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The Regeneration of a Highly Disturbed Ecosystem: A Mined Peatland in Southern Québec

Marc Girard, Claude Lavoie,* and Marius Thériault

Centre de Recherche en Aménagement et en Développement, Université Laval, Sainte-Foy, Québec, G1K 7P4, Canada

Abstract

We studied the natural regeneration of an ombrotrophic peatland (Cacouna bog) located in southern Québec that was disturbed by peat mining and other anthropogenic activities over a 200-year period. Using an extensive collection of historical documents, as well as dendrochronological data, we reconstructed the history of the peatland. We also sampled vegetation and environmental variables, and integrated the data in a geographic information system. More than 60% of the total area of the bog was mined between 1942 and 1975, and 98 km of ditches were dug to drain the site. The peatland lost 34% of its initial peat volume between 1946 and 1998. Although the bog was severely disturbed, the spontaneous revegetation of the site by vascular plants was successful (90%–100% cover). However, only 10% of the total mined area has been recolonized by *Sphagnum* species, mainly because drainage ditches are still operational and contribute to drying out the bog. Water table level, peat deposit thickness, and pH are abiotic factors strongly influencing the vegetation composition in the bog. Spatial and historical factors are also important components in this study since they explain, either alone or in interaction with abiotic factors, 44% of the variation of the species data. The intensity of mining activities and the pattern of abandonment of mined sectors strongly influenced abiotic factors, which in turn affected the revegetation process. Even if the *Sphagnum* cover of the bog is low, the rapid "recovery" of the vegetation cover in the peatland indicates that after the reestablishment of an appropriate hydrological regime, a highly disturbed peatland has a considerable potential for regeneration.

Key words: bog; canonical correspondence analysis; detrended correspondence analysis; drainage; geographic information system; historical ecology; hydrology; restoration ecology; revegetation; *Sphagnum*.

Introduction

Because almost all ecosystems located at temperate latitudes in North America and Europe have been disturbed to various degrees by anthropogenic activities, it is important to know to what extent these ecosystems regenerate after the end of a disturbance. If natural regeneration processes fail to reestablish vegetation communities similar to those present before the disturbance, this indicates that thresholds in the regeneration potential have been crossed and restoration activities are needed. These thresholds must be rapidly identified to mitigate detrimental environmental factors. One way to identify thresholds is to study successful and unsuccessful regeneration cases.

There are very few studies on the regeneration potential of highly disturbed wetlands because these ecosystems are usually totally destroyed by drainage or filling associated with the expansion of agricultural lands or urban communities (Groupe de travail national sur les terres humides 1988; Mitsch and Gosselink 2000). Ombrotrophic peat-

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Current address for Marc Girard: Département de géographie, Université de Montréal, C.P. 6128, succursale Centre-ville, Montréal, Québec H3C 3J7, Canada
**Corresponding author; e-mail:* claude.lavoie@ame.ulaval.ca

lands, one of the most widely distributed wetland types in Canada and Europe (Groups de travail national sur les terres humides 1988; Joosten 2000), are severely disturbed by the extraction of horticultural or fuel peat (Lappalainen 1996; Mitsch and Gosselink 2000). Nevertheless, most bogs are completely abandoned after the end of mining activities. Their residual peat deposit allows the establishment of typical peatland vegetation and the eventual regeneration of the ecosystem. Numerous mined peatlands have been "spontaneously" revegetated (that is, without manmade reintroduction of plant diaspores) with typical bog plants, and particularly by *Sphagnum* species. Most of these sites are block-cut peatlands where peat was extracted by hand using shovels (Smart and others 1986, 1989; Buttler and others 1996; Grosvernier 1996; Matthey 1996; Robert and others 1999; Soro and others 1999). The rapid reestablishment (less than 5 years in some cases) of the vegetation cover in block-cut peatlands is remarkable compared to the slow revegetation of recently abandoned vacuum-mined sites (peat extracted using modern vacuum machines), (Salonen 1990; Salonen and others 1992; Lavoie and Rochefort 1996; Bérubé and Lavoie 2000). The history of mining activities and the vegetation communities established in mined peatlands have been described extensively, but to our knowledge, no detailed study on physico-chemical and historical characteristics of block-cut peatlands has been conducted to learn how such highly disturbed ecosystems were able to regenerate.

Understanding the processes that favor the regeneration of ombrotrophic peatlands is essential for rapidly identifying sites with a high potential for spontaneous recovery; it can also help to keep additional restoration activities to a minimum and consequently reduce restoration costs. Moreover, in sites with poor potential for spontaneous regeneration, it helps ecological engineers to initiate natural revegetation processes, thus improving restoration success.

In this study, we selected an ombrotrophic peatland located in southern Québec (Cacouna) that was severely disturbed by peat mining and other anthropogenic activities over a 200-year period and has since been densely recolonized by bog vegetation. Using an extensive collection of historical documents exclusive to this site, as well as dendrochronological data, we reconstructed the history of the peatland since the beginning of the 19th century. We also sampled vegetation and environmental variables, and integrated the data in a geographic information system (GIS). As previously demonstrated for forest ecosystems (Foster 1992; Foster and others 1998; Fuller and others 1998), we hypothesized that spatio-historical factors (that is, location of mined sectors, mining history, climatological events prevailing during the regeneration period) were as important as physico-chemical (abiotic) factors for explaining spontaneous revegetation patterns.

Study Site

The Cacouna peatland is located in the Bas-Saint-Laurent region (47°53′N, 69°27′W) on the south shore of the St. Lawrence River, eastern Québec, Canada. The bog covers an area of 172 ha at a mean elevation of 83 m. It is located in an agricultural plain that is bordered to the northwest by the St. Lawrence River and to the southeast by the Appalachian foothills near Rivière-du-Loup. This plain is a narrow (16-km) strip of sand, silt, and clay surficial marine deposits (Fulton 1995). On mesic and xeric sites, the vegetation is mainly composed of sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and balsam fir (*Abies balsamea*) forests (Grondin 1996). Large ombrotrophic peatlands are common in wet depressions and are dominated by black spruce (*Picea mariana*), ericaceous shrubs, and *Sphagnum* species (Gauthier and Grandtner 1975). Data from the meteorological station at Saint-Arsène, close to the study site (2 km), indicate that the mean annual temperature is about 3°C; the mean temperature for the coldest month (January) is −12°C and that of the warmest month (July) is 18°C. The mean annual precipitation totals 924 mm, 27% of which falls as snow (Environment Canada 1993).

The Cacouna bog was disturbed several times during the last 200 years (Figure 1). In 1839, a road was built in the southwestern part of the bog (Lebel 1975), and by 1850, the peatland was completely surrounded by agricultural fields. In 1876, the Intercolonial Railway crossed the peatland and divided the bog into two parts (Fortin 1993), thereby creating a barrier for water movement as increasing loads from the railroad compressed the underlying peat (Price and Whitehead 2001). In 1901, a company operated a fuel peat plant in the bog, but the plant was destroyed by fire the same year and never reopened (Warner and Buteau 2000). A fire also burned the northwestern part of the bog (near N sector) around 1945 (Pellerin and Lavoie 2000). Between 1942 and 1975, the site was mined for the production of horticultural peat (Lavoie and Rochefort 1996). During this period, peat was extracted manually using the block-cut method: hundreds of men dug trenches to extract peat blocks (30 × 20 ×

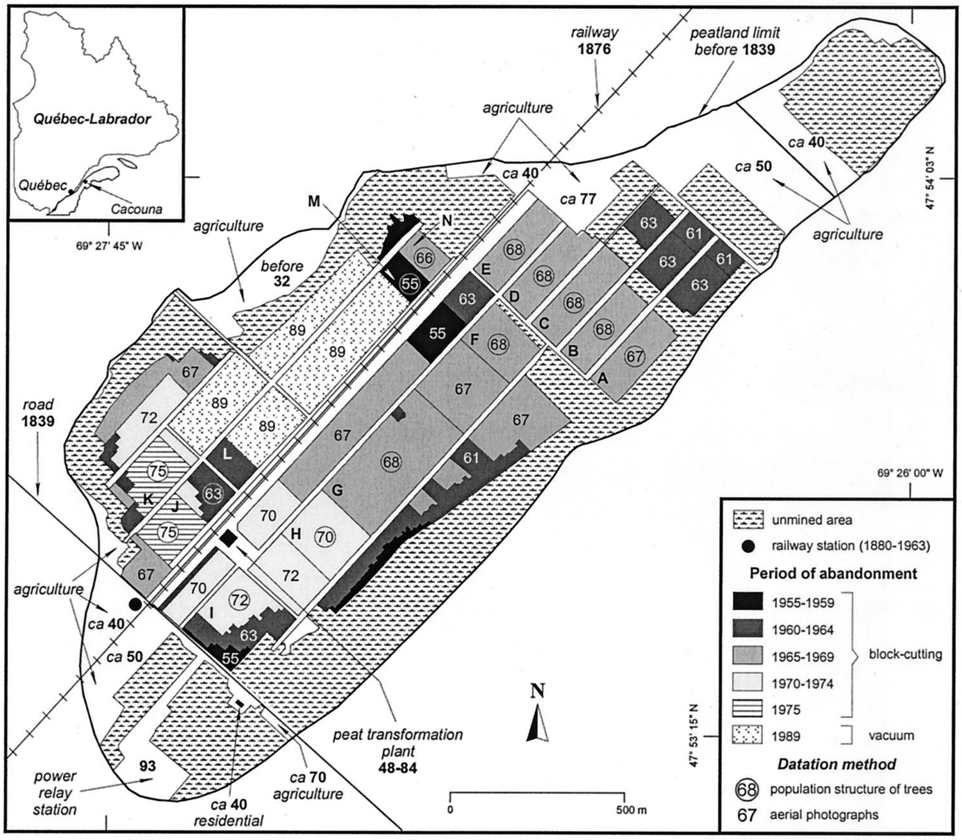

Figure 1. Historical and spatial reconstruction of disturbances in the Cacouna bog, Québec, during the 19th and 20th centuries. The year (the last two digits for the 20th century) and the location of each disturbance are indicated. Mining activities for the extraction of horticultural peat occurred between 1942 and 1975 (block-cut) and between 1983 and 1989 (vacuum). In the mined area, the year of abandonment for mining activities in each sector is indicated, as reconstructed through analysis of aerial photographs or the population structure of trees (Girard 2000). Mined sectors that have been sampled are indicated by a letter (A–N).

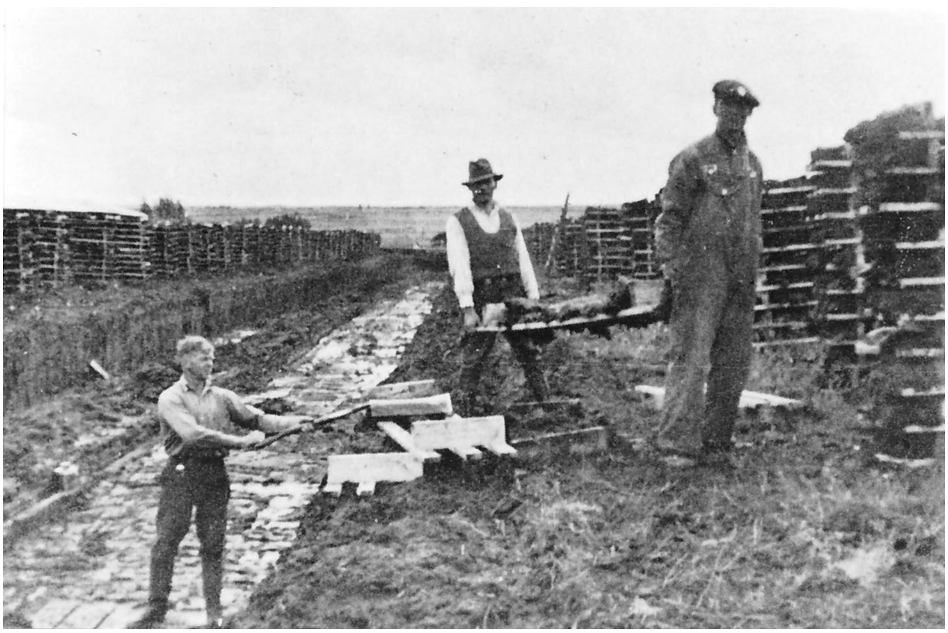

Figure 2. Block-cut mining activities in the Isle-Verte peatland, 18 km east of Cacouna bog, Québec, during the 1940s. The mining trench is bordered by two baulks where peat blocks were deposited for drying (from Risi and others 1953; courtesy of Ministère des Ressources naturelles du Québec).

15 cm) using shovels. Peat blocks were deposited for drying on the baulk (unmined strip of peat) separating two adjacent mining trenches (Figure 2). As soon as the trenches were large enough (3–4 m), living vegetation and other wood fragments were dumped into the middle of the trenches. The microtopography of an abandoned mining trench (cross section) is thus usually characterized by a rounded profile (Lavoie and Rochefort 1996). Once a peat layer was completely extracted, the next series of mining trenches was dug in the residual peat deposit. The introduction of vacuum machines

at the end of the 1960s resulted in the rapid abandonment of the block-cutting technique and of several mined peatlands. These abandoned bogs are characterized by a particular landscape of trenches alternating with baulks (Robert and others 1999). Between 1983 and 1989, an area of 16 ha located in the northwestern half of the Cacouna peatland was bulldozed and leveled to allow an additional peat harvest using vacuum machines (Lavoie and Rochefort 1996). The site was completely abandoned in 1989.

METHODS

Historical Reconstruction of Disturbances

The Cacouna bog is probably the only mined peatland in Québec with such an extensive collection of historical documents. Several reports containing information about the mining history of the bog were consulted (Bureau de la recherche sur l'industrie de la tourbe dans l'Est du Québec 1979, 1984; Girard 1947). Thirteen aerial photographs, taken in 1932, 1948, 1961, 1963, 1970, 1973, 1974, 1978, 1979, 1983, 1986, 1991, and 1995, were used to reconstruct the history of the peatland, and particularly the year of abandonment of mining activities for each sector of the bog. Signs of mining activities were obvious on these photographs: expanding mining trenches, drying peat-block piles (Figure 2), or sheds protecting peat. Abandoned trenches were identified by the absence of these signs and by the presence of trees growing in the trenches; trees are usually unable to establish in a peatland during mining activities, but there is a rapid and massive establishment of trees after abandonment (Lavoie and Rochefort 1996). Each aerial photograph was digitized, registered in space, corrected to limit geometrical distortions using Geographic Transformer software (Blue Marble Geographics 1998), and integrated into a GIS (MapInfo Professional; MapInfo Corporation 1999).

The loss of peat caused by mining, agricultural activities, and industrial activities was estimated. The thickness of the peat deposit had been mapped in 1946 using a grid of 70 points 150 m apart (Drolet 1946). We registered these points in space in the GIS and relocated them in the field during summer 1998 using a global positioning system. The thickness of the peat deposit was estimated again for each point using an iron rod driven into the soil. Maps of peat thickness (1946 and 1998) were created using Kriging's method of Surfer software (Golden Software 1996).

We used climatological data from La Pocatière meteorological station (1920–94), located 70 km southwest of the Cacouna bog (Environment Canada unpublished), to detect whether the climate of the study area during the period of abandonment of mining activities could have had some influence on the revegetation of the bog. Data from the Saint-Arsène station were not used because the record was shorter, incomplete, and did not cover a large part of the period of abandonment of mining activities. Annual, growing season (May–September), and winter (October–April) precipitation data were considered in our analysis. Furthermore, using precipitation and temperature data, we calculated the De Martonne aridity index for the 1920–1994 period (Hufty 1976).

Field Sampling

The Cacouna bog has 511 trenches, 445 baulks, and 16 vacuum peat fields. We concentrated our sampling effort on trenches because their revegetation patterns were much more diverse than those of baulks (Lavoie and Rochefort 1996) and because the vacuum peat fields have already been the subject of other studies (Lavoie and Rochefort 1996; Bérubé and Lavoie 2000). In May 1997, 14 homogeneous sectors (A–N) were delineated in the peatland according to their vegetation structure (tree and *Sphagnum* cover) and topography (presence/absence of baulks separating trenches). Two trenches were randomly selected in each sector for sampling (Figure 1). In two sectors (M and N), only one trench was selected because of the small number of trenches ($n = 5$).

The vegetation in each trench was described during summer 1997 using the sampling point method of Lavoie and Rochefort (1996). Sampling points (diameter, 1 cm) were set at 2-m intervals along six transects (2–3 m apart and 90–180 m long). Species of lichen, liverwort, moss, *Sphagnum*, and vascular plants covering a small point (diameter, 1 cm) were noted for each sampling point. Either even or odd transects were randomly selected to sample trees for dendrochronological analysis. Every 4 m along a selected transect, the nearest tree within a 4-m radius circle from the sampling point was sampled. A cross section of the trunk was taken as close as possible to the collar using an increment borer for large trees, or a saw or pruning shears for small trees or seedlings. In the laboratory, tree rings were counted on the finely sanded cross sections, and the establishment year of each individual was dated. The construction of the population structure of trees from dendrochronological data was used as an indirect method to date the abandonment of min-

Table 1. Abiotic and Spatio-historical Variables Collected for Each Sampled Mining Trench in the Cacouna Bog, Québec, and Used in the Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) Models

Variable	Note
Abiotic	
Mean water table level	Data collected during summer 1998 in the well located at the center of the trench
Water table level fluctuation	Standard deviation of water table level data collected during summer 1998 in the well located at the center of the trench
Mean peat thickness	Along the trench
Water pH	Sample collected in the well located at the center of the trench
Importance of the rounded profile	Mean difference between the relative elevation of the center of the trench and its borders
Water conductivity	Sample collected in the well located at the center of the trench
Slope	Along the trench
Spatio-historical	
Duration of mining activities	Years
Time since abandonment of mining activities	Years
Distance separating the center of the trench from the closest unmined border	
Mined perimeter	Percentage of the sector perimeter bordered by ongoing mining operations when the sector was abandoned

Variables considered by CANOCO software as significant components of the models

ing activities in a particular trench (Lavoie and Rochefort 1996).

At 10-m intervals along transects located at the borders of the trench, and along a line in the center of the trench, the relative elevation of the sampling point was measured with a surveying level. The total peat thickness was estimated using an iron rod driven into the soil at 10-m intervals along a line in the center of the trench. The depth of the water table was monitored on a weekly basis during summer 1998 (19 May–28 August) at three wells located at the center and both ends of each trench. A water sample was taken in the well located at the center of each trench for chemical analyses (pH, conductivity). All data sampled in this study were registered in space and integrated in the GIS.

Nomenclature follows Esslinger and Egan (1995) for lichens, Stotler and Crandall-Stotler (1977) for liverworts, Anderson and others (1990) for mosses (except *Sphagnum* spp.), Anderson (1990) for *Sphagnum* species, and Scoggan (1978–79) for vascular plants, except Farrar (1996) for trees. Each plant species was associated with a particular trophic regime using the works of Scoggan (1978–79), Gauthier (1980), Gérardin and others (1984), Gignac and Vitt (1990), and Gignac and others (1991).

Data Analysis

To evaluate the relative importance of physico-chemical (abiotic) and spatio-historical factors on the distribution of plant communities in the Cacouna bog, we constructed a vegetation matrix including the 26 sampling trenches and the 71 plant species noted in these trenches. Matrix cells contained the percentage of sampling points where a species was noted. We also constructed a data matrix for seven abiotic variables characterizing each trench and a data matrix for four spatio-historical variables associated with each trench (Table 1). All water table data have negative values indicating the position of the water table below the soil surface. Major gradients in vegetation composition were identified using Detrended Correspondence Analysis (DCA). A Canonical Correspondence Analysis (CCA) was then used to relate the vegetation gradients to trench factors. The combined use of DCA and CCA, detailed elsewhere (Borcard and others 1992; Jean and Bouchard 1993), is appropriate for revealing the proportion of vegetation variability that could be accounted for by the abiotic and spatio-historical data sets.

First, the species matrix was analyzed using CCA with the abiotic matrix as constrained variables (step 1). Second, the process was repeated using the spatio-historical variables as constraints (step 2). Third, step 1 was repeated after removing the effects of the spatio-historical matrix (step 3). Finally, step 2 was repeated after removing the effects of the abiotic matrix (step 4). The canonical eigenvalues obtained are measures of the amount of variation accounted for by the explanatory variables. These measures were transformed into percentages of the total variation of species data by dividing the sum of all canonical eigenvalues by the total inertia. Within each CCA, Monte Carlo permutation tests were performed to assess the significance of the trace statistics and of the first eigenvalue (Borcard and others 1992; Jean and Bouchard 1993). All ordinations were carried out using the CANOCO software (ter Braak 1986; ter Braak and Smilauer 1998).

We analyzed the relationship between the water table level in mining trenches and associated vegetation cover by grouping wells used to monitor the water table according to the surrounding (10-m radius) vegetation structure. For grouping, only the cover of trees and *Sphagna* was considered. These plants seem to be particularly influenced by the water table level in bogs (Ivanov 1981; Andrus and others 1983; Foster and Glaser 1986; Laine and others 1995). Because the exact location of wells and vegetation sampling points were incorporated into the GIS, we were able to calculate the *Sphagnum* and tree cover (all species considered) inside a 10-m radius for each well. We used the following four classes to group wells: S = *Sphagnum* cover greater than 25% and tree cover less than 25%, ST = *Sphagnum* cover greater than 25% and tree cover greater than 25%, T = *Sphagnum* cover less than 25% and tree cover greater than 25%, E = *Sphagnum* cover less than 25% and tree cover less than 25% (that is, with only a dense cover of ericaceous shrubs).

Results

Peatland Area

In 1839, the total area of the Cacouna bog was 210.6 ha (Figure 1). That same year, a road was built across the peatland, resulting in the loss of 0.9 ha of bog. The construction of the railway (1876) and a train station (1880) destroyed an additional 3.8 ha of bog. Between 1839 and 1932, 5.3 ha of bog were transformed into agricultural land. Between 1932 and 1963, an additional area of 19.5 ha was converted into agricultural land. Between 1963 and 1995, the total peatland area was reduced by 8.9 ha as a result of agricultural activities (5.1 ha), residential construction (0.6 ha), and the construction of a power relay station (3.2 ha). In 1995, the total peatland area was only 172.2 ha, or 82% of the original area.

Mining History

Mining of the Cacouna bog began in 1942 in the southwestern part of the peatland. The total area mined reached 102.8 ha in the 1950s (maximum extension) and more than 98 km of ditches were dug to drain the site. Aerial photographs and tree population structures indicate that some exploited sectors bordering the unmined area were abandoned between 1955 and 1963 (Figure 1). Large mined sections were abandoned in 1967 and 1968, including the sectors that were subsequently (1983) bulldozed for vacuum mining. All sectors still mined at the beginning of the 1970s were localized in the vicinity of the peat transformation plant. Block-cut mining activities ceased in 1975 after the abandonment of the two remaining exploited sectors (J and K).

Peat Deposit

A comparison of peat deposit maps (Figure 3) indicates that the Cacouna peatland lost 34% of its initial peat volume between 1946 and 1998, mainly as a result of peat mining, peat subsidence, and agricultural activities. In 1946, the maximum peat thickness was located in the southwestern part of the bog, near the peat transformation plant. In 1998, the maximum peat thickness was located in the central part of the bog. More peat was extracted in the vicinity of the peat transformation plant than anywhere else in the peatland during the period of mining activities.

Vegetation and Environmental Gradients

The trenches of the Cacouna bog have been densely recolonized (plant cover, 90%–100%) (Table 2) by a minimum of 71 plant species, most of them (64) frequently found in undisturbed peatlands. Species usually not associated with peat bogs had a cover of less than 1% in the trenches, except for the fern species *Pteridium aquilinum*, which had a cover of 21% in the N sector. Mining trenches were largely dominated by ericaceous shrubs (cover; 70%–97%), such as *Chamaedaphne calyculata*, *Kal-*

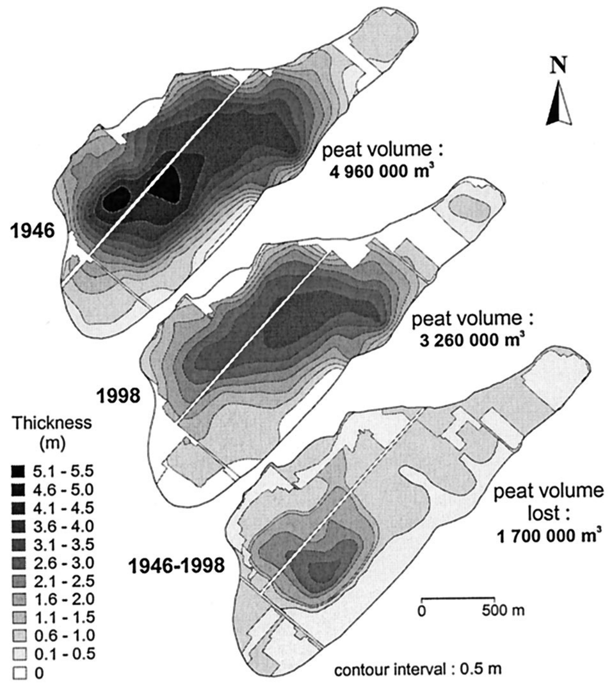

Figure 3. Spatial distribution of the thickness of the peat deposit in the Cacouna bog, Québec, in 1946 (according to Drolet 1946) and in 1998 (this study). The spatial distribution of peat thickness losses between 1946 and 1998 is also illustrated.

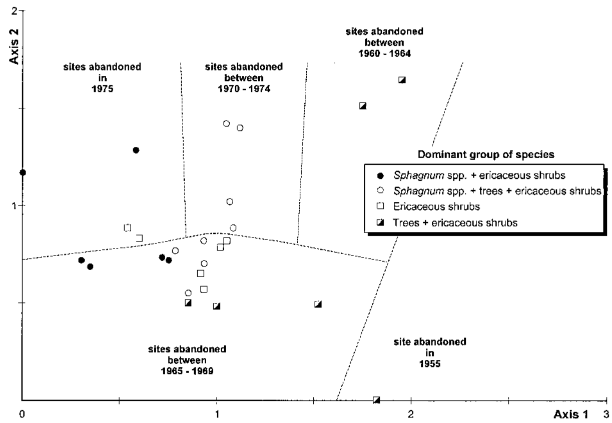

Figure 4. Detrended Correspondence Analysis (DCA) ordination of all mining trenches sampled in the Cacouna bog, Québec. The dominant group of plant species is indicated for each trench.

mia angustifolia, and *Ledum groenlandicum*. Tree cover was variable, from 3%–22% in the C, D, F, G, J, and K sectors to 50%–86% in the I, L, M, and N sectors. Tamarack (*Larix laricina*) and black spruce were the most frequently sampled tree species in the peatland, although jack pine (*Pinus banksiana*) dominated the M and N sectors. *Sphagnum* cover was also highly variable, from 4%–12% in the B, C, K, L, M, and N sectors to 31%–64% in the A, D, I, and J sectors. *Sphagnum capillifolium* was by far the main *Sphagnum* species sampled. If we include baulks, where *Sphagnum* colonies are very rare, we estimate that approximately 10% of the total mined area of the Cacouna bog has been recolonized by *Sphagnum* species.

DCA (Figure 4) produced a clearer segregation of trenches than CCA (data not shown), especially along axis 1. Trenches with a high *Sphagnum* cover are located in the left part of the figure, whereas trenches with a high *Sphagnum* and tree cover are in the central part of the ordination, and those dominated by trees (without *Sphagnum*) are at the right end of axis 1. Five of the seven abiotic variables were considered to be significant components of the model (Table 1). The first two ordination axes explain 62% of the variance. Abiotic variables are strongly related to axes 1 and 2 (Table 3). In particular, there is a strong negative correlation between the water table level and the importance of the rounded profile and axis 1, and peat thickness and axis 2 (Table 4). There is also a strong positive correlation between pH and axis 2. For spatio-historical factors, three of the four variables were considered as significant components of the model (Table 1). The first two ordination axes explain 39% of the variance. DCA successfully distinguished sites according to the abandonment periods of mining activities. Sites abandoned before 1965 are located in the right part of the ordination; those abandoned more recently (1975) are in the left part (Figure 4). There is a strong positive correlation between the time since abandonment of mining activities and axis 1, and the duration of mining activities and the distance separating the trench from the closest unmined border and axis 2 (Table 4).

CCA carried out with plant species and abiotic factors (Figure 5A and Table 4) clearly showed that *Sphagnum* species are located in trenches with a high water table level. Tree species are more abundant in drier sites. Minerotrophic species (and particularly tree species) are mainly associated with high pH values and shallow peat deposits. Several *Sphagnum* and lichen species also seem to be associated with mining trenches with a marked rounded profile. CCA carried out with plant species and spatio-historical factors (Figure 5B and Table 4) produced a complex ordination diagram in which minerotrophic species are associated with trenches that were mined for a long time period and are located far from the closest unmined border. Ombrotrophic species and most *Sphagnum* species are

Table 2. Main Characteristics of Mining Trenches in the Cacouna Bog, Québec, Sampled in 1997 and 1998

Trench	A1	A2	B1	B2	C1	C2	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I1	I2	J1	J2	K1	K2	L1	L2	M1	N1
Length (m)	96	96	88	88	90	90	90	90	88	88	176	175	179	180	180	180	129	110	118	118	120	120	107	119	114	120
Width (m)	14	13	12	13	13	12	14	13	11	11	12	11	9	11	10	9	12	11	15	14	13	12	13	14	10	11
Mean difference between the relative elevation of the center of the trench and its borders (cm)	14	21	19	37	21	33	31	19	17	16	8	9	39	37	21	17	16	16	17	17	14	30	–6	–2	–9	22
Mean peat thickness (cm)	364	342	388	371	369	382	367	373	342	286	382	389	361	324	252	213	139	160	236	232	212	203	307	361	335	291
Mean water table level (cm)[a]	–43	–39	–48	–42	–55	–70	–29	–41	–46	–37	–34	–40	–62	–64	–52	–45	–39	–37	–36	–13	–30	–45	–71	–65	–73	–47
Water table level fluctuation (cm)	12	11	14	13	13	13	9	10	13	12	12	11	9	11	9	11	16	14	8	10	8	13	7	8	9	15
Water pH	4.3	4.0	3.9	4.3	3.9	4.1	3.5	3.5	3.6	3.6	3.5	3.5	4.3	3.8	4.5	4.9	5.1	5.1	4.5	4.5	3.7	3.6	4.0	3.9	3.7	4.4
Duration of mining activities (y)	12	13	13	13	13	12	13	13	13	13	12	13	25	21	28	26	30	29	31	33	33	33	21	20	3	11
Time since abandonment of mining activities (y)	30	29	29	29	29	30	29	29	29	29	30	29	30	29	27	29	25	26	24	22	22	22	34	35	42	31
Distance separating the center of the trench from the closest unmined border (m)	74	75	106	110	150	150	173	197	124	124	130	128	213	237	175	194	132	145	78	145	190	190	260	311	86	50
Total plant cover (%)	99	100	100	100	100	99	99	99	100	99	99	98	98	98	96	99	100	100	100	99	92	90	99	100	99	99
Tree cover (%)	37	24	32	21	22	17	3	5	27	29	9	9	20	20	31	50	50	57	22	16	11	12	86	80	76	64
Ericaceous shrub cover (%)	91	93	95	92	97	96	95	91	94	91	95	94	92	93	86	85	94	88	88	79	85	85	84	93	70	87
Sphagnum cover (%)	31	33	4	9	4	4	33	40	30	17	25	23	21	15	21	47	39	51	64	57	5	7	9	4	10	12
Total number of plant species sampled	23	21	18	19	17	16	27	30	20	17	21	24	33	32	31	38	25	30	23	21	19	21	22	17	23	35

See Table 1 for details about variables.
[a]*A negative value indicates a water table level below the soil surface.*

Table 3. Comparison of the Ordination Results by Detrended Correspondence Analysis (DCA), Canonical Correspondence Analysis (CCA), and Partial CCA

Analysis	λ_1	λ_2	r_1	r_2	$P(\lambda_1)$
DCA with abiotic	0.21	0.12	0.91	0.71	—
DCA with spatio-historical	0.21	0.12	0.82	0.79	—
CCA (abiotic)	0.18	0.13	0.92	0.91	0.007
CCA (spatio-historical)	0.15	0.13	0.89	0.86	0.007
CCA (abiotic) [spatio-historical]	0.08	0.05	0.82	0.77	0.025
CCA (spatio-historical) [abiotic]	0.10	0.04	0.89	0.71	0.005

Eigenvalues (λ), species–environment correlation coefficients (r) for the first two axes, and significance of first canonical axis ($P(\lambda_1)$) are shown.
Constraining variables are indicated by parentheses, covariables by brackets

Table 4. Correlation Coefficients of Abiotic and Spatio-historical Variables with 1st and 2nd Canonical Axes of Various Ordinations using Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA)

	DCA Passive Correlations		CCA Without Covariables		CCA Spatio-historical Variables as Covariables	
Variable	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Abiotic						
Mean water table level	–0.78	0.11	–0.74	0.42	0.53	–0.49
Water table level fluctuation	–0.08	–0.21	–0.10	–0.05	–0.57	–0.08
Mean peat thickness	0.02	–0.58	–0.07	–0.80	0.50	0.24
Water pH	0.14	0.50	0.21	0.69	–0.47	–0.32
Importance of the rounded profile	–0.52	–0.24	–0.55	–0.15	–0.10	0.49
Spatio-historical						
Duration of mining activities	–0.22	0.73	–0.34	0.77	–0.62	0.48
Time since abandonment of mining activities	0.70	–0.35	0.81	–0.31	0.53	–0.20
Distance separating the center of the trench from the closest unmined border	0.27	0.51	0.13	0.53	–0.83	–0.04

mainly associated with more recently abandoned trenches. However, the influence of spatio-historical factors on plant species seems to be less important than that of abiotic factors, as suggested by the shortness of the arrows representing each spatio-historical factor.

Partial canonical ordinations (steps 3 and 4) were carried out, and the trace and sum of all canonical eigenvalues were calculated for each. In total, 66.1% of the amount of variation can be explained. Abiotic and spatio-historical variables explain 21.8% and 19.5% of the species data, respectively. The interaction between these two sets of explanatory variables explains 24.8% of the variation in the species data. Lastly, 33.9% of the variation cannot be explained by the two explanatory data sets, likely owing to lack of fit of data to the response model (Økland 1999). Permutation tests on the trace value showed that the available explanatory variables explain a significant part of the variation in the species data.

Vegetation and Water Table Level

During summer 1998 (9 May–28 August), total rainfall in the peatland was 270 mm (Van Seters and Price 2001), representing a below-average (353 mm) value for the same period of the year at the Saint-Arsène meteorological station (1963–90) (Environment Canada 1993). However, precipitation in July 1998 (102 mm) was above average (87 mm). The wetter conditions in July were followed by a dry spell in August (Figure 6). There were differences between the water table levels measured for the four vegetation types. These differ-

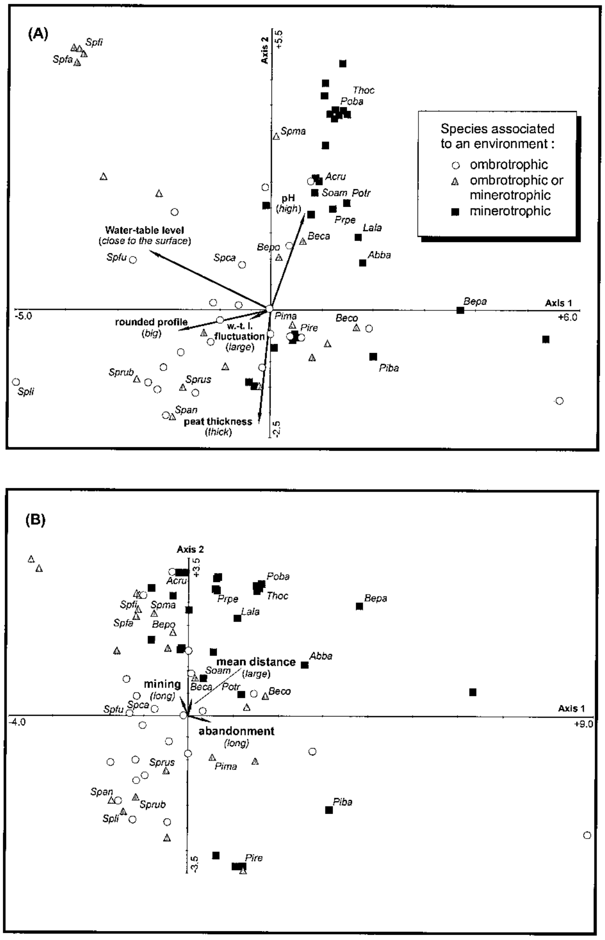

Figure 5. Canonical Correspondence Analysis (CCA) ordinations of all plant species sampled in mining trenches of the Cacouna bog, Québec. Abiotic (**A**) and spatiotemporal (**B**) variables are superimposed. The trophic regime associated with each species is indicated. Species name is indicated only for trees and *Sphagna*. Trees: Abba = *Abies balsamea*, Acru = *Acer rubrum*, Beca = *Betula xcaerulea*, Beco = *Betula cordifolia*, Bepa = *Betula papyrifera*, Bepo = *Betula populifolia*, Lala = *Larix laricina*, Piba = *Pinus banksiana*, Pima = *Picea mariana*, Pire = *Pinus resinosa*, Poba = *Populus balsamifera*, Potr = *Populus tremuloides*, Prpe = *Prunus pensylvanica*, Soam = *Sorbus americana*, Thoc = *Thuja occidentalis*. *Sphagna*: Span = *Sphagnum angustifolium*, Spca = *Sphagnum capillifolium*, Spfa = *Sphagnum fallax*, Spfi = *Sphagnum fimbriatum*, Spfu = *Sphagnum fuscum*, Spli = *Sphagnum lindbergii*, Spma = *Sphagnum magellanicum*, Sprub = *Sphagnum rubellum*, Sprus = *Sphagnum russowii*.

ences were constant throughout the monitoring period (19 May–28 August) (Figure 6). The water table level beneath the vegetation type dominated by *Sphagnum* species (S) was higher (and thus closer to the soil surface) than that of the other vegetation types.

Climate History

Climate reconstruction clearly showed that the period of abandonment of mining activities at Cacouna (1955–75) was probably the driest period of the last 80 years, at least in the La Pocatière region (Figure 7). Precipitation levels during the winter seasons were particularly low. De Martonne aridity indexes also suggested that the 1960–70 period was dry. Other dry periods were recorded during the 1920s and 1980s.

Discussion

The Cacouna bog was highly disturbed during the last 200 years, but the mining of approximately 60% of the peatland area (mainly between 1942 and 1975) was by far the main disturbance. During this period, the vegetation cover was removed, an extensive network of drainage ditches was excavated, and a large proportion of the peat deposit was extracted. Nevertheless, the spontaneous revegetation of the bog by vascular plants was successful. The block-cut sectors of the peatland were recolonized almost exclusively by typical bog plants. This contrasts strongly with the situation found in most abandoned vacuum-mined sites in southern Québec and Ontario (Jonsson-Ninniss and Middleton 1991; Lavoie and Rochefort 1996; Lavoie and Saint-Louis 1999; Bérubé and Lavoie 2000), which are almost devoid of vascular and nonvascular plants or invaded by a dense population of gray birch (*Betula populifolia*) or European white birch (*Betula pendula*). Near the English/Welsh border (United Kingdom), abandoned mined peatlands are also recolonized mainly by nonmire species (Berry and others 1996).

Water table level, peat deposit thickness, and pH are abiotic factors that strongly influence the vegetation composition in the Cacouna bog. This is not surprising, since the same factors also have a very strong influence on the vegetation of undisturbed bogs (Jean and Bouchard 1987, 1993; Økland 1990; Anderson and Davis 1997). However, this indicates that although the Cacouna site was severely disturbed, the determining factors playing a fundamental role in the ecology of this peatland have not changed.

Although the spontaneous revegetation of the Cacouna bog by vascular plants was successful, *Sphagnum* colonies cover only 10% of the mined surface. During the mining period, drainage ditches probably drew off a large quantity of water from the peatland. Removal of the acrotelm and mining of peat from the upper part of the catotelm contrib-

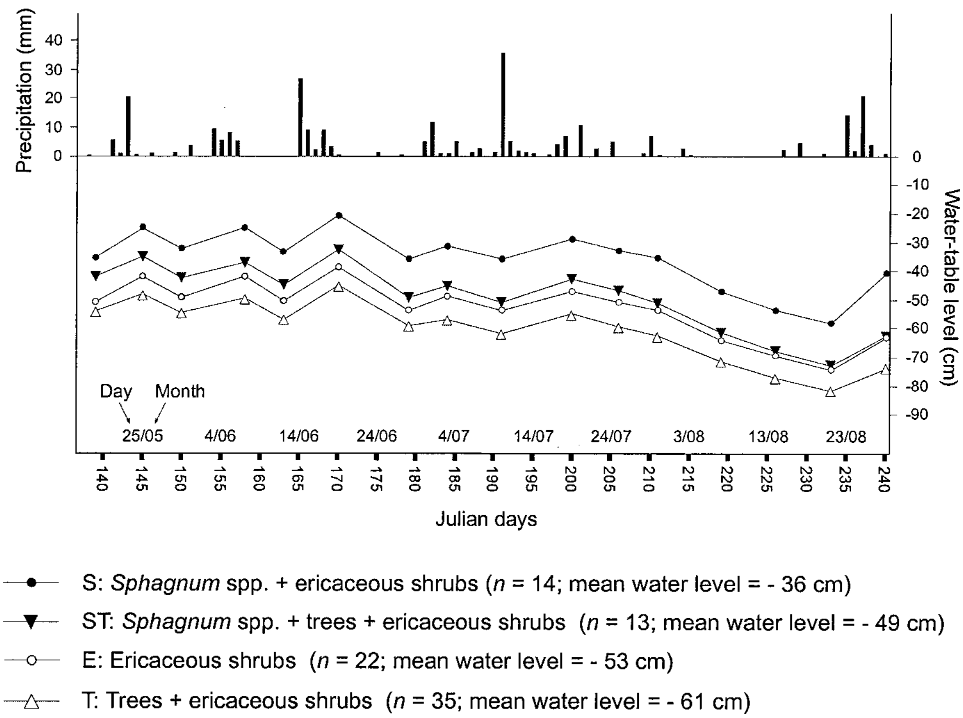

Figure 6. Monitoring of atmospheric precipitation (Van Seters and Price 2001) and water table levels beneath four different types of vegetation cover in mining trenches of Cacouna bog, Québec (summer 1998). S = *Sphagnum* cover more than 25% and tree cover less than 25%, ST = *Sphagnum* cover more than 25% and tree cover more than 25%, T = *Sphagnum* cover less than 25% and tree cover more than 25%, E = *Sphagnum* cover less than 25% and tree cover less than 25% (that is, with only a dense cover of ericaceous shrubs). The number of wells used for monitoring and corresponding to a particular vegetation type is indicated. Additional wells from a previous study (Lavoie and Rochefort 1996) were also monitored.

uted to increasing water table fluctuations (Price 1996; Van Seters and Price 2001). During the 1960s and 1970s, mining activities ceased and drainage ditches were abandoned; some of these ditches were blocked. However, although half of the drainage ditches are inactive or operating at only a fraction of their original efficiency, they still draw off 12%–24% of summer precipitation more than 30 years after abandonment (Van Seters and Price 2001). All these conditions contribute to drying out the bog and limit the recolonization of the mined area by *Sphagnum* species.

It is noteworthy that some sectors of the bog (A, D, I, and J) had a very high *Sphagnum* cover. The lower end of most trenches was also densely recolonized by *Sphagnum* species (Lavoie and Rochefort 1996; Girard 2000; Price and Whitehead 2001). These sectors or trench sections were characterized by a high water table level (less than 40 cm from the soil surface for most of the summer), which appears to be the most important abiotic factor facilitating the establishment and survival of *Sphagnum* colonies. A detailed hydrological study conducted in the Cacouna bog (Price and Whitehead 2001) indicated that soil moisture greater than 50%, and especially soil–water pressure greater than −100 mb, were better predictors of the presence of *Sphagnum* colonies than water table levels. However, there was a good relationship between water table and soil–water pressure values when the water table was not deeper than 40 cm below the soil surface. Some trenches with a markedly rounded profile also had a relatively high *Sphagnum* cover. *Sphagnum* colonies were concentrated near the borders of trenches where there was flowing water. In the middle of the trenches' cross sections, the water table was usually too deep and soil moisture too low to allow the establishment of *Sphagnum* or other moss species (Price and Whitehead 2001). On the other hand, the dryness of the soil surface facilitated the establishment of lichen species.

Studying only abiotic factors would provide an incomplete picture of the regeneration of the Cacouna bog. Spatial and historical factors are also important components in this study because they explain, either alone or in interaction with abiotic factors, 44% of the variation of the species data. The intensity of mining activities and the pattern of abandonment of mined sectors strongly influenced abiotic factors (mainly water level and peat thickness), which in turn affected the revegetation process. Plant species are thus only indirectly influenced by spatio-historical factors, which may explain the shortness of the arrows representing

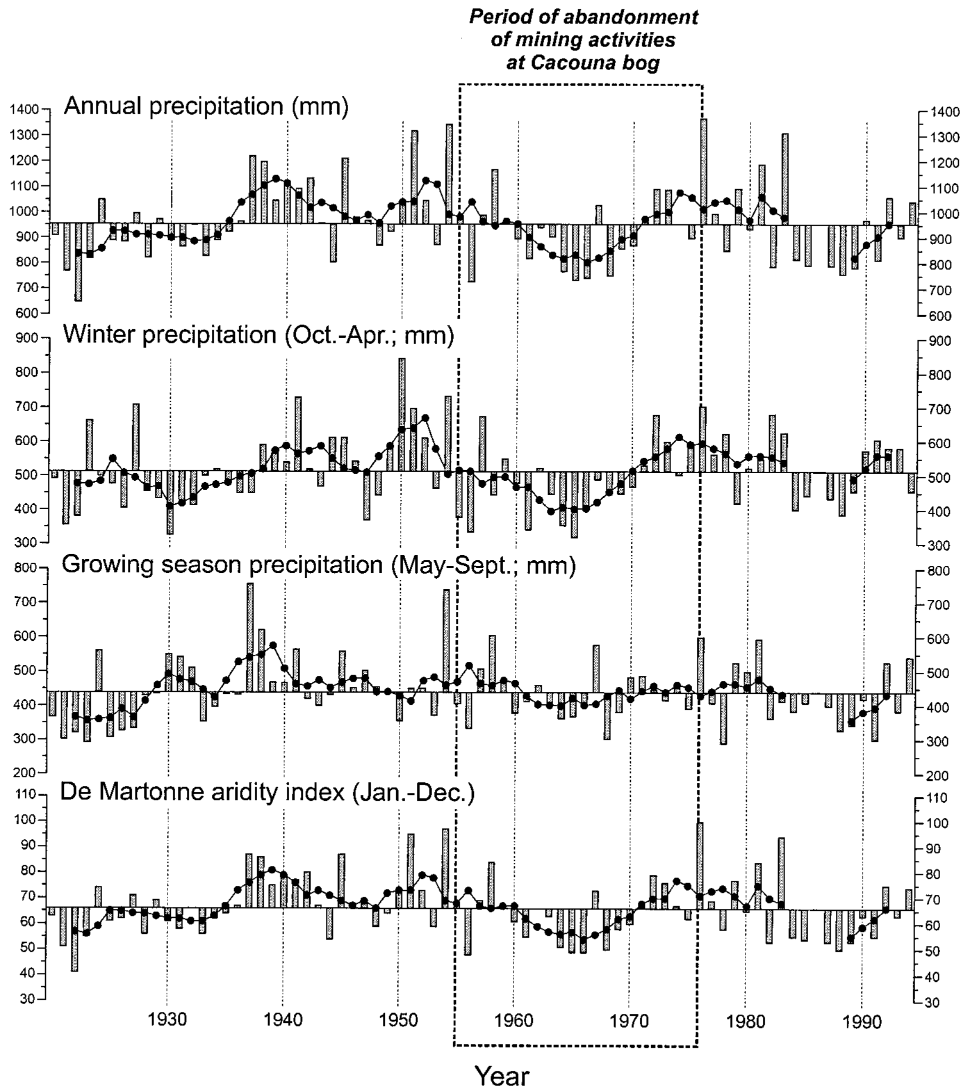

Figure 7. Reconstruction of climatic anomalies at La Pocatière meteorological station, Québec, between 1920 and 1994 (Environment Canada unpublished). Vertical bar: precipitation or index value for each year or winter or growing season. Solid line: 5-year running mean. Missing values: 1986. The lower the De Martonne index, the drier the climate.

those factors in the CCA ordination (Figure 5B). For example, the intensity of mining activities in the southwestern part of the bog (from 1942 to 1970–75) created depressions and resulted in the displacement of the site with maximum peat thickness from the southwestern to the central part of the peatland. In 1998, the highest elevation of the peatland was also located in the central part of the peatland, where little peat was extracted (Van Seters 1999; Girard 2000). After the total abandonment of block-cut mining activities, the depressions (I and J sectors) stored water drawn off by drainage ditches from other mined sectors located at higher elevations (Van Seters 1999). This probably explains why the water table level and consequently the *Sphagnum* cover of I and J sectors, were higher than any other sectors in the peatland (Berry and others 1996). On the other hand, trenches that were abandoned early (L, M, and N sectors) were rapidly recolonized by a dense population of trees. Ditches that drained sectors still being mined probably contributed to maintaining dry abandoned trenches, thereby facilitating the massive establishment of trees.

The climate of the abandonment period is another historical factor that should be taken into account. Although it is difficult to test whether climatic anomalies had some influence on revegetation patterns, it is noteworthy that the abandonment period of the Cacouna bog coincided with the driest climatic period registered at La Pocatière meteorological station between 1920 and 1994. The success of *Sphagnum* reintroduction experiments recently conducted in mined peatlands of southern Québec has been strongly influenced by dry spells occurring during the growing season (Chirino and

Rochefort 2000). Consequently, it is possible that the *Sphagnum* cover would have been higher in the Cacouna bog if the climate had been more humid in the years following the abandonment of the mining trenches.

CONCLUSIONS

A few variables (water level, peat thickness) can predict the revegetation patterns of an abandoned block-cut peatland. However, the spatial and historical context should also be considered to explain particular situations that do not fit with the model, as observed for regenerating forest ecosystems (Foster 1992; Foster and others 1998; Fuller and others 1998). This study provides insights about peatland restoration. First, a water level just below the soil surface (less than 40 cm) seems to be sufficient to allow the rapid reestablishment of *Sphagnum* colonies, as previously suggested by Schouwenaars (1988). The slow recovery of vacuum-mined peatlands compared to block-cut sites is probably related (in part) to the improvement of drainage techniques due to the use of heavy tractor-drawn vacuum machines (Lavoie and Rochefort 1996; Price 1996). Furthermore, drainage of vacuum-mined peatlands increases soil oxidation and compression, and such changes are considered irreversible (Price 1996). Consequently, it is much more difficult to rewet a vacuum-mined peatland—that is, to obtain a water level close to the soil surface over most of the summer, even after blocking drainage ditches (Price 1996; Bugnon and others 1997; Ferland and Rochefort 1997; Price and others 1998). Second, a rapid evaluation of the topography of an abandoned bog and of its drainage network can be useful for identifying wet sectors prone to spontaneous revegetation by typical peatland vegetation, and particularly by *Sphagnum* colonies (Berry and others 1996). Third, large mined areas should be abandoned simultaneously. Small sectors, and especially those surrounded by actively mined areas, tend to be invaded by trees, which intercept precipitation and lose water through transpiration, further contributing to the drying out of the bog (Van Seters and Price 2001).

Even if the *Sphagnum* cover of the Cacouna bog is low, the rapid "recovery" of the vegetation cover in the peatland is remarkable. This indicates that after the reestablishment of an appropriate hydrological regime, a highly disturbed peatland, and possibly other wetland types (Mitsch and others 1998), can show a considerable potential for regeneration. This does not mean that the Cacouna bog is now a fully functional ecosystem; the absence of a widespread *Sphagnum* cover, a keystone plant in a bog environment (van Breemen 1995), suggests that the fundamental carbon accumulation function has not been restored (Waddington and Price 2000). It is unlikely that the *Sphagnum* cover will expand in the near future because drainage ditches are still active and the water storage capacity of a residual peat deposit is usually poor (Berry and others 1996). It may take hundreds of years before one could confuse the Cacouna bog with an undisturbed ombrotrophic peatland. However, spontaneous revegetation processes could and should be integrated into peatland restoration programs to accelerate the reestablishment of functional bog ecosystems.

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