpets. Cover values presented for each mixture and age were averaged over the four trials (retro transformed averages obtained from the statistical analyses). Results for each of the nine species mixtures (treatment codes F, R, FR, etc. as described in Table 1) are grouped on two separate plots according to presence (**A**) or absence (**B**) of hummuck species in the mixture. Average cover for treatments with and without hummock species are presented in **C**.

## Discussion

### *Effect of climatic conditions on Sphagnum development*

Our results demonstrate that the establishment of a moss carpet from introduced diaspores is most strongly affected by climatic conditions during the re-introduction year (Hypothesis 1) even though the four trials were carried out during years of varying humidity and temperature conditions. Although some significant differences are observed across time between trials, the establishment success of *Sphagnum* for the four trials generally increase at each age according to the sequence 1995 < or = 1997 < 1998 = 1996. This series of trial years corresponds to the sequence of years according to theoretical favourability to *Sphagnum* growth, from the warmest and driest year (1995) to the wettest year (1996). Re-introduction attempts in very dry years lead to persistently retarded long-term development of the moss carpet, that is not outweighted by favourable climatic conditions in later years. Accordingly, re-introduction attempts in wet years (in which days with precipitation > 2 mm is well distributed over the growing season) results in a moss carpet that tends to develop in subsequent years independently of climatic conditions.

*Sphagnum* mosses grow well under high-humidity conditions (Lindholm & Vasander 1990; Campeau & Rochefort 1996; Grosvernier et al. 1997; Karofeld & Toom 1999; Rochefort et al. 2002). Measures of total precipitation do, however, not fully account for the relative success of our re-introductions. The success of the 1998 trial can be explained by an early spring as well as by a relatively high frequency of precipitation, even though total summer precipitation was below average. Total precipitation in the summer of 1997 is similar to that of 1998 but the extended period without rain in 1997 negatively affected *Sphagnum* growth, in accordance with the poikilohydric behaviour of *Sphagnum*. A previous study on predictors of *Sphagnum* growth on a Swedish bog reaches conclusions similar to those of this study on *Sphagnum* establishment on bare peat substratum, that is, that the temporal distribution of the moisture is more important than mean values for specific periods (Backéus 1988).

Extreme conditions of low humidity can cause mortality of diaspores (Clymo 1973; Li et al. 1992; Sagot & Rochefort 1996). It is thus likely that diaspore mortality is the major reason for retarded initial development of the moss carpet in very dry years (e.g. 1995). The extended monitoring of the 1995 and 1996 trials (for six and five years, respectively) seemingly indicate that the development of the *Sphagnum* carpet reach a plateau, the level of which depends on climatic conditions during the re-introduction year. Thus mosses re-introduced during critical years may perhaps never reach the same carpet densities as those re-introduced during favourable years. We believe that if the moss carpet does not re-establish extensively within two years after re-introduction, a dense crust forms on the residual peat surface between the newly established mosses which prevents complete colonization of the substratum by *Sphagnum* in the short term.

### *Effects of species richness and species identity on performance*

We hypothesized that treatments including more than one species of *Sphagnum* have higher establishment success than single-species treatments (Hypothesis 2). Accordingly, we expected *S. angustifolium*, a species thriving in more humid habitats than *S. fuscum*, to be at great advantage when establishing during a wet year. Our results, on the contrary, show that the establishment success of moss species relative to each other remains the same in all trials, independent of climatic conditions, and that the establishment success of the moss carpet is not related to the number of species in the combination. Thus the presence of certain species in the re-introduction material is more important than species richness for regeneration success of the moss carpet. Re-introduction of moss species adapted to dry habitats, i.e. hummocks in natural bogs (*S. fuscum* and *S. rubellum*), in all cases favour the development of the moss carpet on bare peat substratum (Hypothesis 3). The positive effect of these species is, however, primarily linked to the higher success of mixtures with *S. fuscum* (Chirino et al. unpubl. results). This accords with results of Waddington et al. (2003) showing that *S. fuscum* is more productive and less prone to decomposition than *S. rubellum* in exploited peatlands following abandonment. Successful re-introduction of *S. fuscum* on bare peat is well known for greenhouse trials and the field (Campeau & Rochefort 1996), but in the present study we demonstrate that this is invariant of climatic conditions.

Contrary to our findings, Grosvernier et al. (1997) and Buttler et al. (1998) proposed that *S. fallax,* a species of the Section *Cuspidata*, closely related to *S. angustifolium,* is the most useful species for restoration of cut-over peatlands. These authors attribute a competitive advantage to *S. fallax* because this species grows and reproduces rapidly under humid conditions. Their experiments are carried out under very humid conditions and fail to include effects of drought on interspecific interactions. In our study, climatic conditions were highly variable in the experimental period and the drought periods affected development of the moss carpet most strongly. Among the species tested, *S. fuscum* is the one best adapted to variable climatic conditions. Extreme drought can negatively affect *S. fuscum* diaspores (Sagot & Rochefort 1996) but once small colonies have been formed, this species has very efficient water uptake and retention (Clymo & Hayward 1982; Rydin & McDonald 1985; Campeau & Rochefort 2000). Even though (and contrary to some other species) *S. fuscum* may delay formation of new branches when submerged, it eventually produces large numbers of capitula when conditions improve (Rochefort et al. 2002).

One might argue that the lesser performance of *S. magellanicum* stems from the collection procedure because one square meter of *S. magellanicum* contains less meristematic material (for potential regeneration) than one square meter of *S. fuscum*. This is true *per se* but on the other hand, *S. fuscum* capitula and stems are much smaller and more slender than those of *S. magellanicum*. At re-introduction, the density used results in one layer (no overlapping) of stems laid at short distance apart from each other for both species. When new *S. fuscum* capitula begin to form, they remain smaller than the one of *S. magellanicum* and thus have no greater advantages in covering the ground. Furthermore, the potential of *S. fuscum* for regeneration is rather low at 5 - 6 cm below the capitulum whereas *S. magellanicum* can still produce innovations from 9 - 10 cm below the capitulum (Line Rochefort unpubl. data).

*Conclusions and implications for restoration*

This study addresses the establishment success of several combinations of *Sphagnum* species under a variety of environmental conditions over several years. Our results show that combined humidity and temperature conditions during the re-introduction year control the speed by which the moss carpet re-establishes. For the next few years, the carpet continues to be affected by climatic conditions, but to a lesser extent than in the first year. The relative performance of *Sphagnum* species does not vary according to climate.

In general, it is not the number but the identity of re-introduced species that determine the long-term establishment success of the *Sphagnum* carpet. We find *S. fuscum* to be the best choice for restoration of ombrotrophic bogs. This species is very resilient to drought (Campeau & Rochefort 2000), while at the same time being able to cope very well with periods of shallow inundation (Rochefort et al. 2002).

From a practical viewpoint, the collection of diaspores from zones where *S. fuscum* and *S. rubellum* occur together may be an acceptable compromise when pure material of *S. fuscum* is not available. In cases where burial of the re-introduced moss by wind-blown peat is likely, the use of *S. rubellum* may even be preferable to *S. fuscum* since *S. rubellum* is more resistant to burial (Faubert & Rochefort 2002).

Detailed analysis of the further development of coverage for each *Sphagnum* species within different re-introduction combinations is needed to test the hypothesis that interspecific competition and or facilitation occurs between mosses in peatland community restoration.

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