Initiation of microtopography in revegetated cutover peatlands

Rémy Pouliot, Line Rochefort & Edgar Karofeld

Pouliot, R. (corresponding author, remy.pouliot.1@ulaval.ca) & **Rochefort, L.**: Département de phytologie and Centre d'études nordiques, Université Laval, Pavillon Paul-Comtois, 2425 rue de l'Agriculture, Québec, Québec, Canada G1V 0A6
Karofeld, E. (edgar.karofeld@ut.ee): Institute of Ecology and Earth Sciences, University of Tartu, Lai 40, 51005, Tartu, Estonia.

Abstract

Question: How many years are required for a gradient of microtopography to be initiated in revegetated cutover peatlands and become similar to natural bogs?

Location: Newly formed *Sphagnum* carpets on cutover peatlands that revegetated spontaneously after site abandonment (in Estonia), or following active restoration (in Canada) and on undisturbed natural bogs nearby.

Methods: Moss surface height was measured along linear transects above a local reference level (the lowest point for a given transect). Heights of at least 20 cm were associated with hummocks. Frequency distributions of surface height and principal component analyses (separately for Canada and Estonia) were conducted to follow the evolution of microtopography in revegetated sites and their similarity with those of natural peatlands. In Canada, regressions were also performed to estimate the time required for the microtopography in revegetated cutover peatlands to become similar to that found in natural bogs.

Results: Only 10–30 yr were needed for microstructures comparable to those in natural bogs to develop on restored peatlands where *Sphagnum* diaspores have been reintroduced. However, this process may take more than a century in cutover peatlands left to revegetate spontaneously.

Conclusions: In cutover peatlands with spontaneous revegetation, hummock–hollow formation starts on bare peat which lacks both plant propagules and viable seed banks, and the initiation of microstructures is probably more akin to the process that occurs naturally. Nonetheless, hummock–hollow microtopography resembling that found in natural bogs without pools appeared, in all of the examined cutover peatlands, over periods that are short in terms of peatland development time-scales. Active peatland restoration could effectively reduce the time required for initiation of microtopography by about 70 yr.

Introduction

Peatland surfaces exhibit topographical heterogeneity at diverse spatial scales, and hummock–hollow alternation is the characteristic microtopography for almost all extensive boreal bogs. The positive feedback between acrotelm thickness and net rate of peat formation is a convincing explanation for the differentiation of hummocks and hollows in hummock–hollow formation (Belyea & Clymo 2001). This is linked with spatial differences in the intrinsic decomposition rates of *Sphagnum* species (Vitt 1990; Johnson & Damman 1993; Belyea 1996). Hummock–hollow formation is also influenced by interactions between plant species (Malmer et al. 1994, 2003), nutrient regimes (Damman 1978), water table position (Rydin 1985; Belyea 1996) and pH (Clymo 1963). The microstructures have been described in terms of water table position, plant species and physicochemical properties (Campbell & Rochefort 2001; Rydin et al. 2006). In this study, we define a hummock–hollow alternation as a mosaic of three microstructure types, namely hummocks

where the peatland surface lies at least 20 cm above the maximum water table, hollows where the surface is close to the water table and frequently inundated, and more or less flat intermediate zones called lawns (Payette & Rochefort 2001; Weltzin et al. 2001). In some cases, pools or mud bottoms constitute hollows. There have been few studies of the development of hummock–hollow formation in bogs, but information is available about the factors that trigger temporal changes once microtopography is well developed.

Hummocks and hollows are extremely resilient to environmental change (Belyea & Clymo 2001; Nungesser 2003). Peat stratigraphy indicates that they generally remain in the same positions over time even if their area can be expanded or contracted in response to climatic variations (Walker & Walker 1961; Karofeld 1998). However, shifts of microstructures can be triggered by gradual changes in environmental conditions. For example, Belyea & Malmer (2004) showed a shift on landscape scale (appearance of hollows) once a certain threshold in climatic conditions was reached. Other examples related to climate are drought or inundation that could alter the production and decomposition rates of plant species (especially *Sphagnum* mosses) when they are sufficiently prolonged (Jeník & Soukupová 1992) and, consequently, they could cause changes in microtopography. Thus, there is some evidence that particular climatic events can stimulate shifting of microstructures over short periods of time.

The development of mud bottoms is an example of an event that can trigger changes in microtopography. Mud bottoms are areas of bare peat or dense algal growth with sparse vascular plants, which develop from necrotic *Sphagnum* patches caused by local disturbance (Karofeld & Toom 1999). Although often associated with hollows, they can be found in all of the hummock–hollow microstructure types, and their evolution through time is determined principally by location within the hummock-hollow alternation (Karofeld & Pajula 2005). Once formed, they may be revegetated by *Sphagnum* mosses if the ecological conditions become again appropriate for *Sphagnum* growth. Otherwise, the height difference between hummock tops and mud bottoms will increase over a period of years because the mud-bottom peat has a higher net decomposition rate than the surrounding *Sphagnum* carpet. In an Estonian case study, a surface reduction of ca. $2 \, mm \, yr^{-1}$ was seen in mud bottoms, whereas $17 \, mm \, yr^{-1}$ growth was measured in adjacent *Sphagnum* carpets (Karofeld 2004). Thus, the formation of mud bottoms can rapidly accentuate microtopography.

Boreal bogs may be resilient to fire at millennial timescale, but fire events are a recurrent cause of disturbance (Magnan 2009) which cause major modifications to plant communities that often persist for several decades and can also modify microtopography. Bog vegetation burns differentially because of spatial variations in surface wetness and plant composition, and this can alter microstructures by differentially changing effective peat accumulation rates (Benscoter et al. 2005a), such that the variability of fire intensity and duration regulates microtopography (Benscoter et al. 2005b). Thus, a range of factors associated with climate must be regarded as potential modifying agents of microtopography.

Some animals and plants can also cause changes in microstructures. Ant hills are an excellent example of microstructural modifications created by animals (Luken & Billings 1986; Lesica & Kannowski 1998). Hummocks offer relatively dry habitats and are preferentially utilized, but tunnelling by the ants severs the upward pathways for water movement which are essential to *Sphagnum* growth. Thus, the hummocks eventually collapse and may become lawns or hollows. Similarly, the activities of herbivores (e.g. goose grubbing or reindeer trampling) create small depressions which constitute microhabitats with different ecological conditions within microstructures. Pathways of larger animal can also modify the microtopography. The abundance and distribution of microstructures such as hummocks, hollows and lawns could be determined by the architecture of the associated vascular plant life forms (Malmer et al. 1994), and the presence of microtopography has been associated with the establishment and growth of *Sphagnum* mosses through the branches of ericaceous shrubs (Clymo & Hayward 1982; Kenkel 1988). Moreover, recent greenhouse and field experiments carried out by the authors have shown that ericaceous shrubs and sparse cover of *Eriophorum* species increase the rate of vertical growth (length increment) of *Sphagnum* by providing support for the moss stems (R. Pouliot, unpubl. data). Thus, the presence and abundance of vascular plants, and to a lesser extent animals, may be important in the formation and subsequent evolution of microstructures.

While existing evidence indicates that local disturbance, climatic events, flora and fauna can all play significant roles in driving spatial and/or temporal changes in the microstructures that make up the microtopography of boreal bogs, and these microstructures can shift over short periods of time, some questions remain about the initiation of hummocks and hollows: How many years are required for the microstructures to develop, mature and reach equilibrium, and which species are involved? In this study, we aimed to estimate the time needed for the initiation of microtopography in boreal peatlands by following its development after peat extraction. Vacuum-milled peatlands that have been restored by the *Sphagnum* moss transfer method (Rochefort et al.

2003) are ideal subjects because the peat fields are scraped and levelled to create surfaces without residual relief before a mixture of plant species typical of boreal bogs is reintroduced. Peatlands that have been spontaneously recolonized by *Sphagnum* mosses after peat extraction also offer potentially relevant information. Our approach involved comparing the microtopography of cutover peatlands that had revegetated, both spontaneously and as a result of active restoration, with that of adjacent unmodified (natural) bogs. We hypothesized that microtopography can appear rapidly in terms of peatland development timescales, and probably within a decade, especially where typical vegetation has been actively reintroduced.

Methods

Study areas

The field studies were carried out on six natural bogs and six extracted peatlands with well re-established vegetation in Canada (Québec province) and Estonia (Eastern Europe) (Fig. 1). Peatland restoration is not common in Estonia and not enough sites were available when the study was done. Also, zones with spontaneous revegetation are not large enough in Québec province to make a comparison with restored peatlands. As our goal was not to compare the regions, both were used. Mean annual temperature and mean annual precipitations were of 2.3 °C and 941 mm in Québec and 6.1 °C and 677 mm in Estonia (EMHI 2010; Environment Canada 2010). Even if climatic conditions were different between Québec province and Estonia, all peatlands studied (in both regions) were located within the boreal zone. In addition, natural bogs had comparable plant species composition (R. Pouliot, unpubl. data). Revegetated peatlands had been mined mechanically (vacuum milling method) in Québec, but manually (block cutting method) in Estonia. The three peatlands in Québec had been restored in sections at different times during the previous years by the *Sphagnum* moss transfer method (Rochefort et al. 2003), and the field work was done 2–11 yry post-restoration. Those in Estonia had been spontaneously recolonized over periods of 30 or 70 yr by *Sphagnum* and vascular plant species typically found in natural bogs. With the active approach to restore post-vacuum milled peatlands, moss fragments were reintroduced uniformly on the sites whereas the quantity of residual living vegetation left on sites following the operation of peat block cutting was less certain. Furthermore, the residual substrate between the two extracting methods was definitively different: residual peat of milled peatland is more compacted and its soil structure is destroyed more because of the repeated passages of machinery than in the block-
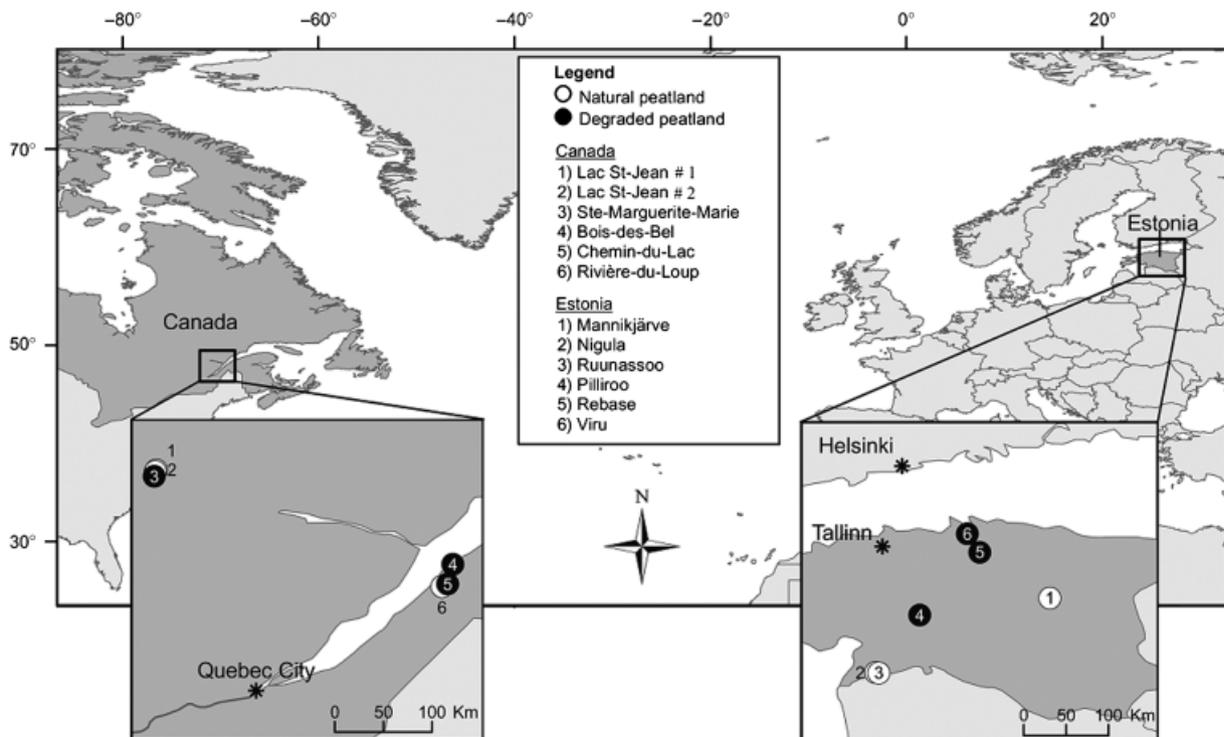

Fig. 1. Locations of the peatland sites studied. Degraded peatlands are (cutover) sites where peat extraction has ceased and revegetation has occurred either as a result of restoration work (in Québec Province, Canada) or spontaneously (in Estonia).

cut peatlands where we studied the spontaneous revegetation. For structural comparisons, areas on three unmodified peatlands in each country were selected to encompass the range of microtopography typical of natural bogs (with and without pools and with mud bottoms). Natural bogs were selected for their proximity to revegetated peatlands and their accessibility. Relevant attributes of the study sites are summarized in Table 1. See Appendix 1 for photography of studied sites.

Microtopography

The microtopography of the peatland surfaces was recorded on linear transects. For each peatland type or section studied, the transect was located randomly within an area where moss cover was at least 75%. Total transect length was adjusted to fit the area of moss carpet available, and ranged from 100 to 500 m. In a few cases where the moss carpet was particularly heterogeneous (e.g. in areas with trees), several shorter transects were surveyed

and combined to make up the total transect length. All data were recorded between Jun and Sep 2007.

The height of the moss surface above a local reference level was measured to an accuracy of ± 1 cm at 1-m intervals along each transect (a similar method was used by Ehrenfeld 1995). The reference level for restored peatlands was the clear junction that becomes visible, with time, between the surface of well-decomposed catotelm peat which was exposed by peat extraction prior to restoration (dark brown) and the slightly-decomposed *Sphagnum* fibres that have accumulated since (light brown to red). For natural and spontaneously revegetated cutover sites, which lack this clear stratigraphical reference level, the measurements were related to a temporary reference level established above the mire surface by stretching a rope between two metal posts. The posts were placed at maximum spacing 20 m to avoid sagging of the rope, initially along the first portion of the transect, and adjusted until the rope was level. When the measurements for this (and each subsequent) portion were

Table 1. List of the 12 peatlands investigated, showing details of the various sections. Surface heights are in cm. BDB = Bois-des-Bel, CdL = Chemin-du-Lac, SMM = Ste-Marguerite-Marie. R = restored peatland, A = Abandoned with spontaneous re-vegetation, N = Natural bog. CV = coefficient of variation of surface height.

Site	Type	Years post-restoration or abandonment or features of natural bog	Total transect length (m)	Mean surface height $\pm$ SD	Maximum surface height	Fraction of hummock points	# hummock/ 100 m of transect	Mean hummock height $\pm$ SD	CV
Canada									
BDB	R	6	200	10.2 ± 7.0	26	10	9	13.9 ± 7.5	69
BDB	R	7	600	11.4 ± 6.9	29	15	10	14.5 ± 6.3	61
CdL	R	3	200	1.2 ± 0.7	3	0	0	0	59
CdL	R	4	200	2.1 ± 1.7	9	0	0	0	80
CdL	R	6	100	7.0 ± 4.9	21	1	1	13.5 ± 2.1	70
CdL	R	7	100	9.2 ± 5.6	28	2	4	18.1 ± 4.1	61
CdL	R	9	200	8.6 ± 7.2	29	9	8	20.6 ± 3.6	84
CdL	R	11	100	13.5 ± 9.4	36	27	18	20.3 ± 7.1	70
SMM	R	2	200	3.0 ± 1.6	7	0	0	0	55
SMM	R	3	200	3.2 ± 1.7	9	0	0	0	52
SMM	R	4	200	4.1 ± 2.5	13	0	0	0	60
SMM	R	5	200	7.7 ± 4.1	21	1	1	12.0	53
SMM	R	6	200	11.8 ± 6.2	32	14	13	14.3 ± 6.1	52
SMM	R	7	200	12.7 ± 6.7	30	18	12	14.1 ± 4.7	53
Lac-St-Jean #1	N	Without pools	100	21.6 ± 8.3	39	67	19	15.0 ± 7.4	38
Lac-St-Jean #2	N	Without pools	100	33.9 ± 13.6	60	84	12	23.0 ± 11.9	40
Rivière-du-Loup	N	Without pools	100	24.8 ± 11.1	57	67	20	24.6 ± 9.4	45
Estonia									
Rebase	A	30	100	13.1 ± 9.5	37	30	15	17.7 ± 6.1	72
Viru	A	30	100	9.9 ± 6.0	25	6	3	17.0 ± 4.9	61
Pilliroo	A	70	100	14.8 ± 9.4	41	31	12	19.0 ± 7.2	64
Mannikjärve	N	Without pools	500	20.8 ± 7.4	43	54	18	13.9 ± 7.9	36
Mannikjärve	N	With pools	500	23.7 ± 13.1	54	64	7	26.7 ± 11	55
Nigula	N	Without pools	200	19.8 ± 10.5	41	54	17	21.3 ± 8.7	53
Nigula	N	With pools	200	12.3 ± 10.1	50	23	10	21.7 ± 8.4	82
Nigula	N	With mud bottoms	200	4.5 ± 4.5	33	2	1	26.8 ± 7.3	99
Ruunassoo	N	With mud bottoms	100	6.5 ± 6.2	29	7	5	20.1 ± 6.9	96

complete, only one post was moved and adjusted to cover the next transect portion so that the reference level was preserved. When the whole transect had been surveyed, the reference level was redefined as the lowest point recorded, and the heights of all the other points recalculated accordingly.

The surface height data were used to identify individual hummocks and to calculate their heights. As the reference level for each transect was never under the water table, points with recorded surface heights of at least 20 cm were considered to lie on hummocks, and where adjacent points on a transect met this criterion they were assumed to lie on the same hummock. Hummock height was calculated as the difference between the maximum surface height value recorded on the hummock and the mean of the surface height minima at either side; for example, if the highest value for an individual hummock was 45 cm and the two lowest flanking values were 13 cm and 19 cm, the height of the hummock was 29 cm $[((45 - 13) + (45 - 19))/2]$. The number of individual hummocks per 100 m and the mean hummock height for each peatland or peatland section were then derived. The number of points on hummocks divided by total number of points of each transect was also calculated (fraction of hummock points).

Statistical analyses

A frequency distribution of surface height (5 cm classes) was constructed for each peatland or peatland section. The evolution of microstructures in revegetated sites and their similarity with those of natural peatlands were then explored separately for Canada and Estonia using principal component analysis (PCA). For each revegetated peatland (or revegetated peatland section), mean and maximum surface height, number of individual hummocks per 100 m of transect, fraction of hummock points and mean hummock height were used as response variables. To be comparable, variables were standardized before to analysis. The PCAs were conducted using the VEGAN library of R software (version 2.2.1; The R Development Core Team Vienna, Austria). For the restored peatlands (Canada), regressions were used to test the effect of time since restoration on mean and maximum surface height, coefficient of variation of height, number of individual hummocks per 100 m of transect, fraction of hummock points on transect and mean hummock height. The regression equations for the significant relationships were then used to estimate the time required for restored peatlands to become comparable to natural peatlands in terms of microtopography. The regressions were conducted using the GLM procedure available in SAS software (version 9.1; SAS Institute Inc., Cary, NC, USA).

Homogeneity and normality were respected for all variables and significant probability levels were set to $\alpha = 0.05$.

Results

Morphometrics of hummock–hollow alternation

For the restored peatlands in Québec, both maximum surface height and the spread of the surface height frequency distributions increased with time since restoration, indicating that the heterogeneity of surface height was increasing towards that observed in natural peatlands (Fig. 2a–c). Surface height variation along the transects (Fig. 3) changed remarkably as the number of growing seasons since restoration increased. Within a decade (3–7 yr post-restoration), clear hummocks appeared. There were small differences in surface height between the 3-yr-old restorations, but the hummock–hollow alternations of 7-yr-old restorations (the only common period for all three restored peatlands) were very similar. The same pattern was observed for the other measured variables. Mean and maximum surface heights, number of hummocks per 100 m of transect and mean hummock height all increased with time and approached the values for natural bogs. For example, at Ste-Marguerite-Marie, mean and maximum surface height were, respectively, 86% and 82% lower than in an adjacent natural open bog 2 yr post-restoration, but only 41% and 23% lower after 7 yr. No hummocks were recorded 2 yr post-restoration, but after 7 yr there were about 12 hummocks per 100 m of transect, which is 37% less than the 19 recorded in the more similar natural open bog nearby (Lac-St-Jean #1). By this stage, mean ($\pm$ SD) hummock height (14.1 ± 4.7 cm) was almost equal to that in the natural open bog (15.0 ± 7.4 cm). Fraction of hummock points is 3.7 times higher in the natural bog. The situations at the other restored peatlands were comparable to that at Ste-Marguerite-Marie (Table 1).

The surface height frequency distributions for the spontaneously revegetated peatlands in Estonia, especially Pilliroo (abandoned 70 yr ago), were similar to those for natural open bog without pools (Fig. 2d); the characteristic peak (0–5 cm) for natural open bog with mud bottoms or pools was absent. As in Canada, the variation of surface height along transects in revegetated peatlands was similar to that in open bog without pools (Fig. 4). Hummock–hollow microtopography was evident at all three sites, but the microstructures were broader at Pilliroo than at the two sites abandoned 30 yr ago. The other measured variables seemed to be within the ranges observed for natural peatlands (Table 1). For Pilliroo, mean surface height was 28% lower. The number of hummocks per 100 m of transect was 1.4 times less and fraction of hummock point was 1.7 times lower than in natural open bog without pools. Conversely,
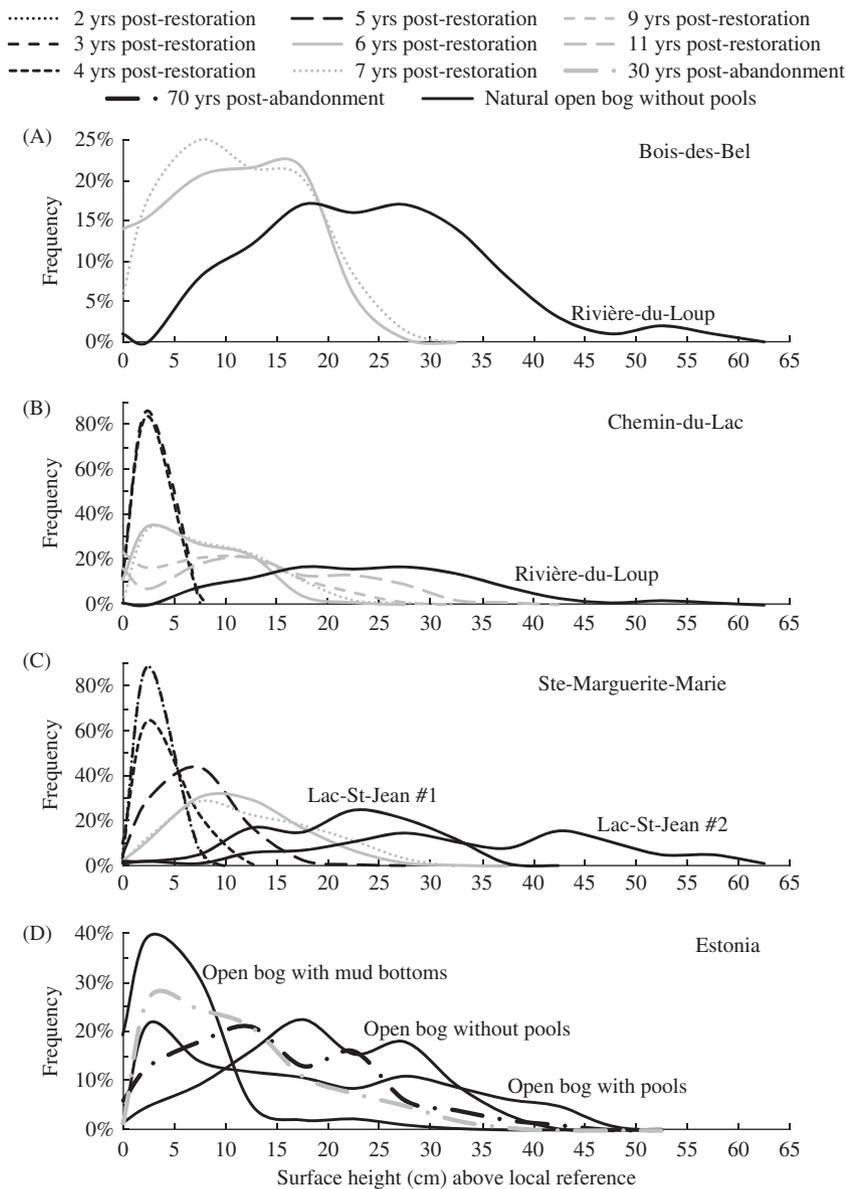
Fig. 2. Frequency distributions of surface height (5 cm classes) for revegetated peatlands or peatland sections and nearby natural peatlands: (**a**) Bois-des-Bel (restored) and Rivière-du-Loup (natural), Canada; (**b**) Chemin-du-Lac (restored) and Rivière-du-Loup (natural), Canada; (**c**) Ste-Marguerite-Marie (restored) and Lac-St-Jean (two natural areas with and without trees), Canada; and (**d**) three cutover peatlands with spontaneous revegetation and three natural hummock–hollow alternation (data pooled across alternation type) found in Estonian natural bogs. See Table 1 for further details of sites.

the values for maximum surface height (41 cm) and mean (± SD) hummock height (19 ± 7 cm) were almost identical to those for the natural bog (42 and 18 ± 8 cm, respectively). The two peatlands abandoned 30 yr previously differed from one another in that microtopography was less developed at Viru than at Rebase. Mean surface height was almost 25% lower at Viru than at Rebase, and there were only three hummocks per 100 m of transect at Viru versus 15 at Rebase. However, all variables were lower 30 yr post-abandonment compared with natural bogs without pools.

Principal component analyses

The first two axes of the PCA comparing restored and natural peatlands in Canada account for 94% of the data variability (Fig. 5a). Axis 1 seemed to be principally linked with maximum surface height whereas no particular variable was related to axis 2. Restored and natural peatlands are clearly distinguished. The centroids for natural bogs are situated to the right of the PCA, close to the ends of the variable vectors. Thus, the highest values for the
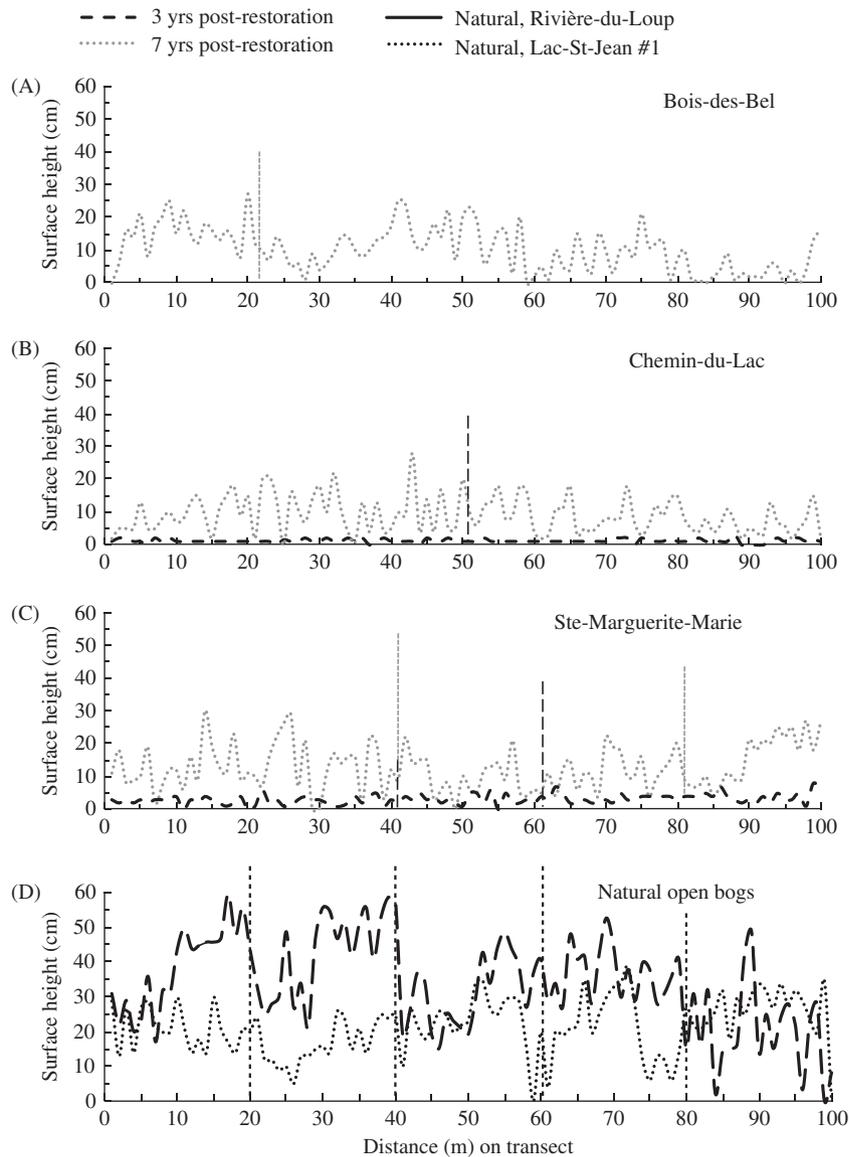
Fig. 3. Surface relief of example 100 m portions of the transects surveyed in Canada on (**a-c**) cutover peatland sections sampled 3 yr and 7 yr after restoration; and (**d**) natural peatlands. The vertical dashed lines indicate junctions between separate transects which were combined to make up the total transect length required (see the Methods section). In (**d**), the dashed lines apply for all sites.

selected variables originated from natural peatlands. The positions of the centroids for restored peatland sections illustrate clearly the evolution of microtopography with time since restoration. The centroid for the oldest restored section (at Chemin-du-Lac, sampled 11 yr after restoration) was closer to the natural bogs than other restored sections. The centroids for peatland sections sampled 2, 3 and 4 yr after restoration are grouped together, whereas the centroids for sections sampled at 5, 6, 7 and 11 yr are more widely spaced, indicating that the evolution of microtopography towards those observed in natural peatlands accelerated after 4–5 yr. Microstructures evolution

was slowest at Chemin-du-Lac, whose 6-yr centroid, for example, lies farther from the centroid for natural peatlands than do the 6-yr centroids for Ste-Marguerite-Marie and Bois-des-Bel. However, overall, hummock–hollow alternation at all of the restored site evolved towards characteristics observed in natural peatland within a decade.

The first two axes of the PCA that was conducted to test similarity between the hummock–hollow alternation of spontaneously revegetated and natural peatlands in Estonia account for 92% of the data variability (Fig. 5b). Axis 1 and 2 were mainly linked with, respectively, mean
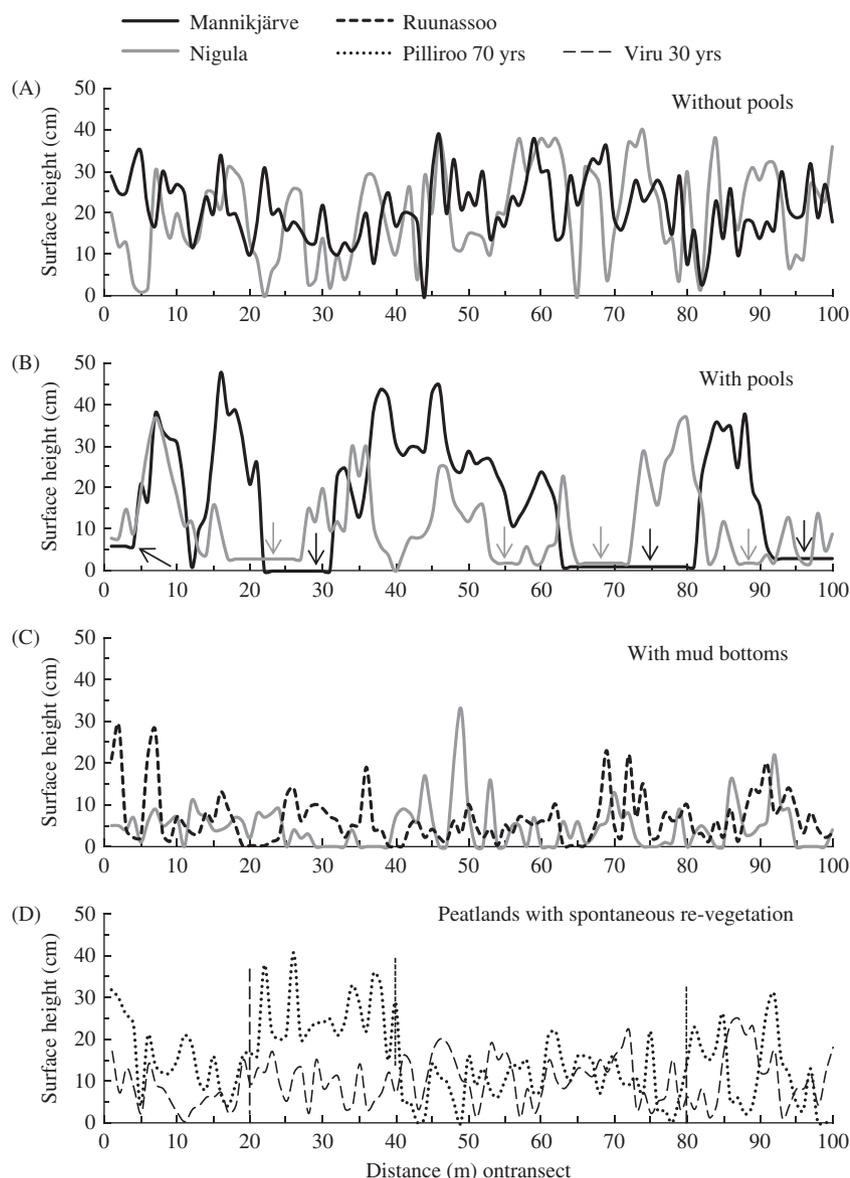
Fig. 4. Surface relief of 100 m portions of the transects surveyed on Estonian peatland areas of different categories: (**a**) natural open bog without pools; (**b**) natural open bog with pools (arrows indicate the locations of pools); (**c**) natural open bog with mud bottoms; and (**d**) spontaneously revegetated cutover peatland. The vertical dashed lines represent the junctions between separate transects which were combined to make up the total transect length required (see the Methods section).

surface height and mean hummock height. The PCA groups the samples from natural peatlands according to microtopography type rather than location. For example, the centroids for the three different microtopography types sampled at Nigula Bog lie farther apart than the centroids for a single microtopography type sampled at different peatlands (e.g. open bog without pools at Nigula and Mannikjärve). Microtopography was least developed in open bog with mud bottoms, for which the centroids are opposed to the vector ends for mean and maximum surface height and number of hummocks per 100 m. The

hummock–hollow alternation at Pilliroo and Rebase are similar to one another, but it is not totally clear how they relate to those of natural bogs because their centroids are situated at approximately equal distances from the centroids for natural bog with and without pools. Conversely, the centroid for Viru Bog lies close to the centroids for natural bog with mud bottoms, again confirming the poor development of hummock–hollow microtopography at this site. In summary, the microtopography in spontaneously revegetated peatlands tended towards that of natural bog with or without pools, but was still dissimilar
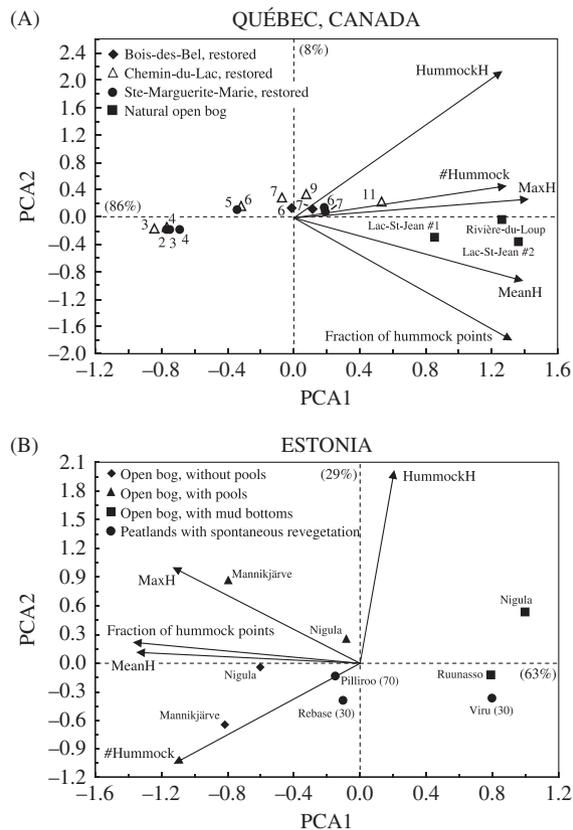
(A)

(B)

Fig. 5. Principal component analyses (PCA) on the first two axes (scaling focuses on inter-sample distances) for the Canadian (**a**) and Estonian (**b**) peatlands. Numbers close to the symbols in (**a**) indicate the number of years since restoration. Numbers in parenthesis in (**b**) indicate the number of years since peat extraction ceased on cutover peatlands. Key to axis labels: MeanH = mean surface height; MaxH = maximum surface height; #Hummock = number of individual hummocks per 100 m of transect; and HummockH = mean hummock height.

from natural microtopography even 70 yr after peat extraction had ceased.

Regressions

No significant differences were found between the slopes of the regressions for individual restored peatlands, and interactions between site and years post-restoration were always non-significant (all $P > 0.20$). Therefore, all of the data from restored peatlands were pooled for the regression analyses (Fig. 6). Linear equation was the best fit for the variables number of hummocks per 100 m of transect and fraction of hummock points on, whereas logarithmic equation was the best fit for mean and maximum height as well as mean hummock height. The relationships between time since restoration and mean or maximum surface height, number of hummocks per 100 m of transect, fraction of hummock points on transect and mean

hummock height explained 64–85% of the data variability (see R^2 values in Fig. 6). Moreover, the effect of time since restoration was significant for these variables ($P < 0.01$). The relationship between time since restoration and coefficient of variation of height was not significant ($R^2 = 0.18$; $P = 0.13$). According to the regression equations, the mean surface height measured in natural peatlands will be attained in restored peatlands after about 65 yr and the maximum surface height in 23 yr, while the number of hummocks per 100 m of transect will take 12 yr, the fraction of hummock points 29 yr and mean hummock height 10 yr to reach 'natural' values.

Discussion

Comparisons with natural bogs

As expected, the morphometrics of hummock–hollow alternation, PCA and regressions demonstrated a rapid initiation of microstructures in restored peatlands and the subsequent evolution of microtopography towards that found in natural bogs. Our analysis indicates that hummocks are comparable between restored and natural peatlands in terms of number and height around one decade post-restoration, but it can take triple this time for the fraction of hummock points. The discrepancy may arise because hummocks are larger in natural peatland. Consequently, the fraction of hummock points is lower in restored peatland and more time will thus be needed to observe hummocks as large horizontally as in natural peatlands. By contrast, maximum surface height will be comparable in restored and natural peatlands around three times more rapidly than mean surface height. Because of ecological constraints (mainly linked with water table depth) surface height cannot increase indefinitely. Slopes of maximum surface height and mean hummock height gradually decrease as time since restoration and peat accumulation increase (as we see by the logarithmic relations). As *Sphagnum* species of hollows have higher rates of decomposition than hummock species (Johnson & Damman 1993), the increase of hollow surface height is difficult, increasing the time needed to mean surface height values to become similar between restored and natural peatlands.

In addition, occasional hollows on natural peatland are very close to the water table, and these were used to define the reference level. If the majority of hollow and lawn surfaces lay at a higher level, mean hummock height would be biased towards low values because hummock height was calculated relative to the mean altitude of the two flanking low points that would mostly lie above the reference level, whereas the mean and maximum surface heights were always referred to the reference level. This probably explains why the
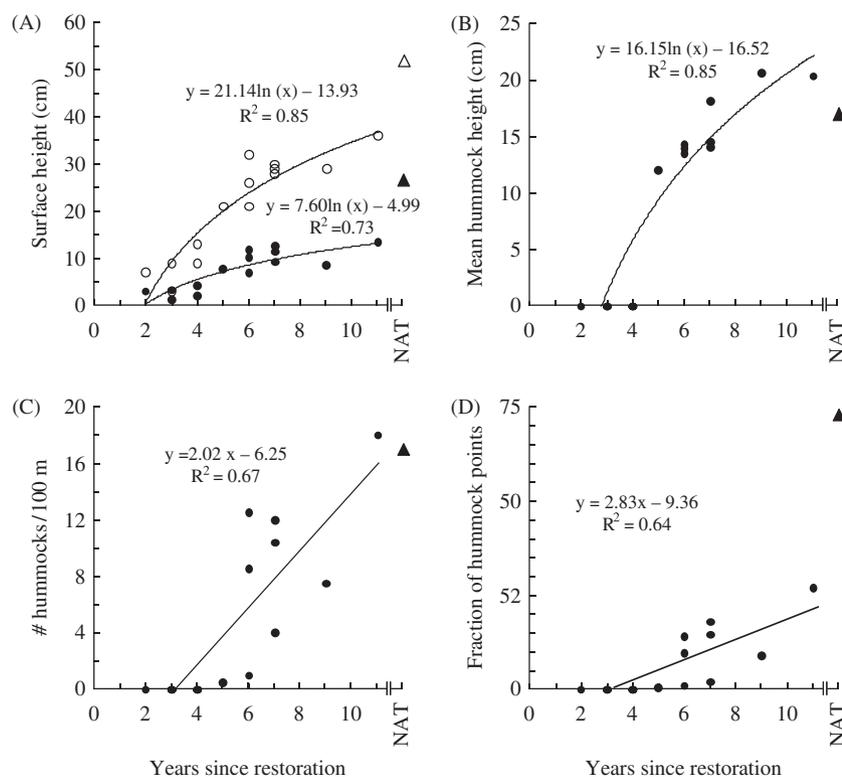
Fig. 6. Linear regressions performed on pooled data for all of the Canadian restored peatlands sampled, showing the effects of time since restoration on (**a**) mean surface height (filled symbols) and maximum surface height (open symbols); (**b**) mean hummock height height; (**c**) number of individual hummocks per 100 m of transect; and (**d**) fractions of hummock points on transect. Mean values for the neighbouring natural peatlands (NAT; $n = 3$) are represented by triangles.

regressions indicate that values similar to those observed in natural peatland will be achieved in restored peatland over a shorter period (10–12 yr) for the hummock metrics (excepted for fraction of hummock points) than for maximum and mean surface height (23–65 yr). The possibility that values in restored peatlands never reach those in natural ones is real, so extrapolation has to be used with caution. Despite that, we estimate that microtopography in restored peatlands will become similar to those in natural bogs around two to three decades after restoration. This is in accord with some modelling results indicating that 17 yr are needed to accumulate a 19-cm thick *Sphagnum* moss layer required to compensate for the summer water table decrease (Lucchese et al. 2010).

The prognosis for cutover peatland that is left to revegetate spontaneously is less clear. Seventy years after abandonment (Pilliroo site), microtopographical heterogeneity was present but still differed from the microtopography observed in natural bogs nearby, although the data suggested that evolution towards natural bog without pools could be in progress. Often, the presence of hummocks and hollows typically leads to a bimodal frequency distribution of surface heights (Baird et al.

2009) and that bimodal distribution was observed in natural peatlands (especially in bogs without pools) as well as in the revegetated peatland 70 yr post-abandonment. As only three peatlands with two abandonment dates were sampled, the course of evolution through time could not be observed as for restored peatlands. However, some variables are comparable 70 yr post-abandonment and we speculate that microtopography in cutover peatlands that have been left to revegetate spontaneously could become comparable to those in natural open bogs without pools over the course of a century.

Large-scale structures such as mud bottoms, strings, flarks and pools do not yet occur on the revegetated peatlands studied. This is an unsurprising result because several centuries are required for these macrostructures to form (Payette 2001; Kuhry & Turunen 2006). The absence of hummock–hollow alternation with trees was also to be expected, as many decades are required for trees to establish successfully on *Sphagnum* carpet. The time required for *Pinus sylvestris*, a common tree on European peatlands, to reach a diameter of 20 mm and thus be able to impede *Sphagnum* growth is 30–90 yr (Ohlson et al. 2001). Before that, young seedlings survive with

difficulty because of the too rapid vertical growth of *Sphagnum* mosses. The same constraint probably applies for *Picea mariana*, the most common tree of peatlands in North America, and could explain why microtopography in peatland which was restored within the last 11 yr is similar to that in the less forested open bogs (LSJ #1). However, the spontaneously revegetated peatlands in Estonia have been abandoned long enough for *P. sylvestris* to become established, and the possibility that microtopography in these peatlands is evolving towards a wooded stage without pools has been considered. However, *P. sylvestris* was slightly more abundant on natural bogs with pools than on those without pools (R. Pouliot, unpubl. data) and, unfortunately, no naturally wooded bogs near the spontaneously revegetated peatlands were studied. However, it appears that a century is insufficient time for either macrostructures or mature trees to develop on spontaneously revegetated cutover peatland, whose hummock–hollow alternation is consequently most similar to that of natural open bog without pools.

Influence of peatland features

The time needed for the initiation of hummocks and hollows on disturbed peatlands depends upon whether plants spontaneously recolonize or are actively reintroduced to the site, as well as on site wetness. The bare peat surface left after peat extraction by vacuum milling presents harsh hydrological conditions for plant growth (Price et al. 2003): no viable seed bank or propagules are available (Salonen & Setälä 1992) and frost heaving events combine with wind erosion to impede plant establishment (Campbell et al. 2002; Groeneveld & Rochefort 2005). This means that bog plants, and especially moss species, usually regenerate slowly on vacuum-milled peatland without human intervention (Poulin et al. 2005). Nonetheless, the spontaneously revegetated milled peatlands studied here had a well-developed microtopography. Growth conditions in the trenches of block-cut peatlands are comparatively rather favourable for plant establishment at the bare peat surface left after peat extraction by vacuum milling (high humidity with presence of plant fragments; Soro et al. 1999; Price & Whitehead 2001). There are other possible explanations: (1) rapid collapse or blocking of unmanaged drainage ditches; (2) intensive peat extraction creating an uneven surface with a tendency to accumulate water; (3) absence of significant frost heaving; and (4) fortuitous selection of peatlands with atypical microtopography as study sites. Whichever explanation is the correct one, many centuries may be required for *Sphagnum* to establish spontaneously after land uplift (Sundberg et al. 2006) or mechanical peat extraction (120 yr, L. Rochefort, personal observation); in

this context our observations indicate that hummock–hollow alternation can develop very rapidly after manual peat extraction even if no vegetation is actively reintroduced, if the hydrological setting is right (e.g. if water table is enough high).

The general goal of peatland restoration is to promote recovery of the essential structures and functions of the peatland ecosystem in order to ensure its self-perpetuation (Rochefort 2000). Several steps of the restoration process encourage the re-establishment of appropriate vegetation. Rather than waiting for seeds or propagules to arrive by chance, small fragments of mostly hummock plants are actively introduced, including such species as *Sphagnum rubellum*, *Sphagnum fuscum* and *Polytrichum strictum* (Rochefort & Lode 2006). New shoots (innovations) can be formed from fragments of *Sphagnum* only 0.5 cm long (Campeau & Rochefort 1996). These are encouraged to grow by blocking the former drainage system to keep the water table high (Price & Whitehead 2001) and applying straw mulch to create a favourable microclimate (Rochefort & Lode 2006). The presence of *P. strictum* also improves microclimate and stabilises the peat surface by reducing the intensity of frost heaving (Groeneveld & Rochefort 2005). All of these measures promote the rapid return of bog plants and in particular accelerate the establishment of *Sphagnum*. When they were well established (after 4–5 yr), an acceleration of microtopography formation was seen. Moss cover was almost 50% 4 yr after the restoration work at Bois-des-Bel, and reached about 100% in 10 yr (Mazerolle et al. 2006; Peatland Ecology Research Group, unpubl. data). Thus, the peatland restoration procedure promotes rapid regeneration of *Sphagnum* followed by the initiation of hummock–hollow microtopography, which reaches full development earlier than in spontaneously revegetated peatlands.

Conclusions

Hummock–hollow alternation can form within a short period of time in boreal bogs, unlike larger-scale surface structures such as pools, flarks and strings. We estimate that, when seeds or plant fragments are applied to the bare peat surfaces created by peat milling (e.g. as a peatland restoration procedure), around three decades are needed for microstructures similar to those found in natural peatlands (bogs without pools) to develop. However, in cases where there is no active reintroduction of plants and revegetation occurs spontaneously by a natural succession, we estimate that at least a century is required for the regeneration of microstructures analogous to those in natural peatlands. The latter cases are possibly more representative of the situation occurring

naturally, when natural succession drives changes in vegetation. There is also a possibility that spontaneous revegetated peatlands will never reach a development stage comparable to natural peatland in term of microtopography. However, hummock–hollow alternation in revegetated peatlands could be as stable as the one observed in natural peatland. The development interval between peatland initiation and maturity is often several millennia (Payette 2001; Kuhry & Turunen 2006), and microstructures appeared rapidly in terms of these time-scales at all of the revegetated peatlands studied. However, peatland restoration could bypass 70 yr of the time required for hummock–hollow microtopography to develop on cutover surfaces which had been left to recover by natural succession.

The fact that hummock–hollow alternation can develop within a decade or two does not necessarily mean that the typical assemblages of plant species for the different microstructures can develop over the same period, and further investigations are needed to determine how the vegetation evolves in parallel with microtopography. Moreover, the initiation of microtopography has so far been studied only in situations where vegetation has recently recolonized bare peat, and it would be informative to observe the initiation of hummocks and hollows in natural ecosystems following land uplift or during paludi-fication. Continued monitoring of the evolution of microstructures on revegetated (especially restored) peatlands over future decades could substantially improve our knowledge of macrostructure development by validating our extrapolations in regressions and by describing the initial development stages of pools (by the transformation of hollows) or linear strings and flarks (by merging of adjacent microstructures). Finally, an increasing number of peatlands will be restored in coming decades and it will be easier to compare the initiation of microtopography in restored and spontaneously revegetated peatlands within the same region.

Acknowledgements

References

Baird, A.J., Belyea, L. & Morris, P.J. 2009. Upscaling peatland-atmosphere fluxes of carbon gases: small-scale heterogeneity in process rates and the pitfalls of 'bucket-and-slab' models. In: Baird, A.J., Belyea, L.R., Comas, X., Reeve, A. & Slater, L. (eds.) *Carbon cycling in Northern Peatlands*. pp. 37–54. Geophysical Monograph Series, American Geophysical Union, Washington, DC, US.

Belyea, L.R. 1996. Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland. *Oikos* 77: 529–539.

Belyea, L.R. & Clymo, R.S. 2001. Feedback control of the rate of peat formation. *Proceedings of the Royal Society of London – Biology* 268: 1315–1321.

Belyea, L.R. & Malmer, N. 2004. Carbon sequestration in peatland: patterns and mechanisms of response to climate change. *Global Change Biology* 10: 1043–1052.

Benscoter, B.W., Vitt, D.H. & Wieder, K. 2005a. Association of postfire peat accumulation and microtopography in boreal bogs. *Canadian Journal of Forest Research* 35: 2188–2193.

Benscoter, B.W., Wieder, K. & Vitt, D.H. 2005b. Linking microtopography with post-fire succession in bogs. *Journal of Vegetation Science* 16: 453–460.

Campbell, D.R. & Rochefort, L. 2001. La vegetation: les gradients. In: Payette, S. & Rochefort, L. (eds.) *Écologie des tourbières du Québec-Labrador*. pp. 129–140. Les Presses de l'Université Laval, Québec, CA.

Campbell, D.R., Lavoie, C. & Rochefort, L. 2002. Wind erosion and surface stability in abandoned milled peatlands. *Canadian Journal of Soil Science* 82: 85–95.

Campeau, S. & Rochefort, L. 1996. *Sphagnum* regeneration on bare peat surfaces: field and greenhouse experiments. *Journal of Applied Ecology* 33: 599–608.

Clymo, R.S. 1963. Ion exchange in *Sphagnum* and its relation to bog ecology. *Annals of Botany* 27: 309–324.

Clymo, R.S. & Hayward, P.M. 1982. The ecology of *Sphagnum*. In: Smith, A.J.E. (ed.) *Bryophyte ecology*. pp. 229–289. Chapman & Hall, London, UK.

Damman, A.W.H. 1978. Distribution and movement of elements in ombrotrophic peat bogs. *Oikos* 30: 480–495.

Ehrenfeld, J.G. 1995. Microtopography and vegetation in Atlantic white cedar swamps: the effects of natural disturbances. *Canadian Journal of Botany* 73: 474–484.

EMHI. 2010. Available at: http://www.emhi.ee/?ide=7 (March 2010).

Environment Canada. 2010. Canadian Climate Normals or Averages 1971–2000. Available at: http://www.climat. meteo.gc.ca/climate_normals/index_e.html (May 2010).

Groeneveld, E.V.G. & Rochefort, L. 2005. *Polytrichum strictum* as a solution to frost heaving in disturbed ecosystems: a case study with milled peatlands. *Restoration Ecology* 13: 74–82.

Jeník, J. & Soukupová, L. 1992. Microtopography of subalpine mire in the Krkonose Mountains, the Sudetes. *Preslia* 64: 313–326.

Johnson, L.C. & Damman, A.W.H. 1993. Decay and its regulation in *Sphagnum* peatlands. *Advances in Bryology* 5: 249–296.

Karofeld, E. 1998. The dynamics of the formation and development of hollows in raised bogs in Estonia. *The Holocene* 8: 697–704.

Karofeld, E. 2004. Mud-bottom hollows: exceptional features in carbon-accumulating bogs? *The Holocene* 14: 119–124.

Karofeld, E. & Pajula, R. 2005. Distribution and development of necrotic *Sphagnum* patches in two Estonian raised bog. *Folia Geobotanica* 40: 357–366.

Karofeld, E. & Toom, M. 1999. Mud-bottoms in Männikjärve bog, central Estonia. *Proceedings of the Estonian Academy of Sciences, Biology and Ecology* 48: 216–235.

Kenkel, N.C. 1988. Spectral analysis of hummock-hollow pattern in a weakly minerotrophic mire. *Plant Ecology* 78: 45–52.

Kuhry, P. & Turunen, J. 2006. The postglacial development of boreal and subarctic peatlands. In: Wieder, R.K. & Vitt, D.H. (eds.) *Boreal peatland ecosystems.* pp. 25–46. Springer-Verlag, Berlin, DE.

Lesica, P. & Kannowski, P.B. 1998. Ants create hummocks and alter structure and vegetation of a Montana fen. *American Midland Naturalist* 139: 58–68.

Lucchese, M., Waddington, J.M., Poulin, M., Pouliot, R., Rochefort, L. & Strack, M. 2010. Organic matter accumulation in a restored peatland: evaluating restoration success. *Ecological Engineering* 36: 482–488.

Luken, J.O. & Billings, W.D. 1986. Hummock-dwelling ants and the cycling of microtopography in an Alaskan peatland. *Canadian Field Naturalist* 100: 69–73.

Magnan, G. 2009. *Fréquence passée des feux et successions végétales dans les tourbières ombrotrophes près de Radisson, Québec nordique.* MSc thesis, Département de géographie, Université Laval, Québec, Canada.

Malmer, N., Svensson, B.M. & Wallen, B. 1994. Interactions between *Sphagnum* mosses and field layer vascular plants in the development of peat-forming systems. *Folia Geobotanica* 29: 483–496.

Malmer, N., Albinsson, C., Svensson, B.M. & Wallen, B. 2003. Interferences between *Sphagnum* and vascular plants: effects on plant community structure and peat formation. *Oikos* 100: 469–482.

Mazerolle, M., Poulin, M., Lavoie, C., Rochefort, L., Desrochers, A. & Drolet, B. 2006. Animal and vegetation patterns in natural and man-made bog pools: implication for restoration. *Freshwater Biology* 51: 333–350.

Nungesser, M.K. 2003. Modelling microtopography in boreal peatlands: hummocks and hollows. *Ecological Modelling* 165: 175–207.

Ohlson, M., Økland, R.H, Nordbakken, J.-F. & Dahlberg, B. 2001. Fatal interactions between Scots pine and Sphagnum mosses in bog ecosystems. *Oikos* 94: 425–432.

Payette, S. 2001. La stratigraphie. In: Payette, S. & Rochefort, L. (eds.) *Écologie des tourbières du Québec-Labrador.* pp. 345–370. Les Presses de l'Université Laval, Québec, CA.

Payette, S. & Rochefort, L. 2001. *Écologie des tourbières du Québec-Labrador.* Les Presses de l'Université Laval, Québec, CA, 621 p.

Poulin, M., Rochefort, L., Quinty, F. & Lavoie, C. 2005. Spontaneous revegetation of mined peatlands in eastern Canada. *Canadian Journal of Botany* 83: 539–557.

Price, J.S. & Whitehead, G.S. 2001. Developing hydrological thresholds for *Sphagnum* recolonization on an abandoned cutover bog. *Wetlands* 21: 32–40.

Price, J.S., Heathwaite, A.L. & Baird, A.J. 2003. Hydrological processes in abandoned and restored peatlands: an overview of management approaches. *Wetlands Ecology and Management* 11: 65–83.

Rochefort, L. 2000. *Sphagnum* – a keystone in habitat restoration. *The Bryologist* 103: 503–508.

Rochefort, L. & Lode, E. 2006. Restoration of degraded boreal peatlands. In: Wieder, R.K. & Vitt, D.H. (eds.) *Boreal peatland ecosystems.* pp. 9–24. Springer-Verlag, Berlin, DE.

Rochefort, L., Quinty, F., Campeau, S., Johnson, K. & Malterer, T. 2003. North American approach to the restoration of *Sphagnum* dominated peatlands. *Wetlands Ecology and Management* 11: 3–20.

Rydin, H. 1985. Effect of water level on desiccation of *Sphagnum* in relation to surrounding Sphagna. *Oikos* 45: 374–379.

Rydin, H., Gunnarsson, U. & Sundberg, S. 2006. The role of *Sphagnum* in peatland development and persistence. In: Wieder, R.K. & Vitt, D.H. (eds.) *Boreal peatland ecosystems.* pp. 47–65. Springer-Verlag, Berlin, DE.

Salonen, V. & Setälä, H. 1992. Plant colonization of bare peat surface: relative importance of seed availability and soil. *Ecography* 15: 199–204.

Soro, A., Sundberg, S. & Rydin, H. 1999. Species diversity, niche metrics and species associations in haversted and undisturbed bogs. *Journal of Vegetation Science* 10: 549–560.

Sundberg, S., Hansson, J. & Rydin, R. 2006. Colonization of *Sphagnum* on land uplift islands in the Baltic Sea: time, area, distance and life history. *Journal of Biogeography* 33: 1479–1491.

Vitt, D.H. 1990. Growth and production dynamics of boreal mosses over climatic, chemical and topographic gradients. *Botanical Journal of the Linnean Society* 104: 35–59.

Walker, D. & Walker, P.M. 1961. Stratigraphic evidence of regeneration in some Irish bogs. *Journal of Ecology* 49: 169–185.

Weltzin, J.F., Harth, C., Bridgham, S.D., Pastor, J. & von der Harr, M. 2001. Production and microtopography of bog bryophytes: response to warming and water-table manipulations. *Oecologia* 128: 557–565.

Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Examples of the sampled microtopography in: (A) natural peatlands and (B) revegetated cutover peatlands.

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.