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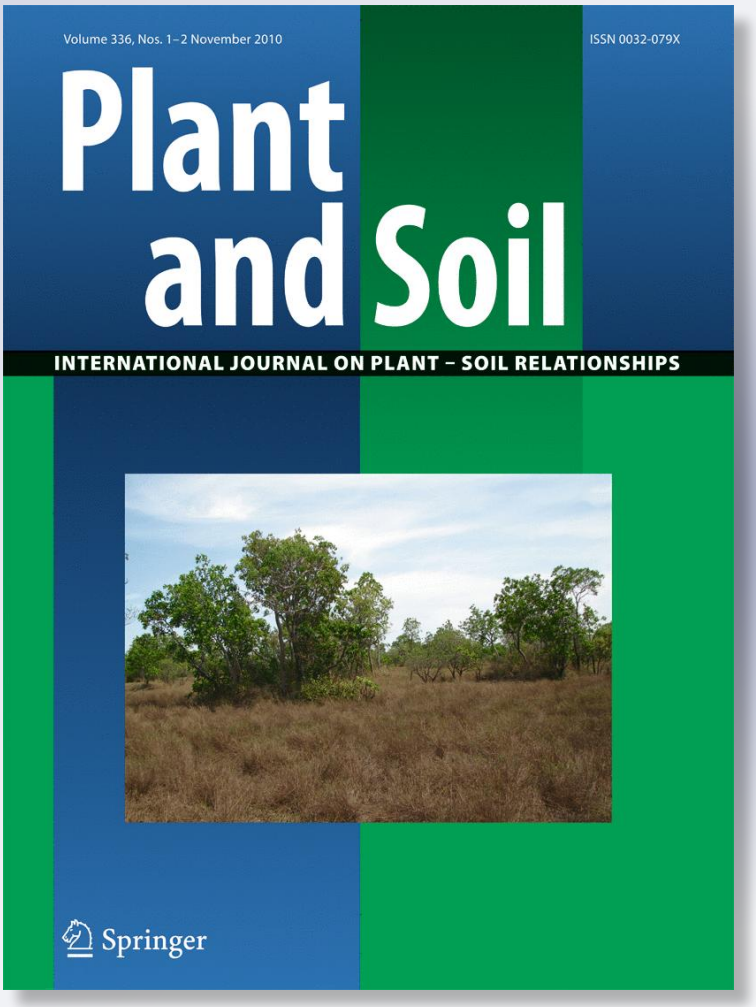
Plant and Soil
An International Journal on Plant-Soil Relationships

ISSN 0032-079X
Volume 336
Combined 1-2

Plant Soil (2010) 336:499-508
DOI 10.1007/s11104-010-0506-z



Springer

Plant Soil (2010) 336:499–508
DOI 10.1007/s11104-010-0506-z

REGULAR ARTICLE

Decomposition rates of bryophytes in managed boreal forests: influence of bryophyte species and forest harvesting

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Received: 21 December 2009 / Accepted: 20 July 2010 / Published online: 4 August 2010

Abstract The slow decomposition rate of boreal forest floor bryophytes contributes both to maintaining high soil C reserves as well as affecting conditions for tree growth by maintaining excessively high soil water content, cooling the soil and slowing nutrient cycles. In this study, mass loss of three bryophyte species (*Pleurozium schreberi*, *Sphagnum capillifolium*, *S. fuscum*) was measured in unharvested, partial cut and low-retention cut forest blocks. Mesh decomposition bags containing the three species and wood sticks were placed at two depths in colonies of either *P. schreberi* or *S. capillifolium* (environment) in the three harvest treatments and retrieved after two growing seasons. Mass loss was primarily related to substrate type (*P. schreberi* > *S. capillifolium* > wood sticks > *S. fuscum*) and secondarily to depth. Harvest treatment and environment (*P. schreberi* or *S. capillifolium*) only weakly affected sphagna mass loss. The weak effect of harvest treatment suggests that conditions created by low retention cuts do not to stimulate decomposition in this system and are not important enough to stimulate carbon loss, or to counteract paludification. On the other hand, the strong effect of bryophyte type indicates that conditions affecting bryophyte colonization and succession are of great importance in driving carbon and nutrient cycles.

Keywords Feather mosses · *Sphagnum* · Organic matter · Partial cuts · Black spruce · Forest floor

Responsible Editor: Erik A. Hobbie.

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Introduction

Boreal forests and peatlands represent one of the great carbon stocks on the globe. Black spruce (*Picea mariana*) forests cover much of the North American boreal forest and contain more carbon than other forest types (Gower et al. 1997), mainly due to the accumulation of thick forest floors (Wang et al. 2003). More carbon is accumulated in these soils because of the low decomposition rate of the organic layer, which is composed mostly of decaying bryophyte litter, conifer needles and wood. A variety of regional factors may also decrease the decomposition rate of the organic layer, including the development of

permafrost due to a thick feather moss (*Pleurozium schreberi, Ptilium crista-castrensis*, *Hylocomium splendens*) cover (Viereck et al. 1993), the presence of ericaceous species (DeLuca et al. 2002), the invasion of *Sphagnum* spp. (Lawrence 1958) or the expansion of neighbouring wetlands (Glebov and Korzukhin 1992; Bauer et al. 2009). In certain regions, the organic layer can accumulate to the point where forests are converted to peatlands (Viereck 1983; Foster 1985; Glebov and Korzukhin 1992; Fenton et al. 2005) in the process of edaphic paludification (Simard et al. 2007).

The decomposition rates of sphagna have been extensively studied in peatlands and wetlands (Johnson and Damman 1991; Clymo et al. 1998). Recent studies have examined the decomposition rate of boreal peatland species (Turetsky et al. 2008) and subarctic species (Lang et al. 2009). However, despite the importance of bryophytes (particularly feather mosses and *Sphagnum* spp.) in the accumulation of carbon in boreal forest ecosystems (Wang et al. 2003; Lecomte et al. 2006) and their role as drivers of paludification (Fenton et al. 2005), few studies have reported on the decomposition dynamics of boreal forest bryophytes (see Turetsky 2003; Cornelissen et al. 2007).

Within the deep organic layer of black spruce–moss ecosystems, the decay rates of soil organic matter are controlled both by the substrate itself and by environmental conditions such as soil water content, temperature and pH (Prescott et al. 2000a). These environmental conditions are in turn influenced by the bryophyte species themselves (Johnson and Damman 1991; Fenton and Bergeron 2006). Forest harvest may affect substrate quality (e.g., C:N ratio, secondary metabolites) in the long run by influencing moss succession (Fenton and Bergeron 2007) and, in the short term, by modifying soil environmental conditions. The degree of canopy opening will affect the amount of heat reaching the ground as well as the soil water balance.

Recent literature has focused on the dynamics of carbon accumulation in boreal forests and climate change (e.g., Preston et al. 2006; Bond-Lamberty et al. 2009; de Groot et al. 2009), however, forest harvest continues to be a major disturbance agent in the boreal forest. The classic study of Covington (1981) suggested that post-harvest, the decomposition rates of the forest floor and mineral soil increased in response to the increased incident radiation and, therefore, temperature. However, studies have since found a wide variety of responses in decomposition rate in reaction to forest harvest (Prescott et al. 2000b; Yanai et al. 2003), which is linked to the degree to which increased temperatures result in desiccation in the soil layer where decomposition is measured (Yanai et al. 2003; Palviainen et al. 2004). Decomposition in partial harvests (retention levels vary, but generally 20–80% of pre-harvest basal area) has been less studied; however, some studies suggest these decomposition rates are more similar to those found in unharvested stands than in clear cut stands (e.g., Lindo and Visser 2003; Brais et al. 2004; Prescott et al. 2003)

Within this context, this study addresses three questions: (1) how do decomposition rates vary among bryophyte species, (2) how does the decomposition rate of different bryophyte species vary with decomposition environment (i.e., host patch species) and depth within the organic layer, and (3) does forest harvest (partial cut and clear cut) change the decomposition rate of different bryophyte species?

Methods

Study area

The Clay Belt of Ontario and Quebec is a major physiographic region created by the deposits left by Lakes Barlow and Ojibway after their maximum extension during the Wisconsin glaciation (Vincent and Hardy 1977). In its northern portion, it is dominated by black spruce (*Picea mariana*)-feather moss (*Pleurozium schreberi*) forests and is particularly prone to paludification between fires due to its poorly drained clay-dominated soil, low topographic relief, and moderately humid and cold climate (892 mm of precipitation annually and annual mean temperature of 0.1°C; Environment Canada 2009). The dominant disturbances are large fires that kill all aboveground vegetation. Between 1850 and 1920, the fire cycle was ca. 135 years, and it has since increased to ca. 398 years (Bergeron et al. 2004). The study area lies just south of the Hudson Bay-James Bay Lowlands, the second largest peatland complex on the globe.

This study is part of a larger project that aims to compare the effects of partial harvest and low-retention cut systems on ecosystem function, diversity and merchantable timber supply. Each site in the network, including the one used in this study, consists of one block of three treatments: low-retention cut

(cut with protection of regeneration and soils, CPRS), partial harvest with variable retention, and unharvested. The partial cut (90 ha) and low-retention cut blocks (99 ha; the unharvested block was 79 ha) were harvested during the winter of 2003–2004, with harvesting of 85% of the living basal area of merchantable timber, i.e. trees >9.0 cm in diameter at breast height, and 12% of the basal area of dead stems. All merchantable stems were harvested in the low-retention block. For more information on the partial cut trials see Fenton et al. (2009). The type of low-retention cut practiced in Québec (CPRS) mandates that all trees with a diameter over 10 cm need to be harvested; however, previously established regeneration and the soil are protected by restricting vehicle movement to trails that are approximately 10 m apart. The site (including the three treatment blocks) chosen for this study was dominated by black spruce established approximately 120 years after a stand-replacing fire. Given its large size (>150 ha), it included all positions along a slope from moderately well-drained to poorly drained, typical for this region. Canopy openness and surface organic layer thickness both increased along this slope. Surface organic layer thickness varied from 20 cm to 60 cm. The understory was dominated by bryophytes; feather mosses, and sphagna (*Sphagnum capillifolium, S. russowii, S. fallax, S. fuscum*) were the most common species. Lichens *Cladina rangifera* and *C. stellaris* were also common. The herb layer was dominated by ericaceous shrubs and saplings of black spruce and balsam fir.

Substrates for decomposition

Decomposition rates were compared among environments and substrates using decomposition bags. The decay rates of four species with differing nutrient compositions (Table 1) were studied. These include *Pleurozium schreberi* (a feather moss), *Sphagnum capillifolium* (an early succession hummuck sphagna), *Sphagnum fuscum* (a late succession hummock sphagna; Fenton and Bergeron 2006), and purchased white birch (*Betula papyrifera*) wood with no bark. Ten live stems of each bryophyte species were selected from large colonies and inserted into 10×10 cm decomposition bags constructed from mosquito mesh with a 1 mm mesh size. Stems were taken below the growing tip in *P. schreberi* and below the capitulum in the sphagna. In order to obtain a dry weight without air drying, which could potentially change the nature and decomposition rate of the material (Moore et al. 2007), each bundle of ten stems was soaked in water for 1 min and spun in a salad spinner. The number of times was predetermined by soaking and then spinning the bundles one time and weighing, and then re-soaking the bundles and spinning them two times and weighing them and so on, until weight no longer decreased with increasing number of spins. This process was repeated for each species separately (see Appendix A for the regression curves). The final wet weight at a constant hydration state could then be used to calculate dry weight using previously established regression curves created from samples that were weighed at a constant hydration state and then dried (see Appendix A). This method has previously been used in determining the dry weight of samples that would be followed in growth experiments (Frego and Carleton 1995; Mulligan and Gignac 2001). For the bags containing wood sticks as the decomposition matter, four sticks (4 in long, 5 mm thick) were broken in two, weighed and inserted into the bags. After the decomposition substrate and a non-reactive metal tag for labelling were inserted into the bags, they were sown shut.

Study design

Within each 50 ha treatment (unharvested, low-retention cut and partial harvest), five 100 m^2 plots were randomly selected within stratified positions

Table 1 Total nutrient contents [% for C and N and (mg/g) for the other nutrients] for *Pleurozium schreberi*, *Sphagnum capillifolium*, and *S. fuscum* inserted in the decomposition bags

	C	N	P	K	Ca	Mg	C/N	C/P
P. schreberi	46.59	0.90	3.10	8.23	5.88	2.45	51.53	122
S. capillifolium	48.65	0.56	NA	NA	4.61	3.59	69.00	NA
S. fuscum	43.94	0.70	1.42	6.51	3.85	3.20	63.00	303

along the slope to ensure that all treatments included the same variability in environmental conditions. The minimum distance between each plot within a treatment type was 100 m, the maximum distance was 1,000 m and the spatial dispersion was scattered across the treatment block. Within each plot, two of the most common environments were selected, *Pleurozium schreberi* and *Sphagnum capillifolium*; *S. fuscum* was absent from these plots. One bag of the four substrate types was placed at each of two depths (10 cm and at the interface between the humus layer and the mineral soil i.e. >20 cm) beneath the organic layer surface. A total of 240 decomposition bags were installed. The five replicates of each treatment combination actually are pseudoreplicates, as they are found within one harvest block of each type. However, because of the large area of each block, they include most of the diversity of forest types found across the landscape (from upland to lowland black spruce).

The bags were placed in the appropriate environment and harvest treatment in late June 2004. The bags were retrieved in September 2006. They were dried, cleaned of roots and other new material, opened and the material was removed and weighed.

Analyses

All weights were converted into percentage of mass loss. After testing for normality, a General Linear Model with Bonferroni post-hoc tests was performed using SPSS v. 12.0 with % mass loss as the dependent variable and substrate (moss species and wood), environment (*P. schreberi* or *S. capillifolium*), depth (10 cm vs. >20 cm) and harvest treatment (unharvested, partial cut and low-retention cut) as independent variables. Subsequently, the data set was split by substrate type and the models were re-run. The data for the substrates *P. schreberi* and wood were re-run with each depth analysed separately.

Results

Substrate (species or wood) and depth (10 cm vs. >20 cm) influenced mass loss overall (Table 2). *Pleurozium schreberi* had the highest rate of mass loss (40–47%), *S. capillifolium* (22–26%) and wood (16–27%) were intermediate, and *S. fuscum* lost only 5–9% of its original mass over 14 months (Fig. 1).

Table 2 Results of GLMs comparing mass loss among substrates (species), environment (patch species), depth (10 cm, >20 cm) and forest harvest treatment. Only interactions with a $P \leq 0.1$ are shown for brevity

Model	Factor	d.f.	Sig.
Complete	Model (R^2=0.650)	46	<0.001
	Intercept	1	<0.001
	Treatment	2	0.107
	Environment	1	0.42
	Matter	3	<0.001
	Depth	1	0.001
	Treat*environment *matter*depth	5	0.031
	Error	183	
	Total	230	
	Corrected total	229	
Pleurozium	Model (R^2=0.254)	10	0.19
	Intercept	1	<0.001
	Environment	1	0.35
	Depth	1	0.003
	Error	43	
	Total	54	
	Corrected total	53	
Pleurozium 10 cm	Model(R^2=0.040)	5	0.63
	Intercept	1	<0.001
	Treatment	2	0.96
	Environment	1	0.09
	Error	24	
	Total	30	
	Corrected total	29	
Pleurozium >20 cm	Model(R^2=0.126)	4	0.94
	Intercept	1	<0.001
	Treatment	2	0.80
	Environment	1	0.92
	Error	19	
	Total	24	
	Corrected total	23	
S. capillifolium	Model (R^2=0.490)	11	<0.001
	Intercept	1	<0.001
	Treatment	2	0.003
	Environment	1	0.108
	Depth	1	0.094
	Environment* depth	1	<0.001
	Error	46	
	Total	58	
	Corrected total	57	
S. fuscum	Model (R^2=0.355)	11	0.021
	Intercept	1	<0.001

Table 2 (continued)

Model	Factor	d.f.	Sig.
	Treatment	2	0.023
	Environment	1	0.46
	Depth	1	0.185
	Treat*environment	2	0.061
	Treat*depth	2	0.038
	Error	47	
	Total	59	
	Corrected total	58	
Wood	Model (R^2=0.204)	11	0.39
	Intercept	1	<0.001
	Treatment	2	0.967
	Environment	1	0.69
	Depth	1	0.047
	Error	47	
	Total	59	
	Corrected total	58	
Wood 10 cm	Model (R^2=0.111)	5	0.48
	Intercept	1	<0.001
	Treatment	2	0.54
	Environment	1	0.48
	Error	23	
	Total	29	
	Corrected total	28	
Wood >20 cm	Model (R^2=0.168)	5	0.70
	Intercept	1	<0.001
	Treatment	2	0.66
	Environment	1	0.89
	Error	24	
	Total	30	
	Corrected total	29	

The environment (i.e., patch of *P. schreberi* or *S. capillifolium*) and harvest treatment (unharvested, partial cut, low-retention cut) were not significant factors in the complete model.

Species were also examined individually. Mass loss of *Pleurozium schreberi* did not vary with treatment, and only depth showed a significant effect (Table 2). When the two depths are analysed separately, environment (*P. schreberi* vs. *S. capillifolium*) approached significance at 10 cm (P=0.09).

Harvest treatment and depth both had an effect on mass loss in *S. capillifolium* and there was an interaction between environment and depth (Fig. 1). Specifically, *S. capillifolium* had a significantly higher mass loss in the unharvested block than in the partial cut block. Mass loss in the low-retention cut was intermediate. Furthermore, mass loss was greater at 10 cm than at >20 cm in the *S. capillifolium* environment, while the inverse was true in the *P. schreberi* environment (Table 3).

Mass loss in *S. fuscum* also varied among harvest treatments (Table 2; Fig. 1) with a greater mass loss in the low-retention cut than in the partial cut. The unharvested treatment was intermediate. However, two interactions were also significant, i.e. harvest treatment x depth and harvest treatment x environment. In the unharvested block, mass loss was greater at the >20 cm depth than at the 10 cm depth, and while mass loss was generally greater in the *P. schreberi* environment, in the low-retention cut it was greater in the *S. capillifolium* environment (Table 3).

The wooden sticks did not vary in mass loss, except between 10 cm and >20 cm depths (Table 2; Fig. 1).

Discussion

The role of substrate

Substrate type had the largest influence on the percentage of mass lost. Substrate type, rather than abiotic environmental factors, has been shown to be the most important factor determining the decomposition rate of sphagna in other habitats (Johnson and Damman 1991; Belyea 1996; Turetsky et al. 2008) and for other litter types in a variety of habitats (Prescott et al. 2000b; Dorrepaal et al. 2005). The relatively high levels of mass loss in *P. schreberi* compared with *S. capillifolium* and *S. fuscum* are consistent with the results of other studies that compared feather mosses and hummock sphagna (Turetsky 2003; Turetsky et al. 2008; Lang et al. 2009). However, it is interesting that the slow decomposition rates of sphagna that are usually partly attributed to the anoxic and acidic environment of peatlands (Moore et al. 2007) are retained in a forest soil environment. Furthermore, these slow decomposition rates were relatively independent of environmental factors.

Mass loss was not related to C:N ratio in this study. When compared to vascular plants, traditional "substrate quality" is a poor predictor of decomposition for bryophytes (e.g., C:N ratio and/or quantity

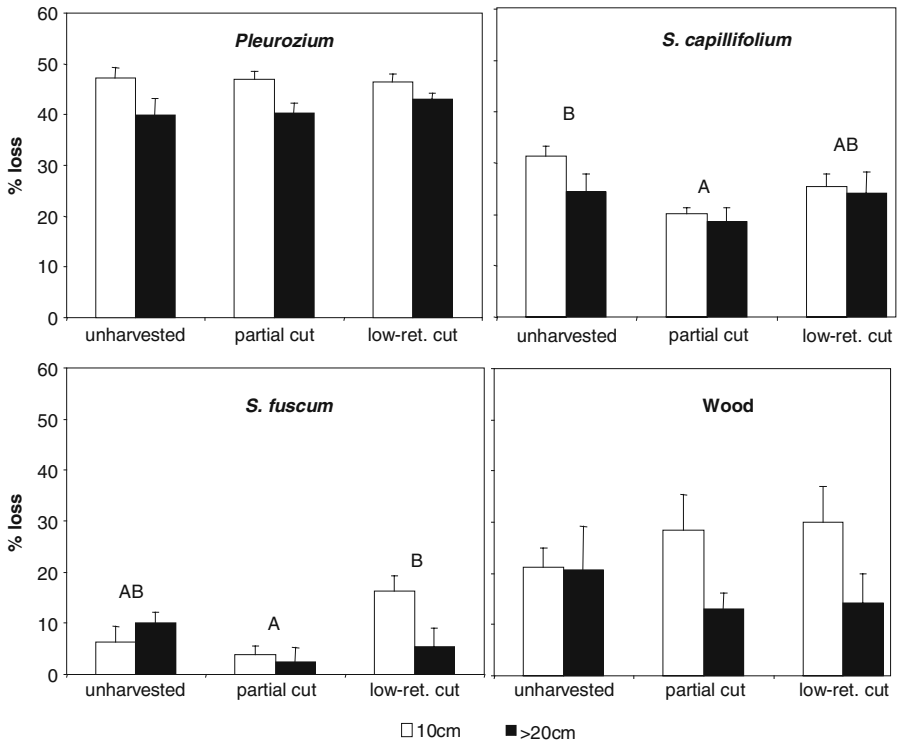

Fig. 1 Percent mass loss for different substrates (*P. schreberi, S. capillifolium, S. fuscum* and wood) in the different harvest treatments (unharvested, partial cut and low-retention cut) at two soil depths (10 cm and >20 cm). *Letters* indicate statistical differences among harvest treatments tested individually for each species

of lignin present; Hobbie 1996; Dorrepaal et al. 2005), and particularly for sphagna. The slow rate of decomposition of some sphagna is believed to be due to a variety of secondary metabolites, including polyphenols, and sphagnum acid (Verhoeven and Liefveld 1997), structural carbohydrates (Turetsky et al. 2008) and proteins and metabolic carbohydrates (Lang et al. 2009). Within sphagna, species with a lower C:N ratio appear to decompose faster (Bragazza et al. 2007; Turetsky et al. 2008), but this was not observed in this study. While it has been previously determined that non-*Sphagnum* mosses also decompose more slowly than their C:N ratio would predict (Berg 1984; Nakatsubo et al. 1997), the reasons for this remain unclear. In contrast, C:P ratio was more closely related to decomposition rate. Phosphorous is believed to be a rate-limiting factor in the decomposition of bryophytes (Moore and Basiliko 2006; Bragazza et al. 2007) and plants in general (Enriquez et al. 1993). Further studies are necessary to have a greater understanding of this relationship.

The role of the abiotic environment

The depth at which the decomposition bag was placed in the organic layer was the only significant

Table 3 Mean ± SE % mass loss of *S. capillifolium* and *S. fuscum* in different harvest treatments, in the two environments (patches of *P. schreberi* and *S. capillifolium*) and two soil depths (10 cm, >20 cm)

	Unharvested		Partial cut		Low-retention cut	
	10 cm	>20 cm	10 cm	>20 cm	10 cm	>20 cm
S.capillifolium						
S.capillifolium	35.98±1.83	17.7±4.06	21.28±2.17	15.39±3.45	28.12±4.32	16.18±5.64
P. schreberi	26.96±1.67	31.11±3.73	18.97±1.38	21.73±4.18	22.97±1.86	32.13±3.28
S. fuscum						
S.capillifolium	4.61±4.26	5.49±2.77	1.26±1.77	−0.32±4.50	16.87±1.57	10.85±2.23
P. schreberi	7.86±5.13	13.67±1.71	6.41±2.76	5.16±2.98	15.82±6.01	−0.15±6.20

factor influencing mass loss (greater mass loss at 10 cm than at >20 cm) other than substrate type. While temperature was not measured in this study, previous work has consistently shown that deep soil layers were cooler and more humid than shallow soil layers (Van Cleve et al. 1981; Klenk 2001; Simard et al. 2007) and this was probably the cause of the lower mass loss at the >20 cm depth, as temperature is one of the main driving forces in nutrient cycling in boreal forests (Van Cleve et al. 1981).

Other factors that would affect the abiotic environment did not influence mass loss overall; however mass loss of individual *Sphagnum* species was influenced by harvest treatment and patch environment, along with depth. While *S. capillifolium* mass loss appears to be reduced in partial harvest and low-retention sites, *S. fuscum* mass loss appears to have been both repressed by partial cuts, and stimulated by low-retention cuts, depending on patch type (environment) and depth. The *S. fuscum* results are difficult to interpret, particularly given the observation by Rice et al. (2006) that the efficiency of fungal conversion of *S. fuscum* mass to fungal mass varied considerably. They also remarked that in some cases the carbon assimilated from the *S. fuscum* and from the surrounding environment resulted in a net increase in fungal mass masking mass loss in *S. fuscum*. This may have been the case in this study as well. It would have been interesting to use a longer period of incubation because a great proportion of the material still remained after 26 months (>70%). Nevertheless, we think that it is likely that the trends observed would persist in time because the effect of treatment would vanish with canopy closure and because organic matter typically loses greater mass in the early stages of decomposition.

Sphagnum capillifolium mass loss was influenced by an interaction between environment (patch type, i.e. *P. schreberi* or *S. capillifolium*) and depth, with higher mass loss at >20 cm compared with 10 cm in *P. schreberi* and the inverse in *S. capillifolium*. Decomposition in the *P. schreberi* patch may be limited by dry conditions at 10 cm, as loosely held water along individual shoots (Silvola 1991) is lost repeatedly during the growing season. However, at the base of the colonies (at >20 cm), where the shoots are decomposing, the moss mat remains moist throughout the growing season (Price et al. 1997), and water would not be a limiting factor. In contrast, sphagna, particularly hummock sphagna such as *S. capillifolium*, retain water within individual shoots, and also within the tightly packed colony so that water content varies little with depth (Hayward and Clymo 1983; Schipperges and Rydin 1998). Therefore, potentially lower temperatures at greater depth could limit decomposition.

Interestingly, the mass loss rate of *P. schreberi* was high and consistent across all conditions, while that of both sphagna was lower and was influenced by several abiotic factors. The many secondary metabolites of sphagna are believed to make them unpalatable to most decomposers (Verhoeven and Liefveld 1997). Microfungi (Rice et al. 2006; Thormann 2006) and specialised bacteria (Kulichevskaya et al. 2007) have however been shown to decompose sphagna tissue. Mass loss rate in sphagna may be more influenced by variations in abiotic environmental conditions than that of feather mosses because sphagna are limited to a narrow group of decomposers, which may not adapt to different environmental conditions. Similarly, the decomposition of recalcitrant organic matter, such as *Sphagnum* spp. tissue (Hobbie 1996), has been shown to be more temperature-sensitive than that of labile organic matter (Conant et al. 2008).

The role of decomposition in forest succession

The increasing thickness of the forest floor in paludifying stands has important consequences in terms of stand productivity and nutrient cycling (Lavoie et al. 2007; Simard et al. 2007). The presence of sphagna has been shown to increase the rate of organic matter accumulation (Fenton et al. 2005), and canopy opening and water table rise facilitate the spread of sphagna over feather mosses (Fenton and Bergeron 2006). This study adds an additional piece to the puzzle, as the lower decomposition rates of sphagna compared to feather mosses in a forest environment suggest that sphagna contribute to forest floor accumulation not only via their high production rates (Silvola 1991; Williams and Flanagan 1998) but also through their low decomposition rates. Furthermore, low decomposition rates may promote the process of physically overtopping feather mosses on the forest floor, as the undecomposed material would cause sphagna colonies

to rise above the feather moss carpet, thus facilitating the typical "wave" overtopping pattern (Foster 1985; Fenton et al. 2007). On a global scale, the large variation in decomposition rates measured in this study is consistent with the findings of Cornwell et al. (2008) who reported that, across the globe, decomposition rates vary widely within climate types, and that changes in dominance among already co-existing plant groups determine how carbon cycles change more than climate itself.

Implications for forest management

Based on the single site examined in this study, forest harvest (partial and low-retention cut) had little effect on bryophyte decomposition. While these results are similar to those reported in studies using other forest and litter types (e.g., Prescott et al. 2000b), they are the first, to our knowledge, for bryophytes. In a landscape such as the Clay Belt, where paludification of black spruce forests is a dominant process, these results have important consequences since they suggest that forest harvesting, even with low-retention cuts, does not stimulate organic matter decomposition and carbon loss (Chertov et al. 2009). Although this is a positive result from a carbon storage perspective, it also causes a problem for forest managers (Simard et al. 2007) because paludified stands are less productive than unpaludified stands. Given the relatively high importance of substrate type and the limited effect of forest harvesting on the decay rates of bryophytes observed in this study, forest management practices in this forest type may have greater impacts on ecosystem carbon, forest productivity and nutrient cycles through their effect on moss colonization and succession than through their effect on soil environmental conditions.

Acknowledgements We gratefully acknowledge the assistance of Catherine Béland, Maude Beauregard, Suzie Rollin, and Mylène Francoeur in the field. Hervé Bescond also provided field support. The comments of three anonymous reviewers greatly improved the manuscript. This study was financed by a National Science and Engineering Research Council of Canada scholarship, the Lake Abitibi Model Forest, the NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management, the Canadian Forest Service, Action concertée fonds nature et technologies fonds forestier II, and by an NSERC partnership grant with forest industries and the Canadian Forest Service.

Appendix A

Description of the method of wet weight determination

The constant hydration state was established for each species using the method described in Frego and Carleton (1995), Mulligan and Gignac (2001). Briefly, a constant weight was assured by removing all of water from the bryophytes that is held in exterior macropores by centrifugation in a salad spinner. The water remaining in micropores and inside the plant can be said to be a constant amount. This state was determined by performing a series of standardization curves for each species, where shoots are initially soaked and weighed and then subjected to increasingly longer periods of centrifugation until a constant weight is achieved. Once the weight of the sample does not decrease with increasing centrifugation, only water held tightly in micropores and internal water (inside the hyalocyst cells of the sphagna) is present. The graph for *Pleurozium schreberi* is shown as an example (Fig. A1). This indicates the amount of centrifugation necessary to reach a standard hydration state that is comparable between samples and across time, and allows the comparison of wet weights. This method has the advantage of not assuming that different stems of the same species have a similar dry weight, and it does not damage the experimental stems via drying.

In order to determine the initial dry weight of the sample stems, and in order to compare it with the final dry weight, regression curves were constructed for each species by comparing the wet and dry weights of several bundles of stems that were centrifuged and then dried (Fig. A2).

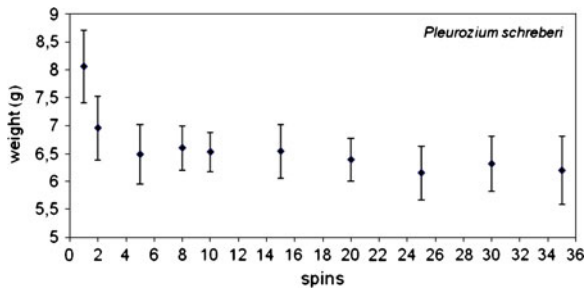

Fig. A1 Mean weight (g) and standard error of *Pleurozium schreberi* bundles after increasing numbers of spins in the salad spinner. Weight was constant after five spins, and experimental bundles were subsequently spun five time

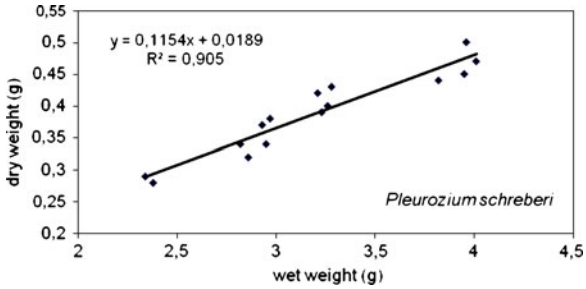

Fig. A2 Regression curve of wet (constant) and dry (oven dried) weights for *Pleurozium schreberi* with the regression equation

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