Wetlands (2013) 33:811–821
DOI 10.1007/s13157-013-0438-5

ARTICLE

Above-Ground Net Primary Production from Vascular Plants Shifts the Balance Towards Organic Matter Accumulation in Restored *Sphagnum* Bogs

Roxane Andersen · Rémy Pouliot · Line Rochefort

Received: 24 January 2013 / Accepted: 16 May 2013 / Published online: 9 July 2013

Abstract The organic matter accumulation potential of a restored bog was estimated over 2 years as a balance between losses to decomposition and inputs through above-ground net primary productivity (AGNPP) in five micro-habitats of increasing complexity (relating to the moss carpet thickness and the number of vegetation functional groups). Decomposition and accumulation rates variations were hypothesized to lead to higher organic matter accumulation potential in the more complex micro-habitats. In general, for a given litter type, the mass losses and decomposition rates were rather homogeneous between micro-habitats, but, they were correlated to the cover of particular species: *Eriophorum vaginatum* with slower decomposition rates, and *Ledum groendlandicum* or *Kalmia angustifolia* with higher rates. Therefore, the abundance of some peatland species, rather than the habitat complexity itself, was a driver of decomposition rates. While the *Sphagnum* AGNPP did not compensate for decomposition losses, the organic matter accumulation potential was tipped towards a sink (positive) by the contribution of vascular species to the AGNPP. The organic matter accumulation potentials are much improved by the presence of *Sphagnum,* but from a restoration perspective, promoting the growth of vascular peatland species might also be a key to achieving a positive balance of organic matter accumulation.

R. Andersen · R. Pouliot (✉) · L. Rochefort
Peatland Ecology Research Group (PERG), Université Laval,
2425 Rue de l'Agriculture,
Quebec City, Québec, Canada G1V 0A6
e-mail: remy.pouliot.1@ulaval.ca

R. Andersen
The James Hutton Institute (MLURI), Craigiebuckler,
Aberdeen AB15 8QH, UK

R. Andersen
Environmental Research Institute (ERI), Thurso, Caithness
KW147JD, UK

Keywords Potential sequestration potential · Decomposition · Ericaceous shrubs · Peatland restoration · Primary production · *Sphagnum*

Introduction

Boreal peatlands are estimated to store up to a third of all the terrestrial carbon (Strack et al. 2008) as a result of the long-term positive imbalance between net primary production and decomposition that has led to the storage of massive quantities of decaying organic matter over the past millennia. In peatland ecosystems, most of the decomposition occurs in the acrotelm, the uppermost oxic layers, while peat accumulation occurs in the catotelm, the deeper and permanently water-saturated layer where rates of decomposition are exceptionally slow (Belyea and Clymo 2001). The interface between those oxic and anoxic layers is now recognized as the mesotelm (Clymo and Bryant 2008) and represents the horizon within which the water table fluctuates.

Vacuum-extraction of peat for horticultural purposes irreversibly modifies the ecosystem structure. The acrotelm layer is removed, causing the loss of the seed bank and exposing more decomposed peat layers to the surface. At the same time, drainage and repeated passages of machinery compact the peat and lowers the hydraulic conductivity, hindering upward capillary flow and leading to stronger soil suction and thus limiting water availability for plants (Price and Schlotzhauer 1999). Phosphorus and potassium are limited in those newly exposed layers (Fisk et al. 2003) and increases in ammonification and nitrification rates following water table drawdown lead to lower C/N ratios (Williams and Wheatley 1988). Therefore, extracted sites represent a carbon- and nutrient-limited system where biomass buildup in the microbial community is reduced (Fisk et al. 2003; Andersen et al. 2006). Similarly, spontaneous colonization processes are limited and peatland plants rarely re-establish (Poulin et al. 2005; Graf et al. 2008). Given that

there is little or no further input of organic matter but that oxidation and decomposition of surface layers continues, the abandoned sites become carbon sources rather than sinks (Waddington et al. 2002). Ecological restoration is an option favored by the horticultural peat industry in North America to bring back a plant cover dominated by peatland species including *Sphagnum* mosses, and ultimately to reset a self-sustainable peatland ecosystem that accumulates carbon (Rochefort et al. 2003).

To achieve this, the imbalance between accumulation and decomposition of organic matter must be restored. Following restoration, fresh organic matter is added to the old peat in the upper layers as vegetation grows, but the water table continues to fluctuate, producing alternating periods of water logging and aeration in a large portion of the profile for many years (Price et al. 2003; Shantz and Price 2006). These conditions promote the immobilization of carbon in the microbial biomass and stimulate microbial respiration leading to high carbon losses in the first decade post-restoration (Glatzel et al. 2004; Andersen et al. 2006; Basiliko et al. 2007; Andersen et al. 2010). Lucchese et al. (2010) used eco-hydrological models to show that a *Sphagnum* carpet thickness of 19 cm would be needed to offset the water table decrease induced by the summer water deficit, and predicted that this is achievable in less than 20 years post-restoration.

However, small-scale variations in environmental conditions influence the success of establishment of mosses, shrubs and herbs and *Sphagnum* growth does not occur at the same rate across the whole restored system (Pouliot et al. 2011a). Differences in the *Sphagnum* carpet thickness and in the number of vegetation functional groups present at a given point (referred hereafter as micro-habitat complexity and detailed in Fig. 1) are thus observed in restored peatlands and the result is the creation of different microtopographic features (Pouliot et al. 2011a). Variation in both *Sphagnum* primary production and decomposition rates could thus lead to heterogeneous distribution of the organic matter accumulation potential in restored sites: if this is the case, a correction of productivity and decomposition values integrated in models could be developed according to spatial distribution of hummocks and hollows. Most studies so far have used measures of respiration rates, often ex situ incubations, to estimate the recovery of belowground processes. Furthermore, the sharp transition between new growth *Sphagnum* and residual compacted peat found in restored peatlands is strikingly contrasting to the acrotelm-mesotelm-catotelm transition of natural sites, and has not been taken into account so far when estimating both decomposition and organic matter accumulation processes following restoration.

We used reciprocal transplant of litter bags containing newly formed *Sphagnum* fragments or surface residual peat from an industrial peatland to characterize the decomposition dynamics in situ along a gradient of micro-habitats going from non-restored conditions to more complex communities in natural reference peatland, with intermediate micro-habitats found in a restored peatland. We simultaneously evaluated above-ground net primary production (AGNPP) for *Sphagnum* and vascular plants to estimate organic matter inputs. We hypothesized that 1) decomposition rates would be highest in habitats where there is a combination of fresh organic matter input and greater hydrological variation (POL, SPH, ERI) and lowest where there is no organic matter input (UNR) or less hydrological variation (NAT); 2) AGNPP for *Sphagnum* mosses would be higher where there are increased abundance of vascular plants that creates opportunities for *Sphagnum* vertical growth (Pouliot et al. 2011b); and 3) the resulting organic matter accumulation would increase with micro-habitat complexity following the gradient described in Fig. 1.

Materials and Methods

Study Sites

The study took place at the Bois-des-Bel Ecological field station (47° 58′ N, 69° 26′ W), in the province of Québec, Canada and in the natural peatland that served as a donor site of plant material for the field station restoration (47° 78′ N, 69° 47′W). In fall 1999, an ecosystem-scale restoration using the *Sphagnum*-moss layer transfer technique (Rochefort et al. 2003) was attempted over 11.5 ha of the Bois-des-Bel cutover peatland following 20 years of abandonment. An area remained un-restored for comparison with the restored zone. Seven years post-restoration (in 2007), *Sphagnum* moss frequency was present in 47 % of the 5,610 points systematically distributed, with a cover estimated of 63±29 % (mean ± SD; from n=192 permanent quadrats) across the restored area (unpublished data, Peatland Ecology Research Group). However, *Sphagnum* carpet thickness was rather heterogeneous (13.2±6.6 cm (mean ± SD); also see Fig. 3 in Lucchese et al. 2010). The natural peatland is semi-forested bog and the vegetation mosaic includes *Picea mariana* (Mill.) Britton, Sterns & Poggenb. and *Larix laricina* (Du Roi) K. Koch as dominant tree species, hummocks formed with *Sphagnum fuscum* (Schimp.) Klinggr., *S. magellanicum* Brid., and *S. rubellum* Wilson and a dense ericaceous shrub cover including *Kalmia angustifolia* L., *Ledum groenlandicum* Oeder, *Chamaedaphne calyculata* (L.) Moench and *Vaccinium angustifolium* Aiton (Lachance and Lavoie 2004).

Gradient of Micro-Habitats

Decomposition dynamics and AGNPP were estimated over 2 years in a gradient of micro-habitats going from absence

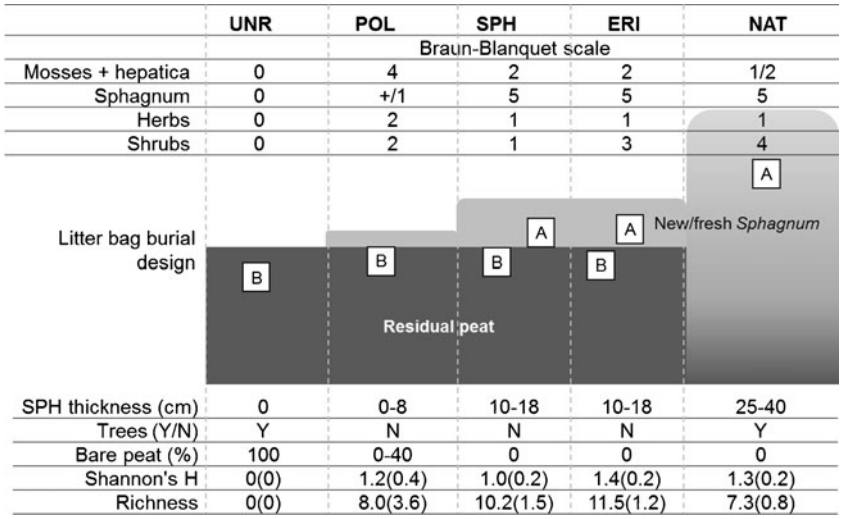

Fig. 1 Details of the vegetation composition, *Sphagnum* thickness, and position of the decomposition bags characterizing the different micro-habitat. UNR = bare peat in cutover peatlands following vacuum extraction, un-restored; POL = carpet of *Polytrichum strictum*, restored; SPH = *Sphagnum* spp. dominated carpet, restored; ERI = mixed carpet of *Sphagnum* spp. and ericaceous shrubs, restored; NAT = intact bog community, natural peatland. Litter bags were placed in fresh Sphagnum (**a**) or residual peat (**b**)

of *Sphagnum* in non-restored conditions to more complex communities in the natural reference peatland. Intermediate stages of *Sphagnum* carpet thicknesses and vegetation organization found in a restored peatland were also used (Fig. 1; Table 1). The five selected micro-habitats were: 1) bare peat in cutover peatland following vacuum extraction, un-restored (UNR), 2) carpet of *Polytrichum strictum* Brid., restored (POL), 3) *Sphagnum* spp. (mainly *S. rubellum*) dominated carpet without shrubs, restored (SPH), 4) mixed carpet of *Sphagnum* spp. (mainly *S. rubellum*) and ericaceous shrubs (*Chamaedaphne calyculata*, *Kalmia angustifolia* and *Ledum groenlandicum*), restored (ERI) and 5) intact bog community in the natural peatland that served as donor site with *Sphagnum* spp. and ericaceous shrubs (NAT).

Decomposition Dynamics

A reciprocal transplant experiment was set up with litter bags containing *Sphagnum* fragments collected from the newly formed moss carpet of the restored sector and residual peat collected in the un-restored sector. Bags were buried within the top 20 cm below the surface of the five different micro-habitats, as this is where highest mass losses are generally observed in bogs (Belyea 1996). However, under SPH and ERI, this meant that the bags could be buried in the newly formed *Sphagnum* carpets (or "depth A") or in aerated old catotelm peat (or "depth B", see schematic representation in Fig. 1). Thus, were bags were buried horizontally in a total of 7 locations: in residual peat (UNRB, POLB), in *Sphagnum* carpet found (NATA) or in both peat types where they co-occur (SPHA, SPHB, ERIA, and ERIB). The litter bags (5.5×6 cm, 1 mm nylon mesh) were filled with ~1.5–2 g of either residual peat or *Sphagnum rubellum* (the newly growth *Sphagnum* fragments), oven dried at 70 °C to a constant weight, and weighted. In October 2006, 6 years post-restoration, three sets of three replicates containing five litter bags each were buried under all micro-habitats x substrate combinations (two different burial depths for ERI and SPH as described above) and for both litter types (residual peat *or Sphagnum* fragments), totalizing 630 litter bags. One set was retrieved 7 months later (June 2007) and the two other sets were retrieved 1 and 2 year(s) post-burial (October 2007 and 2008). Once collected, the litter bags were washed, roots of vascular plant were removed and bags were oven dried at 70 °C until constant weight (a minimum of 48 h) and weighted to calculate mass loss. To correct for manipulation-related losses, 90 extra bags were also filled with either residual peat or *Sphagnum* fragments (45 each) and went through the same steps as the other bags with the exception that those bags were retrieved within a day. The average mass losses estimated from those bags (3.5 % for residual peat and 3.9 % for *Sphagnum* fragments) were used as a correction factor.

Percent of mass loss (Rochefort et al. 1990) was calculated using:

$$M = \left[(X_o - X) \Big/ X_o\right] * 100$$

where X_o is the dry mass of the initial plant material and X is the dry mass of the plant material after litter bag retrieving. Bags that were no longer totally buried when retrieved (possibly due to action of the fauna) were discarded from the dataset. Bags with negative mass loss values, indicating a mass gain possibility due to the presence of small roots into the bags (too small to be removed) were also discarded. Discarded bags represented <10 % of the total dataset. Individual decomposition rates were also estimated for each replicate using the single exponential model (Wieder and Lang 1982; Hobbies 2008), as:

$$M_r = M_0 e^{-kt}$$

where M_r is the mass remaining, M_0 is the initial mass, k is the decomposition rate and t is the time.

Table 1 Initial peat parameters (SD in parenthesis) in the different micro-habitat x depths combinations. *EC corr* corrected electrical conductivity, *AWCD* average well colour development (measure of microbial functional diversity) and *PLFA* phospholipid fatty acids (measure of microbial composition). UNR = bare peat in cutover peatland following vacuum extraction, un-restored; POL = carpet of *Polytrichum strictum*, restored; SPH = *Sphagnum* spp. dominated carpet, restored; ERI = mixed carpet of *Sphagnum* spp. and ericaceous shrubs, restored; NAT = intact bog community, natural peatland. A (in the *Sphagnum* fragments) and B (in residual peat) indicated the layer where litter bags were buried

Micro-habitat	pH	EC corr. (µS cm^{-1})	Bulk density (g cm^{-3})	AWCD (nm)	
				June	October
UNR	3.96 (0.07)	61 (2)	68 (3)	655 (54)	206 (29)
POLB	4.17 (0.04)	73 (3)	89 (4)	696 (29)	572 (72)
SPH-A	4.34 (0.05)	69 (3)	32 (1)	863 (30)	961 (14)
SPH-B	4.33 (0.06)	79 (2)	76 (3)	787 (49)	860 (19)
ERI-A	4.15 (0.01)	53 (1)	25 (1)	1032 (1)	694 (27)
ERI-B	4.01 (0.02)	75 (5)	72 (2)	914 (27)	572 (41)
NAT	3.94 (0.03)	53 (5)	22 (1)	652 (32)	575 (55)
Micro-habitat	PLFA (µg g^{-1}*Sphagnum* fragments)		Fungi: Bacteria		
	June	October	June	October	
UNR	0.26 (0.16)	1.04 (0.47)	0.21 (0.04)	0.18 (0.05)	
POLB	0.26 (0.16)	9.59 (8.03)	0.30 (0.07)	0.20 (0.09)	
SPH-A	0.27 (0.13)	2.70 (0.49)	0.17 (0.03)	0.17 (0.04)	
SPH-B	0.22 (0.07)	3.65 (1.92)	0.22 (0.07)	0.15 (0.02)	
ERI-A	0.14 (0.02)	28.54 (22.76)	0.14 (0.02)	0.14 (0.02)	
ERI-B	0.22 (0.03)	2.02 (1.70)	0.22 (0.03)	0.16 (0.01)	
NAT	1.60 (1.12)	3.79 (3.62)	0.26 (0.04)	0.15 (0.04)	

We included microbial and physicochemical parameters derived from a previous study that characterized the environmental conditions and the microbial communities in the same restored site in order to determine their relationship with in situ decomposition process (detailed methods and original data can be found in Andersen et al. 2010), but briefly, the average well color development obtained from Biolog Ecoplate™ was used as a measure of microbial activity, and the total microbial phospholipid fatty acids (PLFAs) as well as the ratio of fungal:bacterial PLFAs were used as measures of microbial community structure.

Above-Ground Net Primary Production (AGNPP) and Other Variables for Vegetation

AGNPP of *Sphagnum* (g m^{-2}) was estimated both years (in October 2007 and 2008) at each burial site with the following equation (adapted from Vitt and Pakarinen 1977):

$$YI*D*SW*SC$$

where YI = length of year increment (cm), D = density of *Sphagnum* mosses (stem m^{-2}), SW = weight for 1 cm of *Sphagnum* stem (g cm^{-1}stem^{-1}) and SC = cover of *Sphagnum* mosses (%). With the assumption that canopy of mixed moss species grows upward at an even rate (Vitt 2007; Glime 2007), we can use the annual vertical increment of *Polytrichum strictum* to estimate the vertical growth of dense carpet of *Sphagnum* mosses. Thus, 15 stems of *P. strictum* were collected in each burial site (in October 2007 and 2008) and their annual increment was measured (YI). Then, a 0.0082 m^2 sample was cored in the middle of each burial site and *Sphagnum* capitula were counted to obtain density of *Sphagnum* mosses (D). Fifty *Sphagnum* stems were taken in each sample. Capitula were removed and the first 1 cm of each stem was clipped, dried and weighted (SW). Percent cover of *Sphagnum* mosses was estimated in vegetation quadrats of 25×25 cm done at the sampling location (SC).

The utilisation of innate markers had been compared with two other methods in an Arctic environment and showed the lowest coefficient of variation (Pouliot et al. 2010). Innate markers are easy to find in almost all restored and natural peatlands, and the collection is not time consuming as only one visit on the field is required. Innate markers also provide an increment for the entire growing season, which was generally not the case for other methods (e.g. cranked wires) that can only be put in place after snowmelt or thawing of the peat. Since mosses grow rapidly after snow melt and sometimes even under the snow (Collins and Callaghan 1980; Lösch et al. 1983; Woolgrove and Woodin 1996), a part of year increment is lost.

AGNPP for vascular species was estimated at each burial site (only in 2007, 7 years post-restoration) in a circular plot (diameter=70 cm) as follows: 1) for ericaceous species, new leaves, young branches (light green parts), flowers, fruits or seeds were harvested, dried and weighted and 2) for herbs (i.e. all plants growing from the moss surface each year were

included), all above-ground biomass was considered as AGNPP of the current year. AGNPPs of vascular plants were used to calculate organic matter accumulation potential (see below).

Percent covers of all plant species were estimated in a 25×25 cm quadrat above each burial site in June and October 2007 (7 years post-restoration), and were used to estimate aboveground Shannon's diversity index (H) and species richness.

Organic Matter Accumulation

The organic matter accumulation (OM) over the 2 years was estimated as the difference between losses in the aerobic zone and inputs through AGNPP for 1) *Sphagnum* only, and for 2) *Sphagnum* + vascular plants.

The losses associated with *Sphagnum* in the aerobic zone were estimated for a square meter area at any given micro-habitat as:

$$\textit{Sphagnum}\ \text{OM loss}\left(\text{g m}^2\right) = ((\text{WT}-\text{SphTh})*\text{BD}_\text{B}) \times \text{M}_\text{B} + (\text{SphTh}*\text{BD}_\text{A}) \times \text{M}_\text{A})$$

where WT is the mean site water table level of the water table (m), SphTh is the thickness of newly formed *Sphagnum* fragments, BD is the dry bulk density (g m^3) of either the *Sphagnum* fragments (layer A) or the residual peat (layer B) in which the bags were buried, M is the mass loss (%) of the *Sphagnum* fragments (layer A) or the residual peat (layer B). WT-SphTh thus gives us the actual depth of the residual peat still exposed to oxic conditions. The lowest WT position might have been more relevant (Belyea and Clymo 1998), but we used average WT because of the fluctuations in WT occurring in the restored site which are greater than in natural sites (Price et al. 2003; Price and Ketcheson 2009). The values used were 42 cm (UNR), 22 cm (POL, SPH, ERI) and 30 cm (NAT) with ranges of 24 to 68 cm (UNR), −17 to 70 cm (POL, SPH, ERI; negative denotes WT above surface) and 9 to 48 cm (NAT).

Losses of vascular species were estimated as:

$$\text{Vascular OM loss}\ \left(\text{g m}^2\right) = \text{Ve}^{-\text{kt}}$$

where V was the vascular biomass (g), t was set at 2 years, and k, the decomposition rate, was set at 0.20 $year^{-1}$, a conservative average taken from reviews done by Bragazza et al. (2009) and Moore et al. (2007). Total losses over the 2 years were estimated as the sum of *Sphagnum* and vascular OM losses. The total inputs were the sums of *Sphagnum* AGNPP (g m^2) and vascular AGNPP (g m^2) over the two-year period. Losses and inputs were calculated for each replicate and averaged for a given micro-habitats to give OM and a balance was then calculated as (total inputs-total losses)/2 years; negative balance being net loss of OM, while positive balance being net gain of OM.

Statistical Analyses

We used two way ANOVAs followed by Tukey comparison to test the effect of litter type and the micro-habitats on mass losses after 2 years (M) and on decomposition rates (k). Heteroscedasticity and normality were verified beforehand and appropriate transformations were used. We used Pearson's correlation to test the relationships between environmental variables (physicochemical and microbial variables from Table 1 and percent cover of all plant species) and the decomposition rates for each type of litter separately. The correlations were performed with and without the UNR micro-habitats since they introduced mainly zeros in the plant percent cover matrix, and we wanted to see if patterns changed once vegetation was present. *Sphagnum* AGNPP was compared between micro-habitats using two-way ANOVAs following by Tukey comparisons with year and micro-habitats. Shannon's diversity index (H) and species richness of the vegetation assemblages of each burial site were estimated using the VEGAN library (Oksanen et al. 2008). The relationships between *Sphagnum* AGNPP and diversity/richness of the above-ground vegetation assemblages were tested using Pearson correlations. All the statistical analyses were computed in R (R development team 2010).

Results

Decomposition Rates

Between litter type (*Sphagnum* fragments or residual peat), the largest difference was found in NAT, where the organic matter loss and the decomposition rate for the *Sphagnum* fragments were three and four times higher than for the residual peat respectively (Fig. 2). The mass losses and decomposition rates of residual peat and *Sphagnum* fragments were rather homogeneous between micro-habitats. The mass losses differed between three of the micro-habitats only for residual peat, ($F_{\text{mass loss}}=6.9$; $p<0.001$; grey columns; Fig. 2c), with significantly higher mass losses in UNR than in POL and SPH. The decomposition rate of *Sphagnum* fragments was significantly lower in ERI than in NAT when buried in *Sphagnum* fragments ($F_k=3.7$; $p<0.001$; white columns; Fig. 2b).

When all micro-habitats were used for the correlations, the decomposition rates of residual peat was positively correlated with the percent cover of bare peat and negatively correlated with pH, plant species richness and diversity, as well as the percent

cover of some dominant species (see Table 2). When the analysis was performed using only vegetated micro-habitats (UNR removed), the correlations changed: plant diversity was positively correlated with decomposition rates, while bulk density was negatively correlated with it, among others. The decomposition of *Sphagnum* fragments, on the other hand, was positively correlated with the cover of *Kalmia angustifolia* and *Ledum groenlandicum*, and negatively correlated with the electrical conductivity, plant species richness and the percent cover of *Eriophorum vaginatum* L. var. *spissum* (Fernald) B. Boivin and of *Chamaedaphne calyculata*. However, in the case of *Sphagnum* fragments litter, removing UNR from the analyses had little impact (Table 2). There were no significant correlations with the microbial parameters.

Above-Ground Net Primary Production (AGNPP) and Other Variables for Vegetation

Sphagnum AGNPP was similar between the 2 years (F= 0.69; p=0.41) where it was evaluated, but varied significantly between the different micro-habitats, with UNR and POL having significantly lower values than the three micro-habitats dominated by *Sphagnum* (SPH, ERI, NAT) (F= 18.26; p=0.001; Fig. 3a). *Sphagnum* AGNPP was significantly positively correlated to Shannon's diversity index H (0.61, p<0.001) and species richness (0.70, p<0.001). Vascular plant AGNPP was significantly higher in the natural micro-habitat (NAT) compared to other micro-habitats (F= 7.09; P=0.006; Fig. 3b).

Balance Between Accumulation and Decomposition

When only the *Sphagnum* AGNPP values are taken into account, SPH (75±20 g OM m^{-2} y^{-1}) is the only micro-habitat which displayed a small potential to accumulate organic matter over the course of the 2 years of the study, as losses by decomposition were greater than inputs by primary productivity in all other micro-habitats (Fig. 4). When accounting for all the vegetation (*Sphagnum* and vascular AGNPP), the NAT micro-habitat stands out with highest accumulation potential (409±222 g OM m^{-2} y^{-1}). Since UNR sites were devoid of any vegetation, and hence lacked carbon uptake, they showed higher losses than inputs (−1,105±369 g OM m^{-2} y^{-1}). The three restored micro-habitats (POL, SPH and ERI) were in between, showing a small accumulation potential (two to three times lower than for the natural micro-habitat; Fig. 4).

Discussion

Eight years post-restoration, organic accumulation potential was influenced by the abundance of some plant species rather than by differences between decomposition rates and mass losses associated to the structural complexity of selected micro-habitats. As the *Sphagnum* AGNPP was similar in micro-habitats with *Sphagnum* mosses, the contribution of vascular plants became important to tip the balance of organic accumulation potential towards a carbon sink.

Decomposition Rates of Old Peat and Fresh *Sphagnum* Litter

Decomposition rates and mass losses observed in this study fall within the values found in the literature (e.g. Moore et al. 2007) where k values for *Sphagnum* of 0.01 to 0.14 have been reported depending on species and habitat. However our range of average values (0.03 to 0.07) are slightly above the average of 0.02 reported for *Sphagnum* species over longer periods of time (6 years in Moore and Basiliko 2006). This may be a reflection of a more active microbial community in restored conditions than in natural peatlands (Andersen et al. 2010). It is also in line with recent observations by Fenner et al. (2005); Fenner and Freeman 2011) and Tveit et al. (2012) who suggest that if peat soils get oxygenated (e.g. following drainage) this might remove inhibition on phenol-oxydase and increase the degradation rate of complex organic compounds, such as *Sphagnum* fibers, even after rewetting has occurred.

It was expected that residual peat would decompose less readily than *Sphagnum* fragments in similar conditions because it is strongly carbon limited (Fisk et al. 2003; Andersen et al. 2006). Interestingly, the decomposition of this recalcitrant residual peat was highest in un-restored micro-habitats. Given that in the unrestored section, the microbial population had been exposed to highly degraded peat for nearly 30 years, this could be an example of microbial adaptability to a substrate (Bragazza et al. 2007): a group of organisms more adapted to the degradation of highly recalcitrant carbon compounds might inhabit the residual peat where there is generally no easy accessible carbon available. The mass loss and the decomposition rates of *Sphagnum* fragments litter buried in the bare peat of the un-restored micro-habitat were similar to those of the restored and natural micro-habitats. The only significant difference was the rate of decomposition in ERIA which was significantly lower than in NAT for the *Sphagnum* fragments; however there were no differences in mass loss between those two sites, or in fact any sites. This follows Turetsky et al. (2008) who suggested that changes in environmental conditions have little influence into the early degradation of litter formed by hummock *Sphagnum* species, which is not likely to decompose readily. This is the case even under drier and less acidic conditions that are more conducive to organic matter turnover. Studies have

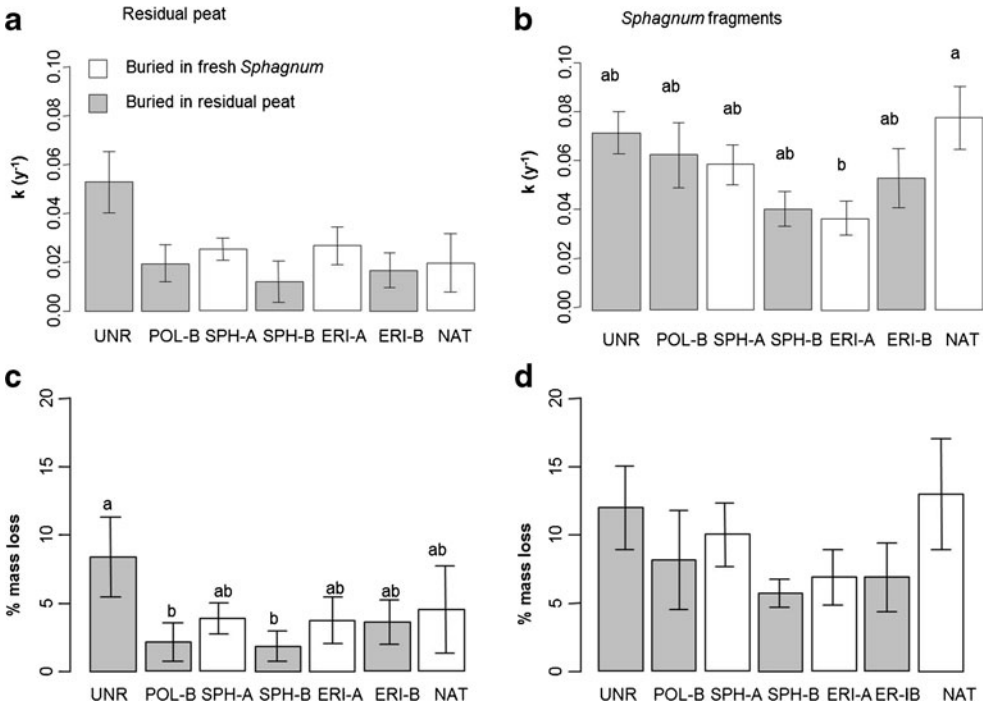

Fig. 2 Exponential decay rate (k) of **a**) residual peat and **b**) *Sphagnum* fragments litter and % mass loss after 2 years for **c**) residual peat and **d**) *Sphagnum* fragments in the different micro-habitats (mean ± SE). For **b**) and **c**), different letters indicates significant differences between micro-habitats according to the 2-way ANOVAs and Tukey tests. For **a**) and **d**) there are no significant difference. Note the difference of scales between **a**) and **b**)

also shown that fungal community respond more strongly to litter type than other environmental variables (e.g. Thormann et al. 2004; Trinder et al. 2008; Straková et al. 2011) and so similar litter types might attract similar fungal assemblages. Interestingly, we observed the presence of dense fungal mycelium in the *Sphagnum* fragments litter bags even under bare peat, possibly from neighboring trees (e.g. *Picea mariana*, *Larix laricina*, *Betula papyrifera* Marsh.), which can create a vast network of superficial roots colonized by ectomycorrhizal fungi (Smith and Read 2008). Yan et al. (2008) suggested that "new" carbon inputs from plants colonising abandoned cutover peatland may support communities of microorganisms that have functionally distinct roles in carbon turnover. We further suggest that in cutover sites, sudden input of new fresh organic matter, even recalcitrant *Sphagnum* fragments, triggers localized changes in the belowground dynamics by attracting micro-organisms in a harsh environment otherwise highly limited in readily

Table 2 Pearson's correlations (only significant correlations were shown) between environmental variables and decomposition rates (k) in the litter bags, and associated *p*-values, estimated with and without the UNR micro-habitat

Residual peat					
All micro-habitats	All vegetated micro-habitats (without un-restored micro-habitat)				
Variable	*R*	*p*	Variable	*R*	*p*
pH	−0.37	<0.01	Bulk density	−0.27	0.01
Species richness	−0.31	<0.01	Water	−0.26	0.02
E. vaginatum cover	−0.31	<0.01	*E. vaginatum* cover	−0.22	0.04
Hepatica cover	−0.28	<0.01	*K. polifolia* cover	0.25	0.02
S. rubellum cover	−0.26	0.01	Plant diversity	0.25	0.02
Plant diversity	−0.24	0.01			
Bare peat area	0.40	<0.01			
Sphagnum fragments					
All micro-habitats	All vegetated micro-habitats (without un-restored micro-habitat)				
Variable	*R*	*p*	Variable	*R*	*p*
E. vaginatum cover	−0.27	0.01	*C. calyculata* cover	−0.27	0.02
C. calyculata cover	−0.26	0.01	Species richness	−0.27	0.02
Species richness	−0.25	0.02	*E. vaginatum* cover	−0.24	0.04
Electrical conductivity	−0.23	0.03	*Sphagnum* carpet thickness	0.30	0.01
L. groenlandicum cover	0.23	0.03	*L. groenlandicum* cover	0.31	0.01
K. angustifolium cover	0.31	<0.01	*K. angustifolium* cover	0.37	<0.01

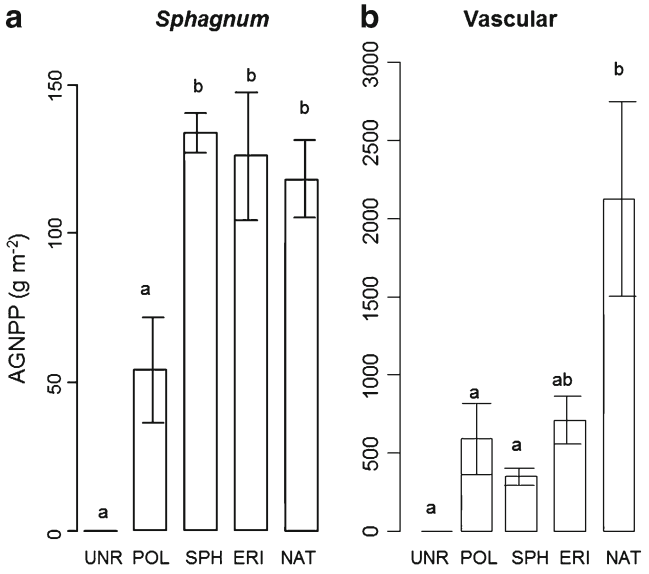

Fig. 3 Above-ground net primary production of **a**) *Sphagnum* mosses and **b**) vascular plant species along the gradient of micro-habitats (mean ± SE, n=3). Significant differences between micro-habitats are indicated with different letters according to 2-way ANOVAs and Tukey tests

available carbon and nutrient (Andersen et al. 2006). Contrarily to what we had hypothesized, there were no correlations between the decomposition rates and any of the microbial proxies, which could be a consequence of relatively homogeneous microbial community structure within the restored site (Andersen et al. 2010, see also Table 2) or lack of specificity of microbial indices. For example, we observed that decomposition rates of the residual peat correlated negatively with pH, and Hartman et al. (2008) showed that pH has a strong influence on bacterial community composition in wetland soils. Therefore, the reduction in decomposition rates at higher pH may be a consequence of suboptimal conditions for peatland specific micro-organisms such as acidobacteria (Dedysh et al. 2006). Although not available at the time of this study, microbial parameters such as bacterial RNA composition, diversity of ericoid fungi, or activity of polyphenol enzymes could be interesting to relate to in situ decomposition rates in the future.

On the other hand, we observed significant correlations between decomposition rates and some above-ground vegetation parameters. In restored peatlands, the changing above-ground vegetation therefore seems to modulate decomposition rates. Within the vegetated micro-habitats, decomposition rates augmented with increased above-ground diversity, which was mostly associated with the diversification of the shrubs and herbs in restored micro-habitats. Such species could impact decomposition rates by improving the aeration and by attracting micro-organisms in the rhizosphere. For instance, decomposition rates increased with increased cover of *Kalmia polifolia* Wangenh., *K. angustifolia* and *Ledum groenlandicum.* Those are all ericaceous shrubs that harbor ericoid mycorrhiza, which are known to have some saprotrophic capacities and might play a significant role in C and N turnover in bogs (Bending and Read 1997). Artz et al.

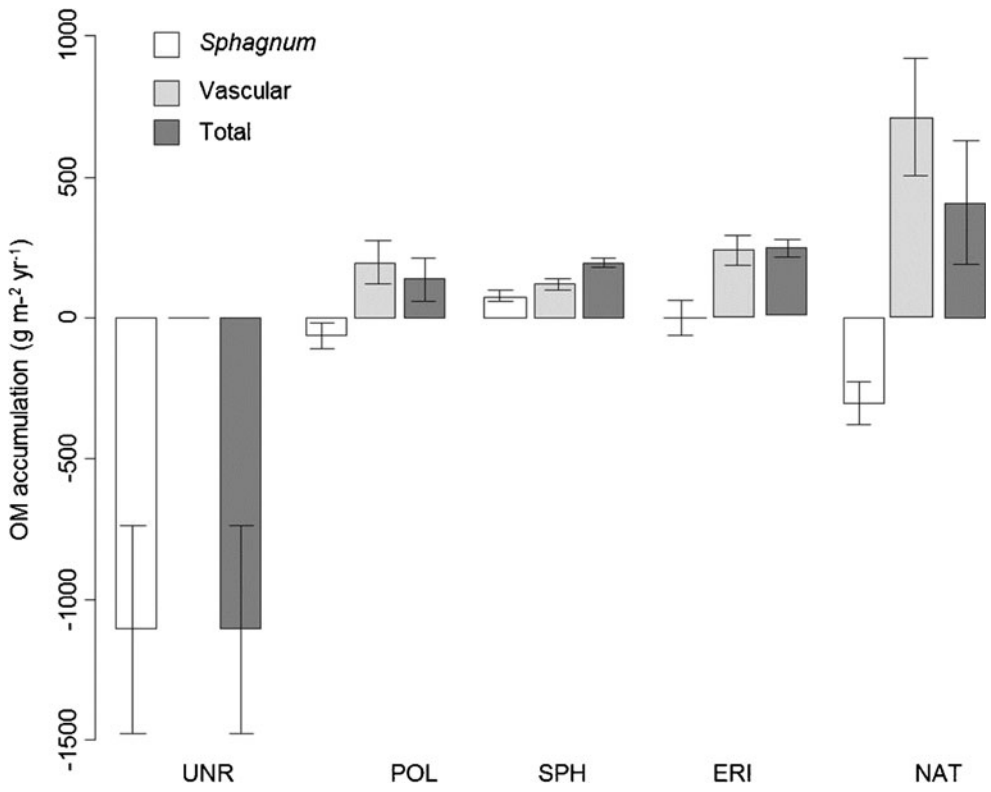

Fig. 4 Balance between accumulation (including *Sphagnum* AGNPP, vascular plant AGNPP and total AGNPP) and organic matter losses through decomposition over the 2 years of the experiment

(2007) observed changes in fungal communities associated with vegetation succession in restored peatlands, where more advanced stages of regeneration were dominated by sequences types belonging to ericoid associated and saprotrophic Agaricales common in peatland, but did not relate these changes to microbial activity, A more recent study by Andersen et al. (2013) showed that the presence of mycorrhizal hosts overrid peat properties in regulating microbial activity in the uppermost horizons of degraded and restored peatlands, but did not relate this to the fungal composition. Future research should address the question of the role of microbial group in carbon turnover by combining these approaches.

Then again, the decomposition rates were lower where there was more *Eriophorum vaginatum* and *C. calyculata* for both litter types. This could be related to competition for nutrients with *E. vaginatum* roots, or to modification of the litter chemistry around tussock dead parts that are known to be recalcitrant to decay (Silvan et al. 2004). This could also be an indirect effect of small hydrological changes, as those two species were generally found in wetter conditions than the other ericaceous shrubs. Once *Sphagnum* was established, higher rates of decomposition were found under thicker carpets, but this might be a consequence of higher number of ericaceous species, who associated with higher rates of decomposition, and only found in thicker carpets. For old peat only, the decomposition rates were lower where bulk density was higher and water table deeper, perhaps suggesting that water can also be limiting the decomposition process. Litter type and water table position have been known to impact decomposition rates in a complex way (Belyea 1996; Moore and Basiliko 2006; Trinder et al. 2008).

AGNPP and its Effect Organic Accumulation Potential

The hypothesis stating that organic accumulation would increase with an augmentation of *Sphagnum* AGNPP along micro-habitat complexity was only partially confirmed. As presence of vascular plants can favour the hummock formation by increasing anchor points for *Sphagnum* vertical growth (Malmer et al. 1994, 2003; Pouliot et al. 2011b), we believed that *Sphagnum* AGNPP would be higher for micro-habitats where the cover of ericaceous shrubs was well developed but not dense enough to block all light access. AGNPP rates were rather divided into two classes: low-productivity micro-habitats without a well-developed *Sphagnum* carpet (non-restored and with *Polytrichum strictum*), and high productivity micro-habitats with a well-developed *Sphagnum* carpet (with or without ericaceous shrubs as well as in natural micro-habitats). Once *Sphagnum* is established, its AGNPP is very similar between micro-habitats. *Sphagnum* AGNPP of this study (130 g m^{-2}) was similar to other studies done at the Bois-des-Bel experimental station (mean of 179 g m^{-2} over the first 6 years post-restoration, Lucchese et al. 2010; 105 g m^{-2} 10 years post-restoration, F. Salvador, unpublished data). Nevertheless, in the context of potential for organic matter accumulation, a relevant question to further investigate is why *Sphagnum* mosses establishes well in places and not in others, e.g. in micro-habitats dominated by *P. strictum*. A threshold in micro-habitat conditions or water table level fluctuations could be present allowing or preventing development of the moss carpet. In micro-habitats that are too dry, ericaceous shrubs can establish because they are more tolerant to drought than *Sphagnum*. With time, wetter and less variable microclimates created by the presence of vascular plants in ericaceous dominated habitats could then promote *Sphagnum* establishment (Pouliot et al. 2011b) and thus trigger the accumulation of organic matter. On the other hand, conditions found in the *Sphagnum* and ericaceous shrubs micro-habitat (SPH and ERI) might already be wet enough to overcome the need of microclimates created by ericaceous shrubs and lead to a homogenous organic matter production by *Sphagnum* mosses.

When AGNPP of vascular plants was also taken into account, organic accumulation seems possible even with a thin *Sphagnum* carpet. However, the values of AGNPP for vascular plants in this study for the natural micro-habitat (1,064 g m^{-2}) were slightly higher than other estimates (80–1,020 g m^{-2} from Moore 2002) perhaps because our data came from only one natural bog on which the cover of ericaceous shrubs was high, around 65 %. In contrast, the difference between the AGNPP that we estimated for ericaceous shrubs in restored micro-habitats and estimates in other studies was smaller (our study, mean of 102 g m^{-2}; Lucchese et al. 2010, mean of 66 g m^{-2}; F. Salvador, unpublished data, mean of 30 g m^{-2}).

There are a certain number of assumptions in the calculations: we used average water table depths to estimate the thickness of the aerated layer, and we did not consider any losses to decomposition in the catotelm (permanently waterlogged horizon) or losses from decomposition of roots (e.g. Moore et al. 2007) or other contributions to carbon input like mycelium. For those reasons, the organic matter accumulation values should be considered with caution. Furthermore, although the model we have used to estimate decomposition rate yielded consistently good fit, there are other models which could be used too (see e.g. Moore et al. 2007). Nevertheless, to our knowledge, it was the first time that the dual nature of the aerobic layer in the restored area, with residual compacted peat being covered with newly formed *Sphagnum* fragments, was taken into account for estimating both decomposition and organic matter accumulation processes.

Conclusion

Organic matter accumulation in peatlands depends upon the imbalance between inputs and losses. We showed that

organic matter accumulation potential is rather homogenous in restored bogs despite differences in *Sphagnum* carpet thickness and complexity of the vegetation assemblages. In conclusion, while *Sphagnum* AGNPP was similar across all the micro-habitats with a carpet thickness >10 cm, it does not compensate for losses. In contrast with the natural peatland, the restored site did not have a significant proportion of litter coming from other species. Because the residual peat is so much denser, it contains more organic matter than the *Sphagnum* fragments in the aerated layer for a similar volume of peat. Therefore, even a slow decay rate due to energy constraints (carbon, water and nutrients) can cause great organic matter losses over time. We argue that from a restoration perspective, ensuring a rapid establishment of *Sphagnum* and promoting the growth of vascular peatland species might help achieving a positive balance of organic matter accumulation more quickly.

Acknowledgments Financial support was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC), the Ministry of Natural Resources and Energy of New Brunswick, the Canadian Sphagnum Peat Moss Association, Acadian Peat Moss (1979) Ltd, ASB Greenworld Ltd, Berger Peat Moss Ltd, Fafard & Frères ltée, Fafard Peat Moss Company Ltd, Lambert Peat Moss Inc., Lamèque Quality Group Ltd, Les Tourbes Nirom Peat Moss Inc., Modugno-Hortibec inc., Premier Horticulture Ltd, and Sun Gro Horticulture Canada Ltd. Roxane Andersen was also supported by a post-doctoral fellowship from the Fonds québécois de recherches sur la nature et les technologies (FQRNT) and a doctoral fellowship from the NSERC. Rémy Pouliot was also supported by a doctoral fellowship from the FQRNT. Special thanks go to Markus Thormann for his help during field planning and all field assistants who have worked on that project.

References

Andersen R, Wells C, Price JS, Macrae M (2013) Nutrient mineralization and microbial functional diversity in a restored bog approach natural conditions 10 years post restoration. Soil Biology & Biochemistry 64:37–47

Andersen R, Francez A-J, Rochefort L (2006) The physicochemical and microbial status of a restored bog in Québec: identification of relevant criteria to monitor success. Soil Biology and Biochemistry 38:1375–1387

Andersen R, Grasset L, Thormann MN, Rochefort L, Francez A-J (2010) Changes in microbial community structure and function following *Sphagnum* peatland restoration. Soil Biology and Biochemistry 42:291–301

Artz RE, Anderson CA, Chapman SJ, Hagn A, Schloter M, Pott JM, Cambell CD (2007) Changes in fungal community composition in response to vegetational succession during the natural regeneration of cutover peatlands. Microbial Ecology 54:508–522

Basiliko N, Blodau C, Roehm C, Bengston P, Moore TR (2007) Regulation of decomposition and methane dynamics across natural, commercially mined, and restored northern peatlands. Ecosystems 10:1148–1165

Belyea LR (1996) Separating the effect of a litter quality and microenvironment on decomposition rates in a patterned peatland. Oikos 77:529–539

Belyea LR, Clymo RS (1998) Do hollows control the rate of peat bog growth? In Standen V, Tallis JH, Meade R (eds) Proceedings of Patterned mires and mire pools: origin and development; flora and fauna. Mires Research Group, British Ecological Society. London, UK, p 55–65

Belyea LR, Clymo RS (2001) Feedback control of the rate of peat formation. Proceedings of the Royal Society, London B 268:1315–1321

Bending GD, Read DJ (1997) Lignin and soluble phonolic degradation by ectomycorrhizal and ericoid mycorrhizal fungi. Mycol Res 101:1348–1354

Bragazza L, Siffi C, Iacumin P, Gerdol R (2007) Mass loss and nutrient release during litter decay in peatland: the role of microbial adaptability to litter chemistry. Soil Biology and Biochemistry 39:257–267

Bragazza L, Buttler A, Siegenthaler A, Mitchell EA (2009) Plant litter decomposition and nutrient release in peatlands. In: Baird AJ, Belyea LR, Comas X, Reeve AS, Slater LD (eds) Carbon cycling in northern peatlands. Geophysical monograph series 184. American Geophysical Union, Washington, DC, pp 99–110

Clymo R, Bryant C (2008) Diffusion and mass flow of dissolved carbon dioxide, methane, and dissolved organic carbon in a 7-m deep raised peat bog. Geochimica et Cosmochimica Acta 72:2048–2066

Collins NJ, Callaghan TV (1980) Predicted patterns of photosynthetic production in maritime Antarctic mosses. Annals of Botany 45:601–620

Dedysh SN, Pankratov TA, Belova SE, Kulichevskaya IS, Liesack W (2006) Phylogenetic analysis and in situ identification of bacteria community composition in an acidic Sphagnum peat bog. Applied and Environmental Microbiology 72:2110–2117

Fenner N, Freeman C (2011) Drought-induced carbon loss in peatlands. Nature Geoscience. doi:10.1038/NGEO1323

Fenner N, Freeman C, Reynolds B (2005) Hydrological effects on the diversity of phenolic degrading bacteria in a peatland: implications for carbon cycling. Soil Biology and Biochemistry 37:1277–1287

Fisk MC, Ruether KF, Yavitt JB (2003) Microbial activity and functional composition among northern peatland ecosystems. Soil Biology and Biochemistry 35:591–602

Glatzel S, Basiliko N, Moore T (2004) Carbon dioxide and methane production potentials of peats from natural, harvested and restored sites, Eastern Québec, Canada. Wetlands 24:261–267

Glime JM (2007) Bryophyte ecology (Volume 1 - Physiological ecology). Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Available at http://www.bryoecol.mtu.edu/

Graf MD, Rochefort L, Poulin M (2008) Spontaneous revegetation of harvested peatlands of Canada and Minnesota, USA. Wetlands 28:28–39

Hartman WH, Richardson CJ, Vilgalys R, Bruland GL (2008) Environmental and anthropogenic controls over bacterial communities in wetland soils. Proceedings of the National Academy of Sciences of the United States of America 105:17842–17847

Hobbies SE (2008) Nitrogen effects on decomposition: a five-year experiment in 8 temperate sites. Ecology 89:2633–2644

Lachance D, Lavoie C (2004) Vegetation of *Sphagnum* bogs in highly disturbed landscapes: relative influence of abiotic and anthropogenic factors. Applied Vegetation Science 7:183–192

Lösch R, Kappen L, Wolf A (1983) Productivity and temperature biology of two snowbed bryophytes. Polar Biology 1:243–248

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

Malmer N, Svensson BM, Wallén 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 BM, Wallén B (2003) Interferences between *Sphagnum* and vascular plants: effects on plant community structure and peat formation. Oikos 100:469–482

Moore PD (2002) The future of cool temperate bogs. Environmental Conservation 29:3–20

Moore T, Basiliko N (2006) Decomposition in boreal peatlands. Ecological Studies 188:125–143

Moore TR, Bubier JL, Bledzki L (2007) Litter decomposition in temperate peatland ecosystems: the effect of substrate and site. Ecosystems 10:949–963

Oksanen J, Kindt R, Legendre P, O'Hara B, Simpson GL, Solymos P, Stevens MHH, Wagner H (2008) Vegan: community ecology package. R package version 1.15-0. Available at http://cran.r-project.org/, http://vegan.r-forge.r-project.org/

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

Pouliot R, Marchand-Roy M, Rochefort L, Gauthier G (2010) Estimating moss growth in arctic conditions: a comparison of three methods. Bryologist 113:322–332

Pouliot R, Rochefort L, Karofeld E (2011a) Initiation of microtopography in revegetated cutover peatlands. Applied Vegetation Science 14:158–171

Pouliot R, Rochefort L, Karofeld E, Mercier C (2011b) Initiation of *Sphagnum* moss hummocks in bogs and the presence of vascular plants: is there a link? Acta Oecologica 37:346–354

Price JS, Ketcheson SJ (2009) Water relations in cutover peatlands. In: Baird AJ, Belyea LR, Comas X, Reeve AS, Slater LD (eds) Carbon cycling in northern peatlands. Geophysical monograph series 184. American Geophysical Union, Washington, DC, pp 277–287

Price JS, Schlotzhauer SM (1999) Importance of shrinkage and compression in determining water storage changes in peat: the case of a mined peatland. Hydrological Processes 13:2591–2601

Price JS, Heathwaite AL, Baird AJ (2003) Hydrological processes in abandoned and restored peatlands: an overview of management approaches. Wetland Ecology and Management 11:65–83

R Development Core Team (2010) R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. Available at http://www.R-project.org.

Rochefort L, Vitt DH, Bayley SE (1990) Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. Ecology 71:1986–2000

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

Shantz MA, Price JS (2006) Hydrological changes following restoration of the Bois-des-Bel peatland, Quebec, 1999–2002. Journal of Hydrology 341:543–553

Silvan N, Tuittila E-S, Vasander H, Laine J (2004) *Eriophorum vaginatum* plays a major role in nutrient immobilisation in boreal peatlands. Annales Botanici Fennici 41:189–199

Smith SE, Read DJ (2008) Mycorrhizal symbiosis, 3rd edn. Academic, New York

Strack M, Waddington JM, Turetsky M, Roulet NT, Byrne KA (2008) Northern peatlands, greenhouse gas exchange and climate change. In: Strack M (ed) Peatlands and climate change. International Peat Society, Jyväskylä

Straková P, Niemi RM, Freeman C, Peltoniemi K, Toberman H, Heiskanen I, Fritze H, Laiho R (2011) Litter tupe affects the activity of aerobic decomposer in a boreal peatland more than site nutrient and water table regimes. Biogeosciences 8:2741–2755

Thormann MN, Bayley SE, Currah RS (2004) Microcosm tests of the effects of temperature and microbial species number on the decomposition of sedge and bryophyte litter from southern boreal peatlands. Canadian Journal of Microbiology 50:793–802

Trinder CJ, Johnson D, Artz RE (2008) Interactions among fungal community structure, litter decomposition and depth of water table in a cutover peatland. FEMS Microbiology Ecology 64:433–448

Turetsky MR, Crow SE, Evans RJ, Vitt DH, Wieder RK (2008) Trade-offs in resource allocation among moss species control decomposition in Boreal peatlands. Journal of Ecology 96:1297–1305

Tveit A, Schwacke R, Svenning MM, Urich T (2012) Organic carbon transformations in high-Arctic peat soils: key functions and microorganisms. ISME Journal 7:299–311

Vitt DH (2007) Estimating moss and lichen ground layer net primary production in tundra, peatlands, and forests. In: Fahey TJ, Knapp AK (eds) Principles and standards for measuring primary production. Oxford University Press, USA, pp 82–105

Vitt DH, Pakarinen P (1977) The bryophyte vegetation, production and organic components of Truelove Lowland. In: Bliss LC (ed) Truelove Lowland, Devon Island, Canada: a high arctic ecosystem. University of Alberta Press, Edmonton, pp 225–244

Waddington JM, Warner KD, Kennedy GW (2002) Cutover peatlands: a persistent source of atmospheric CO_2. Global Biogeochemical Cycles 16:2.1–2.7

Wieder RK, Lang GE (1982) A critique of the analytical methods used in examining decomposition data obtained from litter bags. Ecology 63:1636–1642

Williams B, Wheatley R (1988) Nitrogen mineralisation and water-table height in oligotrophic deep peat. Biology and Fertility of Soils 6:141–147

Woolgrove CE, Woodin SJ (1996) Ecophysiology of snowbed bryophyte *Kiaeria starkei* during snowmelt and uptake of nitrate from meltwater. Canadian Journal of Botany 74:1095–1103

Yan W, Artz RRE, Johnson D (2008) Species-specific effects of plants colonising cutover peatlands on patterns of carbon source utilisation by soil microorganisms. Soil Biology and Biochemistry 40:544–549