

Sphagnum production and decomposition in a restored cutover peatland

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Abstract

Natural peatlands represent a long-term sink of atmospheric carbon dioxide (CO₂), however, drained and extracted peatlands can represent a source of atmospheric CO₂. The restoration of *Sphagnum* mosses on abandoned milled peatlands has the potential to sequester atmospheric CO₂ thereby returning the peatland to a peat accumulating system. Micrometeorological and chamber measurements of net ecosystem CO₂ exchange are proven methods for investigating production and decomposition processes in both natural, extracted, and restored peatlands. However, this approach is relatively expensive because of infrastructure and human resources that not only limits potential use for ecological managers but it limits the number of sites that can be monitored due to high spatial variability. Here we present crank wire and destructive sampling production measurements, litter bag decomposition measurements and measurements of net ecosystem CO₂ exchange made in a restored peatland and natural peatland sites nearby. The objectives were to assess production and decomposition rates in the two systems as well as to compare the different measurements techniques.

Estimates of *Sphagnum fuscum* production at a restored peatland, using the different methods, followed the trend: crank wire < destructive sampling < gas exchange, with the two last methods providing comparable estimates. Production estimates using crank wires in cutover peat surfaces with a thin newly formed *Sphagnum* mat were shown unreliable due to peat subsidence. Results using the destructive sampling method suggest that *Sphagnum* production varies between species (*S. fuscum* > *S. capillifolium*) according to their ability to withstand harsh conditions on restored peat surfaces. Decomposition rate was also significantly greater (p <0.05) for *S. capillifolium* than *S. fuscum*, resulting in an overall plant accumulation greater for *S. fuscum*. Although the restored surfaces were fairly young, production rates estimated on cutover surfaces that were fully covered with a thin *Sphagnum* mat compared with production rates observed in natural sites nearby.

Introduction

Natural peatlands represent an important component of the global carbon cycle containing about one-third of the world's soil carbon (Gorham, 1991) despite covering only 4 to 5% of the global land area (Matthews and Fung, 1987). The accumulation of carbon in peatlands is controlled by the balance between vegetation production and decomposition rates. The latter includes the combined decomposition of live vegetation and the well to weakly humified remains of vegetation (peat). *Sphagnum* mosses are the dominant peat-forming vegetation in northern peatlands and a key plant in the development of most Canadian peatlands (Kuhry et al., 1993).

Peat extraction for horticultural or other industrial uses in North America is usually achieved by milling the peat to let it dry by the sun and then harvesting it with the aids of large vacuums drawn by tractors (Crum, 1988; Rochefort, 2001). The method entails the drainage of extensive peat fields and the removal of the living *Sphagnum* layer. With time a varying quantity of the underlying acrotelm and catotelm peat are extracted. This industrial process causes evapotranspiration to increase and changes the physical properties of the catotelm which restricts moisture availability (Price et al., 1998). Water fluctuations, retention and soil moisture tension remain higher than pre-extraction levels even when the water table rises due to blockage of drainage ditches (Price, 1998). Active management is therefore necessary to restore the *Sphagnum* layer (Rochefort et al., this issue).

Recent research indicates it is possible to reestablish Sphagnum vegetation cover on post-extracted Sphagnum bogs (Rochefort et al., 1995; Campeau and Rochefort, 1996; Quinty and Rochefort, 1997; Rochefort, 2000; Rochefort et al., this issue). One of the stated goals for peatland restoration in Canada, is the return of cutover sites back to peat accumulating ecosystems (Rochefort, 2000). The rate at which the carbon balance of restored peatlands will return to the natural conditions will depend on the rate of production and decomposition of the restored peatland. In pristine northern peatlands, Sphagnum moss productivity averages 70 to 600 g m⁻² y⁻¹ depending on the year (Rochefort et al., 1990). Mass losses (% of original mass) per year will usually be in the range of 8 to 25% (Johnson and Damman, 1993). For production and decomposition, no value for Sphagnum moss has been published yet for restored peatlands. It is essential to assess the rates of Sphagnum production and decomposition on restored peatlands, once the moss mat is established. This is important from not only a scientific understanding basis but also from an ecological management perspective as well - evaluating the success (or lack thereof) of the restoration approach (Gorham, this issue; Hobbs and Norton, 1996).

CO₂ exchange studies on restored cutover peatland plots suggest that *Sphagnum* production is similar to natural peatlands (Waddington and Warner, 2001) and under optimal water level conditions can revert the restored peatland to a net carbon sink (Tuittila et al., 1999). While net CO₂ exchange measurements using chambers and infra-red gas analyzers provide detailed production data, which is essential for linking to ecosystem scale measurements (e.g., Petrone et al., 2001) and model development (e.g., Tuitilla et al., 1999), the approach has limitations as a restoration evaluation approach. Because the approach is relatively expensive, due to large infrastructure and human resource costs, it not only limits potential use for ecological managers but it limits the number of sites that can be monitored due to the high spatial variability in CO₂ exchange (Waddington et al., in press).

Crankwire and litter bag techniques have had good success for determining *Sphagnum* production and decomposition, respectively, in natural peatlands. Both of these methods are relatively inexpensive thereby permitting an extensive spatial coverage of production and decomposition estimates. However, the simple and inexpensive crank wire approach may be limited by the depth of the newly forming *Sphagnum* layer. Alternatively, it may be possible to use the distinct surface of the cutover peat as a marker to estimate the production of the newly grown *Sphagnum* mat. Such clear markers are usually lacking in natural peatlands. This approach and the suitability of crankwire methods remain untested in restored cutover peatlands.

The objective of this study, therefore, is to quantify and compare the production and decomposition rates measured using different methods in a recently restored cutover peatland and natural sites nearby. We present data using decomposition bag, crankwire, CO₂ exchange, and destructive sampling approaches.

Materials and methods

Study area

This study was carried out at the Sainte-Marguerite-Marie peatland (48°47'N, 72°10'W) in the Lac-Saint-Jean region, Québec, Canada. The average annual temperature at the experimental site is 2.2 °C and the mean annual precipitation is 909 mm, of which two-thirds occurs as rain (Environment Canada, 1993). The Sainte-Marguerite-Marie peatland is situated on a terrace of deltaic sands (Price, 1997), forming a 4315-ha bog-poor fen complex. A portion of the peatland has been drained and peat was extracted with a mechanized block-cut operation that commenced in 1990.

Restoration procedure

Principles and details of the techniques used to restore peatland vegetation cover on bare peat are summarized in Rochefort (2000, 2001) and Rochefort et al. (this issue). Briefly, the techniques used are based on 1) active re-introduction of peatland plant diaspores to cutover peat fields and 2) the use of mulches to ameliorate the otherwise harsh substrate conditions in which diaspores are developing and 3) blockage of the former drainage system, in order to allow partial rewetting of the cutover surfaces (Price, 1997). In some instances, low bunds or shallow basins are also used in order to improve water retention at the site, thereby improving the summer hydrological conditions of the peat surfaces (Price et al., this issue, in press).

In our particular study case, experimental restored plots were located on peat fields where drainage ditches were blocked to ensure at least partial rewetting of the peat substrate (Price, 1997). Ditches were blocked in 1992 and *Sphagnum* was reintroduced in 1996. Experimental plots were established in 20 to 25 cm excavated basins bordered with bunds 50 to 100 cm high.

Sphagnum plants used as diaspores were collected by hand from nearby natural peatland areas. The selected monospecific stands of the targeted species (Sphagnum fuscum and S. capillifolium [sensu lato]) had to be large enough to accommodate a 1 m^2 quadrat. The top portion (~10 cm) of Sphagnum was collected by hand over the entire surface of the quadrat. Although manual collection of material for reintroduction mainly targets Sphagnum plants, numerous seeds, rhizomes, seedling and spores of other peatland plant species are also present in the collected material. Sphagnum diaspores were hand-sown in the experimental plots within a few days of collection. The density of the reintroduction was standardized based on ratios between surfaces of collected areas to surfaces of restored areas. In all cases mixtures of diaspores were spread at a density ratio of $1:10(1 \text{ m}^2 \text{ over})$ 10 m^2). Within a few days following diaspore reintroduction, experimental plots were covered with straw mulch at an approximate density of 3000 kg ha^{-1} . All straw mulch application was done by hand.

Decomposition estimates using the litter bag approach

Experimental restored plots used for decomposition studies measured 60 m² and were located in rectangular, 3.5 m wide by 40 to 70 m long basins. These basins were handsown in spring 1996 with an equal mixture of *Sphagnum magellanicum*, *Sphagnum fuscum* and *S. capillifolium* diaspores. In spring 1998, *Sphagnum* cover on these plots had reached 50%, with an additional 5% cover provided by other mosses and vascular plants.

Sphagnum decomposition rates were determined over two growing seasons (1998 and 1999) using 60 litter bags (Johnson and Damman, 1993) containing either S. fuscum or S. capillifolium material. Fresh Sphagnum material (only the top 2.5 cm portion of the plant under the capitula) was collected from nearby natural areas on May 26th, 1998. Litter bags were approximately 5×6 cm, and made of fine nylon netting with opening sizes varying from 0.2 to 0.9 mm. Bags were weighed, filled with plant material, dried at at 60 °C for 24 hours, then weighed again in order to record the amount of dry material present, which varied between 0.42 to 1.02 g (mean = 0.67 g of dry material). Litter bags were inserted under newly established Sphagnum mats (1 to 3 cm thick) at the peat-mat interface such that they laid flat on the peat surface, and were covered with the mat layer. Bags were located along two transects that ran the length of the plots, with approximately 1 m spacing between bags. Litter bags were placed in the field on June 3rd, 1998 and collected at the end of October, 1999. As some of the bags were not found after the two year incubation period, only 50 bags were retrieved for S. capillifolium, and 55 for S. fuscum. Bags were returned to the lab where roots were removed from outside of the bags and fine particles were removed by rinsing with deionized water. The remaining plant material within the litter bag was dried at 60°C for 24 hours.

Mass loss over the 2 year period was calculated as the difference between the initial dry mass and final dry mass in the bag, in proportion to the initial dry mass. Mass loss was compared between species using a one-factor analysis of variance.

Production estimates and comparison of methods

Restored plots used for production measurements, using the three methods, varied in size from 20 m² to 100 m². These handsown plots were located in 120 m long, 4, 10, or 20 m wide shallow basins (Price et al., in press). Handsown plots were bordered by larger areas where *Sphagnum* had been reintroduced mechanically (see Price et al., in press). Half of the the handsown plots received *Sphagnum fuscum* diaspores in spring 1996. The other half received *Sphagnum capillifolium* diaspores. *Sphagnum* cover on these restored plots had reached 40% for *S. capillifolium* plots and 52% for *S. fuscum* plots in fall 1998, with vascular plants and other mosses adding an extra 4% and 2% cover respectively (S. Campeau, unpublished data). Plant cover continued to increase in subsequent years.

In the spring of 1998, a visual survey of the experimental restored plots indicated that many continuous *Sphagnum* colonies, with a minimum 1 m^2 of surface cover, had already established on bare peat. Several of these colonies (5 per species) were selected at random and used for growth measurements using crankwires in 1998 and 1999. Another set of 32 continuous colonies (16 colonies of each species) were selected in fall 1998 and sampled repeatedly in 1998, 1999 and 2000 using the destructive sampling approach in order to estimate biomass accumulation. Finally, one large continuous S. fuscum area was selected in spring 1998 to monitor net ecosystem CO₂ exchange. As all colonies were sampled from the same large set of experimental plots, the data collected allowed for a comparison of production estimates between methods. Crankwire and gas exchange measurements were also taken from nearby natural areas of the peatland to allow comparison of production between natural and restored peatland sites.

Net ecosystem CO₂ exchange measurements

Estimates of production were also made in 1998 using measurements of net ecosystem CO_2 exchange (NEE). NEE measurements were made with a climatecontrolled chamber and a PP systems EGM-1 or EGM-2 infrared gas analyzer (IRGA) assembly placed and sealed over PVC collars set into the peat. Three collars (within 5 m of each other) were placed on continuous *Sphagnum* mats¹ located in a *S. fuscum* restored plot. Three more collars were located in an adjacent natural peatland area (moss layer composed of a mixture of *Sphagnum* species). Details of this measurement approach, including NEE, total respiration (R_{TOT}) and gross ecosystem CO₂ production parameters, are presented in Waddington and Warner (2001).

Crankwire measurements

Crankwires are fine stainless steel rods 20 cm long, bent to present a short horizontal portion (1 to 1,5 cm) at the lower third portion of the rod (upper part 13 cm, lower part 7 cm). This horizontal portion allows the rod to be held fast by the interwined moss plants once the wire is inserted vertically into the moss layer. Crankwires therefore provide a stable, vertical marker against which linear growth can be estimated (Clymo, 1970). Survey of all established moss mats having an area greater than 1 m² with 100% cover in *Sphagnum* mosses was done in the restored plots. Then, ten continuous Sphagnum colonies (5 for S. fuscum and 5 for S. capillifolium) were randomly selected and used for growth measurements using crankwires in 1998 and 1999. Fifteen crankwires were placed in each colony (i.e. n = 5 sets of crankwires per species, with 15 subsamples). For comparison purposes, twelve sets of 15 crankwires were also placed in the neighbouring natural areas of the peatland (n = 6 sets per species)with also 15 subsamples). The crankwires were inserted in mid-May, 1998 and the length of the visible portion of the wire was measured to the nearest mm every second week (except in September and October) from the spring until mid-October, 1998. The same set of crankwires were again used in 1999, but this time length measurements were only taken at the beginning and at the end of the season (May 6th and October 25th, 1999).

In August 1998, one small *Sphagnum* core with a known surface area (10 cm diameter) was collected adjacent to each set of crankwires in both the restored and natural peatland sites. In the lab, the number of capitula in each core was counted, then a 1 to 2 cm thick section (thickness measured precisely) of the core was sliced out directly below the capitula layer. Any vascular plant parts, other mosses or pieces of straw mulch present in the slice were removed, and the remaining *Sphagnum* biomass dried at 70 °C. From this, a length to biomass conversion factor was calculated for each set of crankwires, to convert linear growth data from both years to estimates of biomass production (g m⁻² yr⁻¹).

Comparison of data between species and type of peatland (natural or restored) were made using standard factorial analysis of variance techniques. As measurement did not exactly cover the same period in both years, analyses were run separately for 1998 and 1999. All analyses were performed using the GLM procedure of the SAS software (SAS Institute Inc.). Density of *Sphagnum* mat data (g mm m⁻²) were log-transformed prior to analysis in order to meet the homogeneity of variances assumption. All other data were analysed untransformed.

Destructive sampling method

In the fall of 1998, 32 continuous, *Sphagnum* dominated vegetation patches of at least 1 m² of surface were selected throughout all the experimental restored plots (16 patches per species). Three 25 cm \times 25 cm quadrats were delimited within each patch.

¹ The word mat has been deliberately chosen to designate the relatively large patches $(> 1m^2)$ where a full cover of *Sphagnum* has established on restored peat field. It differs from the word carpet and lawn which have specific meaning in natural peatlands.

The destructive sampling method consisted of collecting all plant material and residual straw present over the surface of 25×25 cm quadrats. The thickness of the newly grown moss layer was measured at nine points within the quadrat while collecting the plants. While destructive sampling in a natural peatland would be difficult owing to the difficulty in identifying a clear date marker at depth, we found this approach easy to use in cutover peatland where the limit between the underlying peat substrate and the

newly established vegetation was clearly visible. One randomly selected quadrat from each of the sixteen patches was sampled in the fall of 1998, the other in fall 1999 and the third in fall 2000. Plant material was collected by hand and brought back to the lab where it was sorted into the various components: Sphagnum mosses, other mosses (primarily Polytrichum strictum) and vascular plants. When sorting, care was taken to remove all residual straw (mulch) and pieces of underlying peat from the samples. After sorting, samples were dried to constant weight at 70 °C and then weighed to the nearest 0.01 g. From these numbers, accumulated biomass for each vegetation component over a 3, 4 or 5-year period (depending on the age of the plot) was estimated on a dry g m $^{-2}$ basis. For comparison purposes, the initial reintroduced biomass was estimated at 100–150 g m⁻², and consisted primarily of Sphagnum biomass, with a very small amount of vascular plants and other mosses mixed in. The residual straw mulch present in each sample was also dried and weighed.

It should be remembered that biomass accumulation numbers calculated from these samples are not representative of the whole plot, but of fully established colonies with a complete moss cover. However they do represent relevant estimates to compare with crankwire and CO₂ exchange measurements, which were also taken on continuous Sphagnum colonies located in the same set of experimental plots. Accumulated biomass, thickness and density of the mat data were compared between peatland type (natural and restored), species and years using a split-plot analysis of variance. Peatland type and species were used as main plot factors, and year of measurement as the sub-plot factor. A correction was applied to the degree of freedom for year and interactions involving years to account for the repeating nature of the time factor (Milliken and Johnson, 1989). All analyses were performed using the GLM procedure of the SAS software (SAS Institute Inc.). All biomass data were log-transformed prior to analysis.

Results

Estimates of decomposition using litter bags

Litter bag decomposition results are expressed as the mean mass loss in proportion to the initial mass. The mean loss for *S. capillifolium* (17.1 \pm 1.1%) and *S. fuscum* (13.1 \pm 0.7%) over two growing seasons are significantly different (p < 0.05). As decomposition of mosses is generally not linear in time (Johnson and Damman, 1993), we can estimate that roughly two-thirds of the loss took place in the first year, and the last portion in the second year.

Estimates of production and comparision of methods

1998 net ecosystem CO₂ exchange

The seasonal ecophysiological parameters created from GEP-PAR light response curves are presented in Waddington and Warner (2001) for the experimental restored plot and the adjacent natural site. Minimum daily GEP occurred at both sites in early June, while maximum daily GEP occurred in late June / early July with the natural site (6.8 g CO₂ m⁻² d⁻¹) exceeding the experimental restoration plot (5.4 g CO₂ m⁻² d⁻¹). The mean daily GEP at locations in the natural site lacking ericaceous shrubs (2.6 g CO₂ m⁻² d⁻¹) was significantly lower than the experimental restored plot (5.1 g CO₂ m⁻² d⁻¹). Seasonal GEP was 82 and 159 g C m⁻² at the natural and experimental restored plot, respectively.

The seasonal parameters for modeling R_{TOT} are also presented in Waddington and Warner (2001). Modeled R_{TOT} was temporally variable at both sites and the mean daily R_{TOT} was greater at the experimental restored plot (10.5 g CO₂ m⁻² d⁻¹) than the natural site (6.9 g CO₂ m⁻² d⁻¹). The greatest R_{TOT} occurred during mid-summer in the natural peatland hummocks and the seasonal R_{TOT} was the greatest at the restoration plot, with a cumulative summer loss of 326 g C m⁻². The seasonal R_{TOT} from the natural site was 218 g C m⁻². Combining GEP and R_{TOT}, the natural and restoration plots were both a net source of CO₂ to the atmosphere of 136 and 167 g C m $^{-2}$, respectively. These numbers do not suggest that there was no Sphagnum growth at the restoration plot but rather there was no net carbon sink owing to the large soil respiration of the aerobic catotelm below the Sphagnum mat.

Because the trace gas approach does not isolate live *Sphagnum* respiration we have taken two approaches

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Table 1. Estimation of linear growth and biomass production S. fuscum and S. capillilifolium in restored and natural peatland sites using crankwires. Five (restored sites) or 6 sets (natural sites) of crankwires (15 wires per set) were used for each species and peatland type (Mean \pm standard error). For both years and species, growth in length was significantly higher in natural sites than in restored sites. Estimated biomass production was also significantly higher in natural sites compared to restored sites, with the exception of S. capillifolium in 1998. For both years, biomass production was significantly larger in S. fuscum than in S. capillifolium in natural areas. In restored areas, S. fuscum production was also higher than S. capillifolium production in 1999, while no significant differences between species could be detected in 1998. Note the large variation reported in restored areas for S. capillifolium in 1998.

		Increase in length		Dry biomass production	
		1998	1999	1998	1999
		mm	mm	$\mathrm{g}~\mathrm{m}^{-2}~\mathrm{yr}^{-1}$	$\mathrm{g}~\mathrm{m}^{-2}~\mathrm{yr}^{-1}$
S. capillifolium	Natural	12.2 ± 2.0	25.1 ± 2.9	113.9 ± 14.9	231.4 ± 22.5
	Restored	5.0 ± 5.4	5.8 ± 2.0	73.8 ± 80.7	86.6 ± 34.0
S. fuscum	Natural	15.5 ± 2.5	26.9 ± 1.9	162.7 ± 24.2	287.4 ± 30.7
	Restored	-3.2 ± 1.6	10.2 ± 2.0	-62.0 ± 38.2	200.6 ± 41.0

to estimate Sphagnum respiration as a means of estimating the Sphagnum production rate from our restored plot GEP values: 1) using Sphagnum fuscum decomposition amount (\sim 9% from year 1) determined from the litter bags, and 2) assuming that Sphagnum respiration is $\sim 15\%$ of R_{TOT} as was found for naturally revegetated Sphagnum cushions at a block-cut peatland (McNeil, 2001). It was not possible to estimate Sphagnum respiration use the using the difference between R_{TOT} at the restored experimental plots and the adjacent bare plots because of large differences in volumetric moisture content (see Waddington et al., in press). Nevertheless, our estimates of Sphagnum production using our seasonal GEP (159 g C m^{-2}) plus our two estimates of Sphagnum respiration are 173 and 208 g C m^{-2} , for approaches one and two respectively. Assuming a carbon content of 50% this translates into 346 and 416 g m⁻² yr⁻¹ of organic matter for Sphagnum fuscum at the restored plots.

Crankwire production measurements

Total changes in length over the 1998 and 1999 growing seasons were significantly lower in the restored sites than in natural sites for both *S. capillifolium* and *S. fuscum* (Table 1; p < 0.05). Estimated biomass production was also significantly lower in the restored sites compared to natural sites, with the exception of *S. capillifolium* in 1998.

For both 1998 and 1999, biomass production was significantly larger in *S. fuscum* than in *S. capillifolium* in natural sites. In restored areas, *S. fuscum* estim-

ated production was also higher than *S. capillifolium* production in 1999, while no significant differences between species could be detected in 1998. Dry biomass production values calculated for 1999 generally exceeded growth values reported for 1998 for both the natural and restored zones, which could be both attributed to either the slightly longer sampling period, or to better growing conditions during the 1999 growing season.

Closer observations of data however leads us to consider crankwire estimates of growth and production in the restored sites with caution. Indeed, in 1998, S. fuscum showed an apparent decrease in length of – 3.2 ± 1.6 mm over the season in the restored areas, corresponding to a production of -62.0 ± 38.2 g m⁻² yr^{-1} . This apparent 'negative growth' of S. fuscum on restored sites is largely due to a sudden and fairly large decrease in length observed between May 15th and May 28th, 1998 (Figure 1). In contrast, S. fuscum at the natural site demonstrated a 15.4 ± 2.5 mm increase in length equivalent to 287 ± 31 g m⁻² yr¹. A decrease in Sphagnum length for three out of five crankwire restored sites transects also occurred in S. capillifo*lium* in 1998, even though the resulting average for all restored sites transects was positive (Table 1: note the large standard error in S. capillifolium for the restored sites in 1998). As Sphagnum stems obviously cannot suddenly 'shrink', the observed decrease in length is not, we believe, 'negative growth' but rather an artifact of the conditions of the cutover peat. The cutover peat was very wet (mean water table position = -3.0 cm)



Figure 1. Apparent change in length for *S. fuscum* and *S. capillifolium* during the 1998 growing season at the natural peatland and experimental restored plots, as measured using series of crankwires. See Table 1 for statistical comparison of overall seasonnal mean increments.

when the crank wires were installed in 1998 and we suspect that peat subsidence along the wire caused the apparent net decrease in length. In fact, the observed decrease corresponded roughly to a large drop (approximately 20 cm) in water table position in the restored area. The water table stayed low throughout the summer and fall in 1998 and *Sphagnum* crank wire measurements did not quite recover from the initial drop over the season.

In 1999, the mean water table position was – 32.3 cm compared to –41.5 cm in 1998. By late August, 1999 the water level in the experimental restored plots recovered to near spring values and this may explain why no overall 'negative growth' was observed in 1999. However, we lack sequential measurements to see if some 'decrease' in length may have occured in the early portion of the season. The observed interference of water table fluctuations on crankwire measurements leads us to use caution in regard to estimates values for increase in length and biomass calculated for both 1998 and 1999 in the restored sites, as presented in Table 1.

Length (mm) to biomass (g m⁻²) conversion factors determined in 1998 and used in the calculation of biomass production values are presented in Table 2. The *Sphagnum* mat density (in g mm m⁻²) was significantly different between natural and restored sites.

Table 2. Density of Sphagnum mats in natural and restored areas (mean \pm standard error, n = 5 except for *S. fuscum* in the natural site, where n = 6). Significant differences in biomass between site types (p = 0.0001) and species (p = 0.0098) were observed for biomass. Comparison of number of capitula between sites and species follow the same trends (p = 0.07 in both cases).

	Capitula Nb m ⁻²	Biomass $g m^{-2} mm^{-1}$
S. capillifolium		
Natural site	39990 ± 3725	9.5 ± 0.5
Experimental restored plot	55679 ± 4201	15.1 ± 1.4
S. fuscum		
Natural site	55471 ± 7327	10.7 ± 0.9
Experimental restored plot	60252 ± 3892	20.6 ± 1.7

(p < 0.05; Table 2). Differences in the number of capitula followed the same trends than differences in mat density (p values between 0.05 and 0.01). *Sphagnum* developing in restored plots, therefore, seemed to have more capitula and were clearly denser than in natural sites where there is more shade and where the environmental conditions are not as hydrologically harsh. In both environments, *Sphagnum fuscum* colonies were generally denser than *S. capillifolium* colonies.



Figure 2. Thickness and accumulated biomass of *S. fuscum* and *S. capillifolium* newly formed mats developing on experimental restored plots. Peatland plants diaspores (mainly *Sphagnum* mosses) were reintroduced on the plot in spring 1996. For all biomass components (*Sphagnum* mosses, other mosses and vascular plants) as well as for mat thickness, significant differences were observed between *S. fuscum* and *S. capillifolium*. Increase in time was also significant for all variables with the exception of biomass of 'other mosses'.

Destructive sampling estimates of accumulation and production

Destructive samples taken in a given year provide an estimate of mean biomass accumulation (production minus decomposition) over the number of growing seasons since plant reintroduction in spring 1996. Destructive samples were taken in 1998 (after 3 growing seasons), 1999 (4 seasons) and 2000 (5 seasons). Accumulated biomass for each vegetation component at the end of those years are presented in Figure 2. Close to 90% of the total biomass accumulated over the 3 to 5 years period is Sphagnum biomass. Other mosses and vascular plants form smaller fractions, but their relative importance in the newly formed mat tended to increase with time from 9% in 1998 to about 12 to 15% in 2000. In all years, accumulated Sphagnum moss and vascular plant biomass were significantly greater for S. fuscum than for S. capillifolium. The biomass of mosses other than Sphagnum was very small compared to Sphagnum and vascular plant biomass, but this time larger in S. capillifolium than in S. fuscum (Figure 2). Thickness of Sphagnum mats was significantly greater (p < 0.05) for S. fuscum than for S capillifolium (Figure 2). Density of the mat, however, was not significantly different between species or between years, averaging 21.3 g m⁻² mm⁻¹ for *S*. *fuscum* (se=0.58, n = 47) and 21.7 g m⁻² mm⁻¹ for *S*. *capillifolium* (se= 0.52, n = 47).

Accumulated biomass does not represent the total net production over several seasons, as biomass produced in a given year will decompose in the following years while, simultaneously, more biomass is produced by growing capitula at the top of the mat. Accumulated biomass can however be used to calculate an estimate of mean annual production over several years if we model in the decomposition rate as measured from litter bags (see section on decomposition measurements). Estimates of mean annual Sphagnum production rates, based on accumulated biomass as measured for each species in 1998, 1999 and 2000 are presented in Table 3. According to these calculations (see footnote of Table 3 for methods of calculations), net yearly production rate for restored Sphagnum mats averaged 230 g m⁻² yr⁻¹ for S. ca*pillifolium* and of 315 g m⁻² yr⁻¹ for S. *fuscum*. It is important to remember here that these yearly estimates do not represent how Sphagnum production varied between years. Each value is an independant estimate

Table 3. Estimation of annual thickness increase and annual *Sphagnum* net production rates on experimental restoration plots based on *Sphagnum* accumulation (length and biomass) measured in 3 separate years using the destructive sampling method (mean and standard errors, n = 15 or 16). See caption of Figure 2 for statistical comparison of *Sphagnum* accumulation data.

Growing season	1998	1999	2000
	3 seasons	4 seasons	5 seasons
S. capillifolium			
Thickness (mm)	35 ± 2.0	43 ± 3.2	54 ± 3.6
Accumulated Sphagnum biomass (g m ⁻²)	785 ± 40	885 ± 26	1060 ± 46
Mean thickness increase (mm yr ⁻¹) ^a	12 ± 0.7	11 ± 0.8	11 ± 0.7
Mean Sphagnum net production rate $(g m^{-2} yr^{-1})^b$	252 ± 5	223 ± 7.5	222 ± 11
S. fuscum			
Thickness (mm)	48 ± 23	54 ± 3.2	68 ± 2.1
Accumulated Sphagnum biomass (g m ⁻²)	1055 ± 49	1145 ± 47	1552 ± 42
Mean thickness increase (in mm yr ⁻¹) ^a	16 ± 0.8	14 ± 0.8	14 ± 0.4
Mean Sphagnum net production rate $(g m^{-2} yr^{-1})^b$	341 ± 17	286 ± 13	324 ± 9.5

^a Thickness divided by the number of growing seasons.

^b Sphagnum accumulation, minus the estimated remaining material from the material initially reintroduced, plus the estimated Sphagnum biomass lost through decomposition of the material produced in earlier years. The following decomposition factors were used: *S. capillifolium*: year 0 (production year): 100%, year 1: 88%, year 2: 83%, year 3 81%, year 4 80%, year 5: 79% of biomass remaining. *S. fuscum*: year 0: 100%; year 1: 91%, year 2: 87%; year 3: 85% year 4: 84%, year 5: 83% of biomass remaining. Initial reintroduced biomass estimated at 125 g m⁻² for both species. For example to calculate the estimated mean production rate (P) based on accumulation data (Acc) for *S. fuscum* at the end of 2000, we must solve for P in the equation: Acc = (0.83 Init) + 0.84 P + 0.85 P + 0.87 P + 0.91 P + P, where Init is the biomass reintroduced or produced in 1996, and the various coefficients correspond to the remaining percentage of biomass reintroduced or produced in previous years. This method of calculation assumes equal production rates between years and that *Sphagnum* biomass begins to decompose only in the year following its production.

of mean production over 3, 4 or 5 growing seasons, based on accumulated biomass and assuming production and decomposition rates did not vary between years. Yearly estimates of annual thickness increase did not vary much between sampling years and averaged 11 mm yr⁻¹ for *S. capillifolium* and 15 mm yr⁻¹ for *S. fuscum* (Table 3).

Approximately 300 g m⁻² of straw mulch was applied to the surface of the cutover bog during the restoration procedure. Assuming straw is not moved by wind or water, measurements of residual straw mulch biomass using the destructive sampling technique provides a measurement of the rate of straw decomposition. In 1998, approximately 50 g m⁻² of straw remained on the plots on average, which means that ~250 g m⁻² of straw had decomposed in the first three years of establishment. Straw mulch biomass decreased by another ~30 g m⁻² in the fourth year and by the end of the fifth year there was only ~11 g m⁻² of straw left on the experimental restoration plots.

Discussion

Comparison of production estimates among methods

Estimates of *Sphagnum fuscum* production at the experimental restored plot using the different methods followed the trend: crank wire < destructive sampling < gas exchange <. *Sphagnum* production estimated using the gas exchange approach is similar to the destructive sampling measurements. Clearly, production estimates using crank wires in cutover peat surfaces with a thin *Sphagnum* mat should be avoided. When used on a thin *Sphagnum* mat, crankwires are inserted in the underlying cutover peat that can shrink and swell and cause errors in length and production measurements in the overlying *Sphagnum* mat.

Sphagnum production and decomposition function of restored peatlands

Sphagnum production has been measured for a wide range of natural peatlands (Ilomets, 1981; Rochefort et al., 1990; Gerdol, 1995). Production estimates vary widely – even within a single species. *S. capillifolium* production ranges from 70 g m⁻² yr⁻¹ in boreal peatlands (Ilomets, 1981; Moore, 1989) to 454 g m⁻² yr⁻¹ for in a temperate bog (Gerdol, 1995) with an average around 380 g m⁻² yr⁻¹. Growth in length for these studies ranged from 3 mm yr⁻¹ to 23 mm yr⁻¹. For *S. fuscum*, the productivity values range from 70 g m⁻² yr⁻¹ in boreal peatlands (Rochefort et al., 1990) to 320 g m⁻² yr⁻¹ (Lindholm and Vasander, 1990) with an average of about 210 g m⁻² yr⁻¹ among the all the studies. For this species, growth in length varies from 4 to 31 mm yr⁻¹.

Although production estimates are known to vary with annual temperature, precipitation, nutrient supply and species composition (Wieder and Lang, 1983; Grigal, 1985; Rochefort et al., 1990) these literature values, along with our natural site crank wire production estimates (Table 1), provide for a relative measure of Sphagnum restoration success. Not only do both S. fuscum (average: 310 g m⁻² yr⁻¹) and S. capillifo*lium* (average: 235 g m⁻² yr⁻¹) destructive sampling production estimates at the experimental restoration plots fall within the range of natural peatland studies, but they actually exceeded that estimated for the adjacent natural peatland sites for the same species using crankwires (Table 1). This indicates that restoration measures are indeed successful but we caution that the destructive sampling has occurred on portions of plots with 100% Sphagnum cover only.

The similarity of production values observed between the young restored Sphagnum mats and natural peatland is surprising considering that hydrological conditions are generally considered harsher on cutover peat than in natural areas (Price, 1996; Price et al., this issue). These results can possibly be explained by the differences in density and number of capitula of Sphagnum in the experimental restoration plots relative to that in natural peatlands. Clearly, the Sphagnum developing in restored plots have more capitula and are denser than in natural areas where there is more shade and where the environmental conditions are not as harsh. The net effect is that Sphagnum mats developing in the restored site were tighter and therefore able to keep a high moisture content (Campeau and Rochefort, 2000) resulting in high production.

Natural peatland *Sphagnum* decomposition estimates (using litter bags) also demonstrate a wide range among peatlands, among species, as well as within a single species (Johnson and Damman, 1993). Mass loss over two years for *S. fuscum* has been reported from two other studies: 16% (Rochefort et al., 1990) and 15% (Johnson and Damman, 1991). Annual mass loss is reported to be 16% for *S. capillifolium* (Clymo, 1965) but no values are known for over a two year period. Values from our study fall within the natural range reported, but it is interesting to note that the mean mass loss for *S. capillifolium* (17%) and *S. fuscum* (13%) is not much greater (and sometimes even lower) than reported in most studies. Given the dry conditions on cutover peat this surprised us, but recent studies by Waddington and Warner (2001) indicate that a mulch and moss layer cover significantly reduces peat and litter decomposition. Consequently, establishing a *Sphagnum* cover not only increases restored peatland productivity but also indirectly decreases peat and litter decomposition.

Given the harsh conditions of post-mined peatlands, interspecific differences in dessication tolerance are important. Our results suggest that not only is *S. fuscum* more productive on restored peatlands but is also more resistant to decomposition. *S. fuscum* is a hummock species that has been shown to resist decomposition (Johnson and Damman, 1991). Moreover, volumetric moisture content in natural peatland hummocks is often drier than conditions often found in cutover peatlands (Price, 1998) and as such *S. fuscum* can likely better adapt to the harsh conditions found on cutover peatland surfaces. As such using *S. fuscum* diaspores over *S. capillifolium* diaspores will significantly improve peatland restoration success.

Finally, our results also indicate that most of the straw is decomposed within the first three years post-application and that almost all straw is decomposed within five years of application. Straw mulch is used to ameliorate the harsh substrate conditions in which diaspores are developing (Johnson et al., 2000; Rochefort, 2000) thereby enhancing *Sphagnum* production and likely decreasing decomposition (Waddington and Warner, 2001). The rate of straw decomposition, therefore, will directly affect the rates of *Sphagnum* production and decomposition. Consequently, studies on the controls of straw decomposition in restored peatlands are needed to improve our understanding of restored peatland *Sphagnum* production and decomposition functions.

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