Natural revegetation of two block-cut mined peatlands in eastern Canada

Élisabeth Claire Robert, Line Rochefort, and Michelle Garneau

Abstract: Limited areas of post-mined peatlands are recolonized by *Sphagnum*-dominated communities. This study aims to recognize the spontaneous *Sphagnum* re-establishment process and to verify if *Sphagnum* directly colonizes the residual peat. Conditions favoring *Sphagnum* revegetation are suggested. Analyses of vegetation macrofossils of the newly formed peat allow the identification of colonizing species and vegetation succession profile. Botanical components of the pioneer horizon suggest that *Sphagnum* species can directly colonize the residual peat. When *Polytrichum strictum* (Kaulf.) Presl and *Eriophorum spissum* Fernald are present as early colonists, they are rapidly overgrown by *Sphagnum* species in the succession profile. Vegetation succession resulted mainly in the formation of hummocks and lawns dominated by *Sphagnum fuscum* (Schimp.) Klinggr., *Sphagnum capillifolium* (Ehrh.) Hedw., and *Sphagnum magellanicum* Brid., with a more or less dense ericaceous shrub cover. Floristic, hydrological, and chemical features indicate that a fibric peat accumulation ecosystem is progressively or partially restored.

Key words: cut-over peatlands, restoration, *Sphagnum*, vegetation macrofossil, acrotelm.

Résumé : Les communautés végétales dominées par les sphaignes couvrent une faible superficie des tourbières anciennement exploitées. Cette étude a pour objectifs de reconnaître le dynamisme de rétablissement spontané des sphaignes et de vérifier si les sphaignes s'établissent directement sur la tourbe résiduelle. Les conditions ayant favorisé le rétablissement des sphaignes sont suggérées. Les analyses de macrorestes végétaux de la tourbe néoformée ont permis d'identifier les espèces colonisatrices et le profil de la succession végétale. La composition botanique de l'horizon pionnier suggère une colonisation directe de la tourbe résiduelle par les sphaignes. Des colonies initiales de *Polytrichum strictum* (Kaulf.) Presl et d'*Eriophorum spissum* Fernald sont rapidement recouvertes par les sphaignes en cours de succession. La succession converge vers la formation de buttes et de platières dominées par *Sphagnum fuscum* (Schimp.) Klinggr., *Sphagnum capillifolium* (Ehrh.) Hedw. et *Sphagnum magellanicum* Brid. sous couvert plus ou moins dense d'éricacées. Les conditions floristiques, hydriques et chimiques actuelles indiquent la restauration progressive ou partielle d'un écosystème accumulateur de tourbe fibrique.

Mots clés : tourbière résiduelle, restauration, *Sphagnum*, macrofossiles végétaux, acrotelme.

Introduction

The accumulation of *Sphagnum* that characterizes ombrotrophic peatlands (bogs) in northern countries is a slow process initiated many centuries ago (Vitt and Kuhry 1992). Within these ecosystems, the rate of *Sphagnum* growth is faster than its rate of decomposition. Thus, *Sphagnum* accumulates at an approximate mean rate of 0.5 mm/year (Gorham 1991). A deposit of peat is formed by the transfer of *Sphagnum* fragments from the aerated acrotelm (layer of living and dead – poorly decomposed *Sphagnum*) to the catotelm that is the humified and always anaerobic underlying layer (Ingram 1983). This peat moss is a valued natural resource in Canada. Industrial-scale exploitation in certain regions threatens these habitats for which few restoration measures were considered before 1990. Peat moss extraction was first carried out by manual block-cut methods, replaced in the late 1960s by mechanical vacuum methods. Any method leads to altered environmental conditions because the sites are drained, surface vegetation destroyed, and peat layers removed to varying depths.

The peatlands formerly exploited by block-cut methods were characterized by an alternation of trenches and baulks that can be topographically detected on the present-day surface. A grid of drainage ditches was first dug out creating rectangular units. The surface vegetation was then removed and put aside. The trenches were created progressively by cutting parallel rows of peat blocks that were stacked to dry on the undisturbed surfaces (baulks) between the trenches (Fig. 1). Depth of trenches varied from 75 to 150 cm between different exploitation sites.

The main type of mechanized extraction method used nowadays in Canada is the vacuum method. To allow the use of heavy machinery, intense drainage is necessary. Main ditches enclose perpendicular secondary ditches, which are set apart every 20–40 m. The peat fields usually vary in length from 200 to 400 m. The fields have a slightly convex

É.C. Robert and L. Rochefort.[1] Centre d'études nordiques et Département de phytologie, Pavillon Paul-Comtois, Université Laval, Sainte-Foy, QC G1K 7P4, Canada.
M. Garneau.[2] Commission géologique du Canada, Division de la science des terrains, 2535, boulevard Laurier, Sainte-Foy, QC G1V 4M3, Canada.

[1]Author to whom all correspondence should be addressed. e-mail: line.rochefort@plg.ulaval.ca

[2]Present address: Institut national de la recherche scientifique, Géo-Ressources, 2535 boulevard Laurier, Sainte-Foy, QC G1V 4M3, Canada. e-mail: garneau@gsc.nrcan.gc.ca

Fig. 1. Cross-sectional view illustrating the surface topography of peatlands exploited by block-cut methods.
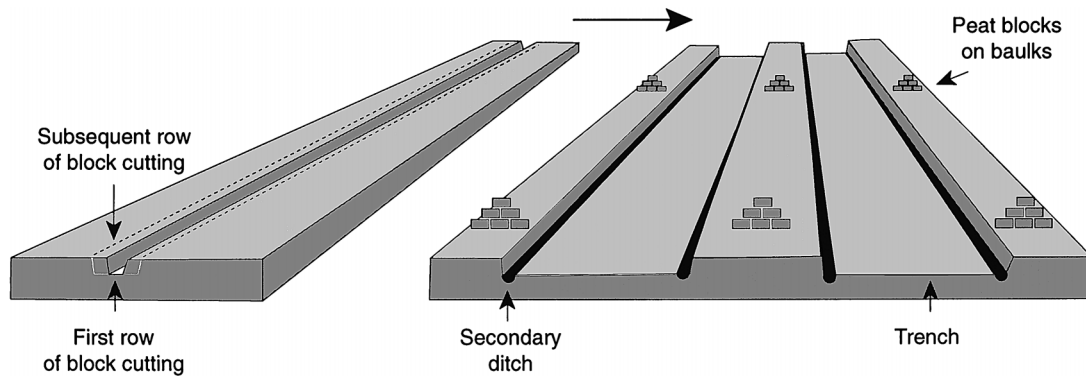
profile to favor water runoff into the ditches. The surface vegetation is entirely removed or chopped up. The surface is then harrowed to allow drying of the peat surface and vacuum-harvested with machines (for more details, see Frilander et al. 1996).

Usually, typical ombrotrophic species recolonize abandoned peatlands, while *Sphagnum*-dominated communities regenerate only in limited areas of block-cut post-mined peatlands (Mörnsjö 1969; Green 1983; Smart et al. 1989; Salonen 1990; Lavoie and Rochefort 1996). The alternation of trenches and baulks influences the pattern of revegetation. *Sphagnum* is mostly absent on baulks. Locally, natural erosion of former ditches allows water to accumulate. The flooded main and secondary ditches may be occupied by floating mats of *Sphagnum* (*Cuspidata* section), often with *Eriophorum angustifolium* Honckeny. In the trenches, the vegetation is generally dominated by ericaceous shrubs. The cryptogam stratum is represented either by lichens or *Polytrichum strictum* (Kaulf.) Presl (Green 1983; Elling and Knighton 1984; Lavoie and Rochefort 1996). In eastern Canada, the invasion of *Sphagnum* species forming hummocks or lawns and showing new fibric peat accumulation occurs in less than 10% of all surface areas of abandoned block-cut peatlands (L. Rochefort, unpublished data).

The opportunity for *Sphagnum* species to colonize residual peat in block-cut trenches seems to be related to (*i*) the proximity, abundance, and random dispersion of their fragments (diaspores) and (*ii*) the prevailing environmental conditions (Mörnsjö 1969; Green 1983; Smart et al. 1989; Salonen 1990, 1994; Joosten 1992; Poschlod 1995; Wheeler and Shaw 1995; Lavoie and Rochefort 1996). The rewetting of the bare substrate, the elevated water table, and the presence of good moisture conditions all appear to be essential for the potential of *Sphagnum* diaspores to regenerate (Clymo and Duckett 1986; Money 1995; Rochefort et al. 1995; Campeau and Rochefort 1996; Rochefort and Bastien 1998). The physical properties of residual peat influence its capacity to keep water in reserve (Price 1996). Oligotrophic and acidic peat conditions (Salonen 1994), as well as prior establishment of peatland companion species, also influence *Sphagnum* re-establishment (Salonen 1990; Schouwenaars 1993; Grosvernier et al. 1995; Joosten 1995). Companion species include ericaceous shrubs, *Polytrichum strictum*, and *Eriophorum spissum* that re-establish along with *Sphagnum* species.

The impacts of vacuum mining are more severe than those of block-cut mining; maintenance of drainage ditches, uni-

form topography, and loss of a diaspore bank in the vicinity of the fields all inhibit *Sphagnum* recolonization. Re-establishment of the former vegetation cover in post-mined peatlands represents an important challenge for ecologists. Recent developments of restoration techniques in post-mined peatlands aim to re-establish *Sphagnum* species by introducing diaspores and reducing moisture deficiencies in the open fields created by the vacuum method (Schouwenaars 1988; Money 1995; Rochefort et al. 1995; Campeau and Rochefort 1996; Quinty and Rochefort 1997; Rochefort and Campeau 1997; Rochefort and Bastien 1998; Price et al. 1998).

Improved knowledge of spontaneous *Sphagnum* recolonization dynamics in trenches of block-cut post-mined peatlands may be helpful in developing restoration techniques. The pattern of surface vegetation in trenches occupied by *Sphagnum* species suggests that the vegetation succession profile will show an overgrowth of typical ombrotrophic peatland species by *Sphagnum*. The objectives of this study are to (*i*) identify the conditions that allow *Sphagnum* species to re-establish and (*ii*) verify whether *Sphagnum* is able to directly colonize residual peat substrate in trenches.

To accomplish these objectives, the analyses of vegetation macrofossils from 20 cores of newly formed peat taken from trenches in two abandoned block-cut peatlands were realized. These analyses allow us to identify colonizing species and to establish a vegetation succession profile since the abandonment of peat extraction. To our knowledge, this is the first North American study which uses vegetation macrofossil analyses to understand the natural revegetation dynamics of post-mined peatlands.

Study sites

Two peatlands, one in Quebec and another in New Brunswick, were studied (Fig. 2). The Rivière-du-Loup peatland, located between the St. Lawrence River and the Appalachian foothills (47°48′N, 69°28′W), is part of one of the biggest peatland complexes in Quebec (Couillard and Grondin 1986). This peatland is classified as an Atlantic boreal peatland (National Wetlands Working Group 1986). The mean annual precipitation is 930 mm, nearly a third of which falls as rain. The mean annual temperature is 4.2°C, with means of –11°C in January and 18°C in July (Environnement Canada 1993*a*). Trenches excavated for peat extraction measured 5×90 m and are separated by baulks 4–10 m wide and up to 1 m high (Fig. 3A). The thickness of residual peat is approximately 3 m. In 1992, the main drainage ditches

Fig. 2. Location of the study sites indicated by stars.
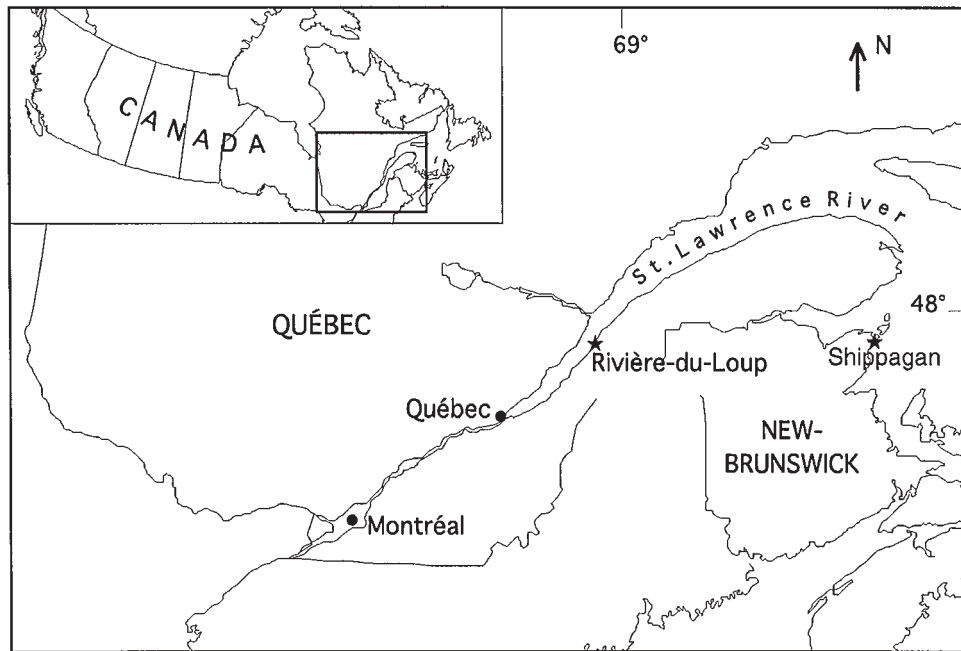
were already blocked by the breakdown of walls cut through the peat, and blockage was completed mechanically. Water accumulates in the main and secondary ditches, with no distinguishable flow.

The Shippagan peatland, in northwestern New Brunswick (47°40′N, 64°43′W), is part of a wide complex of wetlands located near the Gulf of the St. Lawrence (Keys and Henderson 1987). This peatland is classified as a Maritime Atlantic boreal peatland (National Wetlands Working Group 1986). Mean annual precipitation is 1017 mm, nearly half of which falls as rain. Mean annual temperature is 3.3°C, with means of –10°C in January and 19°C in July (Environnement Canada 1993*b*). Trenches excavated for peat extraction measured 18 × 60 m and are separated by baulks 5 m wide and up to 1 m high. Trenches are divided into three longitudinal equal parts, with their central part raised to approximately 40 cm above their lateral parts (Fig. 3B). The thickness of residual peat is approximately 0.6 m in the lateral parts of the trenches and 1 m in their central part. Trenches are still linked by main ditches and narrow secondary ditches are running alongside them. In 1984, water was accumulating in the former ditches that were naturally blocked by the breakdown of the walls cut through the peat and blockage was completed mechanically.

The two peatlands were mined using a manual block-cut method, and peat extraction stopped approximately 25 years ago (ca. 1970). In 1994, a few trenches in both peatlands showed surface vegetation with greater than 75% *Sphagnum* cover. The trenches with this well-regenerated vegetation were chosen to get *Sphagnum* material for the study. The well-regenerated surface vegetation of these trenches is characterized by the presence of natural peatland species of their respective regions (Gauthier and Grandtner 1975; Couillard and Grondin 1986; Keys and Henderson 1987). On both sites, *Sphagnum fuscum* (Schimp.) Klinggr., *Sphagnum capillifolium* (Ehrh.) Hedw., and *Sphagnum magellanicum* Brid. form hummocks or lawns, locally ac-

companied by *Polytrichum strictum* (Kaulf.) Presl (Fig. 3). The shrub stratum is dominated by *Chamaedaphne calyculata* (L.) Moench, *Kalmia angustifolia* L., and *Ledum groenlandicum* Oed., and the herb stratum by *Eriophorum spissum* Fernald, *Eriophorum angustifolium* Honckeny (Shippagan), and *Rubus chamaemorus* L. There are few bare areas in the trenches, and where *Sphagnum* species are absent, a cryptogam stratum of *Cladina rangiferina* (L.) Nyl. (on both sites) or *Mylia anomala* (Hook.) S. Gray (at Rivière-du-Loup) is present, under the ericaceous shrubs. Lichens are rarely found with *Sphagnum* species. Secondary ditches are occupied by *Sphagnum* species from *Cuspidata* section, generally with *Eriophorum angustifolium*.

Methods

Microhabitat identification and coring sites selection

Vegetation succession after cessation of mining activities was only studied in the trenches. At each site, two trenches were randomly selected among 20–30 trenches showing well-regenerated vegetation. The trenches were divided into longitudinal transects 1 m apart. Every 5 m along each transect, the smallest homogeneous unit with regard to microtopography and surface vegetation (microhabitat) was identified. The identification of these microhabitats was done to randomly select five coring sites in each of the four trenches within one microhabitat type occupied by *Sphagnum*, according to the proportion of those microhabitats.

At Rivière-du-Loup, 55% of the microhabitats in the trenches are *Acutifolia* hummocks; 10%, *Cuspidata* lawns; 9%, *Cuspidata* hollows; and 2%, *Acutifolia* lawns. The microhabitats alternate within distances often shorter than 3 m (Fig. 3A). Hence, cores were collected from eight *Acutifolia* hummocks, one *Cuspidata* lawn, and one *Cuspidata* hollow. At Shippagan, *Acutifolia* lawns represent 67% of the microhabitats and *Acutifolia* hummocks represent 10% of the microhabitats in the trenches. The hummocks are present only in the central part of the trenches, whereas the lateral parts are entirely covered by *Acutifolia* lawns (Fig. 3B). Hence, nine cores were collected from *Acutifolia* lawns in the lateral parts

Fig. 3. Topography, microtopography, and vegetation structure of trenches at Rivière-du-Loup (A) and Shippagan (B), showing the distribution of ericaceous shrubs, *Eriophorum spissum*, *Eriophorum angustifolium*, *Sphagnum* spp., *Mylia anomala*, lichens, and *Polytrichum strictum* in the microhabitats.
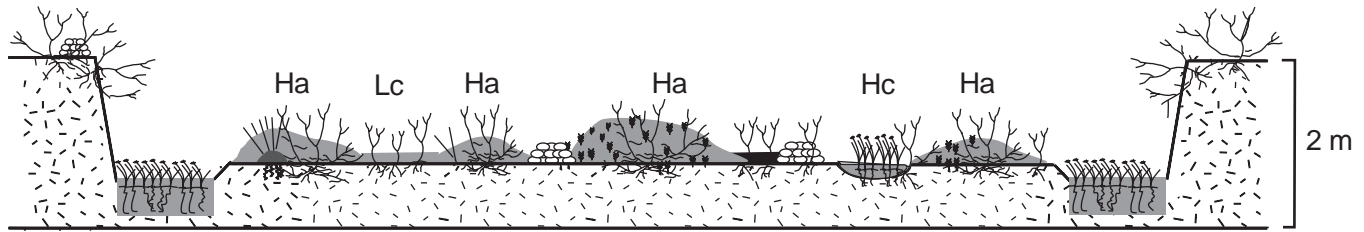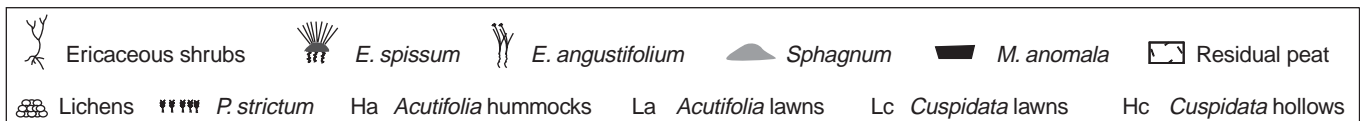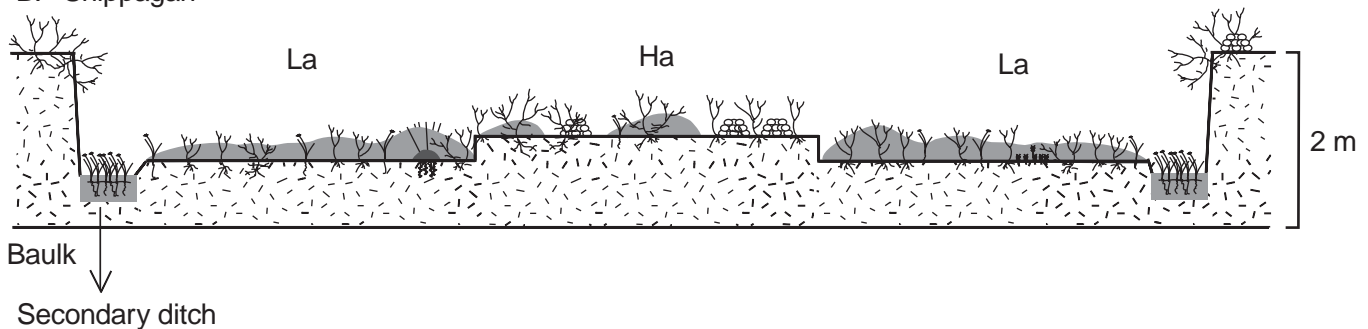
of trenches, and one core was collected from an *Acutifolia* hummock in the central part of one trench.

Surface vegetation characterization at coring sites

The surface vegetation at coring sites was characterized by evaluating the percent cover of each species within the total area of a microhabitat covering a small surface (average of 2 m^2). When microhabitats formed a continuum, the surface vegetation was characterized within a 2-m^2 area. Three vegetation strata were distinguished: cryptogams, herbs, and shrubs. Nomenclature follows Scoggan (1978) for vascular plants, Esslinger and Egan (1995) for lichens, Stotler and Crandall-Stotler (1977) for liverworts, Anderson et al. (1995) for mosses, and Anderson (1990) for *Sphagnum*. *Sphagnum capillifolium* (Ehrh) Hedw. includes *Sphagnum nemoreum* Scop. and *Sphagnum rubellum* Wils. (Flatberg 1983; McQueen 1989). A specimen of each species can be found at the Herbier Louis-Marie (QFA), Laval University.

Measurements of water

The water table position under surface vegetation was measured with observation wells (1994) and PCV pipes (1995). At Rivière-du-Loup, four hummocks and four hollows were selected for measurements in each trench (eight observation points). At Shippagan, three observation points were selected in the two lateral parts and the central parts of each trench (six observation points). In 1994 and 1995, the measurements were made bimonthly from the end of June to the end of September.

Chemical analyses of surface water and physicochemical analyses of peat deposits

One surface water sample was taken from the center of each trench studied (four samples in total). The samples were taken in polyethylene bottles previously rinsed with distilled water and stored at a low temperature until analysis. The water pH was measured with a Fisher Acumet Model 10. Water was then filtered with a cellulose acetate filter (0.45 μm) and measured for corrected conductance (Sjörs 1952). Base cations (Ca^{2+}, Na$^+$, Mg^{2+}, K$^+$) and Fe were analyzed by atomic absorption spectrometry (Varian 1475). NO$_3$-N, NO$_2$-N, SO$_4$, and Cl anions were analyzed by ion chromatography using a Waters chromatographic system. NH$_4$-N concentrations were measured by steam distillation with a Kjeltec 1002 Distillation system. Analyses of total P were done by colorimetric method using UV/vis LKB Urtospec II.

In each trench, two coring sites were chosen for physicochemical analyses of residual peat and newly formed peat. Samples were taken from the first 5 cm on each side of the residual peat – newly formed peat interface. Residual peat was recognized by its darker color and the smaller vegetation fragments, which indicate a more advanced state of decay. The peat samples were stored in polyethylene bags at a low temperature (4°C) until analysis. The peat pH was analyzed using the CaCl$_2$ method. The corrected conductance (Sjörs 1952) analysis was conducted using a 1:10 ratio of fresh peat to distilled water filtered with an 8-μm filter. Base cations, total P, and Fe were measured by agitating the sample in a 1 M ammonium acetate solution at pH 7 to displace cations and then analyzing the filtrate by atomic absorption spectrometry

Table 1. Percent cover of important species in present-day vegetation on *Acutifolia* hummocks (Ha), *Acutifolia* lawns (La), *Cuspidata* lawn (Lc), and *Cuspidata* hollow (Hc) at Rivière-du-Loup (Québec) and Shippagan (New Brunswick).

	Rivière-du-Loup										Shippagan									
	Ha	Ha	Ha	Ha	Ha	Ha	Ha	Ha	Lc	Hc	La	La	La	La	La	Ha	La	La	La	La
	S–E	S–E	S–P	S–P	S–P	S–P	S–P	S–H	—	—	S–E	S–E	S–E	S–E	S–E	S–E	S–E	S–E	S–P	S–H
Cryptogam stratum																				
Mylia anomala		20			10						+							+	5	+
Sphagnum spp., total	100	80	70	70	75	65	75	100	100	80	95	100	95	100	100	100	100	100	80	95
Sphagnum fuscum	60		35	70	20	25	75	90			25		60	75	25	10	15	80	20	45
Sphagnum capillifolium	40	80	35		15	35					70	5	25	25	25	40	85	10	60	30
Sphagnum magellanicum					40						+	95	10		50	20		10		20
Sphagnum flavicomans																30				
Sphagnum fallax									85	70										
Sphagnum cuspidatum										10										
Polytrichum strictum			30	30	25	25	25				5		5	+		+	+		10	5
Herb stratum																				
Eriophorum spissum	+	+	10	20	5	5	+	20	5					+		+		5		+
Eriophorum angustifolium			+							70	5	+	10	10	20	+	10	5	10	
Rubus chamaemorus	20	10		5	15	15	20				25	35	+		+					
Drosera rotundifolia	+	+	+		+		+	+	+		+		+			+	+		+	+
Shrub stratum																				
Empetrum nigrum											10	25	15	+		10	5	10	5	
Chamaedaphne calyculata	45	10	10	5	5	10	15	5	30	25	15	5		5	10	10	20	10	40	15
Kalmia angustifolia	10	10	15	15	10	60	5	10			5	5	30	20	15	25	5	50	15	30
Ledum groenlandicum	10	15	15	5	5	5	10	5	+		10	20	5	+	5	5		5	+	5
Vaccinium angustifolium	+	+	10		+		5	+			5	5	+	5	5	+	5	5		5
Vaccinium oxycoccus	+							5	25	5	5		5	5	5	5	5	5	5	+
Rhododendron canadense	5		5			5	5	25			5		5		5			+	+	+
Andromeda glaucophylla											+		+	5	+	5	+	5		

Note: Each column corresponds to a coring site for determining vegetation succession (Figs. 3 and 4). Study sites are classified by microhabitat (Ha, Hc, La, Lc) and principal colonizing species group (S–E, S–H, S–P). S–E, *Sphagnum* and ericaceous shrubs group; S–P, *Sphagnum* and *Polytrichum strictum* group; S–H, *Sphagnum* and *Eriophorum spissum* group. +, percent cover <5%.

Table 2. Water table position (cm) under the surface vegetation at (A) Rivière-du-Loup, Que., and (B) Shippagan, N.B.

(A) Rivière-du-Loup.

Year	Trenches mean	Hummocks Mean	Range	Hollows Mean	Range
1994	–15	–33	–20 to –45	–7	1 to –16
1995	–25	–37	–23 to –55	–12	–1 to –33

(B) Shippagan.

Year	Trenches mean	Central part Mean	Range	Lateral parts Mean	Range
1994	–23	–29	–25 to –33	–16	–12 to –23
1995	–46	–48	–26 to –57	–44	–19 to –58

(Varian 1475). NH_4-N concentrations were measured by a colorimetric method after KCl extraction. C, S, and N concentrations were determined by gas combustion with a LECO CSN 1000 analyzer. Percent mineral ash was measured by incineration.

Three physical properties of peat deposits were measured: degree of humification, water content, and bulk density. Degree of humification was evaluated following von Post's scale (Parent and Caron 1993). Water content was measured for 100 g of field-moist peat dried at 100°C, as the ratio of weight of water to total weight. Samples of 15 mL mean volume from core cutting residues were used to calculate the bulk density as the ratio of dry weight to initial volume after drying at 100°C.

Vegetation macrofossils analyses

The peat cores were removed in 1994 with a stainless steel sampler ($8 \times 8 \times 60$ cm). Measurements of accumulations of newly formed peat were taken directly from the cores as the distance between surface vegetation and residual peat limits. Cores were wrapped with plastic wrap and aluminum foil, then refrigerated (4°C) until analysis. Peat cores were cut in 2-cm slices starting at 4 cm below the upper limit of residual peat. Analyses were performed on 25 mL subsamples that were cut from the middle of each 2-cm slice. The subsamples were treated with a gently boiling 5% aqueous KOH solution for deflocculation before rinsing with water with a 180-μm sieve (Garneau 1998). In each core, the two samples from residual peat were used to identify botanical components in peat left in place after exploitation. The first sample above the residual peat limit (first 2 cm of newly formed peat) corresponds to the pioneer horizon, and its composition is considered to be representative of colonizing species. The other horizons of the succession correspond to each successive 2-cm slice of the newly formed peat up to the surface horizon.

In the residual peat, 100 *Sphagnum* leaves were subsampled and identified to their section. In the newly formed peat, *Sphagnum* were identified to species. In the first layers of the succession, distinction between *Sphagnum fuscum* and *Sphagnum capillifolium* was principally based on differences between stem leaves, because these two species lose their coloration and their distinctive appearance when they are buried below a certain depth (Mörnsjö 1969; Johnson et al. 1990).

No lichens were found in the peat. Mosses, liverworts, sedges, herbs, and ericaceous fragments were identified to species whenever possible. Ericaceous shrubs were identified to species by their leaves. Nonleaf fragments of ericaceous plants were classified as either ligneous fragments (underground stems and roots), rootlets (diameter <2 mm), or flowers and fruits. *Empetrum nigrum* fragments (Shippagan) were grouped with ericaceous shrubs. In residual peat, fragments of bark and herb leaves (Rivière-du-Loup)

were neither identified to species. Less than 5% of the macrofossil volume was not identified nor considered representative of the dominant colonizing vegetation and its succession. A detailed analysis of each peat core can be found in Robert (1997).

In each 25-mL subsample, the frequency of each species or group of botanical components was estimated as percent volume of the total sample volume. The vegetation succession profile of each core was established and graphically illustrated using the total volume of ericaceous fragments and *Sphagnum* in each 2-cm horizon. The 18 cores from the *Acutifolia* hummocks and lawns were divided into three groups according to the abundance of the principal colonizing species in the pioneer horizon (0–2 cm): *Sphagnum* and ericaceous shrubs (S–E group), *Sphagnum* and *Polytrichum strictum* (S–P group), and *Sphagnum* and *Eriophorum spissum* (S–H group).

Results

Present-day environmental conditions

Surface vegetation at coring sites

At Rivière-du-Loup, *Sphagnum fuscum*, *Sphagnum capillifolium* (*Acutifolia* section), and *Sphagnum magellanicum* (*Palustria* section) form hummocks, generally in mixed cushions (Table 1). *Polytrichum strictum* is abundant in some hummocks. *Eriophorum spissum* and *Rubus chamaemorus* form the major part of the herb stratum. Ericaceous branches are generally well developed in the hummocks as in other microhabitats (Fig. 3A). The selected lawn and hollow are characterized by the presence of *Sphagnum fallax*. *Eriophorum angustifolium* is only present in the hollow.

At Shippagan, *Sphagnum fuscum*, *Sphagnum capillifolium*, and *Sphagnum magellanicum* form lawns and hummocks. *Sphagnum flavicomans* (*Acutifolia* section) appears sporadically and *Sphagnum* species from *Cuspidata* section are absent in the trenches (Table 1). *Polytrichum strictum* is frequent but not abundant in the lawns. *Eriophorum spissum*, *Eriophorum angustifolium*, and *Rubus chamaemorus* form the major part of the herb stratum, with *Eriophorum angustifolium* being more frequent and more abundant than *Eriophorum spissum*. *Empetrum nigrum* forms a locally creeping shrub stratum, and ericaceous shrubs show numerous short stems emerging from the *Sphagnum* stratum in the lawns (Fig. 3B).

Water table position

The water table at Rivière-du-Loup was located at a mean of 15 cm beneath surface vegetation during the summer of 1994 and at 25 cm during the relatively dry 1995 summer (Table 2). The water table at Shippagan was located at a mean of 23 cm beneath the surface during the summer of 1994 and reached a mean depth of 46 cm in 1995 (Table 2).

Surface water chemistry and peat deposit physicochemistry

Surface water of trenches is characterized by an acidic pH (3.6–3.8) and low conductance (63–82 μS). Concentrations of Ca, Mg, Na, K, Fe, NH_4-N, NO_3-N, NO_2-N, Cl, and P are low (Table 3). At Shippagan, the supply of oceanic spray clearly appears in Na and Cl concentrations. The residual peat and newly formed peat also show an acidic pH (3.7–4.2) and a low conductance (30–62 μS). The C/N

Table 3. (A) Surface water chemistry and (B) peat chemistry and physical characteristics of residual peat (residual) and newly formed peat (new) at Rivière-du-Loup, Que., and Shippagan, N.B.

(A) Water chemistry.

	Rivière-du-Loup ($n = 2$)	Shippagan ($n = 2$)
pH	3.80±0	3.60±0.03
Conductance (μS)	63.50±4.95	81.50±12.0
Ca (mg/L)	0.44±0.42	1.67±0
Mg (mg/L)	0.78±0.17	1.04±0.14
Na (mg/L)	1.25±0.16	4.30±0
K (mg/L)	0.94±0.09	0.19±0.04
Fe (mg/L)	0.15±0.06	0.72±0.33
P (mg/L)	0.01±0	<0.01±0
N-NH$_4$ (mg/L)	<0.01±0	0.95±0.44
N-NO$_3$ (mg/L)	0.08±0.01	0.05±0
N-NO$_2$ (mg/L)	0.08±0.03	0.01±0
Cl (mg/L)	0.85±0.21	5.32±0.74
SO$_4$ (mg/L)	0.60±0.03	0.60±0.03

(B) Peat chemistry and physical characteristics.

	Rivière-du-Loup ($n = 4$)		Shippagan ($n = 4$)	
	Residual	New	Residual	New
pH	4.00±0.16	4.20±0.05	3.70±0.08	3.90±0.07
Conductance (μS)	36.10±6.29	29.90±5.06	61.90±7.33	56.80±9.4
Ca (%)	0.08±0.01	0.04±0.01	0.14±0.06	0.18±0.02
Mg (%)	0.10±0.01	0.11±0.01	0.16±0.03	0.19±0.05
Na (%)	0.02±0	0.03±0	0.15±0.02	0.16±0.02
K (%)	0.06±0.02	0.04±0.02	0.05±0.03	0.10±0.02
Fe (%)	0.06±0.02	0.08±0.02	0.21±0.08	0.09±0.04
P (%)	0.04±0.01	0.04±0.02	0.03±0.01	0.03±0.01
N-NH$_4$ (%)	<0.01±0	<0.01±0	<0.01±0	<0.01±0
N-NO$_3$ (%)	1.01±0.11	0.06±0	1.09±0.19	0.89±0.18
S (%)	0.13±0.04	0.11±0	0.15±0.06	0.09±0.03
C (%)	49.00±2.30	47.00±2.34	48.50±1.36	47.90±1.29
N (%)	1.00±0.18	0.85±0.10	0.80±0.27	0.65±0.02
C/N	49.00	55.00	61.00	74.00
Ash (%)	2.53±0.81	3.38±0.52	1.99±0.19	2.16±0.53
Bulk density (g/cm^3)	0.10±0.01	0.07±0.01	0.09±0.19	0.07±0.01
Water (%)	88.40±1.88	89.7±1.66	90.70±2.86	91.40±0.01

Note: Values are means ± SD. n, number of samples.

ratio is less than 75 (Table 3). There are few chemical differences between residual peat and newly formed peat. Nevertheless, residual peat is distinguishable from newly formed peat by its lower pH, lower percent ash, and lower C/N ratio. In both types of deposits, water content is high (89.7–91.4%). Following von Post's scale, residual peat is fibric (H4). Newly formed peat is fibric but with a lower humification scale (H2 and H3). Bulk density is higher (0.09 g/cm^3) in residual peat than in newly formed peat (0.07 g/cm^3).

Vegetation macrofossils

Botanical composition of residual peat

In every sample of residual peat (4 cm below the limit of newly formed peat), branch leaves of *Sphagnum* from *Acutifolia* section are the most abundant botanical components (Figs. 4, 5). Bark fragments are always present at Rivière-du-Loup, whereas they are neither as abundant nor as frequent at Shippagan. At Rivière-du-Loup, residual peat is also distinguishable by the presence of unidentified herb leaf fragments that correspond to the fossilized vegetation cover (Fig. 4, S–P group).

Ericaceous ligneous fragments and rootlets are systematically present in residual peat. They may be associated with either recent or past vegetation cover because of their growth pattern and their ability to accumulate in peat (Lévesque et al. 1988). *Eriophorum* species, identified by fragments of rhizomes, collars, and leaves, are also commonly present peat and abundant in some cores (Fig. 4, S–H group). The presence of recent sedge rhizome fragments is also linked to their growth pattern and rooting system. Fragments (probably rhizomes) of *Rubus chamaemorus* (Fig. 4) may also belong to the recent vegetation succession, as their rhizomes rich in aerenchyma can penetrate deeply into anoxic layers (Clymo and Hayward 1982; Malmer et al.

Fig. 4. Vegetation succession of *Acutifolia* hummocks, *Cuspidata* lawn, and *Cuspidata* hollow at Rivière-du-Loup. *Sphagnum* species are identified by a letter and are arranged following their abundance in the pioneer horizon and in each subsequent horizon where a change in species or in dominance occurs. Groups are as follows: S–E, *Sphagnum* and ericaceous shrubs group; S–P, *Sphagnum* and *Polytrichum strictum* group; S–H, *Sphagnum* and *Eriophorum spissum* group.
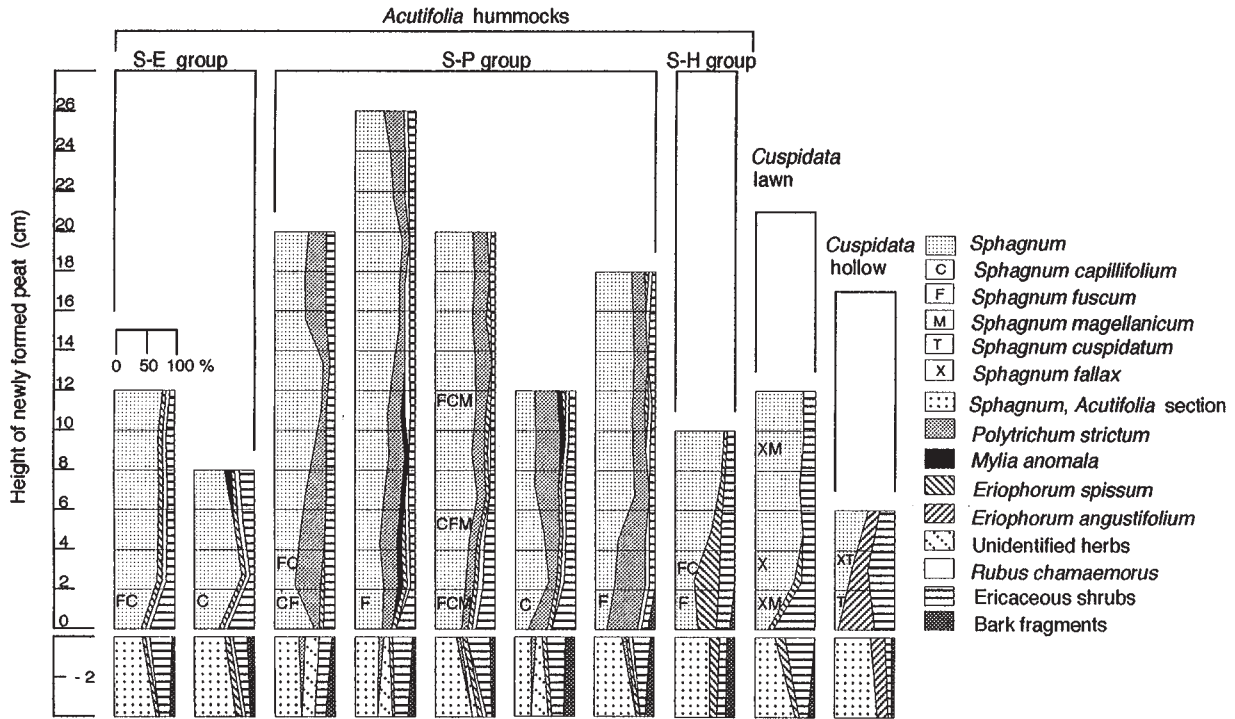

Fig. 5. Vegetation succession of *Acutifolia* lawns and *Acutifolia* hummock at Shippagan. *Sphagnum* species are identified by a letter and are arranged following their abundance in the pioneer horizon and in each subsequent horizon where a change in species or in dominance occurs. Groups are as follows: S–E, *Sphagnum* and ericaceous shrubs group; S–P, *Sphagnum* and *Polytrichum strictum* group; S–H, *Sphagnum* and *Eriophorum spissum* group.
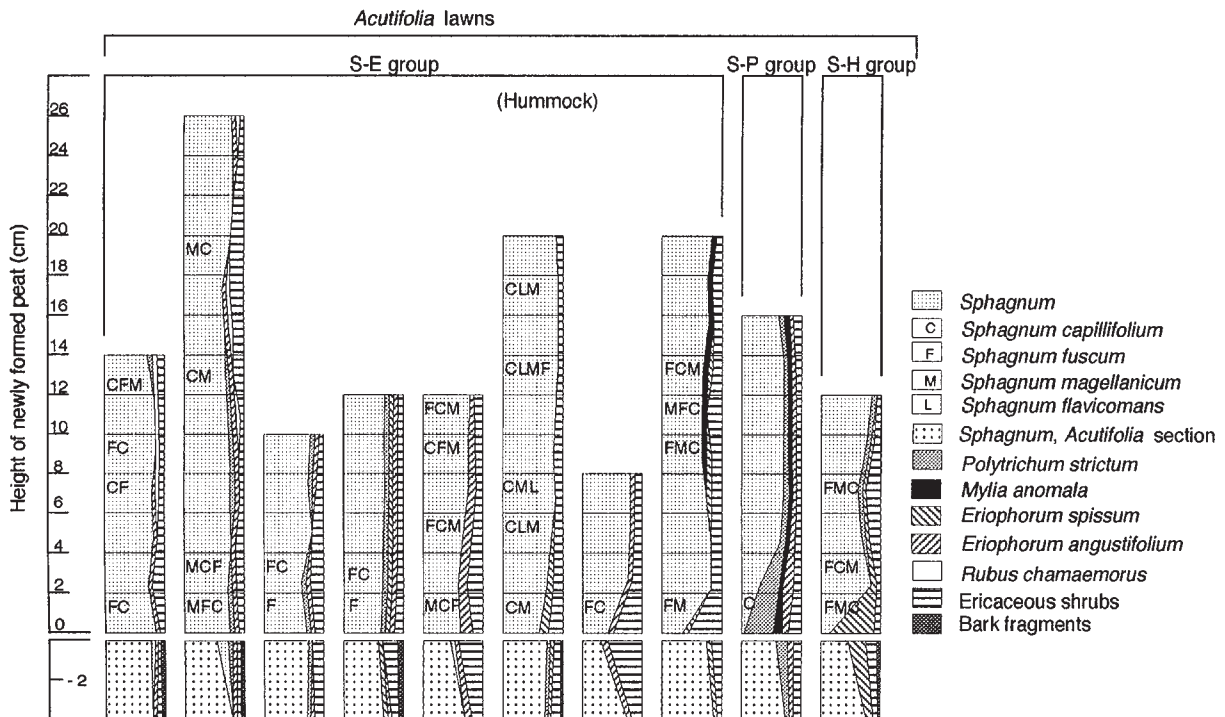
1994). However, dominance (>60%) of *Sphagnum* branch leaves from *Acutifolia* section remains the main characteristic of residual peat.

Colonizing species

The pioneer horizon (0–2 cm) of the 18 cores from *Acutifolia* hummocks and lawns from both sites are characterized by the presence of *Sphagnum fuscum*, *Sphagnum capillifolium*, or *Sphagnum magellanicum*, accompanied by ericaceous fragments (Figs. 4 and 5). *Sphagnum fuscum* and *Sphagnum capillifolium* may or may not be in association, while *Sphagnum magellanicum* is always associated with a least one of those two species. In the *Sphagnum* and ericaceous shrubs group (S–E group), the pioneer horizon is characterized by the dominance of *Sphagnum* and ericaceous fragments (>80%). This group includes two cores from Rivière-du-Loup (Fig. 4) and eight cores from Shippagan (Fig. 5). In the S–P group, the pioneer horizon is characterized by a volume of *Polytrichum strictum* varying between 10 and 60%. It includes five cores from Rivière-du-Loup and only one core from Shippagan. Finally, the two cores in the S–H group have their pioneer horizon distinguished by the abundance of *Eriophorum spissum* (30–50%).

In the pioneer horizon of the three groups, ericaceous shrubs are principally represented by ligneous fragments and rootlets. Even so, leaves, flowers, and fruits are more abundant in the pioneer horizon than in residual peat. Leaves of *Chamaedaphne calyculata*, *Kalmia angustifolia*, and *Ledum groenlandicum* are well represented. At Rivière-du-Loup, the deep growth of *Rubus chamaemorus* rhizomes may result in its representation in the pioneer horizon, even if it appeared later during succession. *Eriophorum angustifolium* only appeared in the pioneer horizon of the *Cuspidata* hollow from Rivière-du-Loup but is frequent, although not abundant, in the pioneer horizon of the *Acutifolia* lawns from S–E and S–P groups at Shippagan. *Mylia anomala* has been identified in the pioneer horizon of the core from S–P group at Shippagan.

The pioneer horizon of the *Cuspidata* lawn from Rivière-du-Loup (Fig. 4) is characterized by the dominance of ericaceous fragments and the presence of *Sphagnum fallax*, accompanied by less than 5% *Sphagnum magellanicum* fragments. The pioneer horizon of the *Cuspidata* hollow is characterized by the dominance of *Eriophorum angustifolium*, the abundance of ericaceous fragments, and by less than 10% *Sphagnum* (*Sphagnum cuspidatum*).

Vegetation succession in the Acutifolia hummocks and lawns

In spite of different initial vegetation stages, the three groups of cores taken from *Acutifolia* hummocks and lawns present a vegetation succession profile with the following common characteristics (Figs. 4 and 5).

(1) Sphagnum species are either dominant in the pioneer horizon (0–2 cm) or they become dominant in the second (2–4 cm) or third horizon (4–6 cm) of succession. They maintain this dominance upwards to present-day surface vegetation.

(2) In most samples, representation of ericaceous shrubs is relatively constant (10–20%) from the pioneer horizon up to the surface horizon. In the remaining samples, their representation becomes constant by the second or third horizon of succession. Ligneous and rootlet fragments are more abundant than other ericaceous fragments throughout succession.

(3) In the S–P and S–E groups, the abundance of *Polytrichum strictum* and *Eriophorum spissum* diminishes throughout succession. However, the S–P group at Rivière-du-Loup is distinguishable by the persistence of *Polytrichum strictum* in relatively significant proportions throughout succession.

(4) All other species followed no particular pattern of abundance over time.

Vegetation succession in the Cuspidata lawn and hollow at Rivière-du-Loup

The vegetation succession profile in the lawn colonized by *Sphagnum fallax* (Fig. 4) is similar to that of *Acutifolia* hummocks and lawns. *Sphagnum fallax* becomes dominant in the second horizon of the succession (2–4 cm), whereas ericaceous shrubs reach a mean proportion of 20%, which is maintained afterwards. In the hollow (Fig. 4), the accumulation of newly formed peat is only 6 cm. The vegetation succession in this microhabitat is distinguishable by the presence of *Eriophorum angustifolium* and ericaceous shrubs in significant proportions in the three horizons of the succession. *Sphagnum fallax* appears in the second horizon (2–4 cm), whereas *Eriophorum angustifolium* decreases. *Sphagnum fallax* then becomes dominant in the surface horizon (4–6 cm), as in hummocks and lawns.

Discussion

Colonization in the trenches

The botanical composition of the pioneer horizon gives an accurate picture of colonizing species, particularly for the cryptogam stratum. The botanical composition of cores from S–E, S–P, and S–H groups indicates that re-establishment of *Sphagnum fuscum*, *Sphagnum capillifolium*, or *Sphagnum magellanicum* was initiated directly on the residual peat. Presence of ericaceous leaves, flowers, and fruits in pioneer horizons is considered a good indicator that ericaceous shrubs were early colonists. On the other hand, the abundance of ericaceous ligneous fragments and their rootlets is evidence of the development of their root systems and branches in the newly formed peat. The presence of ericaceous shrubs in the pioneer horizon is therefore less significant than that of *Sphagnum* for estimating the abundance of those species at the colonization stage.

The abundance or dominance of *Polytrichum strictum* and *Eriophorum spissum* in some pioneer horizons is considered an indicator of a different initial stage of vegetation re-establishment. *Polytrichum strictum* (S–P group) appears to have been locally abundant at the colonization stage, particularly at Rivière-du-Loup. However, there was no general invasion of the trenches by *Eriophorum spissum* (S–H group) as recognized in other post-mined peatlands (Salonen 1990; Campeau and Rochefort 1996).

It is impossible to determine from the botanical composition of the pioneer horizon whether *Sphagnum* re-establishment was initiated before, during, or after coloniza-

Fig. 6. Probable sequences of ericaceous shrubs, *Eriophorum spissum*, *Polytrichum strictum*, and *Sphagnum*, re-establishment at initial stage of revegetation (A, B, C), with vegetation succession and present-day vegetation.
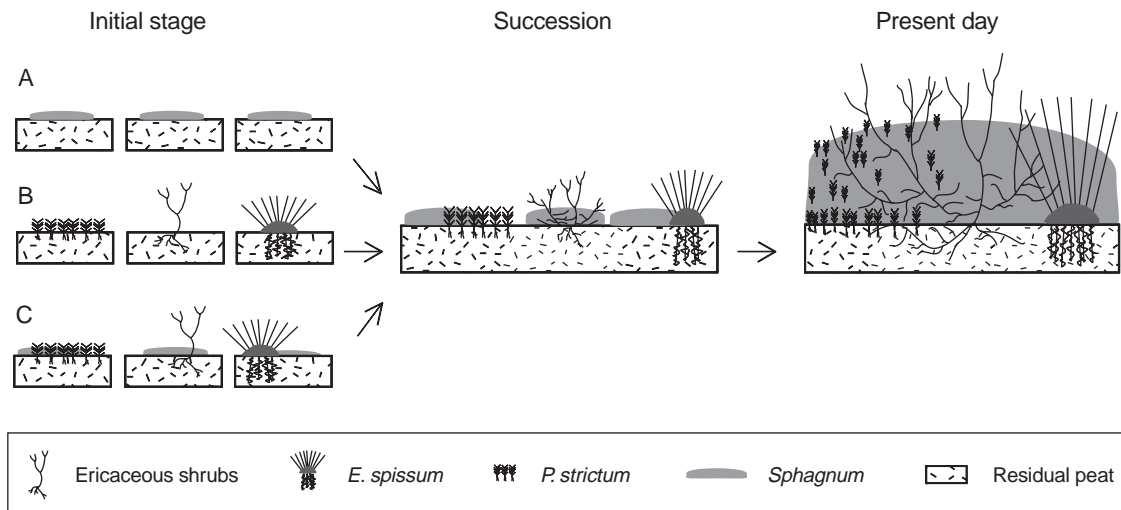
tion by either ericaceous shrubs, *Polytrichum strictum*, or *Eriophorum spissum*. Either *Sphagnum* species (Fig. 6A) or these companion species (Fig. 6B) may have initially colonized the residual peat, or they may have established simultaneously (Fig. 6C). Stages B and C cannot be distinguished in the pioneer horizon. As the moisture deficiency in abandoned peatlands does not benefit precocious *Sphagnum* reestablishment (Joosten 1992; Money 1995; Campeau and Rochefort 1996), the first sequence (Fig. 6A) should be less frequent. The second sequence (Fig. 6B) is a more credible scenario because ericaceous shrubs, *Polytrichum strictum*, and *Eriophorum spissum* can tolerate periods of drought (Ingram 1983; Malmer et al. 1994) and become established before *Sphagnum* species during restoration experiments (Elling and Knighton 1984). On the other hand, presence of *Sphagnum* and companion species together in the pioneer horizon also suggests that their re-establishment occurred simultaneously (Fig. 6C), as was observed following natural or induced rewetting of other abandoned sites (Mörnsjö 1969; Smart et al. 1989; Joosten 1995). It is also possible that *Sphagnum* re-establishment was not initiated uniformly, and that a combination of the three sequences (Figs. 6A, 6B, and 6C) has occurred in the trenches.

Conditions allowing direct *Sphagnum* re-establishment on residual peat

Sphagnum recolonization depends on source of diaspores and suitable environmental conditions for their establishment. The residual peat does not constitute a diaspore bank because *Sphagnum* material loses its regeneration potential if buried deeper than 30 cm, if it is more than 25–60 years old, or if the environment is dry for a long time (Clymo and Duckett 1986; Poschlod 1995; Campeau and Rochefort 1996; Sagot and Rochefort 1996). Hence, no spontaneous *Sphagnum* regeneration can have occurred in situ from the *Sphagnum* fragments in the remaining peat, and the opportunity for *Sphagnum* species to colonize residual peat is primarily related to the abundance and random dispersion of their diaspores (Salonen 1990, 1994; Joosten 1992; Poschlod 1995; Wheeler and Shaw 1995). During the manual block-cut process, some *Sphagnum* fragments may have reached

the residual peat from the living vegetation present in the vicinity of the trenches.

Given a supply of diaspores, the main factors influencing *Sphagnum* re-establishment were probably those controlling moisture, such as the physical properties of residual peat (Mörnsjö 1969; Elling and Knighton 1984; Smart et al. 1989). Physical conditions that favored the rewetting of residual peat were in place on both sites. The residual peat has a fibric texture (H4) and is composed of weakly decomposed *Sphagnum* fragments. Bulk density of residual peat is similar to that found in the upper part of the catotelm in natural peatlands (Malmer and Holm 1984; Clymo 1987; Johnson et al. 1990; Wallén and Malmer 1992), and its water content is high (88–91%). These physical properties indicate the presence of pore sizes that favor water reserves and the availability of water for *Sphagnum* at the air–soil interface (Price 1996). Hence, the partial remains of a catotelm at the end of exploitation may have contributed to direct *Sphagnum* re-establishment on residual peat (Schouwenaars 1988, 1993; Salonen 1990, 1994; Joosten 1992; Wheeler and Shaw 1995).

Contrary to the flat and uniform topography created by vacuum mining methods, block-cut methods produce a varied landscape which can be advantageous for *Sphagnum* re-establishment. Natural blockage of ditches due to cessation of maintenance may have favored water recharge of the residual peat in the trenches (Price 1996; LaRose et al. 1997). The revegetation pattern indicates the impact of topography on mean position of the water table: the secondary ditches are flooded and principally occupied by *Sphagnum* species from the *Cuspidata* section, whereas *Acutifolia* hummocks and lawns developed only in trenches (Fig. 3). Small rough patches resulting from cutting work may also have enhanced chances of direct *Sphagnum* re-establishment on the residual peat by protecting their diaspores against displacement and desiccation by wind (Money 1995; Ferland and Rochefort 1997; Quinty and Rochefort 1997; Rochefort and Bastien 1998).

Abundance and dominance of *Sphagnum* in the pioneer horizon are indicators of its ability to colonize residual peat without previous formation of an important vegetation cover

by other peatland species. Nevertheless, the effect of companion species cannot be neglected even if the exact sequences of *Sphagnum* re-establishment are unknown. Abundance or dominance of ericaceous shrubs, *Polytrichum strictum*, and *Eriophorum spissum* in the pioneer horizon of some cores suggests that moisture deficiency or a variable water table may have persisted for the first post-mining period (Mörnsjö 1969; Green 1983; Elling and Knighton 1984). The companion species may then have generated some local microclimatic conditions of moisture and shading, protecting *Sphagnum* from desiccation by wind at the initial revegetation stage (Salonen 1990; Schouwenaars 1993; Grosvernier et al. 1995; Joosten 1995). *Sphagnum* re-establishment may then have started near the companion species (Fig. 6C) and spread from those small initial cushions during succession to form the present-day vegetation pattern (Fig. 6).

Suitable environmental conditions for *Sphagnum* re-establishment also include the chemical characteristics of residual peat in the trenches (Joosten 1992; Salonen 1994). On both sites, chemical characteristics of water and peat are closer (Table 3) to those found in natural ombrotrophic peatlands, than to those found in post-mined peatlands where no *Sphagnum* re-establishment occurs (Gauthier and Grandtner 1975; Vitt and Chee 1990; Croft 1996; Lavoie and Rochefort 1996; Wind-Mulder et al. 1996). The present-day chemistry of residual peat is influenced by processes occurring in the newly formed peat. Because Ca, Na, Mg, and K have accumulated in the root systems of ericaceous shrubs (Malmer and Wallén 1993), the present-day weak chemical differences between residual peat and newly formed peat may depend on the abundance of ericaceous ligneous fragments and rootlets in the pioneer horizon and in the residual peat (Figs. 4 and 5). The more advanced state of decomposition of *Sphagnum* in residual peat explains why C, N, and S concentrations are slightly higher and why the C/N ratio is lower than in newly formed peat (Malmer and Holm 1984; Malmer and Wallén 1993). Nevertheless, the residual peat of both sites was probably still oligotrophic and acidic at the initial revegetation stage, as most of the colonizing species were ombrotrophic. Sufficient rewetting by natural degradation of the drainage system may have limited decay, oxidation, and mineralization of the residual peat (Joosten 1992; Schouwenaars 1993).

Convergence of vegetation succession

At both sites, the dominant *Sphagnum* re-establishment dynamics correspond to a convergence of succession towards the formation of hummocks and lawns dominated by *Sphagnum fuscum*, *Sphagnum capillifolium*, and *Sphagnum magellanicum*, with a more or less dense cover (25–80%) of *Chamaedaphne calyculata*, *Kalmia angustifolia*, and *Ledum groenlandicum*. The vegetation composition profile shows an initial or rapid dominance of *Sphagnum* and its maintenance throughout succession. The convergence of vegetation composition at the different coring sites shows that a sufficient expansion of *Sphagnum* cushions under ericaceous shrubs led to a complete overgrowth of *Eriophorum spissum* tussocks and partial overgrowth of *Polytrichum strictum* mats. Vegetation succession towards formation of hummocks and lawns, even when succession was initiated in

Polytrichum strictum mats or in proximity to *Eriophorum spissum* tussocks, confirms the ability of *Sphagnum* to direct succession if it successfully colonizes a habitat (Clymo and Hayward 1982). The persistence of *Polytrichum strictum* at Rivière-du-Loup may depend on significant oscillations of the water table (Mörnsjö 1969; Green 1983; Salonen 1990, 1994). Similar convergence of vegetation succession was observed in disturbed peatlands of Jura, Switzerland (Grosvernier et al. 1995).

At Rivière-du-Loup, the present-day spatial alternation of microhabitats indicates that local microscale variations of the physical properties of residual peat may have favored its colonization by different species. At Shippagan, the revegetation pathway indicates delayed rewetting of the higher, central part of the trenches, even if peat extraction ceased earlier there than on the lateral parts. Complete *Sphagnum* re-establishment on the lower, lateral parts of the trenches reveals that topography and high water table have more impact on the development of a *Sphagnum* cover than time since abandonment of exploitation.

Progressive reconstitution of acrotelm

Newly formed peat accumulations provide sufficient evidence that a new *Sphagnum* fibric layer (acrotelm) is progressively reconstituted (Ingram 1983; Schouwenaars 1988, 1993; Joosten 1992). Importance of fibric peat accumulation may be explained by the fact that *Sphagnum fuscum*, *Sphagnum capillifolium*, and *Sphagnum magellanicum* are more productive and more acidifying than *Sphagnum* from other sections, and also because they are more decay resistant and do not collapse rapidly (Wallén et al. 1988; Johnson et al. 1990; Lindholm and Vasander 1990; Ohlson and Dahlberg 1991).

A partially reconstituted acrotelm attenuates the hydrological deficiency, keeps water in reserve, and limits the oscillations of the water table, thereby ensuring favorable hydrological conditions for *Sphagnum* growth (Schouwenaars 1988, 1993; Joosten 1992). Thus, the high water table at both sites may also be attributed to the progressive reconstitution of the acrotelm. Physical properties of residual peat and of newly formed peat contribute to the establishment of internal mechanisms for water regime control. Nevertheless, the position of the water table (Table 2) and the abundance of ericaceous ligneous fragments and rootlets in the first centimetres of residual peat (Figs. 4 and 5) indicate that the mean position of the water table is still located under the newly formed peat.

The formation of a new acrotelm and present-day hydrological, chemical, and floristic conditions in block-cut trenches indicate that restoration of a fibric peat-accumulating ecosystem is possible after abandonment of exploitation. From a restoration perspective, this study confirms that research should continue on interventions favoring direct *Sphagnum* re-establishment on residual peat. Establishment of small cushions of *Sphagnum* can initiate formation of new fibric peat accumulation. Simultaneous introduction of companion species may enhance restoration of vegetation diversity by stimulating natural interactions between species that make up the floristic cohort of natural peatlands. However, the re-establishment of a functional peatland ecosystem remains unsure. Further studies are nec-

essary to determine if residual peat is a substitute for the catotelm or if development of a new catotelm is possible by accumulation of decomposed material at the bottom of newly formed peat.

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