

## THE DYNAMICS OF A COTTON-GRASS (*ERIOPHORUM VAGINATUM* L.) COVER EXPANSION IN A VACUUM-MINED PEATLAND, SOUTHERN QUÉBEC, CANADA

Claude Lavoie<sup>1</sup>, Kathleen Marcoux<sup>1</sup>, Annie Saint-Louis<sup>1</sup>, and Jonathan S. Price<sup>2</sup>

<sup>1</sup>*Centre de recherche en aménagement et développement*

*Université Laval*

*Sainte-Foy, Québec, G1K 7P4, Canada*

*E-mail: claudelavoie@esad.ulaval.ca*

<sup>2</sup>*Department of Geography and Wetlands Research Centre*

*University of Waterloo*

*Waterloo, Ontario, N2L 3G1, Canada*

**Abstract:** We studied from 1998 to 2003 the fine-scale vegetation dynamics of an abandoned vacuum-mined bog located in southern Québec in which cotton-grass (*Eriophorum vaginatum*) has become dominant. A water table no deeper than 30–40 cm below the soil surface combined with a volumetric peat water content >70% in the surface peat layer favored the increase in cotton-grass cover in abandoned peat fields. In one of the two peat fields that was monitored, the density of living tussocks was 30,750/ha in 1998. The density decreased constantly to reach 25,900/ha in 2002, a 16% decrease. The expansion of cotton-grass cover was mainly the result of the growth of established tussocks following a rise of the water table. The strong relationship between cotton-grass cover and water table suggests that the latter could be used as a predictor for cotton-grass cover change in mined bogs. The present study does not provide evidence that cotton-grass facilitates the establishment of moss species. At the study site, moss establishment was more highly associated with particular hydrologic characteristics (volumetric peat water content  $\geq 85\%$ ) than with the presence of a dense cotton-grass cover. The use of cotton-grass to facilitate the establishment of *Sphagnum* colonies in mined peatlands is questionable, particularly where other efficient restoration techniques are available.

**Key Words:** biological invasion, cotton-grass, *Eriophorum vaginatum*, mire, monitoring, peatland, Québec, restoration

### INTRODUCTION

Invasive plants produce reproductive offspring, often in very large numbers at considerable distances from parent plants, and thus have the potential to spread over a considerable area (Richardson et al. 2000). They are generally perceived as weeds because they often negatively impact the diversity of plant communities. Invaders may compete for natural resources, transform entire ecosystems by changing the nutrient composition of soils, and alter the frequency and intensity of natural disturbances (Lodge 1993, Mack and D'Antonio 1998, Mack et al. 2000, Ehrenfeld 2003). In most cases, eradication or control of invasive plants is essential for maintaining the ecological integrity of ecosystems. There are, however, some particular cases where invasive species may be used by managers to improve the environmental conditions of highly disturbed sites, especially where site conditions are so degraded that few plant species are able to establish and survive. Invasive species may be used

to re-establish a plant cover rapidly and restore site fertility, which may subsequently improve establishment conditions for other species (D'Antonio and Meyerson 2002). If the vegetation assemblage dominated by the invasive species persists for only a few years or decades, the introduction of the invader may represent an alternative to costly restoration techniques.

Mined peatlands are one of these particular cases where invasive plants may be useful for restoration. Peatland mining is a widespread industrial activity, especially in Canada (Québec, New Brunswick) and Germany, where peat is used for horticulture or agriculture, and in Finland and Ireland, where peat is used for domestic heating or energy generation. Extraction activities cover approximately 50,000 km<sup>2</sup> and are responsible for 10% of peatland area losses in the non-tropical world (Joosten and Clarke 2002). Peatland mining is a major anthropogenic disturbance—bogs are drained, vegetation is removed, and a thick layer of soil is extracted—and usually occurs over a period

of several decades. A post-mined peatland is a harsh environment for plants, and current mining techniques seriously hamper the natural capacity of bog ecosystems to regenerate after a disturbance. For instance, most sites that have been mined using vacuum machines are almost totally devoid of plants after decades of abandonment (Lavoie *et al.* 2003). There are, however, some vacuum-mined bogs that have been invaded (>60% cover) by cotton-grass (Cyperaceae: *Eriophorum vaginatum* L.). Although cotton-grass is a native species in regions with peatland mining activities, this plant species never dominates plant assemblages in undisturbed ombrotrophic peatlands. For instance, the plant cover occupied by cotton-grass in southern Québec's bogs usually ranges from 1 to 5%, and very rarely exceeds 25% (Gauthier and Grandtner 1975, D. Lachance and C. Lavoie, unpublished data).

Cotton-grass has many characteristics facilitating its establishment and survival in nutrient-poor environments such as mined bogs that have been drained. This plant species can tolerate prolonged drought periods because of its deep root system (Wein 1973). Numerous cotton-grass seeds are produced each year and are easily dispersed by wind (Salonen 1987, Campbell *et al.* 2003). Seeds germinate at high (23–35 °C) temperatures (Wein and MacLean 1973, Gartner *et al.* 1986), and such temperatures are common during the summer season just above the peat surface of abandoned mined bogs (Matthey 1996, Price *et al.* 1998, Marcoux 2000). Cotton-grass forms long-lived (>100–200 years) tussocks (Mark *et al.* 1985), in which the growth of new leaves is supported almost entirely by nutrient retranslocation from older leaves that are senescing (Jonasson and Chapin 1985, Cholewa and Griffith 2004). Furthermore, this non-mycorrhizal plant can absorb organic nitrogen directly and use it as its sole nitrogen source (Chapin *et al.* 1993).

With only minimal water management, it is possible to increase the cotton-grass cover in disturbed peatlands substantially. For instance, the cotton-grass cover increased from 1 to 60–70% two years after the rewetting of a drained fen, and from 18 to 34% five years after the rewetting of a mined bog in southern Finland (Komulainen *et al.* 1998, 1999, Tuittila *et al.* 2000b). In southern Québec and New Brunswick, several abandoned and rewetted mined sites with a >60% cotton-grass cover have been identified (LeQuéré and Samson 1998, Lavoie *et al.* 2003). Whether such invasions are beneficial or detrimental to abandoned mined peatlands remains a controversial issue. Paleoecological studies suggest that cotton-grass is an 'ecosystem engineer' or a nurse plant facilitating the re-establishment of *Sphagnum* species in mined bogs (Buttler *et al.* 1996, Hughes and Dumayne-Peaty 2002). Cotton-grass is presumed to create microcli-

matic conditions facilitating the establishment and growth of other plants, particularly *Sphagnum* species (Grosvernier *et al.* 1995, Matthey 1996, Marcoux 2000, Tuittila *et al.* 2000a, Lavoie *et al.* 2003). On the other hand, cotton-grass may also be considered as an invading weed prohibiting the re-initiation of peat formation, impeding restoration activities and enhancing greenhouse gas emissions (Pfadenhauer and Klötzli 1996, Frenzel and Rudolph 1998, Kumolainen *et al.* 1998, Frenzel and Karofeld 2000, Greenup *et al.* 2000, Rinnan *et al.* 2003, Marinier *et al.* 2004).

To our knowledge, no detailed study on the dynamics of a cotton-grass cover expansion in a mined peatland has been reported. This study, based on five years of detailed monitoring of tussock individuals and cotton-grass cover, has two main objectives, i.e., to understand which factors facilitate an increase in cotton-grass cover, and to verify whether the establishment of typical bog plants is facilitated by the presence of cotton-grass. Our working hypothesis is that the re-establishment of moss colonies is more rapid in mined sites invaded by cotton-grass than in sites with a low cotton-grass cover.

## STUDY SITE AND METHODS

One peatland, in which cotton-grass has become a dominant species, was selected for this study. The Saint-Henri peatland is located 16 km southwest of Québec City, Québec, Canada (46° 42' N; 71° 03' W) and covers 150 ha (Figure 1). Before the beginning of mining activities, this ombrotrophic peatland was dominated by black spruce (*Picea mariana* [Mill.] B.S.P.), tamarack (*Larix laricina* [Du Roi] Koch), ericaceous shrubs, and *Sphagnum* species, with scattered cotton-grass individuals. In 2003, approximately 80% of the bog area had been mined for the production of horticultural peat, mainly using the block-cut method during the 1960s and the vacuum method since the beginning of the 1970s (Marcoux 2000). Data from the meteorological station at Québec City indicate that the mean annual temperature is 4 °C. January is the coldest month (mean temperature: -12 °C) and July the warmest month (mean temperature: 19 °C). The mean annual precipitation is 1208 mm, 27% of which falls as snow (Environnement Canada 1993).

In 2003, approximately 40% of the mined area of the bog had been abandoned. Some abandoned sites with a very thin (<20 cm) peat cover were colonized by gray birch (*Betula populifolia* Marsh.), while the others were colonized by cotton-grass. For this study, we selected two large (180 × 24 m) vacuum-mined peat fields (A and B) bordered by drainage ditches and abandoned the same year (Figure 1). Peat field A (mined between 1979 and 1993) was bordered by oth-



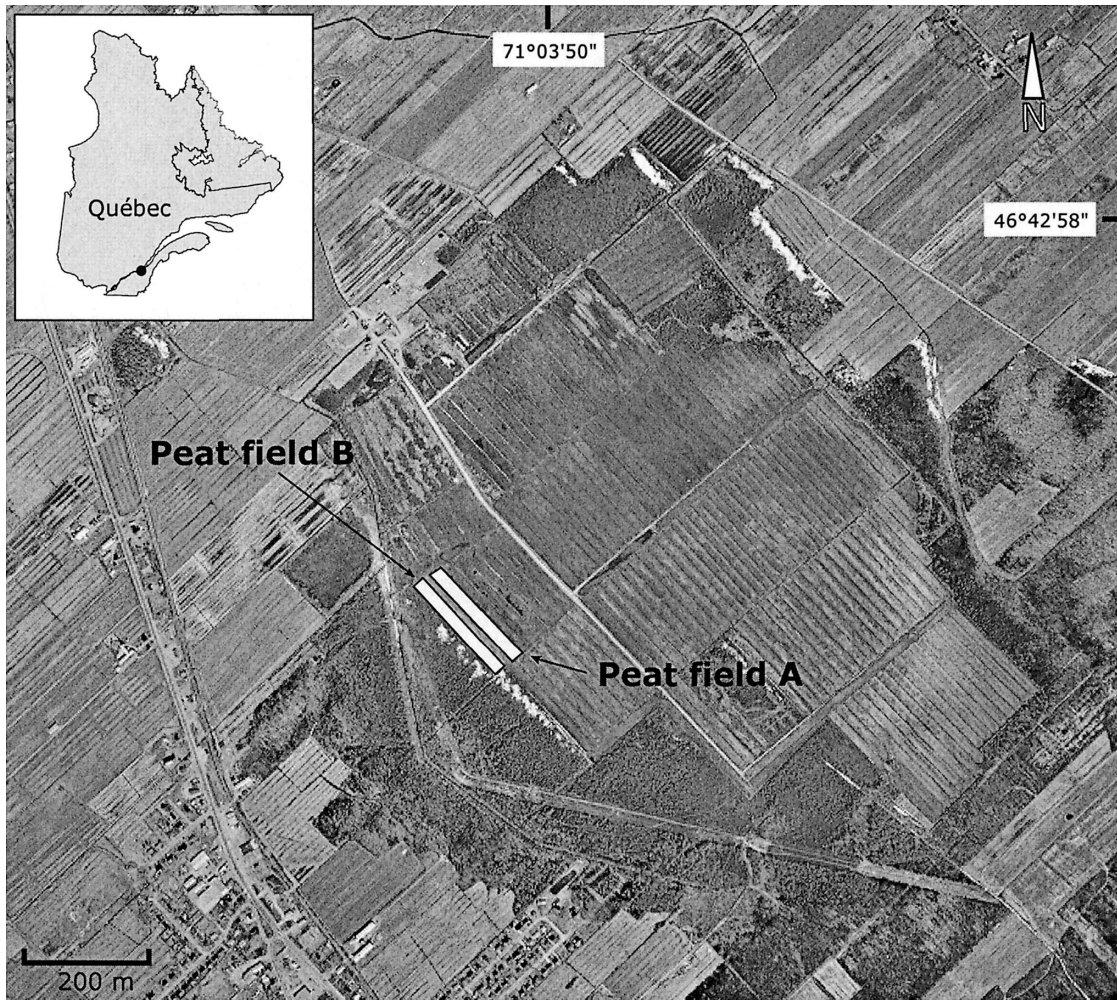


Figure 1. Aerial photograph of the Saint-Henri ombrotrophic peatland, southern Québec, Canada taken in 1993. Approximately 80% of the bog area was mined using vacuum machines. Study sites (peat fields A and B) are indicated (photograph: courtesy of Hauts-Monts Inc., HMQ93106-12).

er peat fields, while peat field B (mined between 1987 and 1993) was located between a peat field and the undisturbed margin of the peatland. An abandoned peat field with similar dimensions separated peat fields A and B. Drainage ditches bordering peat fields A and B were partly blocked in 1993, and in 1998, the cotton-grass cover was very large in peat field A, especially at the lower end of the peat field; this section was very wet (water table close to the peat surface) and had a >90% cotton-grass cover. Several cotton-grass tussocks established at peat field B between 1993 and 1998, but the peat surface remained dry and the cotton-grass cover was very low (<10%) during that period (Figure 2a). In 1998, when we initiated this study, we decided to study peat field B to understand why the cotton-grass recolonization process was so slow in this part of the peatland. However, the owner of the site decided in the fall of 1998 to improve the blockage of drainage ditches and to construct peat

bunds near peat fields A and B, to reduce surface runoff. The cotton-grass cover substantially increased following those operations, especially in peat field B (Figure 2b). Cotton-grass tussocks in peat fields A and B probably originated from seeds produced by the few tussocks established in the unmined parts of the peatland and dispersed by wind toward the peat fields, and from tussocks established in other peat fields that have been previously abandoned.

The cotton-grass cover was not homogeneous in peat field A. Consequently, we used this peat field to describe the spatio-temporal pattern of cotton-grass cover change and to associate this pattern to some hydrologic characteristics. In peat field A, the presence / absence of all species of vascular and non-vascular plants covering a small sampling-point (diameter: 1 cm) every 1 m along 25 transects, 1-m apart and 180-m long (Lavoie and Rochefort 1996) was noted in July 1999. The same survey was repeated in July 2003. The



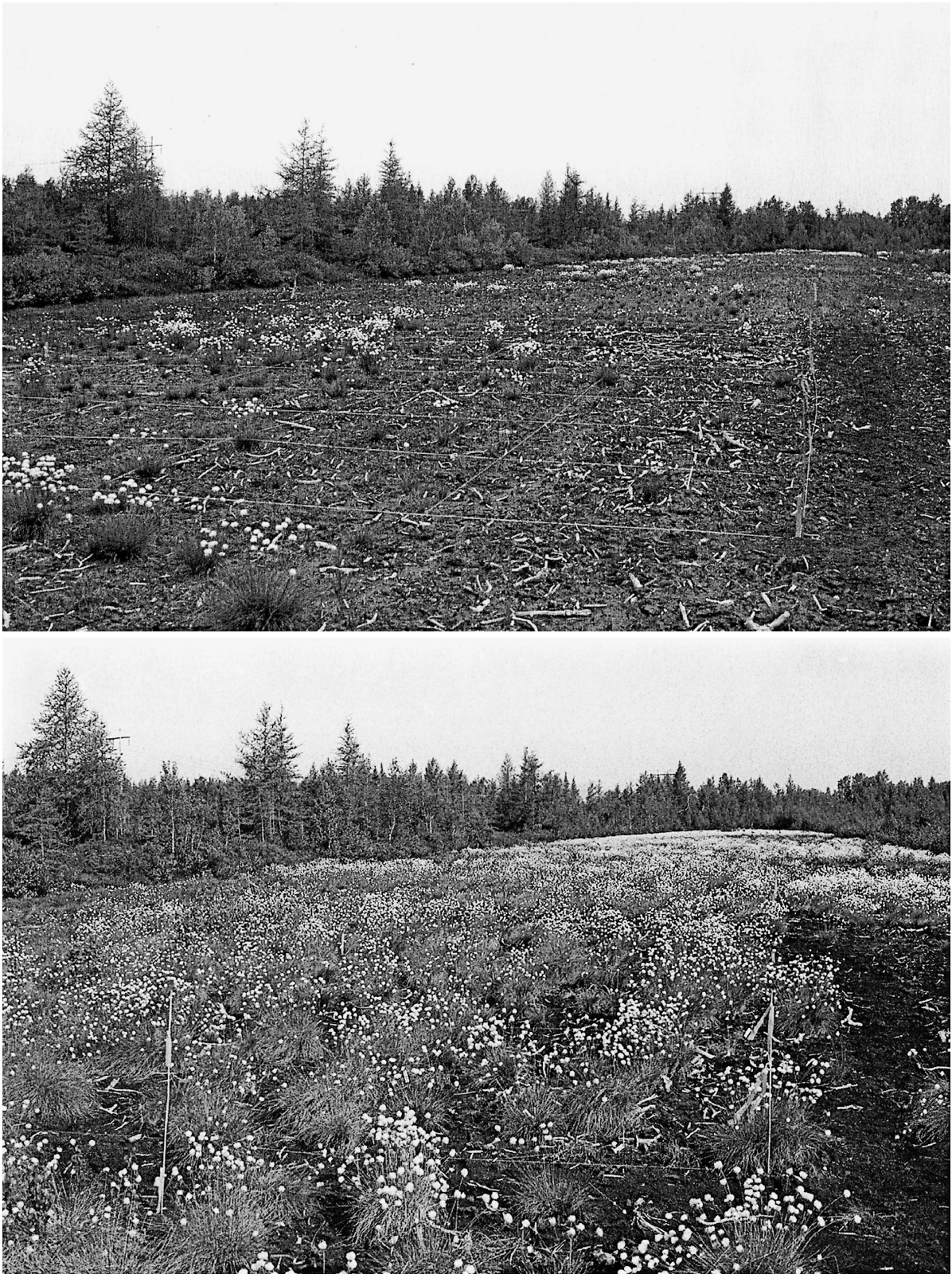


Figure 2. Vacuum-mined site in the Saint-Henri bog that was abandoned in 1993: A) peat field B in 1998, sparsely revegetated by cotton-grass (*Eriophorum vaginatum*) tussocks; B) the same location in 2000, with a dense cotton-grass cover.



1999 and 2003 surveys were compared using a Wilcoxon's signed-ranks test to verify whether they were significantly different (Scherrer 1984). Furthermore, the surveys were compared for each major group of species (cotton-grass, trees, ericaceous shrubs and mosses, including liverworts) using a McNemar's test to detect whether a species group was significantly more or less abundant in 2003 than in 1999. Each sampling point was then considered individually to detect if at least one species of the group was present / absent in 1999 and in 2003 (Scherrer 1984). The Bonferroni's correction was applied to weight the significance level ( $\alpha = 0.05$ ) by the number (N) of McNemar's tests used ( $\alpha / N$ ) (i.e., one for each species group) (Harris 1975, Bérubé and Lavoie 2000). Nomenclature follows Hinds (2000) for vascular plants, Anderson (1990) for *Sphagnum* species, and Anderson et al. (1990) for other mosses.

At peat field A, the relative elevation of the peat surface was measured with a surveying level every 2 m along 13 transects, 2-m apart and 180-m long. The thickness of the peat deposit was also estimated using an iron rod driven into the soil every 10 m along 9 transects, 3-m apart and 180-m long. The volumetric soil moisture content of the surface (12 cm) peat layer was mapped in 1999 (August 11) using a Hydro-Sense™ soil-water content measurement system (Campbell Scientific, Logan, UT, USA). One measurement was taken every 5 m along 7 transects, 4-m apart and 180-m long. Volumetric soil moisture content data were calibrated for peaty soils in the laboratory using peat samples from the same peat field (Marcoux 2000). Maps of relative elevation, peat thickness, and volumetric soil moisture content were created using Kriging's method of Surfer® software (Golden Software Inc. 1996).

The water table at peat field A was monitored during summers of 1999 (July 5–September 5) and 2000 (June 12–August 28) on a daily (1999) or weekly (2000) basis. The water table was measured using well pipes slotted along their entire length and covered with a geotextile screen. Pipes were inserted in hand-drilled holes every 10 m along a 180-m long transect positioned along the centre-line of the peat field. All pipe intakes were above the peat-mineral interface. The distance from the top of the well to the soil surface was measured coincidentally with water-table measurements to account for possible shifting of the pipe due to peat shrinkage. Pearson's product moment correlation coefficients (Gilbert and Savard 1992) between the water table and the cotton-grass cover were calculated for summers 1999 and 2000 using SPSS software (SPSS Inc. 2001). Cotton-grass cover was calculated by the percentage of vegetation sampling points with cotton-grass surrounding a water-table well

(i.e., inside a 5-m distance on either side of the well). For instance, the well located at a distance of 50 m from the beginning of the transect was associated with all sampling points located between 45 and 55 m along the 25 transects used for vegetation sampling.

In peat field A, cotton-grass cover strongly decreased at a distance of 120 m from the beginning of the transect, suggesting the presence of a threshold. We used a categorical variable approach to test the statistical significance of the difference between the intercepts and the regression coefficients calculated using values from either side of this 120-m distance. To do so, the two sets of observations were pooled into one set. To test the difference between the intercepts, we defined a categorical variable, Distance (DIS), which equalled 1 for observations located between 0 and 120 m (large cotton-grass cover), and 0 for observations located between 120 and 180 m (low cotton-grass cover). A significant difference between the intercepts would indicate the presence of a threshold value for the cotton-grass cover. To test the difference between the regression coefficients of water table, we created an interaction variable by multiplying mean water-table values by DIS after having centered the interval scale variable in order to avoid multicollinearity. A significant interaction variable would indicate that the relationship between cotton-grass cover and water table is not the same on either side of the threshold value (Vandersmissen et al. 2003). The SPSS software (SPSS Inc. 2001) was used for all calculations.

Cotton-grass cover was homogeneous in peat field B but changed greatly from 1998 to 2002. Consequently, we used this peat field to monitor precisely a cotton-grass population during a five-year period. We delineated a 10 × 20 m quadrat that was subdivided into fifty 2 × 2 m subquadrats. In each subquadrat, the percent cover of all vascular and non-vascular plants was estimated each year (in late-May, early-June) from 1998 to 2002 using a semi-quantitative scale: 0%, <1%, 1–10%, 11–25%, 26–50%, 51–75% and 76–100%. The species cover was compared year to year by calculating the median value of the cover class occupied by the species in each subquadrat, and totalling all median values from all subquadrats. The position of each cotton-grass tussock was mapped using an  $x - y$  coordinate system, and its status (living or dead) was monitored each year. New tussocks established after 1998 were also monitored, but it is important to note that this growth form can only be clearly distinguished from seedlings after one or two growing seasons. The number of infructescences produced each year by the tussocks was counted. The number of emerging seedlings was also estimated in five randomly selected subquadrats. A Pearson's product mo-

ment correlation coefficient (Gilbert and Savard 1992) between the number of infructescences and the number of seedlings emerging one year later was calculated using SPSS software (SPSS Inc. 2001).

In the 10 × 20 m quadrat, the water table and the volumetric soil moisture content of the surface (12 cm) peat layer were monitored on a weekly basis during the summers (June–August) of 2000 and 2001. The water table was measured using well pipes inserted in holes drilled at three different locations (i.e., at the center and at each extremity of the quadrat). The volumetric soil moisture content was monitored near each well using the HydroSense™ system. Unfortunately, we have no hydrologic data for summer 1998. We did not expect major changes in the hydrology of the site from 1998 to 1999 because the peat company did not initially plan to conduct additional water management operations near peat fields A and B. This decision was made in the fall of 1998.

One peat sample from the surface (5 cm) peat layer was taken from the quadrat for chemical analyses, which were conducted in the Premier Horticulture Laboratory (Rivière-du-Loup, Québec, Canada) using the standard methods suggested by Day *et al.* (1989). Total peat thickness was estimated using an iron rod driven into the soil at eight different locations near the quadrat (near all corners and mid-points between corners). Precipitation data during the monitoring period were taken from the Québec meteorological station (Environnement Canada, unpublished data) and were compared to a reference period (Québec station, 1961–1990; Environnement Canada 1993).

## RESULTS

### Peat Field A

The thickness of the peat deposit at peat field A ranged from 24 cm at the lower end of the field to 143 cm at the upper end. However, two-thirds of the field area had a peat thickness >84-cm and a large *Sphagnum* peat content. Approximately 64% of the field surface was covered with cotton-grass in 1999, but the cover varied greatly from 96% in the lower third of the peat field to 28% in the upper third (Figure 3). Only 18 plant species were found in 1999, including three moss species. No *Sphagnum* colony was detected. Peat field A was more species-rich in 2003, with 13 vascular plant species and 14 moss and liverwort species, respectively. Four *Sphagnum* species were recorded (*S. capillifolium* (Ehrh.) Hedw., *S. rubellum* Wils., *S. russowii* Warnst., and *S. teres* (Schimp.) Ångstr. *in* Hartm.). The 1999 and 2003 vegetation surveys were significantly different ( $p < 0.001$ ). The cover of trees, ericaceous shrubs, and mosses (including

liverworts) was significantly higher ( $p < 0.001$ ) in 2003 than in 1999, while the cover of cotton-grass significantly ( $p < 0.001$ ) decreased from 64 to 58% during the same period. The increase in the tree cover was mainly the result of the growth of birch (*B. populifolia*) saplings, while that of ericaceous shrubs was the result of the establishment of several *Chamaedaphne calyculata* (L.) Moench individuals. Although the spatial distribution of trees and ericaceous shrubs was relatively homogeneous at peat field A in 2003, the distribution of moss and liverwort species was mainly restricted to the wettest part of the field, and essentially in the zone with a volumetric peat water content  $\geq 85\%$ . This zone represented only 14% of the peat field by area but 57% of the sampling points with at least one moss or liverwort species.

There was a significant ( $p < 0.001$ , adjusted  $R^2 = 0.89$  for both years) correlation coefficient between the mean water table and cotton-grass cover in 1999 and 2000. As indicated in the Methods section, the cover of cotton-grass strongly decreased at a distance of about 120 m along the transect (i.e., from 75 to 40% over a 20-m distance) (Figure 3). The decrease in the cotton-grass cover coincided with the location at which the mean water table dropped farther than 30 cm below the soil surface in 1999 and farther than 40 cm below the soil surface in 2000 (Figure 4). The cotton-grass cover was significantly different on either side of the 120-m distance, as indicated by the significant ( $p < 0.001$ ) difference between the intercepts. However, the interaction variable that has been calculated was not significant ( $p = 0.318$ ), suggesting that the relationship between cotton-grass cover and water table was the same on either side of the 120-m distance.

### Peat Field B

Peat field B had a thick (165–189 cm), acidic (pH = 3.14) peat with a large *Sphagnum* content. In general, chemical properties of the peat were similar to those recorded in abandoned mined bogs (Wind-Muller *et al.* 1996):  $\text{Ca}^{2+}$ ,  $\text{Cl}^-$ ,  $\text{Mg}^{2+}$ ,  $\text{Na}^+$ ,  $\text{NH}_4^+-\text{N}$ , and  $\text{NO}_3^--\text{N}$  values ranged from 1 to 8 mg L<sup>-1</sup>. During the summers of 2000 and 2001, except for some very brief periods, the water table and the volumetric peat water content were quite stable, ranging from 10 to 40 cm below the soil surface and from 70 to 85%, respectively.

The spatial distribution of cotton-grass tussocks was fairly homogeneous at peat field B. At the beginning of the monitoring period (1998), the density of living tussocks was 30,750/ha. The density decreased constantly to reach 25,900/ha in 2002, a 16% decrease. The annual mortality rate of tussocks ranged from 5

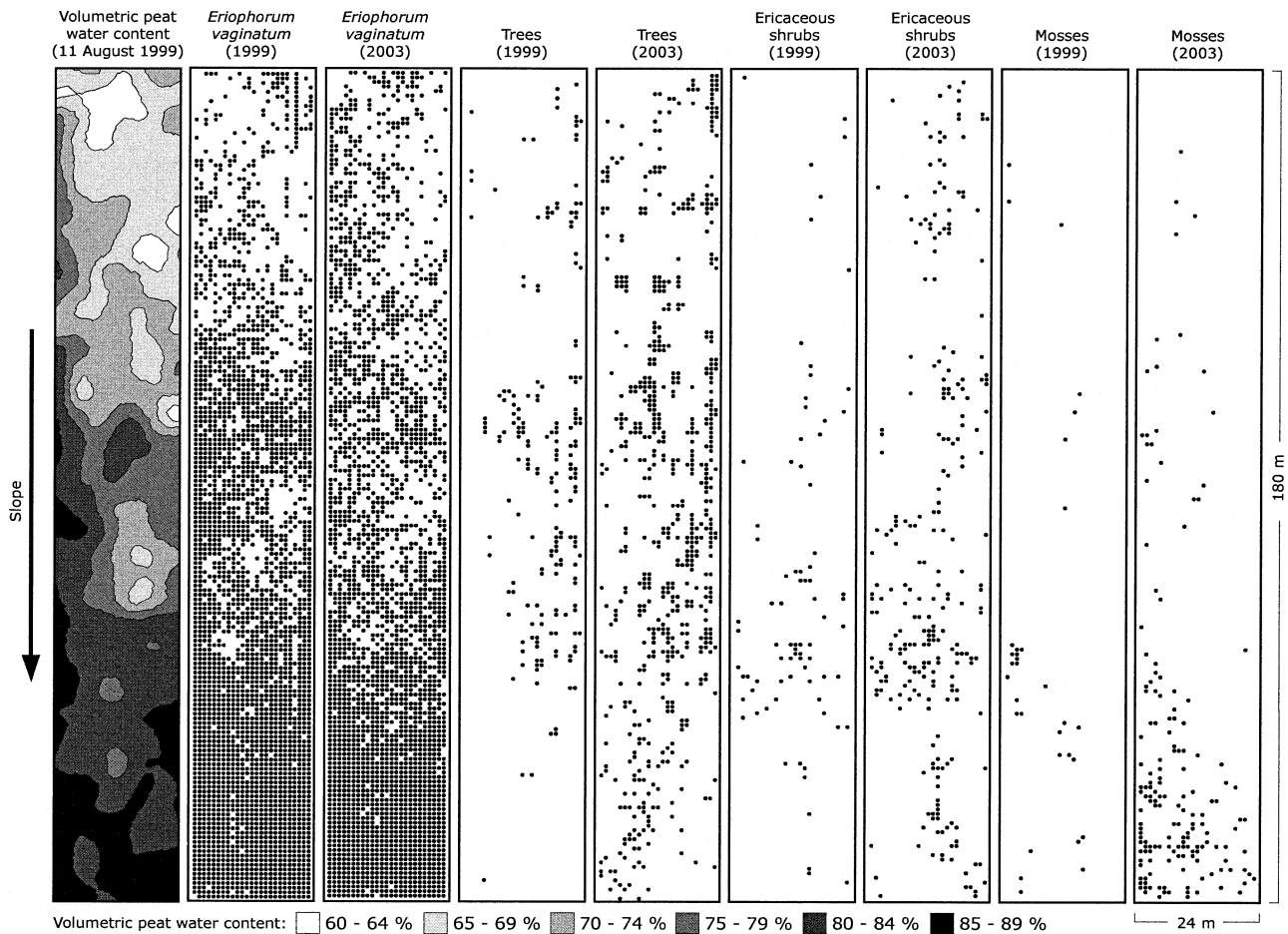


Figure 3. Map showing the volumetric peat water content (data taken August 11, 1999) in peat field A, Saint-Henri bog, and spatial distribution of plant species groups (data taken in July 1999 and 2003) in the same peat field. Mosses include liverworts.

to 6%. Very few new tussocks established during that period (Figure 5). Tussocks produced a large number of infructescences in 1999, 2000, and 2002 but very few in 1998 and 2001 (Figure 6). The number of cotton-grass seedlings increased constantly from 1998 to 2001 but then decreased in 2002 (Figure 6). There was no significant correlation between the number of infructescences and the number of seedlings emerging one year later ( $p = 0.09$ ), but a longer time series would probably be necessary to detect a significant correlation.

Only 14 plant species were found in the  $10 \times 20$  m quadrat delineated in peat field B. All were vascular plants, except two moss species (*Dicranella cerviculata* [Hedw.] Schimp. and *Polytrichum strictum* Brid.). Apart from cotton-grass, only *Eriophorum virginicum* L. had a notable plant cover. The cover of both *Eriophorum* species changed substantially during the monitoring period (Figure 7). The cover of cotton-grass greatly increased from 1998 to 2001. This increase occurred mainly in April–May 1999; the cotton-grass cover was still low in October 1998 (C. Lavoie,

personal observations) and our field sampling was conducted earlier in 1999 (19 May) because of a warm and dry spring triggering the early production of infructescences. The expansion of cotton-grass cover was mainly the result of the growth of established tussocks and not the consequence of the establishment of new tussocks after 1998. The cover of *E. virginicum* also increased from 1998 to 2000 but then decreased in 2001 and 2002.

During the monitoring period, precipitation was generally well below the average, especially from 2000 to 2002 (Figure 8). During the 56-month period covered, only 19 months received above-average precipitation. Most summers were dry, except June and July 1999, which both received well-above-average precipitation. Since plant cover data were taken in mid-May in 1999, it should be noted that 1999 data were not influenced by this wet summer.

## DISCUSSION

Minimal water management (blocking of drainage ditches, construction of peat bunds) can trigger a cot-

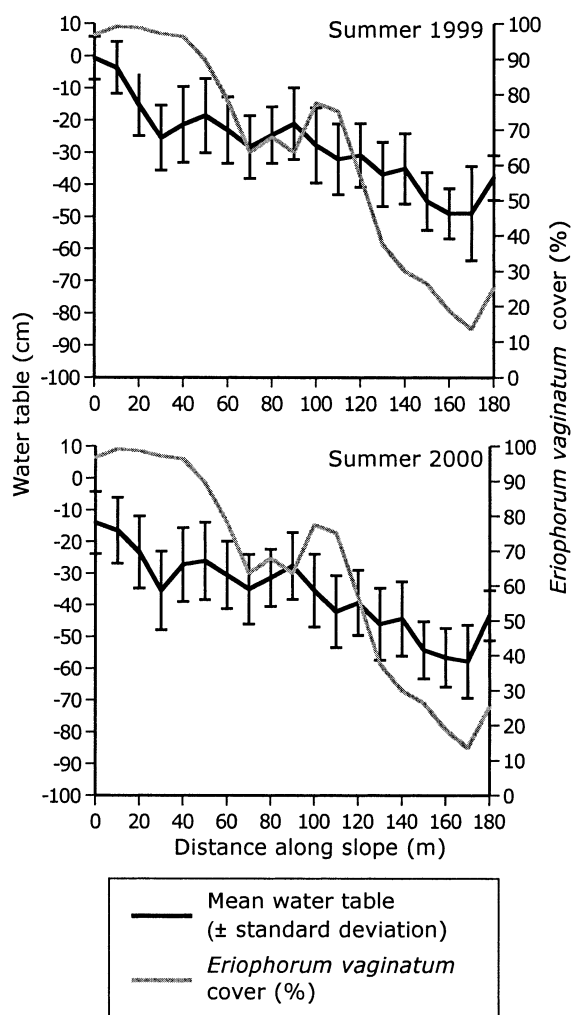


Figure 4. Water table vs distance along peat field A, Saint-Henri bog, during summers 1999 and 2000. The corresponding cotton-grass (*Eriophorum vaginatum*) cover is indicated.

ton-grass expansion in an abandoned vacuum-mined bog. At Saint-Henri peatland, a water table no deeper than 30–40 cm below the soil surface and a volumetric peat water content >70% in the surface (12 cm) peat layer favored the rapid development of a large cotton-grass cover in abandoned peat fields. Once well-established, the cotton-grass cover remained quite stable (at least during the subsequent four-year period), although a decrease in the number of tussocks was observed. The strong relationship between cotton-grass cover and water table suggests that the latter could be used as a predictor for cotton-grass cover change in mined bogs, especially if we compare Saint-Henri data with others taken in similar abandoned peatlands from southern Québec (Table 1). This relationship is consistent with earlier studies conducted in disturbed fens and bogs of Finland and New Brunswick showing that it is essential to raise the water table above 40 cm below the soil surface to trigger a massive cotton-grass

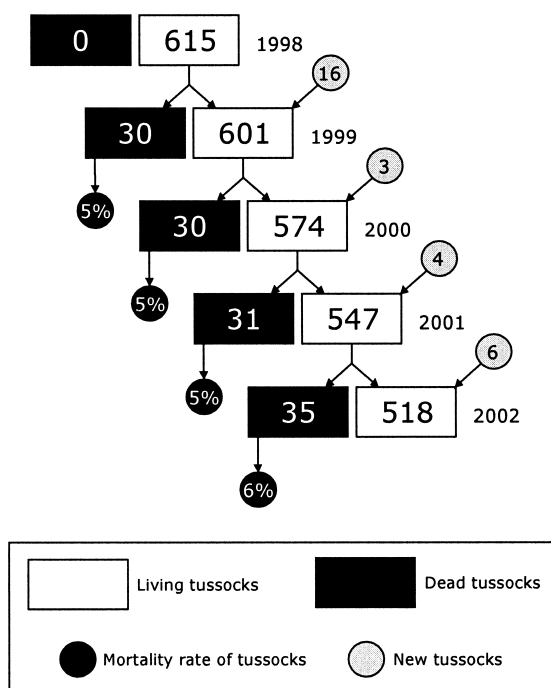


Figure 5. Evolution of the number of cotton-grass (*Eriophorum vaginatum*) tussocks from 1998 to 2002 that were recorded in the 10 × 20 m quadrat in peat field B, Saint-Henri bog.

expansion (Komulainen et al. 1998, Tuittila et al. 1999, 2000b, Price et al. 2003). Below this hydrologic threshold, cotton-grass seedlings may establish and form small tussocks, but the growth of tussocks remains very slow. The present study is the first to iden-

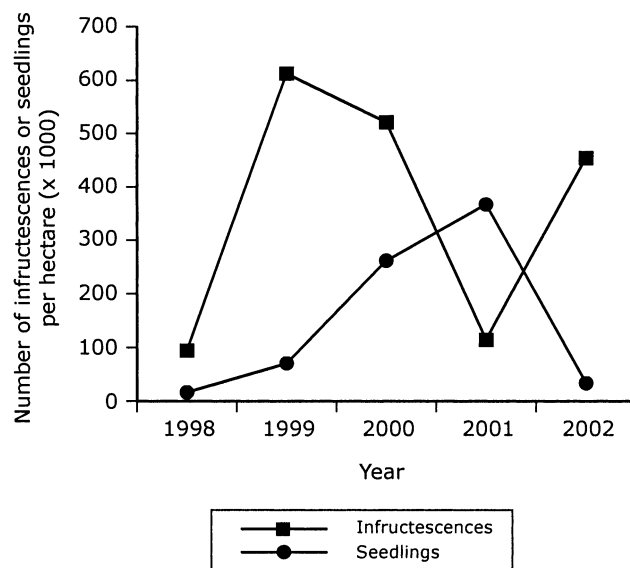


Figure 6. Estimation of the number of cotton-grass (*Eriophorum vaginatum*) infructescences produced and seedlings that have germinated each year from 1998 to 2002 in peat field B, Saint-Henri bog.



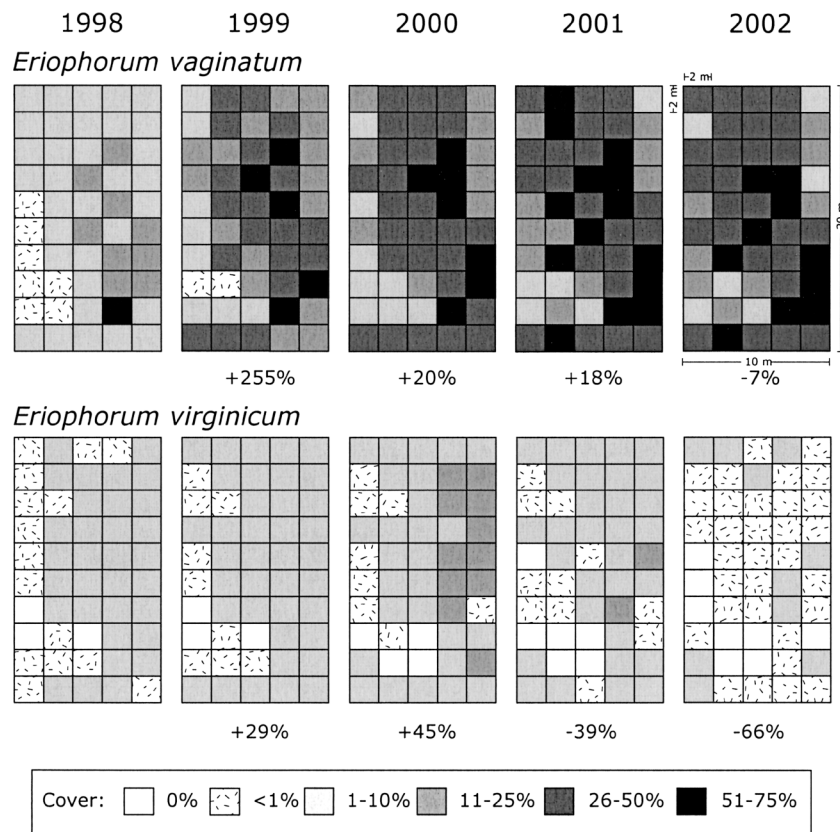


Figure 7. Cover of *Eriophorum vaginatum* and *Eriophorum virginicum* in the  $10 \times 20$  m quadrat in peat field B, Saint-Henri bog. The quadrat was subdivided into fifty  $2 \times 2$  m subquadrats in which the cover of living individuals was evaluated in late-May, early-June, from 1998 to 2002. Cover classes are indicated in the legend. The species cover was compared year-to-year by calculating the median value of the cover class occupied by the species in each subquadrat, and totalling all median values from all subquadrats. Percentage change of the species cover, compared to the previous year, is shown for each year from 1999 to 2002.

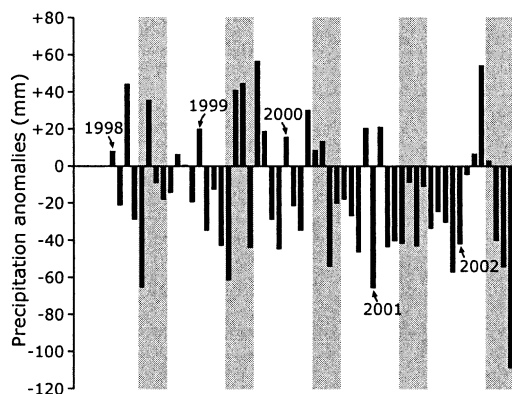


Figure 8. Precipitation anomalies in the Québec City area from January 1998 to August 2002. Vertical bars: difference between precipitation recorded for a particular month and mean precipitation for the same month during the 1961–1990 period. January months are indicated by arrows. Summer months (May–August) are indicated by grey zones.

tify with confidence this threshold and establish a clear link between cotton-grass cover and water table.

Precipitation influences the water table in mined bogs and, consequently, the development of cotton-grass cover. However, at the Saint-Henri peatland, water management operations have certainly had a much stronger effect on the establishment and growth of cotton-grass than precipitation fluctuations. For instance, although peat field B was abandoned for six years, the massive growth of cotton-grass tussocks only occurred in 1999 (i.e., just after better drainage blocking and the construction of peat bunds near the peat field). On the other hand, the warm spring and wet summer of 1999 also probably accelerated the growth of tussocks. Dry weather conditions during the subsequent years had apparently few impacts on the cotton-grass cover. Whether the decreasing cover of *Eriophorum virginicum* in 2001 and 2002 was associated with dry conditions or competition with *Eriophorum vaginatum* remains to be substantiated.

Two previous detailed studies provided some evidence that cotton-grass facilitates the establishment of

Table 1. Cotton-grass cover, water table, and volumetric peat water content monitored during summers 2000 and 2001 in three abandoned mined bogs of southern Québec. The Rivière-du-Loup sites were very similar to the Saint-Henri peat field B. All sites had a thick acidic peat deposit with large *Sphagnum* content that had been vacuum mined, but the cotton-grass cover was much lower at Rivière-du-Loup than at Saint-Henri. Data from the Rivière-du-Loup peatland are from Lavoie *et al.* (2005).

Site	Cotton-grass Cover (tussock ha <sup>-1</sup> ; min.–max. values)	Water Table Level (cm below the soil surface; min.–max. values)	Time Period with a Water Table Level >40 cm Below the Soil Surface (% of days during the summer season; min.–max. values)	Volumetric Peat Water Content of the Surface (12 cm) Peat (%; min.–max. values)
Saint-Henri (peat field B)	27 350–28 700	6–51	32–46	67–87
Rivière-du-Loup (site RDLP2)	9750–10 700	19–53	45–58	55–83
Rivière-du-Loup (site RDLP1)	3600–4000	26–67	92–94	54–81

other bog plant species in mined bogs (Matthey 1996, Tuitilla *et al.* 2000a), but it was difficult to separate the impacts of the cotton-grass from those of abiotic variables associated with the peat deposit. For instance, Tuitilla *et al.* (2000a) found a very strong relationship between the presence of vegetation and the water table in Finnish mined peatlands. To determine whether the composition of vegetation was also related to the presence of cotton-grass tussocks, they eliminated the influence of water table using a statistical procedure. Unfortunately, they did not indicate the percentage of the variance that was explained either by water table or by other variables, which precludes conclusions about the biological significance of results. The present study does not provide evidence for the facilitation hypothesis. At peat field A, mosses and liverworts were confined to the wettest part of the field. This zone with a greater moss and liverwort content covered only 14% of the area of the field, while cotton-grass cover was very large (>60%) over 66% of the surface of peat field A. This suggests that the establishment of mosses and liverworts was associated more with particular hydrologic characteristics than with the presence of a dense cotton-grass cover.

As our study does not provide evidence for cotton-grass facilitation of the establishment and growth of other bog plant species, we question the value of favoring the expansion of cotton-grass in peatland restoration plans. Cotton-grass may contribute to stabilizing the peat surface and minimizing the effects of erosion and frost heaving on other bog plant species (Marcoux 2000, Campbell *et al.* 2002, Groeneveld and Rochefort 2002). Cotton-grass tussocks can also increase levels of relative humidity near the peat surface, which may improve establishment conditions for moss species (Matthey 1996, Marcoux 2000, Lavoie *et al.* 2003). On the other hand, cotton-grass tussocks may

intercept 30–80% of precipitation (Marcoux 2000) and lose large quantities of water through evaporation (Matthey 1996), which may negate any benefits provided by a cotton-grass cover to the establishment of moss species. Rewetted mined sites colonized by cotton-grass also produce large amounts of methane (Kömulainen *et al.* 1998, Rinnan *et al.* 2003, Marinier *et al.* 2004). Assuming that each infructescence contains 40 seeds (C. Lavoie, unpublished data), cotton-grass tussocks may produce as many as 24 million seeds per hectare (peat field B in 1999), which may then potentially contaminate nearby peat areas harvested for horticultural purposes. Finally, the presence of a dense cotton-grass cover hampers bog restoration activities as developed in North America. The North American approach involves the spreading of *Sphagnum* diaspores on bare peat surfaces to accelerate the reconstruction of an acrotelm (Rochefort *et al.* 2003). A large cotton-grass cover prevents contact between mechanically spread *Sphagnum* diaspores and the wet soil surface, resulting in the death of diaspores by desiccation. Removal and disposal of cotton-grass tussocks is then essential before restoration, which represents additional spending. However, in many European countries, the development of a large cotton-grass cover may represent an interesting option considering the low number of *Sphagnum* diaspore sources (*i.e.*, undisturbed bogs).

#### ACKNOWLEDGMENTS

This research was financially supported (grants to C. Lavoie and J. S. Price) by the Natural Sciences and Engineering Research Council of Canada (NSERC) and by the Canadian peat moss industry. NSERC provided scholarships to K. Marcoux. We thank Premier Horticulture for the access to the study sites and for



providing chemical analyses of a peat sample. We also thank M.-È. Bérubé, C. Dufresne, K. Fortin, C. Huot, Y. Jodoin, L. Letarte, N. Rivard, M.-È. Roy, I. Simard, T. Van Seters, and C. Zimmermann for field and laboratory assistance, P. Villeneuve and D. Lachance for help with statistical analyses, and S. Boudreau, R. Budelsky, T. Malterer, L. Rochefort, and an anonymous reviewer for helpful comments on earlier drafts of the manuscript.

#### LITERATURE CITED

- Anderson, L. E. 1990. A checklist of *Sphagnum* in North America north of Mexico. *Bryologist* 93:500–501.
- Anderson, L. E., H. A. Crum, and W. R. Buck. 1990. List of the mosses of North America north of Mexico. *Bryologist* 93:448–499.
- Bérubé, M.-È. and C. Lavoie. 2000. The natural revegetation of a vacuum-mined peatland: eight years of monitoring. *Canadian Field-Naturalist* 114:279–286.
- Buttler, A., B. G. Warner, P. Grosvernier, and Y. Matthey. 1996. Vertical patterns of testate amoebae (Protozoa: Rhizopoda) and peat-forming vegetation on cutover bogs in the Jura, Switzerland. *New Phytologist* 134:371–382.
- Campbell, D. R., C. Lavoie, and L. Rochefort. 2002. Wind erosion and surface stability in abandoned milled peatlands. *Canadian Journal of Soil Science* 82:85–95.
- Campbell, D. R., L. Rochefort, and C. Lavoie. 2003. Determining the immigration potential of plants colonizing disturbed environments: the case of milled peatlands in Quebec. *Journal of Applied Ecology* 40:78–91.
- Chapin, F. S., III, L. Moilanen, and K. Kielland. 1993. Preferential use of organic nitrogen for growth by a non-mycorrhizal arctic sedge. *Nature* 361:150–153.
- Cholewa, E. and M. Griffith. 2004. The unusual vascular structure of the corm of *Eriophorum vaginatum*: implications for efficient retranslocation of nutrients. *Journal of Experimental Botany* 55: 731–741.
- D'Antonio, C. and L. A. Meyerson. 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. *Restoration Ecology* 10:703–713.
- Day, J. H., P. J. Rennie, W. Stanek, and G. P. Raymond. 1989. Manuel d'analyse des tourbes. Conseil national de recherches du Canada, Comité associé de recherches géotechniques, Ottawa, Ontario, Canada.
- Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6:503–523.
- Environnement Canada. 1993. Normales climatiques au Canada. Service de l'environnement atmosphérique, Environnement Canada, Ottawa, Ontario, Canada.
- Frenzel, P. and E. Karofeld. 2000. CH<sub>4</sub> emission from a hollow-ridge complex in a raised bog: the role of CH<sub>4</sub> production and oxidation. *Biogeochemistry* 51:91–112.
- Frenzel, P. and J. Rudolph. 1998. Methane emission from a wetland plant: the role of CH<sub>4</sub> oxidation in *Eriophorum*. *Plant and Soil* 202:27–32.
- Gartner, B. L., F. S. Chapin, III, and G. R. Shaver. 1986. Reproduction of *Eriophorum vaginatum* by seed in Alaskan tussock tundra. *Journal of Ecology* 74:1–18.
- Gauthier, R. and M. M. Grandtner. 1975. Étude phytosociologique des tourbières du Bas-Saint-Laurent, Québec. *Naturaliste canadien* 102:109–153.
- Gilbert, N. and J.-G. Savard. 1992. Statistiques. 2<sup>nd</sup> edition. Éditions Études Vivantes, Laval, Québec, Canada.
- Golden Software Inc. 1996. Surfer. Version 6.04. Golden Software Inc., Golden, CO, USA.
- Greenup, A. L., M. A. Bradford, N. P. McNamara, P. Ineson, and J. A. Lee. 2000. The role of *Eriophorum vaginatum* in CH<sub>4</sub> flux from an ombrotrophic peatland. *Plant and Soil* 227:265–272.
- Groeneveld, E. V. G. and L. Rochefort. 2002. Nursing plants in peatland restoration: on their potential use to alleviate frost heaving problems. *Suo* 53:73–85.
- Grosvernier, P., Y. Matthey, and A. Buttler. 1995. Microclimate and physical properties of peat: new clues to the understanding of bog restoration processes. p. 435–450. In B. D. Wheeler, S. C. Shaw, W. J. Fojt, and R. A. Robertson (eds.) *Restoration of Temperate Wetlands*. John Wiley & Sons, Chichester, UK.
- Harris, R. J. 1975. *A Primer of Multivariate Statistics*. Academic Press, New York, NY, USA.
- Hinds, H. R. 2000. *Flora of New Brunswick*. 2<sup>nd</sup> edition. Department of Biology, University of New Brunswick, Fredericton, New Brunswick, Canada.
- Hughes, P. D. M. and L. Dumayne-Peaty. 2002. Testing theories of mire development using multiple successions at Crymlyn Bog, West Glamorgan, South Wales, UK. *Journal of Ecology* 90:456–471.
- Jonasson, S. and F. S. Chapin, III. 1985. Significance of sequential leaf development for nutrient balance of the cotton sedge, *Eriophorum vaginatum* L. *Oecologia* 67:511–518.
- Joosten, H. and D. Clarke. 2002. *Wise Use of Mires and Peatlands*. International Mire Conservation Group and International Peat Society, Totnes, UK.
- Komulainen, V.-M., H. Nykänen, P. J. Martikainen, and J. Laine. 1998. Short-term effect of restoration on vegetation change and methane emissions from peatlands drained for forestry in southern Finland. *Canadian Journal of Forest Research* 28:402–411.
- Komulainen, V.-M., E.-S. Tuittila, H. Vasander, and J. Laine. 1999. Restoration of drained peatlands in southern Finland: initial effects on vegetation change and CO<sub>2</sub> balance. *Journal of Applied Ecology* 36:634–648.
- Lavoie, C., P. Grosvernier, M. Girard, and K. Marcoux. 2003. Spontaneous revegetation of mined peatlands: a useful restoration tool? *Wetlands Ecology and Management* 11:97–107.
- Lavoie, C. and L. Rochefort. 1996. The natural revegetation of a harvested peatland in southern Québec: a spatial and dendroecological analysis. *Écoscience* 3:101–111.
- Lavoie, C., A. Saint-Louis, and D. Lachance. 2005. Vegetation dynamics on an abandoned vacuum-mined peatland: 5 years of monitoring. *Wetlands Ecology and Management* (in press).
- LeQuére, D. and C. Samson. 1998. Peat bog restoration: industrial scale application. p. 69–72. In T. Malterer, K. Johnson, and J. Stewart (eds.) *Proceedings of the 1998 International Peat Symposium*. International Peat Society, Duluth, MN, USA.
- Lodge, D. M. 1993. Biological invasions: lessons for ecology. *Trends in Ecology and Evolution* 8:133–137.
- Mack, M. C. and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution* 13:195–198.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689–710.
- Marcoux, K. 2000. Les invasions de linaigrette (*Eriophorum vaginatum* L.): aide ou frein à la restauration des tourbières? M.Sc. Thesis. Université Laval, Sainte-Foy, Québec, Canada.
- Marinier, M., S. Glatzel, and T. R. Moore. 2004. The role of cotton-grass (*Eriophorum vaginatum*) in the exchange of CO<sub>2</sub> and CH<sub>4</sub> at two restored peatlands, eastern Canada. *Écoscience* 11:141–149.
- Mark, A. F., N. Fetcher, G. R. Shaver, and F. S. Chapin, III. 1985. Estimated ages of mature tussocks of *Eriophorum vaginatum* along a latitudinal gradient in central Alaska, U.S.A. *Arctic and Alpine Research* 17:1–5.
- Matthey, Y. 1996. Conditions écologiques de la régénération spontanée du *Sphagnion magellanici* dans le Jura suisse. Typologie, pédologie, hydrodynamique et micrométéorologie. Ph.D. Dissertation. Université de Neuchâtel, Neuchâtel, Switzerland.
- Pfadenhauer, J. and F. Klötzli. 1996. Restoration experiments in middle European wet terrestrial ecosystems: an overview. *Vegetatio* 126:101–115.
- Price, J. S., A. L. Heathwaite, and A. J. Baird. 2003. Hydrological processes in abandoned and restored peatlands: an overview of

- management approaches. *Wetlands Ecology and Management* 11: 65–83.
- Price, J. S., L. Rochefort, and F. Quilty. 1998. Energy and moisture considerations on cutover peatlands: surface microtopography, mulch cover and *Sphagnum* regeneration. *Ecological Engineering* 10:293–312.
- Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6:93–107.
- Rinnan, R., M. Impiö, J. Silvola, T. Holopainen, and P. J. Martikainen. 2003. Carbon dioxide and methane fluxes in boreal peatland microcosms with different vegetation cover: effects of ozone or ultraviolet-B exposure. *Oecologia* 137:475–483.
- Rochefort, L., F. Quilty, S. Campeau, K. Johnson, and T. Malterer. 2003. North American approach to the restoration of *Sphagnum* dominated peatlands. *Wetlands Ecology and Management* 11:3–20.
- Salonen, V. 1987. Relationship between the seed rain and the establishment of vegetation in two areas abandoned after peat harvesting. *Holarctic Ecology* 10:171–174.
- Scherrer, B. 1984. *Biostatistique*. Gaëtan Morin, Chicoutimi, Québec, Canada.
- SPSS Inc. 2001. *SPSS for Windows*. Release 11.0.1. SPSS Inc., Chicago, IL, USA.
- Tuittila, E.-S., V.-M. Komulainen, H. Vasander, and J. Laine. 1999. Restored cut-away peatland as a sink for atmospheric CO<sub>2</sub>. *Oecologia* 120:563–574.
- Tuittila, E.-S., H. Rita, H. Vasander, and J. Laine. 2000a. Vegetation patterns around *Eriophorum vaginatum* L. tussocks in a cut-away peatland in southern Finland. *Canadian Journal of Botany* 78:47–58.
- Tuittila, E.-S., H. Vasander, and J. Laine. 2000b. Impact of rewetting on the vegetation of a cut-away peatland. *Applied Vegetation Science* 3:205–212.
- Vandersmissen, M.-H., P. Villeneuve, and M. Thériault. 2003. Analyzing changes in urban form and commuting time. *Professional Geographer* 55:446–463.
- Wein, R. W. 1973. Biological flora of the British Isles. *Eriophorum vaginatum* L. *Journal of Ecology* 61:601–615.
- Wein, R. W. and D. A. MacLean. 1973. Cotton grass (*Eriophorum vaginatum*) germination requirements and colonizing potential in the Arctic. *Canadian Journal of Botany* 51:2509–2513.
- Wind-Mulder, H. L., L. Rochefort, and D. H. Vitt. 1996. Water and peat chemistry comparisons of natural and post-harvested peatlands across Canada and their relevance to peatland restoration. *Ecological Engineering* 7:161–181.

Manuscript received 20 January 2004; revisions received 9 August 2004; accepted 25 October 2004.