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Does prolonged flooding prevent or enhance regeneration and growth of *Sphagnum*?

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Abstract

Site preparation for restoration of peat-mined bogs in eastern Canada frequently involves the construction of bunds or shallow basins to enhance peat moisture content. As a consequence, *Sphagnum* reintroduced within restored areas may be subjected to extended periods of flooding, particularly following snow melt or heavy rainfall. This paper examines two aspects of the effect of flooding on growth and development of *Sphagnum*: (1) the production of innovations (growth buds and shoots) and capitula from plant fragments (six species) under continuous, intermittent or non-flooding conditions, and (2) the growth response of whole plants (10 species) under long-term continuous shallow flooding.

The development response of *Sphagnum* fragments to short-term continuous (8–10 cm), intermittent (–1 to +1 cm) or non-flooding conditions (–3 to 0 cm), was investigated in growth chambers. Environmental parameters were selected to investigate the possible differential effects of early spring flooding (10:7 °C, day:night), or inundation following heavy rainfall events later in the season (20–25:20 °C, day:night). Both temperature regimes yielded similar results. After 1 month of flooding the number of innovations was generally similar to that for non-flooded controls. However, after a further 3 months, fragments that had been flooded for 1 month (either continuously or intermittently) produced more capitula than non-flooded fragments. Although *S. fuscum*, a hummock-forming species, showed delayed formation of innovations, flooding still increased final capitula production.

The growth response of whole *Sphagnum* plants to long-term continuous flooding in the field (+1 cm), revealed that most species grew well, but that several becoming etiolated. These modifications may result in plants more prone to desiccation during drier events than individual with a regular growth form.

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It is concluded that limited periods of shallow flooding could enhance *Sphagnum* development in restored areas. Care must be exercised though, as deep or extensive inundation may result in excessive plant etiolation or cause severe physical disturbances to the restored areas.

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1. Introduction

Recent restoration techniques developed for peat-mined bogs in North America are based on: (1) the blockage of former drainage systems, (2) the active reintroduction of peatland plant diaspores (any part of a plant capable of initiating a new individual), and (3) the use of mulches to ameliorate the microclimate surrounding regenerating plants (Quinty and Rochefort, 1997a,b; Rochefort and Campeau, 1997; Price et al., 1998; Rochefort, 2000; Rochefort et al., in press). Water availability is often a limiting factor in restored areas and the water table of bare peat areas, even when high in early spring, tends to fall lower than in adjacent natural peatland areas during summer (see Price, 1996, 1997 for a review of the underlying hydrological processes involved). Although *Sphagnum* plants are fairly resilient to drought, an insufficient water supply may reduce photosynthesis and growth, and therefore hinder regeneration (Silvola and Aaltonen, 1984; Rydin, 1993; Gerdol et al., 1996; Sagot and Rochefort, 1996). To overcome this, bunds or shallow basins may be used. These serve to improve water retention, so enhancing summer peat surfaces moisture content (Price et al., 2002). A side effect of the use of bunds and basins is that restored surfaces may be exposed to flooding following snow melt or after heavy rainfall events.

Although *Sphagnum* species are adapted to moist or waterlogged environments, the growth of most species takes place above water. This is particularly true for hummock-forming species whose capitula are located well above the water table even in early spring. Under submerged conditions, CO₂ diffusion to the plant may be decreased, which may in turn lower *Sphagnum* photosynthetic rates (Rice and Giles, 1996) and reduce growth (Baker and Boatman, 1985, 1990; Paffen and Roelofs, 1991). It is therefore, possible that extended periods of flooding may retard the regeneration of reintroduced diaspores or the growth of recently established *Sphagnum* plants. Species specific responses may differ depending on whether flooding occurs on fragments of plants that are regenerating innovations (new growth buds generally formed at the junction between stem and branches) or on mature plants with fully developed capitula. The impact of submergence may also vary according to the environmental conditions under which flooding occurs and temperature is likely to be an important variable. Changes in temperature influence both the physiological demand for CO₂ and the diffusion rate of gases in water, but in opposite ways (Proctor, 1982).

In the field, surfaces prone to spring flooding or inundation following heavy rainfall events will generally stay wetter throughout the summer than non-flooded surfaces. This may enhance the establishment of reintroduced *Sphagnum* (Price and Whitehead, 2001; Girard et al., 2002). However, deep or long-term flooding can cause peat erosion and subsequent deposition on restored areas, resulting in poor vegetation establishment success (Quinty and Rochefort, 2000). The growth and establishment response of *Sphagnum* diaspores

reintroduced onto flooding-prone field sites will, therefore, be determined by a balance between the physiological response of diaspores or young mosses to inundation, coupled with the gain obtained from growing in a wetter environment during the summer, and the possible negative effects of physical disturbances associated with water and peat movements.

This paper presents results from two studies documenting the response of *Sphagnum* mosses to flooding in a peatland restoration perspective. The first study examined the effect of flooding on the regeneration and establishment success of diaspores of six *Sphagnum* species on bare peat. This study included two independent experiments, each run under a different temperature regime. The second study examined the growth response of 10 species to long-term, very shallow flooding in the field. Because of the difficulties in separating the physiological effect of inundation from the positive effects of improved substrate humidity and negative effects of physical disturbances experienced by surfaces prone to flooding in the field, this study investigated the effect of flooding under controlled artificial conditions. It was hypothesized that a prolonged period of flooding would retard diaspore establishment of hummock-forming species and enhance establishment of species more adapted to growth in hollows and pools. It was also anticipated that species adapted to wetter conditions would demonstrate a more “natural” growth rates under flooded conditions than hummock-forming species.

2. Methods

2.1. Growth chambers experiment: the effect of short-term flooding on *Sphagnum* regeneration

This part of the study comprised two similar but independent experiments that examined the effect of different degrees of flooding on regeneration of *Sphagnum fuscum* (Schimp.) Klinggr., *Sphagnum capillifolium* (Ehrh.) Hedw. (sensu lato), *Sphagnum angustifolium* (C. Jens. ex Russ.) C. Jens. in Tolf, *Sphagnum fallax* (Klinggr.) Klinggr., *Sphagnum papillosum* Lindb. and *Sphagnum magellanicum* Brid. under two temperature regimes. Growth chambers were used to simulate spring flooding conditions (10:7 °C, day:night) in one experiment (hereafter referred to as the COLD experiment) and summer flooding caused by heavy rainfall in the other experiment (WARM experiment, 20–25:20 °C, day:night). Plants for the two experiments were collected in the field at the same time, and the experiments were run concurrently. In order to examine both the immediate impact of flooding on regeneration and the longer-term effect on capitula development, the experiments were divided into two parts: a 1 month flooding period in growth chambers (flooded phase) followed by a 4 months growth period in a greenhouse under non-flooding conditions (long-term phase).

2.1.1. Flooded phase of the experiment

For both experiments (COLD and WARM) three flooding regimes were compared: (1) continuous flooding with a water depth of 10 cm; (2) shallow intermittent flooding with a water level fluctuating between –1 and +1 cm from the peat surface, and (3) no flooding, with a water level that barely reached the peat surface. Space available in the COLD and WARM growth chambers only allowed one replicate of each flooding treatment

at a time in its flooded phase. Therefore, the experiment was run three times sequentially, for a total of three replicates per treatment per experiment.

Each repetition (block) consisted of three main experimental units (one 54 cm × 38 cm × 23 cm height water bath for each flooding regime) in which six smaller experimental sub-units were placed (one small container per species per water bath, for a total of 18 small containers in each repetition). Experimental sub-units consisted of perforated plastic containers (13 cm × 13 cm × 10 cm height) filled with commercial horticultural peat. The peat surface was firmly compacted and 20 fragments of *Sphagnum* (3 cm long, and originating from the apical portion of the plant but with the capitula removed) were laid horizontally on the peat surface and anchored in place with coarse netting. Peat containers were attached to the bottom of the three water baths using Velcro bands. The water baths were placed in a growth cabinet, randomly assigned a flooding level and filled with a dilute nutrient solution (Rudolph et al., 1988, modified according to Campeau and Rochefort, 1996) to the desired depth. Three times a week, the water levels were readjusted to the targeted values to compensate for evaporation, once using the diluted nutrient solution and twice using deionized water. Water levels in the different treatments fluctuated due to evaporation and refilling, and ranged between 8 and 10 cm above the peat surface in the continuously flooded treatment, between −1 and +1 cm from the peat surface in the intermittently flooded treatment, and between −3 and 0 cm in the non-flooded treatment. A 16 h light:8 h dark photoperiod was used in the growth cabinets, with a photon flux density of 140 μmol/(m² s).

After 4 weeks in the growth chamber, the experimental units were removed from the water baths and the number of newly formed innovations counted under a dissecting microscope at 64×. Innovations are here described as new growth buds that are generally formed at the junction between stems and branches, and that were at least 1–2 mm long.

2.1.2. Long-term phase of the experiment

Once innovation counts were completed, the small peat containers from both COLD and WARM experiments were placed in a greenhouse for a further 16 weeks during which the newly grown innovations would be allowed to develop into fully formed capitula. Containers were watered three times a week using a dilute nutrient solution (Campeau and Rochefort, 1996). As the excess watering solution was allowed to drain out through the holes in the containers, peat and fragments remained wet but were never flooded. Containers were covered with a shade screen approximately 3 cm above the peat surface in order to create a high humidity air layer around the fragments. Similar covering techniques have been shown to improve *Sphagnum* establishment in greenhouse studies (Buttler et al., 1998; Campeau, unpublished data) and mimic the use of mulch in the field (Quinty and Rochefort, 1997b; Price et al., 1998; Rochefort et al., in press). A 16 h light:8 h dark photoperiod (20:15 °C, day:night) was used, using artificial lighting (400 W sodium lamps). After 4 months in the greenhouse, the number of capitula present in each container was counted. As the initial fragments had no capitula, all recorded capitula developed from innovations.

2.1.3. Statistical analyses

Statistical analyses were done using the SAS/STAT software package (SAS Institute Inc., Cary, NC, USA). The two experiments (COLD and WARM) were analysed separately for each dependent variable measured (i.e. number of innovations at the end of flooded

phase period and number of capitula at the end of the long-term phase period). Analyses of variances were carried out according to a split-plot design, with level of flooding as the main factor and species as the subplot factor. Each repetition in time was considered as a block ($n = 3$ blocks). Data sets were checked for normality and heterogeneity of variances prior to analyses. Innovation and capitula data were square-root transformed prior to analyses. Tukey multiple comparison tests were used to locate differences in main effects between flooding levels. When the flooding \times species interaction was shown significant, the SLICE option of GLM in combination with LSMEANS comparison option (protected LSD) was used to detect differences between flooding levels within each species (simple effects). The significance level for statistical tests was set at 0.05. In the case of protected LSD, the sequential Bonferroni method (Rice, 1989) was used to correct the 0.05 probability level for the number of simultaneous comparisons made (three within each species).

2.2. Field experiment: the effect of long-term continuous shallow flooding on *Sphagnum* growth

The effect of continuous shallow flooding on growth of 10 *Sphagnum* species (Table 2) was investigated using plants held in floating, screen-bottomed containers over a 3.5 months period in the field.

Each experimental unit comprised a Styrofoam box (14 cm \times 27 cm \times 10 cm deep), the bottom of which was removed and replaced with nylon mosquito netting. These boxes were attached in three groups of 10 (one box per species per group) using nylon rope and each group was loosely strung between two posts in blocked ditches of a post-mined peatland in the Lac-Saint-Jean region (Quebec). This allowed a flooding level of 1 cm of water above the screen bottom to be maintained, independent of seasonal fluctuations in the water level. Water chemistry conditions in the blocked ditches were representative of typical bog conditions, with the exception of an observed enrichment in nitrogen and sulphur that is often observed in post-mined surface waters (Wind-Mulder et al., 1996, same experimental site, same year).

Sphagnum plants used for this study were collected from adjacent natural peatlands. Each moss stem was cut at 4 cm from the apex, and only the top portion (i.e. with capitula) was used. Each experimental unit within each of the three groups (blocks) was randomly assigned a species. Because species size varied, the number of plants used per container differed (Table 2). The numbers of plants used for each species were chosen to give a similar density of material in all containers (i.e. with moss stems loosely covering the bottom of the containers but with little overlap). Separate samples for each species were dried to constant weight at 70 °C and used to estimate the initial total dry biomass per container.

Sphagnum plants were placed in the floating containers at mid-June 1993. Moss stems were laid horizontal on the screen bottom. With time however, their apices tended to emerge as the plants grew. At the end of the three and a half experimental period, the plants were harvested and washed with deionized water to remove any foreign particles (mainly peat, but possibly also some algae or invertebrates) that may have settled on the plant while flooded. A subsample of plants from each container was measured to evaluate growth in length over the experimental period. The total content of each container was afterward dried to constant weight at 70 °C to obtain the final total dry biomass.

Growth in *Sphagnum* mosses is essentially linear, the production of all new biomass taking place at the apex (capitula). Specific weight (g dry weight/cm), stand density (number of plant/m²) and growth rates (g dry weight/m² per year) vary widely between species. The fragment size used in this study (4 cm including capitula) was chosen for convenience. In small species such as *S. fuscum*, this fragment may represent up to 2 years of growth. In *Sphagnum riparium*, it may be just a fraction of the natural yearly growth (Lindholm and Vasander, 1990). Likewise, numbers of plants per containers were chosen to account for differences in size between species, not to mimic natural densities. Therefore, growth in length and biomass are here reported as absolute values (mm and mg per plant) in order to be compared with literature values for the same species in natural conditions.

To better understand specific responses to flooding, we were interested in examining how flooding affected the form of growth. To do so, we calculated for each container an “etiolation value”, which was the difference between growth in length and growth in biomass in percentage of initial values. Species with denser new growth are species where percent increase in length was significantly smaller than percent increase in biomass. Species where percent increase in length was significantly greater than percent increase in biomass are considered etiolated. Species where no significant differences could be detected between percent increase in length and percent increase in biomass are considered to show unaltered or “normal” growth in comparison to initial plant fragments.

2.2.1. Statistical analyses

Statistical analyses were done using the GLM procedure of the SAS/STAT software package (SAS Institute Inc., Cary, NC, USA). Growth in length and growth in biomass were compared between species using completely randomised block design analyses of variances ($n = 3$ blocks) followed by a Tukey multiple comparison test. Analysis of variance procedures were also used to evaluate if mean etiolation values for each species departed from zero based on the analysis of variance error term (LSMEANS option of the GLM). Data sets were checked for normality and heterogeneity of variances, and were analysed untransformed. The significance level was set at 0.05 for statistical tests. The sequential Bonferroni method (Rice, 1989) was used to correct this probability level for the number of simultaneous comparisons made (10) when comparing etiolation values to zero.

3. Results

3.1. Growth chambers experiment: the effect of short-term flooding on *Sphagnum* regeneration

Continuous or intermittent flooding for 1 month had only a limited impact on the number of innovations produced (Fig. 1, Table 1). After a further 4 months of growth under non-flooded conditions in a greenhouse however, significantly more capitula developed in the treatments that had been flooded than in controls (Fig. 2, Table 1). The number of innovations and capitula produced varied between species (Table 1).

In more detail, results obtained in the COLD experiment showed a significant interaction between species and water level for the number of innovations after 1 month of

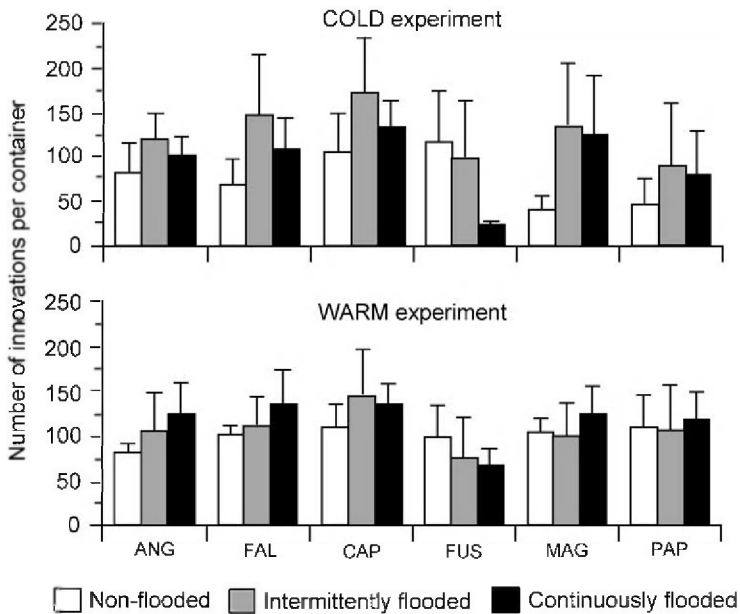


Fig. 1. Effect of short-term flooding (1 month) on the innovation production of *Sphagnum* fragments. The data presented are means and standard errors ($n = 3$) for two separate independent experiments done under COLD (7–10 °C) and WARM (20–25 °C) conditions. ANG: *S. angustifolium*; FAL: *S. fallax*; CAP: *S. capillifolium*; FUS: *S. fuscum*; MAG: *S. magellanicum*; PAP: *S. papillosum*. Flooding levels were 8–10 cm above the peat surface (continuous flooding treatment), between –1 and +1 cm (intermittent flooding treatment) and –3 to 0 cm (non-flooding treatment). See Table 1 for detailed statistical results.

Table 1

Split-plot ANOVA tables for the two experiments on the effect of flooding on short-term innovation production (flooded phase of the experiment) and long-term capitula production (long-term phase of the experiment) for six species of *Sphagnum*

Sources	Flooded phase				Long-term phase			
	d.f.	Mean square	<i>F</i>	<i>P</i>	d.f.	Mean square	<i>F</i>	<i>P</i>
A: WARM experiment								
Block	2	102	11.9	0.02	2	53	13.8	0.016
Flooding	2	2.5	0.3	0.75	2	28	7.34	0.046
Error a (block × flooding)	4	8.6			4	3.9		
Species	5	7.0	2.6	0.04	5	18	5.4	0.001
Species × flooding	10	1.6	0.6	0.81	10	1.4	0.4	0.93
Error b (residual)	30	2.7			30	3.4		
B: COLD experiment								
Block	2	220	26.3	0.005	2	23	94	0.0004
Flooding	2	31	3.7	0.12	2	7.4	30	0.004
Error a (block × flooding)	4	8.4			4	0.25		
Species	5	21	5.6	0.001	5	7.3	3.9	0.008
Species × flooding	10	8.9	2.4	0.03	10	1.7	0.9	0.53
Error b (residual)	28	3.7			30	1.9		

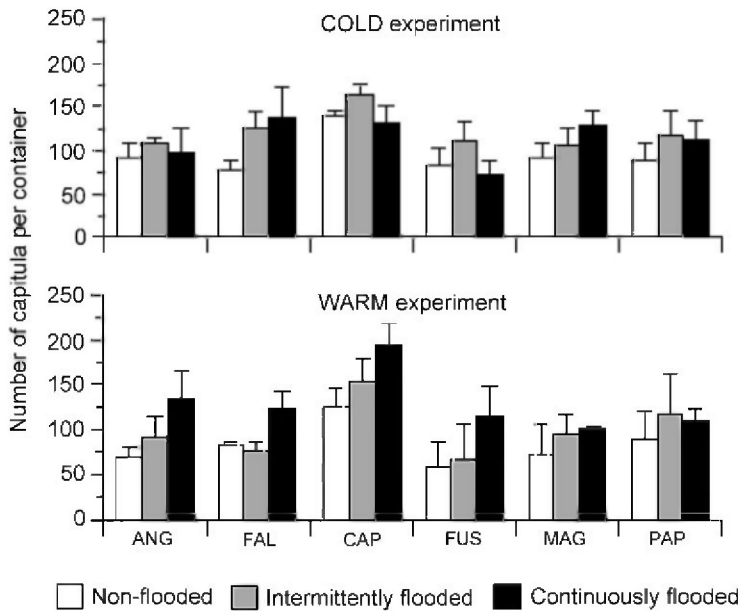


Fig. 2. Effect of short-term flooding (1 month) on long-term (4 months) capitula production of *Sphagnum* fragments. Data presented are means and standard errors ($n = 3$). See Fig. 1 for description of treatments and abbreviations. See Table 1 for detailed statistical results.

flooding (flooded phase of the experiment, Table 1). This interaction is explained by the contrasting behaviour of *S. fuscum* and *S. magellanicum*. Fragments of *S. fuscum* placed in the continuously flooded containers developed significantly less innovations than those in the non-flooded or intermittently flooded treatments. The opposite was observed for *S. magellanicum*, where flooded containers harboured significantly more innovations than non-flooded ones. For all other species tested, no significant differences were detected between the three flooding levels (LSD after SLICE). In the WARM treatment, no significant difference between flooding levels, nor any interaction between flooding and species, were detected for the number of innovations produced (Table 1).

After a further 4 months of development in the greenhouse (Long-term phase of the experiment), counts of capitula showed a pattern different from that observed for innovation counts (Fig. 2). In both the COLD and WARM experiments, significant interspecific differences were observed as well as differences between flooding levels, with no significant interaction between flooding and species (Table 1). In the COLD experiment, containers from the two flooded treatments harboured significantly more capitula at the end of the experiment than non-flooded containers. In the WARM experiment, significantly more capitula were observed in permanently flooded containers than in non-flooded ones, with containers from intermittently flooded treatments displaying intermediate values.

Because the COLD and WARM experiments were not run in the same growth chamber and as replicates were not randomised between the two temperature regimes, the data were not statistically comparable. However, the similarity of conclusions drawn from the two

separate experiments suggests that the response of regeneration to submergence did not vary much with temperature. The overall number of innovations and capitula obtained per experimental unit were also similar in both experiments (Figs. 1 and 2).

3.2. Field experiment: the effect of long-term continuous shallow flooding on *Sphagnum* growth

At the end of the experiment, very few of the submerged stems had produced new capitula or innovations. The observed biomass increase is therefore due to elongation of the initial stems, with the number of capitula (plants) remaining constant over the experiment.

The increase in length of *Sphagnum* plants during the 3.5 months of shallow flooding differed widely among species: from less than 1 cm for *S. fuscum* to 7 cm for *S. riparium* (Table 2). The mean increase in biomass (mg per plant) also varied greatly between species. Differences in total dry biomass did not necessarily rank in the same order as differences in length (Table 2).

Closer examination of the relation between growth in length and growth in biomass suggest that the morphology of the new growth was often different from that of the initial fragment used. Fig. 3 compares the percentage increase in length versus the percentage increase in biomass for each species. If plant morphology stayed the same throughout the experiment, we expect a 50% increase in length to result in a 50% increase in total dry biomass (etiolation value: 0). When the observed value for percent biomass increase is lower than the percent increase in length, it is assumed that the new growth is more etiolated than the initial fragments used (etiolation value greater than 0). Similarly, when percent increase in biomass is larger than the percent increase in length, the new growth is thought to be denser and more compact than the initial fragment (etiolation value smaller

Table 2

Growth data for the 10 species of *Sphagnum* incubated in shallow flooded containers in the field, within a single column, growth values labelled with the same letters are not statistically different at the 0.05 level according to Tukey multiple comparison tests^a

<i>Sphagnum</i> species	Number of plants per container ^b (plants)	Growth during 3.5 months experiment	
		mm	mg per plant
<i>S. riparium</i>	250	73 ^a	32.8 ^a
<i>S. pulchrum</i>	300	57 ^{ab}	10.9 ^{bc}
<i>S. angustifolium</i>	600	45 ^{bc}	5.4 ^{cd}
<i>S. fallax</i>	500	38 ^{cd}	7.8 ^{cd}
<i>S. majus</i>	300	33 ^{cde}	18.3 ^b
<i>S. magellanicum</i>	300	33 ^{cde}	6.4 ^{cd}
<i>S. papillosum</i>	300	28 ^{cdef}	4.2 ^{cd}
<i>S. capillifolium</i>	750	22 ^{def}	1.2 ^d
<i>S. cuspidatum</i>	400	20 ^{ef}	4.3 ^{cd}
<i>S. fuscum</i>	1000	10 ^f	1.8 ^d

^a Standard error for length increment: 3.3 mm ($n = 3$), standard error for increment in biomass: 1.5 mg per plant.

^b Number of plants per container varied to account for differences in size between species.

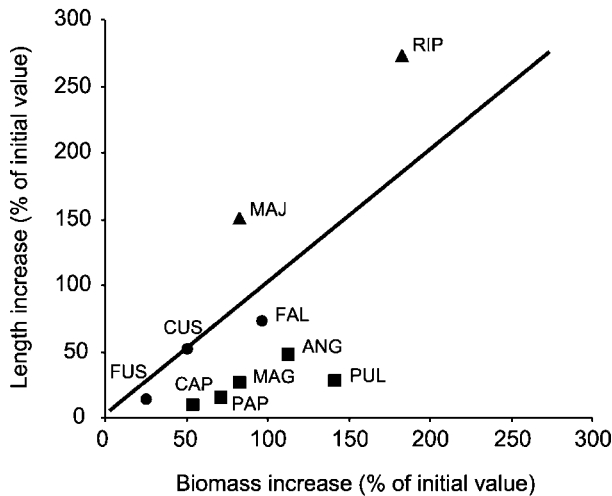


Fig. 3. Growth of *Sphagnum* under long-term shallow flooding (3.5 months) in the field. RIP: *S. riparium*; MAJ: *S. majus*; PUL: *S. pulchrum*; ANG: *S. angustifolium*; MAG: *S. magellanicum*; PAP: *S. papillosum*; CAP: *S. capillifolium*; FAL: *S. fallax*; CUS: *S. cuspidatum*; FUS: *S. fuscum*. Data presented are means and standard errors. ($n = 3$). Species with denser new growth (percent increase in length significantly smaller than percent increase in biomass) are marked with triangles; species with etiolated new growth (percent increase in length minus significantly greater than percent increase in biomass) are marked with squares; species with unaltered new growth (no significant difference between percent increase in length and percent increase in biomass) are marked with circles. The solid line indicates the 1:1 relationship between percent increase in length and percent increase in biomass.

than 0). The greater the difference between the percentage increase in length and biomass, the more important the change in morphology between the new growth and the initial fragment. Comparison of etiolation values to zero value allowed us to divide the species into three groups: (1) those showing significantly denser new growth (*S. riparium* and *S. majus*), (2) those showing significantly etiolated new growth (*S. pulchrum*, *S. angustifolium*, *S. magellanicum*, *S. papillosum* and *S. capillifolium*), and (3) those showing relatively unaltered growth forms (*S. fallax*, *S. cuspidatum* and *S. fuscum*).

4. Discussion

4.1. Effect of flooding on *Sphagnum* regeneration

The individual *Sphagnum* species tested are adapted to various microhabitats characterized by different water availabilities. These range from pools to drier hummocks. *Sphagnum* fragments placed in both flooded and non-flooded conditions all produced innovations, demonstrating that flooding was not essential for any of the species to regenerate. Likewise, short-term flooding (1 month) had no detrimental effect on regeneration. In fact, the levels of flooding applied here even increased capitula production in the long-run. The formation of

innovations was only retarded by flooding in *S. fuscum* in the COLD experiment. This had, however, no effect on longer-term capitula formation. These results are supported by field observations from restoration sites (Ferland and Rochefort, 1997; Quinty and Rochefort, 1997b; Price et al., 1998), which show that *Sphagnum* growth is often favoured in wet depressions or in zones where water tends to accumulate briefly in the spring.

CO₂ limitation due to flooding does not therefore, appear to hinder regeneration under the temperatures and flooding regimes tested (water 10 cm above the peat surface at maximum). From a different perspective, the results may also suggest that flooding during the present study was less detrimental to fragments than continuous exposure to air in the drier non-flooded treatment.

In restored sites, plant establishment in zones subjected to deep or lengthy flooding has been observed as less successful than in other areas (Quinty and Rochefort, 2000). These authors suggested that physical disturbances, such as erosion, subsequent sedimentation and mulch displacement explain the failure of plants to establish. The present study supports this contention, since we did not find any serious impediment to *Sphagnum* regeneration under flooding.

Optimal temperatures for *Sphagnum* photosynthesis lie between approximately 10 and 20 °C, and are probably species-dependent (Kurets et al., 1993; Gerdol, 1995; Maseyk et al., 1999). The experimental temperatures used were in the acceptable range of temperature for *Sphagnum* moss development, and the number of innovations observed for a given species in the COLD and WARM experiments were generally comparable. The similarity of conclusions drawn from both experiments suggests that the observed responses of *Sphagnum* to flooding could be valid over a wide range of environmental conditions. Differences between flooding and non-flooding treatments were greater in the COLD than in the WARM experiment. Although this was possibly due to differences in air temperature, it may also have been due to differences in relative humidity. Ventilation in the COLD growth chamber was probably greater than in the WARM one, which may have increased the drying effect on exposed fragments. In the field, *Sphagnum* diaspores reintroduced onto bare peat are generally covered with a straw mulch (Quinty and Rochefort, 1997b; Rochefort et al., *in press*) to maintain a humid microenvironment around diaspores (Price et al., 1998). The presence of a mulch probably reduces differences between temporarily flooded and non-flooded areas in the field.

4.2. Effect of flooding on *Sphagnum* growth

All of the species tested were able to survive and grow under long-term shallow flooding (3.5 months). Increases in length measured after the 3.5 months field experiment (Table 2) varied between species, but were in the range of growth rates recorded for the same *Sphagnum* species under natural conditions (see Lindholm and Vasander, 1990; Rochefort et al., 1990). Comparisons of biomass increase with values reported in other North American studies (Table 3), including data recorded on the same peatland as our study (Waddington et al., *in press*), suggest that for certain species the increase in biomass was not as high as might be expected from the increase in length. For example the 22 mm increase in length of *S. capillifolium* recorded under flooded conditions is nearly double that recorded in natural areas of the same peatland during the 1998 and 1999 growing seasons (Waddington et al., *in*

Table 3

Growth data recorded for four species of *Sphagnum* in North American field studies

<i>Sphagnum</i> species and study	Total growth over the growing season		
	mm	g/m ²	mg per plant ^a
<i>S. angustifolium</i>			
Bartsch and Moore, 1985	4–9	19–58	0.7–2
Moore, 1989	4–17	29–127	1–4.3
Rochefort et al., 1990	20–39	97–198	3.3–6.8
<i>S. magellanicum</i>			
Rochefort et al., 1990	11–34	52–240	3.1–14
<i>S. fuscum</i>			
Pakarinen and Gorham, 1983	17–29	195–239	3.7–4.5
Moore, 1989	6–7	75–83	1.4–1.6
Rochefort et al., 1990	7–31	69–303	1.3–5.7
Waddington et al. (in press)	15–27	163–287	3.1–5.4
<i>S. capillifolium</i>			
Moore et al., 1989	8–9	70–79	1.6–1.9
Waddington et al., in press ^b	12–16	113–231	2.7–4.4

^a For comparison with results from our experiment, growth per plant in the different studies was estimated by dividing growth values in g/m² by the following density constants: *S. angustifolium*: 29,000 plants/m²; *S. magellanicum*: 17,000 plants/m²; *S. fuscum*: 53,000 plants/m² and *S. capillifolium*: 42,000 plants/m². These specific density of capitula were established from measurements made in natural areas of two Lac-Saint-Jean peatlands (Campeau, unpublished data). Results were similar to those measured for the same species in an Ontario peatland (Rochefort, unpublished data). The *S. fuscum* densities are also similar to those reported by Lindholm and Vasander (1990) in Finland.

^b Data collected from the same peatland as the current study.

press; Table 3). By contrast, the 1.2 mg increase in biomass per plant recorded for the same species is only a fraction of the values recorded by Waddington et al. (in press), (Table 3). *S. magellanicum* and, to a lesser extent, *S. angustifolium* showed similar patterns (Table 3). These observations are coherent with the fact that these three species demonstrated etiolated new growth under submerged conditions. For *S. fuscum*, the 1.8 mg per plant increase in biomass observed in our flooded containers is at the low end of values reported in natural areas and is associated with a comparably low length increment (Table 3). Again, this supports the observed non-etiolated, low growth of this species under flooded conditions.

The major impact of continuous shallow flooding on the growth of fully developed *Sphagnum* mosses was, therefore, a change in growth form. Three types of responses were observed, which could be loosely linked to the original habitat of the species being tested. Species such as *S. riparium*, originating from flooded habitats grew denser (more biomass per cm of stem) in our shallow-flooded containers than in nature, whereas new growth of terrestrial species such as *S. angustifolium*, *S. magellanicum*, and *S. capillifolium* was etiolated, resulting in plants with a lower biomass per cm of stem than the original fragments. Only three of the species tested maintained their initial density: two of those, *S. cuspidatum* and *S. fallax* generally grow in shallow water comparable to the experimental conditions

tested. Unexpectedly at least based on its natural habitat, the third species of this group is *S. fuscum*, a high hummock-forming species and the most “terrestrial” of all *Sphagnum* species tested.

Whilst the ability of certain species to respond to flooding by growing longer stems may seem an advantage for rapid establishment on bare peat, these new stems maybe more prone to desiccation once the water level falls. Field observations on the establishment of *S. fuscum*, *S. capillifolium*, *S. magellanicum* and *S. angustifolium* on peat, show that the latter three species tended to form much looser colonies of etiolated plants in areas that were temporarily flooded in the spring. *S. fuscum*, in contrast, elongates much less (Campeau and Rochefort, field observations). When the peat surface dries out during summer, the looser *S. capillifolium*, *S. magellanicum* and *S. angustifolium* colonies tend to bleach and desiccate more rapidly than adjacent, more compact, *S. fuscum* colonies. Indeed, *S. fuscum* colonies established in shallow peat basins are denser and better able to retain their humidity than *S. capillifolium* colonies during summer dry spells (Campeau and Rochefort, 2000).

4.3. Implications for peatland restoration

Results from our growth chamber experiments suggest that regenerating fragments of all the species of *Sphagnum* tested, whether from hummocks or hollows, can tolerate and even benefit from shallow temporary flooding. Areas that tend to be temporarily flooded also tend to stay wetter throughout the growing season. When this is the case, establishment of reintroduced *Sphagnum* will be enhanced, as establishment success is strongly linked to the level of humidity at the peat surface during summer (Price and Whitehead, 2001; Girard et al., 2002). However, it must be underlined that flooding is by no means an absolute necessity for *Sphagnum* regeneration and growth. On the contrary, severe or lengthy flooding in the field, and even limited flooding of unstabilized fine peat, can lead to erosion and peat deposition, that in turn retard or impede vegetation establishment (Quinty and Rochefort, 2000; Faubert and Rochefort, 2002).

Bare peat peatland surfaces subjected to hydrological restoration measures are characterised by water table fluctuations that are more pronounced than in natural peatlands (Price, 1996). Hummock species, such as *S. capillifolium* and particularly *S. fuscum*, are often recommended for use in peatland restoration in Canada as they have better recolonization success than other species (Campeau and Rochefort, 1996; Campeau and Rochefort, 2000; Chirino and Rochefort, 2000; Waddington et al., in press). It is generally believed that the success of these species—and of *S. fuscum* in particular—is linked to their capacity to survive periods of low water availability during summer. In this study, we hypothesised that hummock species may not be as efficient at coping with temporary flooding as those species usually found in hollows or pools. Our present results however do not confirm this. On the contrary, hummock species can apparently establish efficiently in a wide range of conditions, from temporarily to non-flooded peat surfaces. Furthermore, the peculiar growth response of the hummock-building *S. fuscum* to flooding, i.e. the lack of etiolation as observed in other terrestrial species, may in fact be important in explaining the success of this species when establishing in environments subjected to water level fluctuations.

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