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Source: Ecoscience, 16(2):158-166. 2009.
Published By: Centre d'études nordiques, Université Laval
DOI: http://dx.doi.org/10.2980/16-2-3128
URL: http://www.bioone.org/doi/full/10.2980/16-2-3128

ÉCOSCIENCE

16 (2): 158-166 (2009)

Examining the peat-accumulating potential of fen vegetation in the context of fen restoration of harvested peatlands[1]

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Abstract: In order to focus efforts towards specific vegetation groups in fen restoration, knowledge of the peat-accumulating function of dominant fen species is critical. The decomposition rates of 3 species typical to undisturbed fens and 3 species that spontaneously colonize harvested fens were assessed. These species were incubated in both a restoration site (harvested fen) and an undisturbed fen to compare decomposition according to different environmental conditions. The average exponential decay coefficient (k) for all material types was slightly higher (*circa* $0.04 \cdot y^{-1}$ higher) in the harvested fen than those observed in the undisturbed fen. However, the litter type (leaves, roots/rhizomes, or bryophyte fragments) had the largest impact on the decomposition rates. The 2 tested bryophytes had lower k-values (between 0.14 and 0.11 for *Polytrichum strictum* and 0.06 for *Sphagnum centrale*) than the vascular plant litter (between 0.25 and 0.50). The annual primary production of the tested species was also measured to estimate the peat-accumulating capacity of each species. *Scirpus cyperinus* had an annual primary production that was 3 times higher (1500 $g \cdot m^{-2} \cdot y^{-1}$) than the other species (between 300 and 550 $g \cdot m^{-2} \cdot y^{-1}$). Estimates show that the harvested fen has a high peat-accumulating potential due to the high biomass production observed at this site.
Keywords: decomposition, fen, production, restoration, C storage.

Résumé : Afin de concentrer les efforts en restauration des tourbières minérotrophes sur des groupes spécifiques de végétaux, il est essentiel de connaître la fonction d'accumulation de la tourbe des espèces dominantes. Les taux de décomposition de 3 espèces typiques des tourbières minérotrophes naturelles et de 3 espèces colonisant spontanément les tourbières exploitées ont été évalués. Ces espèces ont été incubées dans un site en restauration (tourbière exploitée) et dans une tourbière minérotrophe naturelle pour comparer la décomposition dans différentes conditions environnementales. Le coefficient exponentiel moyen de décomposition (k) pour tous les types de matières était légèrement plus élevé (environ 0,04 de plus par an) dans la tourbière minérotrophe exploitée que ceux observés dans la tourbière naturelle. Cependant, c'est le type de litière (feuilles, racines/rhizomes ou fragments de bryophyte) qui avait le plus d'impact sur les taux de décomposition. Les 2 bryophytes testées avaient des valeurs de k inférieures (entre 0,14 et 0,11 pour *Polytrichum strictum* et 0,06 pour *Sphagnum centrale*) à celles de la litière de plantes vasculaires (entre 0,25 à 0,50). La production primaire annuelle des espèces testées a été aussi mesurée pour évaluer la capacité d'accumulation de la tourbe de chaque espèce. *Scirpus cyperinus* avait une production primaire annuelle trois fois plus élevée (1500 $g \cdot m^{-2} \cdot an^{-1}$) que les autres espèces (entre 300 et 550 $g \cdot m^{-2} \cdot an^{-1}$). Les estimations montrent que la tourbière minérotrophe exploitée a un fort potentiel d'accumulation de la tourbe en raison de la production élevée de biomasse observée pour ce site.
Mots-clés : décomposition, entreposage de C, production, restauration, tourbière minérotrophe.

Nomenclature: Scoggan, 1978; Anderson, 1990; Anderson, Crum & Buck, 1990.

Introduction

Understanding the link between an ecosystem's structure and function is crucial for setting restoration targets and strategies (Naeem, 2006). Return of the peat-accumulating function is an important long-term goal in peatland restoration (Rochefort, 2000). It is known that species play a major role in the ability of an ecosystem to accumulate peat (Johnson & Damman, 1993); however, there is little consensus on which species are most important to peat accumulation in fens. Roth (1999) focused restoration efforts on reeds and sedges because he felt they were important peat-accumulating species. Chimner, Cooper, and Patron (2002) found 50% of fen peat to consist of structural root material when peat accumulation in fens was simulated. Vitt (2000), on the other hand, found that vascular plant–dominated layers produce less biomass and decompose more readily than the bryophyte-dominated ground layer in fens. Currently, most fen restoration projects focus on restoring vascular plant vegetation (Wheeler & Shaw, 1995; Cooper & MacDonald, 2000; Kratz & Pfadenhauer, 2001; Lamers, Smolders & Roelofs, 2002).

Historical data do not provide a clear picture of which vegetation groups are mainly responsible for peat accumulation in fens. Paleoecological studies of peatlands in North America show a wide range of plant composition in fen peat. Vitt (2000) examined 341 peatland cores across North America and found that the major component of fen peat was bryophytic: *Sphagnum* in poor fens and brown mosses in rich

[1]Rec. 2007-08-14; acc. 2009-02-29.
Associate Editor: Tim Moore.
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DOI 10.2980/16-2-3128

fens. However, Kubiw, Hickman, and Vitt (1989), Nicholson and Vitt (1990), and Lavoie and Richard (2000a,b) all found vascular plants and bryophytes to be equally important components of fen peat, while Griffin (1977), Warner, Tolonen, and Tolonen (1991), and Hu and Davis (1995) found fen peat to be dominated by vascular plants. Macrofossil studies do not give us a clear indication of which vegetation group is most efficient in accumulating peat.

The use of historical data to determine restoration goals is often limited because present environmental conditions may differ greatly from those prevalent during the formation of the system. In the case of harvested peatlands, the hydrology of the restoration sites differs substantially from the hydrology of natural peatlands. Abandoned peatlands are characterized by a water table that fluctuates greatly (Price, Heathwaite & Baird, 2003), while natural fens are characterized by relatively constant water tables (Bedford & Godwin, 2003). The extent to which an altered hydrology will affect the decomposition rates and thereby the peat-accumulation rates of plants is unknown.

The vegetation of the restoration sites also differs from the vegetation common to undisturbed fens. Harvested fens that are no longer being actively drained are quickly recolonized by spontaneous vegetation (Famous, Spencer & Nilsson, 1991). This spontaneous vegetation can be characterized as wetland species, dominated by *Scirpus cyperinus*, *Juncus* sp., and other forbs (Graf, Rochefort & Poulin, 2008). In contrast, undisturbed fens with chemical properties similar to the harvested fens are dominated by *Carex* and *Sphagnum* species (Graf, Rochefort & Poulin, 2008). Although the community structure and species of the harvested fens are different from those of undisturbed fens, it is not known whether this dissimilarity translates to differences in the peat-accumulating potential of the sites.

The goal of this study was to identify which vegetation groups are important in returning the peat-accumulating function of a fen. Specifically, we wanted to know 1) if spontaneously colonizing plants are as efficient in accumulating peat as typical fen species and 2) whether decomposition rates vary greatly between undisturbed and harvested fens.

Methods

Study species

Decomposition rates and annual production were measured for 6 species: 4 vascular plant species and 2 bryophytes. *Scirpus cyperinus*, *Juncus brevicaudatus*, and *Polytrichum strictum* are species that frequently colonize harvested fens (Graf, Rochefort & Poulin, 2008). *Carex rostrata*, *Calamagrostis canadensis*, and *Sphagnum centrale* represent genera commonly found in undisturbed moderate-rich fens of the boreal zone of North America (Vitt & Chee, 1990; Graf, Rochefort & Poulin, 2008). In total, the decomposition rates of 10 litter types were measured: leaves of the 4 vascular species, rhizomes and roots of the same species, and fragments of 2 bryophyte species.

Study area and site descriptions

The decomposition rates of the above-mentioned species were measured in an abandoned harvested peatland and an undisturbed fen. The harvested fen (47° 45' N, 69° 30' W) was located *circa* 15 km southeast of Rivière-du-Loup, Quebec, Canada. This fen site was part of a large complex of bogs interspersed with *Alnus* swamps (Gauthier & Grandtner, 1975) and can be classified as a low boreal peatland (National Wetlands Working Group, 1988). The particular experimental sector, originally a bog, was mined down to its minerotrophic peat layer. Hereafter, it will be referred to as the harvested fen. Harvesting of the fen was abandoned 8 y prior to the start of the experiment, and spontaneous recolonization had begun (46% total vegetation cover). The vegetation was dominated by *Equisetum arvense*, *Scirpus cyperinus*, *Juncus brevicaudatus*, and *Spirea latifolia* (Graf, 2008). The pH of the harvested fen was 4.97 (± 0.07), and its electrical conductivity was 23.9 $\mu S \cdot cm^{-1}$ (± 2.5) (Graf, 2008), indicating that this site was a poor fen (Vitt & Chee, 1990). The harvested fen was drier than the undisturbed fen: the average water table level measured during the summer of 2005 was –19.8 cm (± 6.40) (Graf, 2008). These environmental parameters are typical of cutaway peatlands in North America (Graf, Rochefort & Poulin, 2008).

The undisturbed fen (47° 46' N, 52° 50' W) was located *circa* 25 km southwest of the harvested fen. This site was chosen because its environmental parameters were similar to those of the harvested fen: pH was 4.97 (± 0.24), electrical conductivity was 30.9 $\mu S \cdot cm^{-1}$ (± 7.9). This site was a poor fen (Vitt & Chee, 1990) and was dominated by *Sphagnum centrale*, *Calamagrostis canadensis*, *Salix discolor*, *Carex brunnescens*, and *Glyceria canadensis*. The undisturbed fen had a higher water table (–3.5 cm ± 3.2) (Cobbaert, Rochefort & Price, 2004).

The regional climate is characterized by cold winters and warm summers, with January and July mean temperatures of –13 and 18 °C, respectively. Mean annual precipitation is 963 mm, of which 72% falls as rain (Environment Canada, 2007).

Decomposition

Senesced leaf litter (yellow in colour), belowground biomass of the tested vascular species, and fragments of the tested bryophytes were collected in early September of 2004. The roots and rhizomes of the vascular plants were extracted by cutting peat cores in a 10-cm diameter around individual plants. The roots and rhizomes were rinsed clean of any remaining peat debris. The root material used for this study was randomly selected from all roots (and rhizomes for *Carex* and *Scirpus*) with a diameter of *circa* 3 mm. The fragments of the 2 bryophyte species included the stems, branches, and leaves of live, healthy specimens; the capitula of the *Sphagnum* species were removed.

The plant material was oven-dried at 40 °C until constant mass, and 1 to 2 g (0.5 g for *Sphagnum* species) of plant material was placed in individual mesh bags (5 × 7.5 cm). The litter was placed in pre-weighed fibreglass mesh bags with 1-mm mesh gauge. Litter that was at risk of falling through the mesh at this gauge (*Sphagnum, Polytrichum*, and *Juncus* leaves) was placed in pre-weighed nylon mesh bags with a 0.25-mm mesh gauge. Each filled bag was weighed to the closest 0.001 g.

Within each incubation site (undisturbed and harvested) 3 transects of 10 m located within 30 m of each other were randomly chosen. Six bags were attached to bamboo rods placed 1 m apart along the transects, for a total of 10 rods per transect. The 10 litter types were replicated 6 times per transect, totalling 60 bags per transect. On each site 180 bags and overall 360 bags were deployed. The bags were inserted vertically at a depth of *circa* 5 cm below the surface in mid September 2004. All bags were removed after 2 y of exposure in mid September 2006. In the laboratory, excess peat and debris were cleaned from the bags by rinsing them in a water bath. Growing roots and other vegetation that had penetrated the bags during the 2 y of incubation were carefully removed with forceps. The bags were dried at 40 °C until a constant mass was reached. Each bag was again weighed to the closest 0.001 g.

The linear decay rate (k') over 2 growing seasons was computed for each litter material using the following equation (Reader & Stewart, 1972):

$$k' = [(X_0 - X)/X_0] \times 100 \qquad [1]$$

where X_0 represents the initial dry litter mass (g) before decomposition and X is the final dry litter mass (g) after incubation in the field. The exponential decay coefficient (k) was also computed for each litter material using the following equation (Brinson, Lugo & Brown, 1981):

$$k = \ln (X_0/X)/t \qquad [2]$$

where X_0 and X are the same as described above and t is time in years. The total site decay coefficient was calculated as in Thormann, Szumigalski, and Bayley (1999), where the sum of the total mass loss ($g \cdot m^{-2} \cdot y^{-1}$) was divided by the sum of the litter production of the measured litter material ($g \cdot m^{-2} \cdot y^{-1}$).

Production

Bryophytes

Moss annual primary production (MAPP; in $g \cdot m^{-2}$) was estimated using the following equation (Vitt & Pakarinen, 1977):

$$MAPP = [W * G] / [SS * H] \qquad [3]$$

where W is the bryophyte dry biomass (g), G is the mean annual increment (m), SS is the sample surface (m^2), and H is the mean living bryophyte height (m). The mean annual increment (G) of *Sphagnum centrale,* growing in the undisturbed fen, was measured using the Velcro technique (Glime, 1984). Thirty Velcro strips were placed just below the capitulum along a topographical (hummock–hollow) gradient within a 5-m^2 area in May of 2005. In October of the same year 24 of the 30 Velcro strips were found, and the growth from the Velcro strip to the capitulum was measured to the closest mm. The mean annual increment (G) of *Polytrichum strictum* growing in the harvested fen was measured using its innate marker, the natural growth pattern of this species allows to distinguish the growth from the previous growing season from that of the current one (Vitt & Pakarinen, 1977). The innate markers of 20 stems within a colony of 5 m^2 were measured to the closest mm. For both bryophyte species, the sample surface (SS) was a 50.24 cm^2 core, removed using an aluminium cylinder with sharp cutting edges. Ten cores were randomly sampled from the colonies (an area of *circa* 5 m^2) of each bryophyte species. Only the green, photosynthetically active portions of the bryophytes were used to calculate the bryophyte layer height (H); 3 lengths per core were measured. To calculate the bryophyte dry biomass (W) the photosynthetically active bryophyte fragments of each core were dried at 40 °C until a constant mass was achieved and then weighed to 0.001 g.

Vascular plants

Annual aboveground biomass production was measured in late August of 2005. Ten quadrats of 50 × 50 cm were chosen randomly in colonies (approximate areas of 15 m^2) of the 4 tested vascular species, and all biomass within each quadrat was clipped. Any dead leaves or leaves from other species were removed, and the biomass was dried at 40 °C until the mass was constant. The material collected from each quadrat was weighed to the closest 0.001 g.

Production of root biomass was measured over 2 growing seasons using an ingrowth bag method (Steen, 1991; Finér & Laine, 2000). The ingrowth bags were mesh bags (mesh size 7 mm) with a diameter of 7 cm and a length of 50 cm. Each bag was filled with fen peat from the harvested fen where no vegetation was growing. A wood cylinder was used to compact the peat in the bags so that it approximated the density of the peat in field conditions. Transects of 5 m were set up in communities of the tested vascular plants, and a hand-held auger was used to drill holes of the same diameter as the ingrowth bag every metre along the transects. In May 2005 five bags were deployed for each species, for a total of 20 bags. We were able to find monocultures (no other species within a 2-m radius of transect) for the *Scirpus cyperinus* and *Calamagrostis canadensis.* Transects for *Juncus brevicaudatus* and *Carex rostrata* contained some individuals of other plants, although the target species were still dominant (> 80% of vegetation cover).

After 2 growing seasons (in mid September 2006) the ingrowth bags were removed. Before removal the roots around the bags were cut to a depth of 20 cm. Within 48 h of removal, the bags were placed in a freezer until they could be further processed. Peat was washed away from the root material using a series of sieves (2-mm and 0.5-mm meshes). Forceps were used to remove the roots from the peat and debris that collected in the 0.5-mm sieve. The root biomass from each ingrowth bag was dried at 40 °C until the mass was constant and then weighed to the closest 0.001 g. The masses measured for each vegetation type were extrapolated to primary production measures of biomass ($g \cdot m^{-2} \cdot y^{-1}$).

The peat of the ingrowth bags, the harvested fen, and the undisturbed fen were compared with chemical analyses and bulk density measurements. One peat sample was taken from the middle of each transect and from the peat used to fill the ingrowth bags. The samples were taken from the surface (top 5 cm) after the biological crust (top 1 cm) had been removed. Only one peat sample was taken for the *Juncus brevicaudatus* and *Scirpus cyperinus* communities because these communities were in close proximity (10 m apart). After loss on ignition, the peat ash was analyzed for Ca, Mg, Fe, Cu, Zn, Mn, and K concentrations using an atomic absorption method (ISO number PHL-LA-WI-030 and 031). Total N content was determined after mineralization through acidic digestion following the Kjeldhal method (ISO number PHL-LA-WI-022). Total P was determined after mineralization (ISO number PHL-LA-WI-033).

After 2 growing seasons, the bulk density of the surface (top 5 cm) was measured twice for each transect at random locations along the transect and twice for the ingrowth bags of each transect. Bulk density was calculated by dividing the oven-dry mass by its known volume of peat (Hillel, 1998).

Peat accumulation potentials

Two types of peat accumulation potential were calculated. First, the production to decomposition quotients for each site were determined by dividing total annual plant production ($g \cdot m^{-2} \cdot y^{-1}$) by the total amount lost ($g \cdot m^{-2} \cdot y^{-1}$) as estimated by the linear decay coefficient (k') (Thormann, Szumigalski & Bayley, 1999). Secondly, the asymptotic limit of peat accumulation ($g \cdot m^{-2}$) was calculated using Clymo's acrotelm model (1984), where plant production (ρ_a) is divided by the exponential decay coefficient of litter (α_a).

Statistical analyses

ANOVA and LSD (least squared difference) procedures of SAS (SAS Statistical System software, v. 9.1, SAS Institute Inc., Cary, North Carolina, USA) were used to test the differences in exponential decay coefficients (dependent variable) for each litter type (independent variable). Decomposition rates could not be compared between sites because the main effect (the sites) was not replicated. Therefore, the litter types were analyzed separately for each site.

Results

Peat properties

The chemical properties of the peat for the ingrowth bags were comparable to those of the peat from the incubation sites. However, the peat from the undisturbed fen was slightly richer in some nutrients and base cations (Table I). The bulk density of the ingrowth bags was slightly higher than that of the surrounding areas for all colonies except *Scirpus cyperinus* (Table I).

Exponential decay coefficients

The averaged 2-y exponential decay coefficient (k) for all litter on the undisturbed fen (0.26) was slightly lower than that observed on the harvested fen (0.30). When the individual litter types were compared, similar k-value patterns were observed at both sites (Figure 1). The bryophyte species had significantly lower k-values than the vascular plants at both sites (Figure 1). Of the 2 bryophyte species, *Sphagnum centrale* had a lower k-value than *Polytrichum strictum* on the harvested fen. Among the vascular plants, the k-values observed for *Carex rostrata* and *Calamagrostis canadensis* leaves were higher than those of other litter types on the harvested fen (Figure 1). The k-values of all root litters and the leaves of *Scirpus cyperinus* that decomposed in the harvested fen did not vary among one another, but they were significantly lower than those of the leaves of *C. rostrata*, *C. canadensis*, and *Juncus brevicaudatus* (Figure 1). The differences between the k-values of material that was incubated in the undisturbed fen were less distinct but followed the same general pattern as the harvested fen (Figure 1).

TABLE I. Nutrient concentrations (total elements) and bulk density of the top 5 cm of the peat surface of the study sites and of the peat used for the ingrowth bags.

		Harvested Fen	Undisturbed Fen	
	Ingrowth Bags	*Juncus brevicaudatus/ Scirpus cyperinus*	*Carex rostrata*	*Calamagrostis canadensis*
N ($mg \cdot g^{-1}$)	2.3	2.9	3.5	2.0
P ($mg \cdot g^{-1}$)	0.2	0.7	0.7	0.4
K ($mg \cdot g^{-1}$)	0.4	0.6	1.6	14.1
Ca ($mg \cdot g^{-1}$)	3.9	6.1	12.8	14.1
Mg ($\mu g \cdot g^{-1}$)	0.9	0.9	1.6	2.5
Mn ($\mu g \cdot g^{-1}$)	32.7	37.7	121.6	42.3
Fe ($\mu g \cdot g^{-1}$)	1613.9	1983.6	5176.0	8687.2
Cu ($\mu g \cdot g^{-1}$)	5.8	29.3	56.0	28.7
Zn ($\mu g \cdot g^{-1}$)	6.5	22.8	26.5	13.9
Bulk density ($g \cdot cm^{-3}$) (± SD)	0.19 (± 0.03)	0.14 (± 0.01) (*Juncus*) 0.20 (± 0.04) (*Scirpus*)	0.10 (± 0.01)	0.12 (± 0.01)

TABLE II. The linear decay coefficients (k'), mean above- and belowground plant production (from August 2005), mass loss after 2 y and the total biomass remaining (the sum of above and belowground for each species is shown). The totals of the above-described measurements are shown for each site.

Site species	Linear co-efficient (k')	NPP ($g \cdot m^{-2} \cdot y^{-1}$) (± SD)	Mass loss after 2 y ($g \cdot m^{-2} \cdot y^{-1}$)	Total NPP remaining after 2 y ($g \cdot m^{-2} \cdot y^{-1}$)
Harvested fen				
Polytrichum strictum	0.25	311 (± 195)	78	233
Scirpus cyperinus aerial	0.41	1484 (± 717)	608	943
S. cyperinus roots	0.45	121 (± 53)	54	
Juncus brevicaudatus aerial	0.54	380 (± 97)	205	211
J. brevicaudatus roots	0.42	62 (± 12)	26	
Total	0.30	3258	972	1387
Undisturbed fen				
Sphagnum centrale	0.11	554 (± 239)	61	493
Calamagrostis canadensis aerial	0.49	358 (± 95)	175	256
C. canadensis roots	0.48	141 (± 32)	68	
Carex rostrata aerial	0.56	290 (± 54)	162	235
C. rostrata roots	0.40	178 (± 35)	71	
Total	0.35	1521	538	984

Production

The aboveground biomass production of *Scirpus cyperinus* that grew in the harvested fen was *circa* 3 times higher than the production of the other species (Table II). *Sphagnum centrale* produced the second highest annual biomass. All other plants had similar lower annual aboveground primary production rates. In both the undisturbed and harvested fens, belowground annual primary production was substantially lower than the aboveground production of the vascular plants (Table II).

Peat accumulation potentials

Estimates of accumulation potentials (Figure 2) indicate that the harvested fen has a larger peat-accumulating

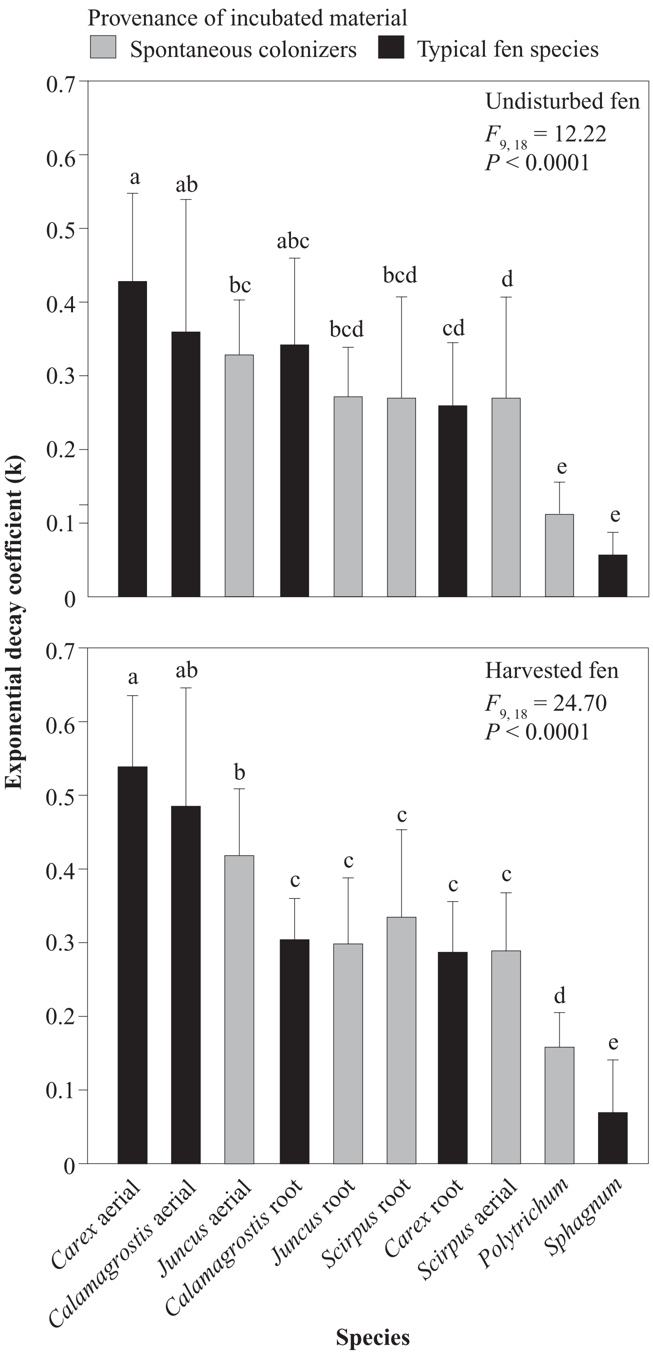

FIGURE 1. The exponential decay values (mean + SD) are shown for the 10 litter types (n = 18) that were incubated in an undisturbed and a harvested fen. For the vascular plants, leaves and roots/rhizomes were incubated separately. Spontaneous colonizing plants are those that frequently colonize harvested fens, while typical fen species correspond to vegetation groups that are common to poor and moderate-rich fens of North America. The lower case letters indicate significant differences (α = 0.05) between litter types.

potential. Both sites had a large ρ_a/α_a; larger for the harvested site (7860 g·m^{-2}) than for the undisturbed site (5850 g·m^{-2}; Figure 2). The production to decomposition quotient differed slightly between the harvested fen (2.4) and the undisturbed fen (2.8; Figure 2). The total NPP remaining after 2 y was larger in the harvested fen than

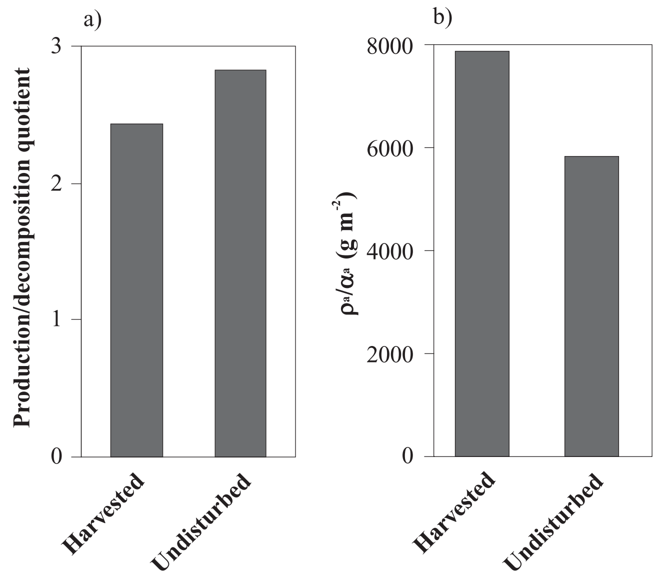

FIGURE 2. Two measures of peat accumulation potentials for an undisturbed and a harvested fen. The production/decomposition quotient (left) is the ratio of production (g·m^{-2}·y^{-1}) to 2-y mass loss (g·m^{-2}·y^{-1}) shown in Table II. The graph to the right shows the asymptotic limit of peat accumulation (Clymo, 1984), where ρ_a is the total plant production (g·m^{-2}·y^{-1}) and α_a is the exponential decay rate of litter.

in the undisturbed fen (Table II). *Scirpus cyperinus* had a remaining NPP that was 3 times larger than that of most species (Table II). The NPP of *Sphagnum centrale* was double that of other tested species (excluding *S. cyperinus*).

Discussion

The aim of this study was to identify the vegetation groups that are important in restoring the peat-accumulating function of fens. Specifically, whether 1) spontaneously colonizing plants are as efficient in accumulating peat as typical fen species and 2) whether decomposition rates vary greatly between undisturbed and harvested fens. Our study shows that the harvested fen had a higher peat-accumulating potential than the undisturbed fen, mainly due to the high aerial biomass production of *Scirpus cyperinus*. The exponential decay coefficients (k) were lowest for the 2 bryophyte species and highest for the leaves of the vascular species.

The k-values varied only slightly between undisturbed and harvested fens despite very different hydrological conditions. The litter bags were placed 5 cm under the surface, meaning they were subjected to near-constant saturation in the undisturbed fen and were seldom saturated in the harvested fen. This shows that litter type influences decomposition more than habitat (undisturbed *versus* harvested), as was also observed by Richert *et al*. (2000).

DECOMPOSITION

ABOVEGROUND

The exponential decay coefficients (k) of the bryophytes over 2 y were substantially lower than the k-values of aboveground and belowground litter of the vascular plants. The k-values of *Sphagnum centrale* did not differ between sites (Figure 1). This lack of variation shows that the intrinsic litter quality of *Sphagnum* is more important in regulating decomposition than habitat factors, as has been shown in numerous other studies (Clymo, 1965; Johnson & Damman, 1991; Johnson, 1992).

Polytrichum strictum also had k-values that were considerably lower than those of the vascular litter material. It is difficult to compare these values with values of other true mosses found in fens because most studies on decomposition in fens do not include true mosses (Brinson, Lugo & Brown, 1981; Moore, 1989; Thormann & Bayley, 1997). Li and Vitt (1997) compared *Sphagnum* decomposition to brown moss decomposition in hummocks and found that *Sphagnum* decomposition rates were 11% lower, similar to the difference in *Polytrichum* and *Sphagnum* observed in this study. Nevertheless, fens dominated by non-sphagnous mosses accumulate peat as proficiently as *Sphagnum* bogs (Vitt, 2000).

Among the litter types of vascular plants, the leaves of the vascular species (except *Scirpus cyperinus*) had the highest k-values. The k-values observed for the *Carex* (0.43–0.50) and *Juncus* (0.33–0.39) species in this study correspond with k-values of the same genus from other studies on northern peatlands (0.37–0.70 for *Carex* and 0.32–0.37 for *Juncus*) (Brinson, Lugo & Brown, 1981; Szumigalski & Bayley, 1996; Aerts & Caluwe, 1997; Richert *et al*., 2000; Moore, Bubier & Bledzki, 2007). *Scirpus cyperinus* leaves had a significantly lower k-value than the leaves of the other vascular plant species. Similarly, in created wetlands *S. cyperinus* was mainly responsible for litter accumulation due to low k-values (Atkinson & Cairns, 2001).

The different mesh size of the decomposition bags used for this study likely influenced the decomposition rates of the litter material because vegetation decomposes more slowly in decomposition bags with smaller mesh sizes (Brinson, Lugo & Brown, 1981; Johnson & Damman, 1993). However, if the mesh size had had a large impact on the mass losses, then *Juncus brevicaudatus*, *Polytrichum strictum*, and *Sphagnum centrale* all should have had much lower mass losses than the other litter types. Actually, *Juncus brevicaudatus* leaves had k-values similar to those of the other leaves of vascular plants despite the smaller mesh size used for this litter type. The k-values of vascular plant leaves and *Sphagnum centrale* observed in this experiment are also largely in agreement with those observed in other experiments (Brinson, Lugo & Brown, 1981; Johnson & Damman, 1993). Therefore, we do not believe that the mesh size greatly altered our results.

Belowground

This study is one of the few to measure belowground decomposition and production in fens, which is strange given the reported importance of belowground biomass to fen systems (Hartman, 1999; Thormann, Bayley & Currah, 2001). Thormann, Bayley, and Currah (2001) included only rhizomes in their tested belowground biomass and found that mass loss was rather high (75%). We included both roots and rhizomes in the *Carex* and *Scirpus* belowground litter to approximate all belowground decomposition and found decomposition rates that were much closer to those observed in other fens (Hartmann, 1999; Moore, Bubier & Bledzki, 2007). Scheffer and Aerts (2000) found that roots of fen plants have lower decomposition rates than either rhizomes or leaves. Indeed, fine roots have been shown to play an important role in carbon accumulation (Minkkinen & Laine, 1998; Scheffer & Aerts, 2000; Chimner, Cooper & Patron, 2002), as they contribute to up to 90% of the belowground biomass of *Carex* species in temperate latitudes (Saarinen, 1996).

Primary production

Aboveground

The annual primary production of *Scirpus cyperinus* (approx. 1500 $g \cdot m^{-2} \cdot y^{-1}$) in the harvested fen was 30 times the primary production value of an undisturbed fen in Alberta (*circa* 53 $g \cdot m^{-2} \cdot y^{-1}$; Szumigalski, 1995). The large standard deviation was due to the fact that the harvested fen was an early successional site and biomass production was not homogeneous, varying between bare peat and large *S. cyperinus* tussocks. Similarly, the primary production of *Juncus* observed in this study was also 30 times the value observed in an undisturbed fen (*circa* 1.9 $g \cdot m^{-2} \cdot y^{-1}$; Szumigalski, 1995). It is likely that the altered hydrology of the harvested fen as well as the lack of competition with other species allowed for higher growth rates and a higher density and abundance of this plant. The extent to which the high primary production of *S. cyperinus* will lead to high peat accumulation remains a question.

Belowground

Belowground primary production has rarely been measured in continental Canada, probably because belowground production is more difficult to measure than aboveground production (Campbell *et al*., 2000). The only study that did measure belowground primary production found great variation in the percentage of net primary production that was accounted for by belowground plant material (28% to 80% of primary production) (Reader & Stewart, 1972). Drawing on the work of Reader and Stewart (1972), recent studies have assumed belowground primary production to be 50% of the aboveground primary production of continental bogs and fens in North America (Campbell *et al*., 2000; Thormann, Bayley & Currah, 2001). In our study belowground primary production was less than 50% of net primary production. The belowground NPP estimates of *Scirpus cyperinus*, *Juncus brevicaudatus*, *Carex rostrata*, and *Calamagrostis canadensis* species from both undisturbed and harvested fens were 8%, 14%, 38%, and 28% of NPP, respectively.

The difference between the percentage of net primary production attributable to belowground primary production in our study and that of Reader and Stewart (1972) may be due to differing methodologies. Reader and Stewart (1972) excavated 25- × 25- × 25-cm blocks of peat and removed and weighed all living roots. It is difficult to understand how Reader and Stewart (1972) could determine annual belowground primary production from this data. We believe our estimates to be closer to the true annual belowground primary production because our methodology allowed us to estimate root growth over a specific period of time.

A disadvantage of the ingrowth bag method is that the peat in the bags differs slightly from the peat at the sites. In our study the bulk density of the peat from the ingrowth bags was slightly greater than that of the peat from the *Juncus brevicaudatus, Carex rostrata*, and *Calamagrostis canadensis* communities (Table I). Additionally, the chemistry of the peat from the ingrowth bags differed slightly from that of the peat found in the incubation sites. This certainly affected to some extent the root growth in the bags. More studies that measure belowground NPP in peatlands using modern methodologies, such as root ingrowth bags or isotope labelling (Wallén, 1992), would be of great assistance in estimating peat accumulation in North American peatlands, as roots are thought to play an important role in the peat accumulation of fens (Chimner, Cooper & Patron, 2002).

Peat accumulation potentials

The harvested fen had a higher peat-accumulating potential than the undisturbed fen in our study. However, the findings of this study are limited due to its short duration. The ρ_a/α_a values we found should not be considered as an absolute asymptotic limit but rather a relative measure of peat accumulation potential. Harvested fens are early successional environments where sparse competition allows for extremely high NPP in a few species. As time goes on, these production rates will surely approach those found in undisturbed fens. A long-term study of the decomposition and production of harvested and undisturbed fens would provide a more reliable estimate of the long-term peat accumulating potentials of these sites.

Conclusion

This study showed that a harvested fen with spontaneously colonizing vegetation had a much higher production rate than an undisturbed fen. The decomposition rate of the undisturbed fen was slightly lower than that of the harvested fen. Finally, the peat-accumulating potential of the harvested fen was higher than the undisturbed fen, due mainly to the high aerial NPP of vascular plants. Will this high rate of production truly create more peat in the long run? Several studies have shown that decomposition rates, not production rates, are largely responsible for peat accumulation (Clymo, 1965; Vitt, 1990).

This study also showed that *Scirpus cyperinus*, a plant that dominates harvested fens in North America (Graf, Rochefort & Poulin, 2008), should be considered to be functionally similar, perhaps even superior, to *Carex* species in peat-accumulating capacity. The NPP of *S. cyperinus* was much higher than that of other vascular plants, and its decomposition rate was slightly lower. Additionally, because of its tussock form, *S. cyperinus* should be able to create the same structure found in undisturbed fens. Tussocks have been shown to be crucial in creating and maintaining species richness in sedge meadows (Peach & Zedler, 2006).

Acknowledgements

We thank the Canadian Peat Moss Association, ASB Greenworld Ltd., Cie de Tourbe Fafard ltée, Fafard et frères ltée., La Mousse acadienne (1979) ltée., Les Tourbes Nirom Peat Moss inc., Les Tourbières Berger inc., Modugno-Hortibec, Premier Horticulture ltée., Sun Gro Horticulture inc., Tourbières Lambert inc., and the Ministry of Natural Resources of New Brunswick for financially supporting this project within an industrial research chair program of the Natural Sciences and Engineering Research Council granted to L. Rochefort. We greatly appreciate the advice of R. Pouliot and C. St-Arnaud on the methodology of this project. The field assistance of M. Bellemare, J. Bussières, G. Clément-Mathieu, T. Graf, G. Lambert, and F. Pelloté is greatly appreciated.

Literature cited

Aerts, R. & J. Caluwe, 1997. Nutritional and plant-mediated controls on leaf detritus decomposition of *Carex* species. Ecology, 78: 244–260.

Anderson, L. E., 1990. A checklist of *Sphagnum* in North America north of Mexico. Bryologist, 93: 500–501.

Anderson, L. E., H. A. Crum & W. R. Buck, 1990. List of the mosses of North America north of Mexico. Bryologist, 93: 448–499.

Atkinson, R. B. & J. Cairns Jr., 2001. Plant decomposition and litter accumulation in depressional wetlands: Functional performance of two wetland age classes that were created via excavation. Wetlands, 21: 354–362.

Bedford, B. L. & K. S. Godwin, 2003. Fens of the United States: Distribution, characteristics and scientific connection versus legal isolation. Wetlands, 23: 608–629.

Brinson, M. M., A. E. Lugo & S. Brown, 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. Annual Review of Ecology and Systematics, 12: 123–161.

Campbell, C., D. H. Vitt, L. A. Halsey, I. D. Campbell, M. N. Thormann & S. E. Bayley, 2000. Net Primary Production and Standing Biomass in Northern Continental Wetlands. Information report No. NOR-X-369. Northern Forestry Centre, Edmonton, Alberta.

Chimner, R. A., D. J. Cooper & W. J. Patron, 2002. Modeling carbon accumulation in Rocky Mountain fens. Wetlands, 22: 100–110.

Clymo, R. S., 1965. Experiments on the breakdown of *Sphagnum* in two bogs. Journal of Ecology, 53: 747–757.

Clymo R. S., 1984. The limits to peat bog growth. Philosophical Transactions of the Royal Society of London Biological Sciences, 303: 605–654.

Cobbaert, D., L. Rochefort & J. Price, 2004. Experimental restoration of a fen plant community after peat mining. Applied Vegetation Science, 7: 209–220.

Cooper, D. & L. MacDonald, 2000. Restoring the vegetation of mined peatlands in the Southern Rocky Mountains of Colorado, USA. Restoration Ecology, 8: 103–111.

Environment Canada, 2007. Normales climatiques au Canada (1971–2000), station St-Arsène, Québec. [Online] URL: http://www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html Accessed 27 February 2007.

Famous, N. C., M. Spencer & H. Nilsson, 1991. Revegetation patterns in harvested peatlands in central and eastern North America. Pages 48–66 *in* D. N. Grubich & T. J. Malterer (eds.). Peat and Peatlands: The Resource and Its Utilization. Proceedings of the International Peat Symposium. Duluth, Minnesota.

Finér, L. & J. Laine, 2000. The ingrowth bag method in measuring root production on peatland sites. Scandinavian Journal of Forest Research, 15: 75–80.

Gauthier, R. & M. M. Grandtner, 1975. Étude phytosociologique des tourbières du bas Saint-Laurent, Québec. Naturaliste Canadien, 102: 109–153.

Glime, J. M., 1984. Physio-ecological factors relating to reproduction and phenology in *Fontinalis dalecarlica.* Bryologist, 87: 17–23.

Graf, M. D., 2008. Restoring Fen Plant Communities on Cutaway Peatlands of North America. Ph.D. thesis. Université Laval, Québec, Québec.

Graf, M. D., L. Rochefort & M. Poulin, 2008. Spontaneous revegetation of cutaway peatlands of North America. Wetlands, 28: 28–39.

Griffin, K. O., 1977. Paleoecological aspects of the Red Lake peatland, northern Minnesota. Canadian Journal of Botany, 55: 172–192.

Hartmann, M., 1999. Species dependent root decomposition in rewetted fen soils. Plant and Soil, 213: 93–98.

Hillel, D., 1998. Environmental Soil Physics. Academic Press, San Diego, California.

Hu, F. S. & R. B. Davis, 1995. Postglacial development of a Maine bog and paleoenvironmental implications. Canadian Journal of Botany, 73: 638–649.

Johnson, L. C., 1992. Species-Regulated *Sphagnum* Decay in Raised Peat Bogs. Ph.D. thesis. University of Connecticut, Storrs, Connecticut.

Johnson, L. C. & A. W. H. Damman, 1991. Species-controlled *Sphagnum* decay on a south Swedish raised bog. Oikos, 61: 234–242.

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

Kubiw, H., M. Hickman & D. H. Vitt, 1998. The developmental history of peatlands of Muskiki and Marguerite lakes, Alberta. Canadian Journal of Botany, 67: 3534–3544.

Kratz, R. & J. Pfadenhauer (eds.), 2001. Ökosystemmanagement für Niedermoore: Strategien und Verfahren zur Renaturierung. Ulmer Verlag, Stuttgart.

Lamers, L. P. M., A. J. P. Smolders & J. G. M. Roelofs, 2002. The restoration of fens in the Netherlands. Hydrobiologia, 478: 107–130.

Lavoie, M. & P. J. H. Richard, 2000a. The role of climate on the developmental history of Frontenac Peatland, southern Quebec. Canadian Journal of Botany, 78: 668–684.

Lavoie, M. & P. J. H. Richard, 2000b. Paléoécologie de la tourbière du Lac Malbaie, dans le Massif des Laurentides (Québec) : évaluation du rôle du climat sur l'accumulation de la tourbe. Géographie physique et Quaternaire, 54: 169–185.

Li, Y. & D. H. Vitt, 1997. Patterns of retention and utilization of aerially deposited nitrogen in boreal peatlands. Écoscience, 4: 106–116.

Minkkinen, K. & J. Laine, 1998. Long-term effect of forest drainage on the peat carbon stores of pine mires in Finland. Canadian Journal of Forest Research, 28: 1267–1275.

Moore, T. R., 1989. Plant production, decomposition and carbon efflux in a subarctic patterned fen. Artic and Alpine Research, 21: 156–162.

Moore, T. R., J. L. Bubier & L. Bledzki, 2007. Litter decomposition in temperate peatland ecosystems: The effect of substrate and site. Ecosystems, 10: 949–963.

Naeem, S., 2006. Biodiversity and ecosystem functioning in restored ecosystems: Extracting principles for a synthetic perspective. Pages 210–237 *in* D. A. Falk, M. A. Palmer & J. B. Zedler (eds.). Foundations of Restoration Ecology. Island Press, Washington, DC.

National Wetlands Working Group, 1988. Wetlands of Canada. Polyscience Publications, Montréal, Quebec.

Nicholson, B. J. & D. H. Vitt, 1990. The paleoecology of a peatland complex in continental western Canada. Canadian Journal of Botany, 68: 121–138.

Peach, M. & J. B. Zedler, 2006. How tussocks structure sedge meadow vegetation. Wetlands, 26: 322–335.

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

Richert, M., O. Dietrich, D. Koppisch & S. Roth, 2000. The influence of rewetting on vegetation development in a degraded fen. Restoration Ecology, 8: 186–195.

Reader, R. J. & J. M. Stewart, 1972. The relationship between net primary production and accumulation for a peatland in southeastern Manitoba. Ecology, 53: 1024–1037.

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

Roth, S., 1999. Etablierung von Schilfröhrichten und Seggenriedern auf wiedervernäßtem Niedermoor. Ph.D. thesis. Philipps-Universität, Marburg.

Saarinen, T., 1996. Biomass and production of two vascular plants in boreal mesotrophic fen. Canadian Journal of Botany, 74: 934–938.

Scheffer, R. A. & R. Aerts, 2000. Root decomposition and soil nutrient and carbon cycling in two temperate fen ecosystems. Oikos, 91: 541–549.

Scoggan, H. J., 1978. The Flora of Canada. National Museums of Canada, Ottawa, Ontario.

Steen, E., 1991. Usefulness of the mesh bag method in quantitative root studies. Pages 75–86 *in* D. Atkinson (ed.). Plant Root Growth: An Ecological Perspective. Special Publication No. 10. British Ecological Society, London.

Szumigalski, A. R., 1995. Production and decomposition of vegetation along a wetland gradient in central Alberta. Ph.D. thesis. University of Alberta, Edmonton, Alberta.

Szumigalski, A. R. & S. E. Bayley, 1996. Decomposition along a bog–fen gradient in central Alberta, Canada. Canadian Journal of Botany, 74: 573–581.

Thormann, M. N. & S. E. Bayley, 1997. Decomposition along a moderate-rich fen–marsh peatland gradient in boreal Alberta, Canada. Wetlands, 17: 123–137.

Thormann, M. N., S. E. Bayley & R. E. Currah, 2001. Comparison of decomposition of belowground and aboveground plant litters in peatlands of boreal Alberta, Canada. Canadian Journal of Botany, 79: 9–22.

Thormann, M. N., A. R. Szumigalski & S. E. Bayley, 1999. Above ground peat and carbon accumulation potentials along a bog–fen–marsh wetland gradient in southern boreal Alberta, Canada. Wetlands, 19: 305–317.

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

Vitt, D. H., 2000. Peatlands: Ecosystems dominated by bryophytes. Pages 312–343 *in* A. J. Shaw & B. Goffinet (eds.). Bryophyte Biology. Cambridge University Press, Cambridge.

Vitt, D. H. & W. L. Chee, 1990. The relationship of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. Vegetatio, 89: 87–106.

Vitt, D. H. & P. Pakarinen, 1977. The bryophyte vegetation, production and organic components of Truelove lowland. Pages 225–244 *in* L. C. Bliss (ed.). Truelove Lowland, Devon Island, Canada: A High Arctic Ecosystem. University of Alberta Press, Edmonton, Alberta.

Wallén, B., 1992. Methods for studying below-ground production in mire ecosystems. Suo, 43: 155–162.

Warner, B. G., K. Tolonen & M. Tolonen, 1991. A postglacial history of vegetation and bog formation at Point Escuminac, New Brunswick. Canadian Journal of Earth Science, 28: 1572–1582.

Wheeler, B. D. & S. C. Shaw, 1995. A focus on fens: Controls on the composition of fen vegetation in relation to restoration. Pages 49–72 *in* B. D. Wheeler, S. C. Shaw, W. J. Fojt & R. A. Robertson (eds.). Restoration of Temperate Wetlands. Wiley & Sons, Chichester.