

Trade-offs in resource allocation among moss species control decomposition in boreal peatlands

Merritt R. Turetsky^{1*}, Susan E. Crow², Robert J. Evans³, Dale H. Vitt⁴ and R. Kelman Wieder⁵

¹Department of Integrative Biology, University of Guelph, Guelph, ON, Canada; ^{2,14}CHRONO Centre, Queen's University Belfast, Belfast, UK; ³National Renewable Energy Laboratory, Golden, CO, USA; ⁴Department of Plant Biology, Southern Illinois University, Carbondale, IL, USA; and ⁵Department of Biology, Villanova University, Villanova PA, USA

Summary

1. We separated the effects of plant species controls on decomposition rates from environmental controls in northern peatlands using a full factorial, reciprocal transplant experiment of eight dominant bryophytes in four distinct peatland types in boreal Alberta, Canada. Standard fractionation techniques as well as compound-specific pyrolysis molecular beam mass spectrometry were used to identify a biochemical mechanism underlying any interspecific differences in decomposition rates.
2. We found that over a 3-year field incubation, individual moss species and not micro-environmental conditions controlled early stages of decomposition. Across species, *Sphagnum* mosses exhibited a trade-off in resource partitioning into metabolic and structural carbohydrates, a pattern that served as a strong predictor of litter decomposition.
3. Decomposition rates showed a negative co-variation between species and their microtopographic position, as species that live in hummocks decomposed slowly but hummock microhabitats themselves corresponded to rapid decomposition rates. By forming litter that degrades slowly, hummock mosses appear to promote the maintenance of macropore structure in surface peat hummocks that aid in water retention.
4. *Synthesis*. Many northern regions are experiencing rapid climate warming that is expected to accelerate the decomposition of large soil carbon pools stored within peatlands. However, our results suggest that some common peatland moss species form tissue that resists decomposition across a range of peatland environments, suggesting that moss resource allocation could stabilize peatland carbon losses under a changing climate.

Key-words: boreal, climate change, decomposition, metabolism, mosses, non-structural carbohydrates, peatlands, resource allocation, *Sphagnum*, structural carbohydrates

Introduction

The boreal region covers about 10% of the world's vegetated surface, but contains 30% or more of the world's soil carbon (C) (Dixon *et al.* 1994; Vasander & Kettunen 2006). Peatland ecosystems occur mainly in boreal regions, and cover approximately 3.5 million km² of boreal and subarctic land (Vasander & Kettunen 2006). These northern peatlands have served as a long-term sink for atmospheric C throughout the Holocene, and today store an estimated 270–370 pg C, a substantial proportion of C stored in the boreal forest region (471 pg C, IPCC 2000; Vasander & Kettunen 2006). Given that northern peatlands currently store large C reservoirs and are experiencing rapid climate warming in many regions (Chapin *et al.* 2005), C exchange between boreal peatlands

and the atmosphere are particularly relevant to the global climate system (Frolking *et al.* 2006). Climate change may lead to enhanced decomposition in peatlands as microbial activity becomes less limited by water-saturated conditions (Freeman *et al.* 2001), possibly triggering positive feedbacks to future climate change. This prediction, however, does not consider variability in plant litter chemistry and/or the role of plant species in controlling ecosystem functions like C exchange, which could influence ecosystem responses to changing climatic conditions (Chapin *et al.* 2000; Hooper *et al.* 2000).

The mosses that dominate northern peatland ecosystems lack root structures and do not synthesize true lignin, and thus may not be able to control the distribution and quality of soil resources to the extent of vascular species (Chapin *et al.* 1990; Shaver & Aber 2004). However, moss litter has been shown to decompose more slowly than vascular plant litter across a variety of ecosystems (Berg 1984; Smith & Walton

*Correspondence author. E-mail: mrt@uoguelph.ca

1986; Hobbie 1996; Aerts *et al.* 1999; Liu *et al.* 2000; Thormann *et al.* 2001). In particular, *Sphagnum* species (the peat mosses) are thought to retard decomposition by producing acidity as a result of high cation exchange capacity (Spearing 1972) as well as recalcitrant tissue that resists microbial breakdown (reviewed by Van Breemen 1995; Turetsky 2003). The mechanisms controlling the recalcitrance of moss tissue in general are not well-understood (Aerts *et al.* 1999), but slow decomposition rates have been attributed to: (i) low-N concentrations, particularly given the high nutrient use efficiency of *Sphagnum* species (Aerts *et al.* 1999) and abundance of dead hyaline cells in their tissue, (ii) soluble phenolic compounds typically produced by some bryophytes (Rasmussen 1994), or (iii) insoluble phenolics (Wilson *et al.* 1989; Verhoeven & Liefveld 1997; Williams *et al.* 1998) that can mask cellulose and make tissue more resistant to microbial breakdown (Verhoeven & Liefveld 1997). Several studies also have demonstrated antimicrobial properties of mosses (Banderjee & Sen 1979; Basile *et al.* 1999) that can alter the decomposition of litter (Verhoeven & Toth 1995).

Given that many peatlands are dominated by a nearly continuous groundcover of mosses, peatland responses to future environmental change may be largely dictated by the physical and chemical qualities of dominant bryophytes (Shaw *et al.* 2003). Several studies have found wide differences in decomposition rates (Clymo 1965; Johnson & Damman 1991) and litter quality (Belyea 1996) among dominant peatland mosses. In particular, the common hummock species, *Sphagnum fuscum*, tends to decay more slowly than other *Sphagnum* spp. across a range of microhabitats (Rocheffort *et al.* 1990; Johnson & Damman 1991; Belyea 1996). While it seems clear that *Sphagnum* species typically decompose more slowly than other peatland plants, the underlying biochemical mechanisms controlling the recalcitrant nature of *Sphagnum* litter remains unclear (Aerts *et al.* 1999).

Understanding species-specific decay rates in relation to microhabitat, growth rates, and tissue chemistry may help identify the mechanisms controlling the slow breakdown of bryophyte litter, which drives peat accumulation in most northern peatlands. Here we used a full factorial, reciprocal transplant of eight dominant moss species into hummocks and hollows of four distinct peatland environments. This design allowed us to statistically separate the influence of species controls on decomposition from environmental controls. To identify a biochemical mechanism underlying any interspecific differences in decomposition rates, we used both standard fractionation techniques as well as compound-specific pyrolysis molecular beam mass spectrometry (pyr-MBMS) to quantify species variation in a variety of litter chemistry traits.

Methods

We selected four distinct peatland environments in central Alberta, which encompassed a wide range in peatland hydrology (ombrotrophic bogs vs. minerotrophic fens), vegetation (open vs. treed canopies), and pH (acidic vs. alkaline sites):

1. Anzac Bog (56°28.3' N, 111°2.5' W): an acidic bog dominated by *Sphagnum fuscum* in hummocks and *Sphagnum angustifolium* in hollows with a sparse canopy of *Picea mariana*. Mean annual temperature and precipitation at this site are 0.2 °C and 465 mm, respectively (1944–90 climate normals derived from the nearest climate station, Environment Canada 1998). Maximum depth of water-table position at the bog is approximately 60–70 cm beneath the moss surface, and the mean surface water pH is 4.6;
2. Anzac Permafrost/Thaw complex (56°28.4' N, 111°2.5' W): a permafrost peatland adjacent to the acidic bog dominated by a dense stand of *Picea mariana* with groundcover dominated by the feather moss, *Pleurozium schreberi*, as well as *Cladina* spp. Active layer depth is 50–60 cm, and the mean surface water pH is 4.4. There is active permafrost degradation in this site that creates internal and lateral thaw pools dominated by *Sphagnum riparium* and *S. angustifolium*;
3. Mariana Fen (55°32.2' N, 112°20' W): a weakly patterned poor fen with no tree cover dominated by *Sphagnum magellanicum* in hummocks and *Sphagnum jensenii* in hollows. Mean annual temperature and precipitation at this site are 0.8 °C and 463 mm, respectively (Environment Canada 1998). The water-table tends to be < 10 cm from the moss surface in hummocks and lies flush with the moss layer in hollows. The mean surface water pH at this site is 4.2; and
4. Upper Pinto Fen (52°50.0' N, 116°51' W): a calcareous extreme-rich fen with a sparse canopy of *Larix laricina* dominated by true mosses including *Scorpidium scorpioides* in hollows and *Tomenhypnum nitens* in hummocks. The mean annual temperature and precipitation at this site are 1 °C and 596 mm, respectively. The mean surface water pH at the site is 7.6.

RECIPROCAL TRANSPLANT DECOMPOSITION EXPERIMENT

We harvested stands of the most dominant hummock and hollow moss species in each site, including *S. fuscum* and *S. angustifolium* (bog), *S. magellanicum* and *S. jensenii* (poor fen), *P. schreberi* and *S. riparium* (permafrost-thaw complex), and *T. nitens* and *S. scorpioides* (rich fen), respectively. Hereafter, species are referred to either as *Sphagnum* or true mosses (including both true and feather mosses; *P. schreberi*, *T. nitens*, *S. scorpioides*). For each species, plants were sorted, cleaned of debris and fine roots, and dried at 40 °C. After removing the top 1 cm of each plant (i.e. the *Sphagnum* capitulum), 2-cm lengths of the top 1–3 cm of individual plants were collected and placed into peat traps following Wieder & Yavitt (1991) to mimic natural bulk density at the sites. Peat traps were reciprocally transplanted into multiple hummocks and hollows of each peatland environment. In both hummocks and hollows, peat traps were placed 10 cm beneath the moss surface. Samples were incubated *in situ* for 1 year and 3 years, after which three replicates were collected from each species × topography × peatland type combination. After ingrown roots were removed, samples were dried at 60 °C to a constant mass.

MOSS LITTER QUALITY

Fresh subsamples of each of the eight moss species used in the reciprocal transplant decomposition experiment were used to characterize moss litter chemistry. Triplicate subsamples of moss were analysed by a sequential chemical extraction procedure (Wieder & Starr 1998) to quantify five proximate fractions: soluble non-polars (fats, oils, waxes), hot water-soluble carbohydrates, water-soluble phenolics, holocellulose, and acid-insoluble material (mixture of

tannins, lignins). Fractions are expressed on an ash-free dry mass basis following measurement of organic matter concentrations (via loss on ignition at 450 °C) of each proximate residue. One subsample of homogenized litter for each species was used to determine carbon and nitrogen concentrations by combustion at 1200 °C on a Carlo Erba NA1500, and total phosphorus concentrations by Kjeldahl digestions and colorimetric determination on a Technicon Autoanalyzer II.

Pyrolysis molecular beam mass spectrometry (pyr-MBMS) was used to characterize the biomolecular composition of initial moss litter. For these analyses, we also included two additional species commonly found in our sites (*Drepanocladus revolvens* and *Polytrichum strictum*) to increase the sample size of true mosses. Triplicate subsamples of homogenized litter from each species were rapidly heated in a flowing helium atmosphere at 500 °C at ambient pressure in a quartz reactor, which was connected to the inlet of a molecular beam mass spectrometer (Evans & Milne 1987). Mass spectral data from 15–200 amu were acquired using 22 eV electron impact ionization. We processed data by averaging the 20–30 spectra that accumulated during each sample pyrolysis. To correct for analytical variation, the absolute signal of each mass was converted to relative intensity by dividing each mass intensity by the sum of all (15–200) mass intensities for that sample. The data as presented is analogous to concentration data (e.g. weight %), but without calibration the results are only semi-quantitative, appropriate for the identification of trends only within the sample set.

Lastly, to examine the relationship between litter quality and chemistry, and the structural features of moss tissue, we performed scanning electron microscopy (SEM) on moss segments using a Hitachi S-570 SEM. Specimens were dehydrated in an alcohol series, dried in a Polaron E-3100 critical point drier, mounted on aluminum stubs, and coated with 12 nm of gold palladium in a Polaron SC 7640 sputter coater prior to analysis.

GROWTH RATES

To provide potential linkages between moss growth rates, litter chemistry, and decomposition rates, we quantified the productivity of a dominant hummock (*S. fuscum*) and hollow (*S. riparium*) species at the Anzac bog and permafrost sites, respectively. These two species were selected due to their widely different litter chemistry and decomposition rates from our initial results. Vertical growth rates of *S. fuscum* were estimated using the cranked wire method (Clymo 1970) and are presented in Vitt *et al.* (2003; Anzac East site). Briefly, in June of 2000, we established five 1-m² plots in hummocks at the bog site dominated by *S. fuscum* and placed 50 cranked wires in each plot. Vertical growth was determined as the difference in the length of each wire exposed above the *Sphagnum* surface at the beginning (early June) and end (mid-October) of the growing season. Vertical growth rates were multiplied by the average bulk density of surface *S. fuscum* (excluding the capitula) at the same site to estimate rates of net primary production (NPP).

We used annual growth markers created by snowpack conditions (Camill *et al.* 2001) to estimate the NPP of *S. riparium*. In 2001, we harvested *S. riparium* plants from five 10 cm² plots and sectioned individual stems according to their previous year's growth. Vertical growth rates were multiplied by the average bulk density of surface *S. riparium* (excluding developing leaves in the capitula) at the same site to estimate rates of NPP.

STATISTICAL ANALYSES

Litterbag decomposition rates were analysed as proportions of original mass remaining (final mass of moss in peat trap ÷ initial mass of moss

in peat trap; hereafter referred to as *remaining mass*) following the 1-year and 3-year field incubations for each species × site × topography combination. Proportions were natural log transformed and analysed using a single general linear model (GLM) with data constrained with 100% *remaining mass* at time zero. We analysed site (bog, permafrost bog, poor fen, rich fen), topographical position (hummock, hollow), and species (6 spp.) as fixed factors, and time (0, 1, and 3 year) as a continuous variable. We started with a full model that included site, topography, species, time, and all possible interactions, and removed terms sequentially from the model in a backward, stepwise procedure based on changes in the likelihood version of Mallows's *Cp* statistic (Insightful 2001). The exponential rate constant (*k*; in units year⁻¹) was determined as the slope of *remaining mass* vs. time. The GLM was designed to explore the effects of species, site, or topography on *k*, which were represented by two-way interactions of each variable with time.

Key pyr-MBMS masses were determined by principal component analysis and by their known importance in biomass pyrolysis (Evans & Milne, 1987). All 200 mass variables were investigated using principal component analysis, which allowed visualization of clustering among the variables and enabled chemical interpretation and the selection of the key mass variables that can be used to compare samples. Mass variables that were called out in this work are *m/z* 126 (C₆H₆O₃, 5-hydroxymethylfurfural), which is a pre-dominant carbohydrate pyrolysis marker. It has higher pre-dominance in hexose monosaccharides than in hexan polysaccharides. Hereafter, *m/z* 126 is referred to as fructose but is a general indicator of C6 sugars. The pyrolysis of polymeric pentosans give high signals of *m/z* 114 (C₅H₆O₃) and in this work it also correlated with the group of products associated with carbohydrates. The methoxyphenols were all highly correlated with each other and were represented at *m/z* 164 (C₁₀H₁₂O₂, isoeugenol). We also investigated *m/z* 67 and 117 (indicative of N containing biopolymers), 94, 120, and 124 (indicative of phenolics), 91 and 105 (fragment ion of aromatics), and 60, 73, 144 (indicative of cellulose).

Correlation tests were used to explore the relationship between select pyr-MBMS products and proximate fractions. We examined the influence of litter chemistry (concentrations of N, P, proximate fractions; C/N and acid-insoluble material/N; pyr-MBMS products), and climatic (soil moisture content upon collection as a proxy for field moisture conditions, mean annual temperature and precipitation from the nearest climate station to each site; Environment Canada 1998) variables on *k* using forward selection multiple regression models.

Results

The final, reduced model of *remaining mass* indicated significant effects of species × time ($P < 0.001$; d.f. 5; $F = 10.255$) and topography × time ($P < 0.002$; d.f. 1; $F = 14.32$). In general, species that occupy peatland hummocks (i.e. *S. fuscum*, *S. magellanicum*) tended to decompose more slowly than species that live in hollows (i.e. *S. riparium*, *S. jensenii*), though this pattern did not hold for the rich fen species (Fig. 1). Averaged across species and peatland sites, decomposition was significantly faster in hummocks ($k = 0.078 \pm 0.006$) than in hollows ($k = 0.056 \pm 0.005$; $n = 240$). Site terms (either single or interaction terms; bog, poor fen, etc.) were not retained during the model procedure, indicating that decomposition rates did not vary among the bog, poor fen, rich fen and permafrost/thaw sites when averaged across species and microenvironments.

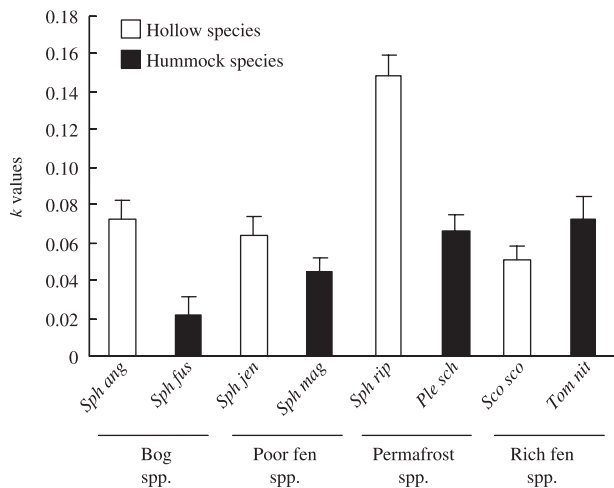


Fig. 1. Mean k values for eight dominant moss species transplanted into both hummocks and hollows of four peatland sites in Alberta, Canada (Table 1). Data are means \pm 1SE, where error represents variability in turnover rates among sites and microtopographic positions (hummocks, hollows).

During the first year of *in situ* decomposition, mass losses exceeded total initial concentrations of soluble material (sum of soluble non-polars, hot water-soluble carbohydrates, and water-soluble phenolics) in moss tissue. Therefore, mass losses during the entire experiment reflect decomposition beyond what could be attributed to leaching losses alone.

Moss tissue showed wide differences in litter chemical variables measured by chemical fractionation across species (Table 1). *Sphagnum* species had greater concentrations of holocellulose and lower concentrations of soluble non-polars and N than the other moss species. The hummock species *S. fuscum* and *P. schreberi* had the lowest C/N. The hollow species *S. jensenii*, *S. riparium* and *S. angustifolium* had the lowest concentrations of acid-insoluble material, while the hummock species *S. fuscum* and *S. magellanicum* had the greatest concentrations of water-soluble phenolics.

Compound specific pyr-MBMS revealed relationships between relative amounts of metabolic carbohydrates (fructose, 5-hydroxymethyl furfural, m/z 126) and structural carbohydrates (pentosans, m/z 114) (Fig. 2) across moss species. Across *Sphagnum* species, there was a negative relationship between relative amounts of metabolic and structural carbohydrates, while the true moss species showed a positive relationship (Fig. 2). Across all moss species, relative amounts of metabolic carbohydrates were positively correlated to concentrations of hot water-soluble carbohydrates derived from proximate analysis (Pearson correlation coefficient = 0.87; $P = 0.005$; $n = 8$). Relative amounts of structural carbohydrates were positively correlated to concentrations of the proximate fraction acid-soluble carbohydrates (Pearson correlation coefficient = 0.90; $P = 0.003$; $n = 8$).

We used multiple regression models to examine the influence of litter chemistry and climate (mean annual temperature and precipitation, sample soil moisture content) variables on litter decomposition rates. The ratio of metabolic

Table 1. Litter chemistry variables for the eight dominant peatland moss species used in the reciprocal transplant decomposition experiment, including (in order) *Sphagnum fuscum*, *Sphagnum angustifolium*, *Sphagnum magellanicum*, *Sphagnum jensenii*, *Sphagnum riparium*, *Pleurozium schreberi*, *Tometyphnum nitens*, and *Scorpidium scorpioides*. Proximate organic matter quality fractions, including holocellulose, acid-insoluble material, soluble non-polars, hot water-soluble carbohydrates, and hot water-soluble phenolics, are expressed in mg g^{-1} ash-free dry mass. Data for these proximate fractions are means (\pm 1SE), where error terms represent variability among triplicate homogenized tissue samples. N and P concentrations are in mg g^{-1} dry mass; C, N and P concentrations were determined on one homogenized sample per moss species

	Sph fus	Sph ang	Sph mag	Sph jen	Sph rip	Ple sch	Tom nit	Sco sco
Holocellulose	641.03 (8.39)	651.33 (43.89)	619.48 (13.21)	655.39 (12.84)	551.73 (25.67)	418.52 (4.72)	543.46 (1.53)	421.53 (0.15)
Acid-insoluble material	349.46 (107.77)	126.79 (14.76)	359.84 (144.38)	154.07 (14.34)	135.45 (13.57)	542.59 (201.83)	308.60 (2.61)	383.97 (14.18)
Soluble-nonpolars	46.03 (4.09)	46.68 (16.36)	45.76 (1.79)	41.28 (2.91)	41.74 (1.88)	57.90 (0.47)	62.50 (1.97)	73.57 (1.05)
Hot water-soluble carbohydrates	33.30 (3.04)	47.83 (14.13)	43.50 (7.99)	74.05 (11.35)	124.75 (19.45)	56.77 (4.05)	32.41 (0.32)	34.13 (1.16)
Hot water-soluble phenolics	4.19 (0.31)	3.27 (0.12)	4.15 (0.29)	2.24 (0.19)	3.86 (0.46)	3.32 (0.56)	1.02 (0.05)	1.07 (0.006)
N	9.44	8.64	8.63	5.93	7.61	12.42	8.80	12.36
P	0.42	0.54	0.44	0.21	1.07	1.49	0.37	0.21
C/N	53.14	58.81	58.38	83.25	66.49	40.62	55.89	38.47

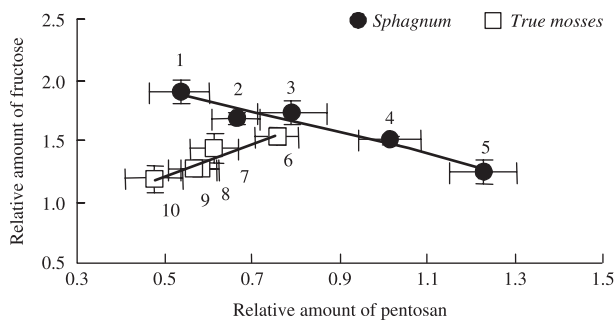


Fig. 2. Relationship between metabolic (fructose) and structural (pentosans) carbohydrates among dominant boreal mosses determined by pyrolysis molecular beam mass spectrometry (pyr-MBMS). We analysed two additional true moss species (*Drepanocladus revolvens* and *Polytrichum strictum*) by pyr-MBMS that were not included in our decomposition experiment in order to increase our sample size in this moss group. Regression model results for *Sphagnum* were: $R^2 = 0.92$; $F = 45.80$; $P = 0.007$; slope = $-0.88 (\pm 0.13)$; intercept = $2.37 (\pm 0.11)$ and for the other species (true and feather mosses): $R^2 = 0.85$; $P = 0.016$; $F = 24.42$; $P = 0.02$; slope = $1.32 (\pm 0.27)$; intercept = $0.56 (\pm 0.16)$. Species are labelled: 1 = *S. riparium*; 2 = *S. angustifolium*; 3 = *S. jensenii*; 4 = *S. magellanicum*; 5 = *S. fuscum*; 6 = *P. schreberi*; 7 = *T. nitens*; 8 = *D. revolvens*; 9 = *P. strictum*; 10 = *S. scorpioides*.

to structural carbohydrates was the only significant predictor of *in situ* decomposition across all eight moss species, and explained 84% of variability in k values (Fig. 3). The relationship between these biochemical constituents and k was strengthened when the true moss species were excluded from the analysis (*Sphagnum* only: $R^2 = 0.94$; $P = 0.0062$; slope = 0.05 ± 0.01 , $t = 6.92$). Neither climatic variables nor additional litter chemical variables (acid-insoluble material, N or P concentrations, C/N, acid-insoluble material/N) significantly predicted k values (Fig. 4).

The two *Sphagnum* species, *S. fuscum* and *S. riparium* (Fig. 1) represent the most dominant moss species in two peatland types, bogs and internal lawns (permafrost thaw), respectively.

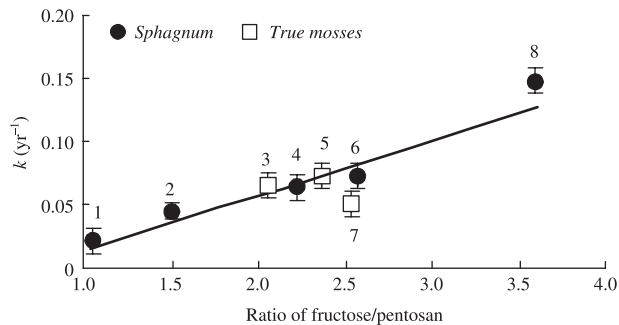


Fig. 3. Relationship between the ratio of fructose/pentosan carbohydrates and k values across moss species. Values are denoted as *Sphagnum* or true moss species. Across all data, regression model results were $R^2 = 0.83$; $P = 0.0017$; $F = 29.25$; slope = 0.044 ± 0.01 ; intercept = -0.03 ± 0.02 . Species are marked: 1 = *S. fuscum*; 2 = *S. magellanicum*; 3 = *P. schreberi*; 4 = *S. jensenii*; 5 = *T. nitens*; 6 = *S. angustifolium*; 7 = *S. scorpioides*; 8 = *S. riparium*.

In our reciprocal transplant experiment, decomposition rates varied the most between these two species (Fig. 1). During a single growing season, we quantified vertical growth and NPP of *S. fuscum* and *S. riparium* in their native habitats, which are located adjacent to one another. Vertical growth rates averaged 0.4 ± 0.02 and 5.6 ± 0.3 cm/year, and annual NPP (estimated by multiplying vertical growth rates by bulk density) averaged 154 ± 6 and 189 ± 14 g/m²/year for *S. fuscum* and *S. riparium*, respectively. Scanning electron microscopy revealed striking differences in the physical appearance of litter from the two species as *in situ* decomposition progressed. After 3 years, little evidence of structural damage to *S. fuscum* tissue was present in all of the subsamples analysed (Fig. 5). In contrast, after just 1 year, *S. riparium* experienced significant degradation to both stem and leaf tissue (Fig. 5). Characterization of litter chemistry showed that *S. fuscum* had the greatest relative amount of structural carbohydrates, while *S. riparium* had the greatest amount of metabolic carbohydrates (Figs 2, 3).

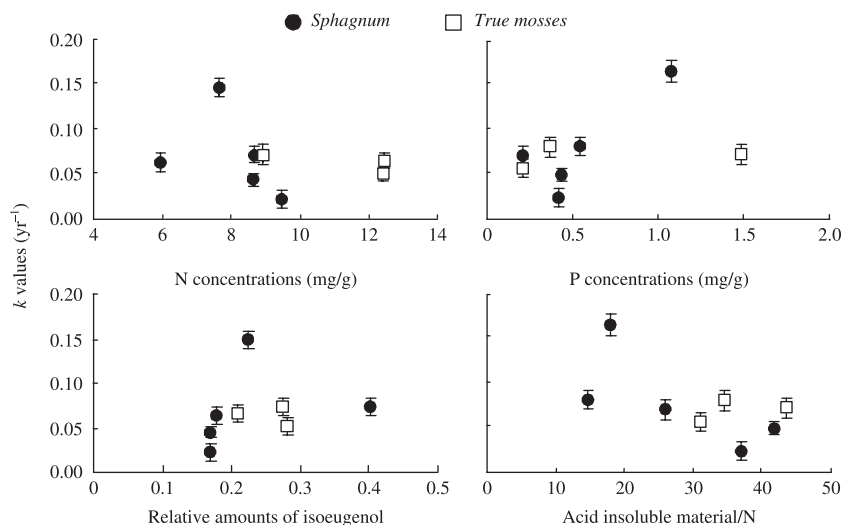


Fig. 4. Relationships between litter chemistry variables (Table 1) and k values across moss species, including (a) N concentrations, (b) P concentrations, (c) levels of the phenolic isoeugenol, and (d) acid-insoluble material/N.

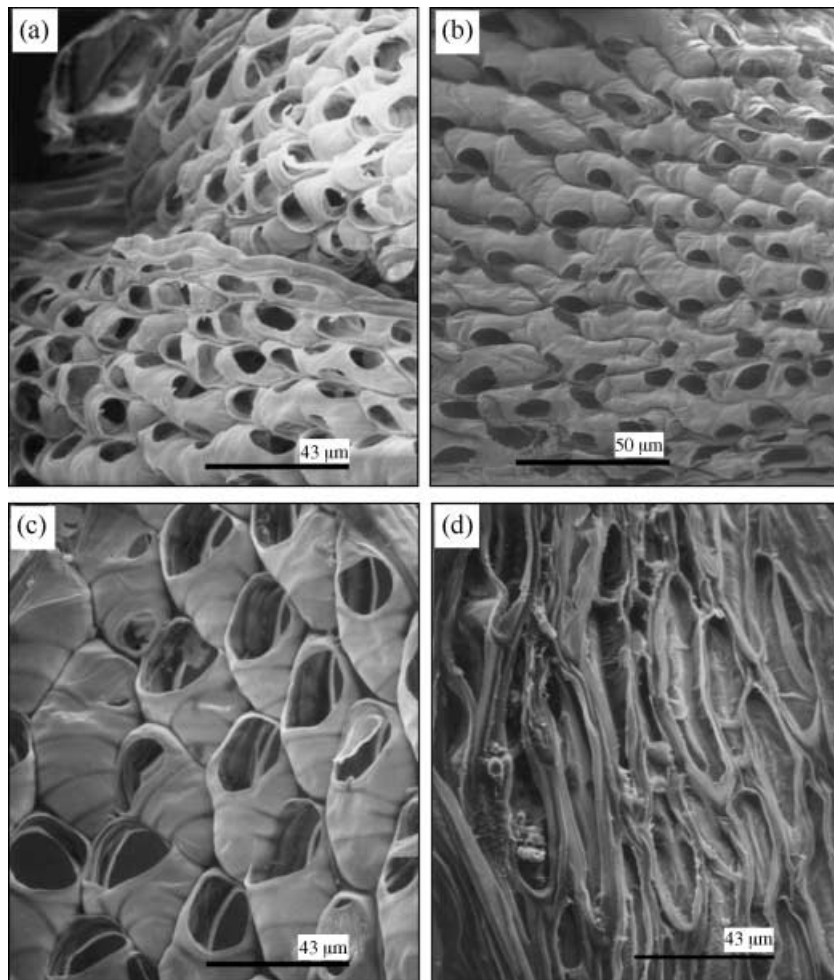


Fig. 5. Scanning electron micrographs of *Sphagnum fuscum* (a) prior to the field incubation, and (b) after 3 years of field incubation. *Sphagnum riparium* (c) prior to the field incubation, and (d) after 1 year of field incubation.

Discussion

Species that thrive in peatland hollows tend to have higher metabolic activity and grow more quickly than hummock species (Pakarinen & Vitt 1974; Luken 1985; Camill *et al.* 2001), although this trend can be reversed during drought (Gerdol *et al.* 1996). Here, vertical growth rates and rates of NPP of *S. riparium* were approximately 90% and 20% faster than the dominant hummock species *S. fuscum*. Hollow species also maintained high relative amounts of metabolic carbohydrates and low amounts of structural carbohydrates (Fig. 2), and biomass produced by these species was more rapidly degraded during an *in situ* decomposition experiment (Figs 3, 5). Alternatively, hummock mosses that tend to grow more slowly (Johnson & Damman 1991; Belyea 1996; Waddington *et al.* 2003) allocated resources to maintain high amounts of structural carbohydrates, which were strongly related to slow decomposition rates across a diversity of soil environments (Figs 2, 3).

Fast specific growth rates of plant and animal species have been predicted to lead to unrecognized trade-offs (Arendt 1997; Elser *et al.* 2000). Here, compound specific analyses revealed a negative relationship between metabolic (fructose) and structural (pentosan) carbohydrates among *Sphagnum*

species. Given that the majority of non-structural carbohydrates are derived from recent photosynthesis, we believe that this relationship represents a previously unreported trade-off of resource allocation by mosses, whereby a *Sphagnum* species can devote resources to maintain high levels of simple sugars to sustain fast growth or high levels of structural carbohydrates, but not both. Interestingly, the true moss species we investigated do not appear to face a trade-off in carbohydrate partitioning, but rather exhibited a positive correlation between metabolic and structural carbohydrates (Fig. 2). This trend suggests that while there were differences in the total amount of carbohydrates among true moss species, there was little variation in the partitioning of these resources into different types of carbohydrates (Fig. 2). It is possible, however, that these true moss species face trade-offs between their allocation to carbohydrates as a whole and other organic compounds that we did not examine, such as proteins or lipids. Alternatively, our results could represent different carbohydrate partitioning strategies within and among genera of mosses. The true moss species represent a number of distinct genera, whereas the *Sphagnum* species we analysed represent a single genus. Our data are, therefore, consistent with variation among species in carbohydrate allocation and variation among higher taxonomic levels (i.e. genera) in carbohydrate acquisition.

Despite potential differences in resource allocation among these peatland moss groups, the ratio of metabolic to structural carbohydrates was a strong predictor of decomposition rates across all of the species we examined (Fig. 3). Thus, acquisition and allocation strategies that influence carbohydrate chemistry in moss tissue have consequences for ecosystem-level carbon cycling by influencing litter chemistry and decomposition rates.

Sphagnum species thrive in nutrient poor environments such as bogs, and generally have high nutrient use efficiency (Aerts *et al.* 1999). Consequently, low-N concentrations often are thought to be responsible for the slow decomposition of *Sphagnum* tissue (Aerts *et al.* 1999). Clymo & Hayward (1982) found strong relationships between rates of decomposition and N concentrations among peatland plant species, including several *Sphagnum* species. Additionally, increasing levels of atmospheric N deposition stimulated CO₂ and DOC production in peat from European bogs (Bragazza *et al.* 2006). However, any differences in nutrient availability between our sites (bog, poor fen, rich fen, permafrost forest/thaw feature) had little influence on decomposition rates, as litter mass losses surprisingly did not differ between sites independent of species or microtopography. Moreover, while *Sphagnum* species had lower N concentrations than other mosses (Table 1), N concentrations, C/N, or acid-insoluble material/N were not significantly related to litter decomposition rates (Fig. 4, C/N data not shown).

High concentrations of inhibitory compounds such as phenolics in *Sphagnum* tissue also are thought to inhibit organic matter decomposition in peatlands (Verhoeven & Liefveld 1997). Herbivory on moss, particularly *Sphagnum*, is thought to be very low (Clymo & Hayward 1982), possibly due to concentrations of secondary metabolites that deter feeding (Gerson 1982). In general, allocation of carbon-based resources such as phenolics is typical of species living in low-nutrient environments (Shaver & Aber 2004). Among the moss species we analysed, we observed a wide range of concentrations of acid-insoluble material (representing a mixture of condensed tannins, insoluble phenolics, etc.) as well as individual phenolic compounds identified by pyr-MBMS. However, concentrations of phenolics or their ratios with N were not related to litter decomposition rates (Fig. 4). Yavitt *et al.* (1997) also found that acid-insoluble material/N was not a strong predictor of C mineralization across several temperate peatlands.

Several studies have found linkages between C mineralization in peat and different types of carbohydrates such as water-soluble vs. acid-soluble carbohydrates (Updegraff *et al.* 1995; Yavitt *et al.* 1997). Building on these past studies and our results, it is tempting to frame our results in resource-based theories of allocation. Species growing in resource poor settings, such as 'bog-like' hummocks, generally are expected to allocate more resources to defence compounds, grow slowly and produce costly tissues with slow within-plant turnover rates (Coley *et al.* 1985). Our results show that hummock species maintained a high investment in structural carbohydrates (Fig. 2) that in turn retarded litter breakdown (Figs 3, 5).

This was particularly true for the common hummock species *S. fuscum*, which also had slower growth rates than *Sphagnum riparium* in adjacent habitats. Conversely, plants from high-resource environments are expected to allocate more energy towards rapid growth. Here we show that hollow species maintained high concentrations of metabolic carbohydrates (Fig. 2), likely to support fast growth rates. Similar to other studies (Camill 1999), the hollow species *S. riparium* had rapid rates of vertical stem elongation although differences in NPP between *S. riparium* and the hummock species *S. fuscum* were smaller due to interspecific differences in branching morphology and plant density. However, all hollow species we investigated generally corresponded to labile litter that decomposed quickly across a range of peatland types (Figs 3, 5), providing an important potential link between moss physiology, biochemistry and ecosystem-scale litter turnover.

These biochemical trends also could be adaptive for mosses in maintaining critical ecohydrologic processes at the surface of peatlands. *Sphagnum* species that thrive in hummocks are known as drought avoiders, as they maintain a high water retention capacity through a number of structural and morphologic characteristics such as dense capitula, spreading and hanging branches, and hyaline cells that store water (Rydin & McDonald 1985). It seems likely that this strategy requires a high investment in structural compounds, although we did not quantify morphologic traits such as hyaline cell density across species. However, Malcolm (1996) concluded that leaf curvature, pore diameter and possibly the relationship between hyaline cell shape and fibril frequency were the most important morphological traits across *Sphagnum* species contributing to water retention.

Interestingly, decomposition rates in this study showed a negative covariation between species and their microtopographic position, as species that live in hummocks decomposed slowly but hummock microhabitats themselves corresponded to rapid decomposition rates (see also Belyea 1996). By forming litter that degrades slowly, hummock mosses appear to promote the maintenance of pore size-structure in surface peat hummocks (Johnson *et al.* 1990) that aid in water retention. Without this species-level biochemical control on decomposition rates, organic matter in the more aerobic hummock microenvironments would degrade more rapidly, compromising the water retention capacity that allows some moss species to thrive well-above the water-table (Rydin 1985). Conversely, species thriving in hollows have a looser canopy structure and overall less well-developed water retention abilities, and tend to be characterized as drought avoiders. Rather than investing resources into structural materials, instead these species appear to maintain higher concentrations of metabolic sugars than hummock species presumably to support fast growth rates.

To our knowledge, this study is the first to examine potential trade-offs in resource allocation among mosses in relation to tissue recalcitrance. As a strong predictor of decomposition rates, the trade-off in carbohydrate allocation has consequences for patterns of organic matter turnover and

likely contributes to hummock and hollow maintenance in many peat accumulating environments. Generalities often made about *Sphagnum* species producing highly recalcitrant litter (cf. Van Breemen 1995) ignore the considerable variation in growth strategies and allocation of carbohydrate resources present across this important genus. Our results show wide variation in litter chemical traits and decomposition rates among dominant peatland mosses. Mosses should not be considered as a single functional group, rather we argue that peatland functional assessments should be based on microtopography (hummock vs. hollow species) to confer important information about growth rates, physiology and litter chemistry. However, given that little is known about species, population or individual variation (i.e. phenotypic plasticity) in moss traits, further research is needed to explore relationships between key moss traits and environmental parameters. Key traits that should be investigated include growth rates, carbohydrate allocation and other biochemical traits, albedo, response to drought stress, and branching morphology and plant density, which affect water retention.

Species controls on decomposition rates are probably large during initial stages of decomposition due to differential turnover rates of labile vs. recalcitrant organic matter pools. The majority of organic matter in peatlands is decomposed in surface peat layers above the water-table (i.e. in the acrotelm) over a relatively short time scale (i.e. years to decades). Over time, however, as the most easily degraded organic matter pools are depleted, environmental factors (temperature, moisture saturation) become increasingly dominant controls on decomposition rates (Trofymow *et al.* 2002). Nonetheless, evidence of species-specific trends in decomposition continues to persist in peatlands over long time scales, ultimately causing certain moss species to be preserved more preferentially than other species in peat stratigraphies.

Our reciprocal transplant experiment shows that differences in the environment do little to influence the degradation of litter formed by hummock mosses such as *S. fuscum* and *S. magellanicum*. Warmer, drier climatic conditions and lower water-table position in peatlands may increase the competitive ability and habitat available for moss species that dominate hummocks, which will stimulate the accumulation of recalcitrant organic matter in surface peat layers (Figs 2, 3). By reciprocally transplanting species into a wide range of environmental conditions present in western Canadian peatlands (wet to relatively dry conditions, acidic to calcareous conditions), our results suggest that litter formed by hummock mosses is not likely to decompose readily, even under drier and less acidic conditions that are more conducive to organic matter turnover. Thus, moss species-level controls on litter chemistry and decomposition rates could help to moderate peatland carbon losses under the drier climatic regimes predicted for many boreal and subarctic regions.

Peatland mosses today occupy relatively narrow niches defined largely by height above the water-table and pH (Gignac *et al.* 1991; Bragazza 1997). However, the geographical distributions of important boreal moss species are predicted to shift under future climate change (Gignac & Vitt 1993). We

suggest that long-term carbon sequestration in boreal peatlands has occurred as moss species have developed strategies of resource utilization (including water) and carbon accumulation that allow them to persist in different chemical and physical microhabitats. These growth strategies, in turn, influence litter chemistry and decomposition, and provide a biological mechanism for the development and persistence of hummocks and hollows in peatlands, which increase the microhabitat diversity of these ecosystems. The trade-offs that we report here for living moss species undoubtedly have developed over long periods of time, and will stabilize peatland carbon reservoirs under changing climatic conditions. However, moss allocation strategies will be less effective in promoting carbon sequestration in peatlands if relatively rapid climate changes at high latitudes displace keystone species such as *S. fuscum* or outpace the adaptive capacity of mosses to tolerate environmental change.

Acknowledgements

Authors thank Kim Magrini for assistance with pyrolysis mass spectrometry measurements, Shelly Manchur, John Navaratnam, Andrew McAdam, Kara Powell and Shannon Ripley for assistance with field work, Kim Scott for assistance with nutrient concentrations, and Mike Waddington, Dan Thompson, Sarah Hobbie, and Joseph Yavitt for comments and discussion on a previous version of this manuscript.

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Received: 2 April 2008; Accepted: 4 August 2008.

Handling Editor: Jonathan Newman