

Litter Decomposition in Temperate Peatland Ecosystems: The Effect of Substrate and Site

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ABSTRACT

The large accumulation of organic matter in peatlands is primarily caused by slow rates of litter decomposition. We determined rates of decomposition of major peat-forming litters of vascular plants and mosses at five sites: a poor fen in New Hampshire and a bog hummock, a poor fen, a beaver pond margin and a beaver pond in Ontario. We used the litterbag technique, retrieving triplicate litterbags six or seven times over 3–5 years, and found that simple exponential decay and continuous-quality non-linear regression models could adequately characterize the decomposition in most cases. Within each site, the rate of decomposition at the surface was generally *Typha latifolia* leaves = *Chamaedaphne calyculata* leaves = *Carex* leaves > *Chamaedaphne calyculata* stems > hummock *Sphagnum* = lawn/hollow *Sphagnum*, with exponential decay constant (k) values generally ranging from 0.05 to 0.37 and continuous-quality model initial quality (q_0) values ranging from 1.0 (arbitrarily set for *Typha* leaves) to 0.7 (*Sphagnum*). In general, surface decay rates were slowest at the bog hummock site, which had the lowest water table, and in the beaver pond, which was inundated, and fastest at the fens. The continuous-quality model site decomposition parameter

(u_0) ranged from 0.80 to 0.17. Analysis of original litter samples for carbon, nitrogen and proximate fractions revealed a relatively poor explanation of decomposition rates, as defined by k and q_0 , compared to most well-drained ecosystems. Three litters, roots of sedge and a shrub and *Typha* leaves, were placed at depths of 10, 30 and 60 cm at the sites. Decomposition rates decreased with depth at each site, with k means of 0.15, 0.08 and 0.05 y^{-1} at 10, 30 and 60 cm, respectively, and u_0 of 0.25, 0.13 and 0.07. These differences are primarily related to the position of the water table at each site and to a lesser extent the cooler temperatures in the lower layers of the peat. The distinction between bog and fen was less important than the position of the water table. These results show that we can characterize decomposition rates of surface litter in northern peatlands, but given the large primary productivity below-ground in these ecosystems, and the differential rates of decomposition with depth, subsurface input and decomposition of organic matter is an important and relatively uncertain attribute.

Key words: bog; fen; sedge; moss; shrub; roots.

INTRODUCTION

The accumulation of large amounts of organic matter in peatland ecosystems (>100 kg m⁻²) rep-

resents an imbalance between input of C from plant production and its export from the peatland as carbon dioxide, methane or dissolved organic carbon, which are the products of the decomposition of plant tissues and organic matter in the soil (Gorham 1991). Rates of net primary production in

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peatlands are generally small (for example, Campbell and others 2000; Moore and others 2002), as are rates of net ecosystem exchange of CO₂ and soil respiration (Frolking and others 1998). Thus, the accumulation of organic matter in peatlands is generally ascribed to slow rates of decomposition associated with cool temperatures, anoxic conditions, functionally limited decomposer communities, and litter and organic matter substrates that are naturally slow to decompose.

Several studies have used the litter-bag technique to determine the short-term (generally <3 years) rate of decomposition of litter in northern peatlands and the main controls on these rates. Rates have been found to be slow, with exponential decay (k) values of generally less than 0.3 y⁻¹ for litters placed on the peat surface (Moore and Basiliko 2006). Controls on rates of decomposition generally fit within the broad climate and litter chemistry postulated by Aerts (1977). Although there may be an over-riding macro-climate control, the evidence for a hydrologic control on decomposition rates in peatlands is mixed: there may be a stimulation of decomposition by short periods of waterlogging whereas prolonged flooding may slow rates (for example, Day 1983; Wylie 1987; Lockaby and others 1996; Baker and others 2001). In a comparison of three pairs of adjacent upland and peatland sites in eastern Canada, Moore and others (2005) were unable to detect major differences after 6 years in decomposition rates of ten foliar litters. The effect of litter chemistry, such as N concentration and lignin content, on decomposition rates has been postulated (for example, Limpens and Berendse 2003; Moore and others 2005) but may be of limited applicability in peatlands where moss chemistry may play an important role (Clymo 1965; Banerjee and Sen 1979; Painter 1991; Johnson and Damman 1993; Verhoven and Toth 1995; Verhoven and Liefveld 1997; Turetsky 2003).

Most litter-bag studies have focused on tissues placed on the peat surface, whereas considerable plant productivity may enter the peat ecosystem below-ground. In many peatlands, the majority of total plant biomass is allocated belowground, presumably to capture nutrients and water resources (for example, Wallén 1986; Backéus 1990; Sjörs 1991; Saarinen 1996; Laiho and Finér 1996). The vertical variation in temperature and aerobic/anaerobic conditions within the peat profile may exert a profound influence on decomposition rates. Johnson and Damman (1991) noted a decrease in the rate of *Sphagnum* decomposition over 22 months when samples were moved from the

peat surface to a depth of 50 cm and Belyea (1996) observed changes in decomposition rate when samples were transplanted between the surface and the water table. In Alberta fens, Thormann and others (2001) determined decomposition rates of roots and rhizomes placed 3–10 cm beneath the peat surface.

Although these studies provide insight into decomposition rates of peat-forming tissues, they generally suffer from being of short duration (generally <3 years), being restricted to a narrow range of sites and focusing mainly on surface litter. Our objectives in this study were to determine the rate of decomposition of important peat-forming plant litters at five sites located in two peatlands using the litterbag technique over 3–5 years, including both surface and three subsurface depths. We relate these rates of decomposition to the type of litter and the environment of emplacement.

MATERIALS AND METHODS

Site Descriptions

Sallie's Fen (SF) is a mineral poor, *Sphagnum*-dominated peatland located in southeastern New Hampshire (43°13'N, 71°04'W). Mean annual temperature for Durham, NH, approximately 15 km southeast of the site, is 8.2°C, ranging from -5.4°C in January to 20.9°C in July. Mean annual precipitation is 1,071, 351 mm of which falls during the summer months of May to August (Barry Keim, NH State Climatologist, 30-year climate normals). The overall fen complex has a nutrient and hydraulic gradient of minerotrophic wet edges to an oligotrophic central area with pH ranging from 4.2 to 5.7 and peat depth ranging from 2 to 4.5 m (Melloh and Crill 1996). *Sphagnum* mosses (for example, *Sphagnum fallax* and *Sphagnum magellanicum*) dominate the surface. Sedges (*Carex rostrata*) dominate the plant communities in the wetter portions of the fen, whereas ericaceous shrubs, such as leatherleaf (*Chamaedaphne calyculata*) and cranberry (*Vaccinium oxycoccus*) dominate the drier areas. Red maple (*Acer rubrum*) is common along the margins of the fen, while speckled alder (*Alnus incana* ssp. *rugosa*) and highbush blueberry (*Vaccinium corymbosum*) are interspersed throughout the fen (Bubier and others 2003a). Sallie's Fen is found near the southern boreal/northern temperate delineation (Mitsch and Gosselink 2000).

The Mer Bleue (MB) peatland is primarily a large ombrotrophic bog located in the Ottawa River Valley, 10 km east of Ottawa, Ontario, Canada (45°24'N lat., 75°30'W long.). Mean annual temperature is

6.0°C, ranging from -10.8°C in January to 20.9°C in July. Mean annual precipitation is 943, 342 mm of which falls during the summer months (Environment Canada; climate normals). Peat began to form approximately 8,500 years ago, but the bog phase began later, about 7,000 years ago (Roulet and others 2007). The peat depth now ranges from 2 m at the edge to greater than 5 m in the middle. Beaver ponds are found at the lagg margin of the bog. Plant communities comprised primarily of the ericaceous shrubs *C. calyculata*, *Ledum groenlandicum*, and *Kalmia angustifolia* dominate the bog. Clusters of the deciduous shrub *Vaccinium myrtilloides* and the tufted sedge *Eriophorum vaginatum* are fairly common across the bog. The most common tree species found in the bog is *Larix laricina*, with *Betula populifolia* and *Picea mariana* occurring less frequently. In the MB poor fen, located to the north of the bog proper, community composition is primarily composed of the ericaceous shrubs listed above, including higher densities of *K. angustifolia* and *Andromeda glaucophylla*. The primary sedge in this area is *Carex oligosperma*. All sites are dominated by an understory of bryophytes, mainly *S. magellanicum*, *Sphagnum capillifolium* and *Polytrichum strictum* in the bog, with *Sphagnum papillosum* and *S. fallax* common in the wetter portions of the poor fen. Plant communities on the edge of the bog leading into the beaver pond are dominated by ericaceous shrubs at the driest end of the gradient, and by an increasing dominance of cat-tail (*Typha latifolia*), sedges (*Dulichium arundinaceum*, *Carex* spp.), and floating *Sphagnum* mosses (for example, *Sphagnum majus*) toward the wetter zones (Bubier and others 2003b, 2006). At the MB beaver pond margin, the vegetation was dominated by sedges and *T. latifolia*, with a few young *B. populifolia* trees. At the MB pond site, the litterbags were placed on the pond sediment, which was about 60 cm thick, under approximately 75 cm of water, but drying of the pond lowered the average depth of inundation to about 50 cm and emergent sedges and herbs grew. Surface water pH ranges from 3.5 in the bog hollows to 6.1 in the poor fen and the beaver pond margin.

The five sites chosen for this comparison of litter decomposition were Sallie's Fen (SF), and bog hummock (MB bog), mineral poor fen (MB fen), the terrestrial margin of a beaver pond (MB margin) and the edge of a beaver pond (MB pond) at Mer Bleue.

Litterbags

We chose litters based on the dominant vascular plants and mosses, which in some cases were the same species at MB and SF. The evergreen shrub

C. calyculata was prevalent at both sites and we used leaves and stems as well as cattail *T. latifolia* leaves. The most abundant sedge at Sallie's fen was *C. rostrata*, whereas at the Mer Bleue poor fen, the smaller *C. oligosperma* was dominant and we used the leaves of these two. *Sphagnum magellanicum* and *S. fallax* were the most common mosses at Sallie's Fen, whereas the hummock species *S. capillifolium* and hollow species *S. angustifolium* were used for this experiment at Mer Bleue.

We collected senesced tissues in the fall, air-dried and placed them in the field; a subsample of each litter type was oven-dried to determine the air-dry to oven-dry conversion. Litter bags were made of fiberglass mosquito netting, mesh size 1.5 × 2 mm. Leaves and stems were placed at the peat surface, *Sphagnum* was placed at 0–5 cm beneath the peat surface, whereas roots were placed at three depths below the surface (10, 30, and 60 cm). In addition, we placed *Typha* leaves at all depths below the peat surface at all sites to compare the decay rate of one similar tissue at all locations. We also conducted a transplant experiment with *Typha* leaves collected at Mer Bleue and placed at all peat depths at Sallie's Fen.

Triplicate litterbags were retrieved over 4–5 years, except at the MB margin and MB pond sites, where rapid growth of vegetation precluded recovery at 5 years. At the MB sites, litterbags were retrieved at 0.3, 0.5, 1.0, 1.5, 2.0, 3.3 and 5.3 years, except at the margin and pond, where we were unable to locate the last set of samples. At SF, retrieval was after 0.3, 1.0, 1.6, 2.4, 3.5 and 4.5 years. We calculated the *k*-values for 4.5 years for MB and compared with 5.25 years *k* values and found no significant difference ($P > 0.05$), so we believe that SF and MB *k* values are similar. After collection, litterbags were oven dried at 70°C. The remaining litter was then weighed and percent of the original mass calculated.

Decay rates for *T. latifolia* leaves grown at SF and those grown at MB but placed at SF, were not significantly different. Two-sample *T* tests indicated that at all depths combined and at each individual depth (10, 30 and 60 cm), the mass remaining was statistically the same ($P > 0.05$).

Modelling

We used a single-exponential linear regression model (Trofyomov and others 2002) to calculate the decay constant *k*-value: $\ln y = a - kt$, where *y* is percent mass remaining, *a* = intercept, *k* = decay constant and *t* = time of exposure in years.

Table 1. Temperature Data (°C) for Sallie's Fen and Mer Bleue Bog Hummock, 2000–2004

Site	Air		10 cm		30 cm		60 cm	
	Ann.	M–O	Ann.	M–O	Ann.	M–O	Ann.	M–O
Sallie's Fen	7.4	15.6	6.9	12.1	6.5	10.6	6.8	10.5
Mer Bleue Bog hummock	5.8	14.9	7.8	15.3	7.0	12.8	6.6	10.5

Values are means for annual (Ann.) and from May to October (M–O).

We also applied the continuous-quality non-linear regression model (Hyvönen and others 2005; Joffre and others 2001):

$$m(t) = \frac{m_0}{(1 + f_c \beta \eta_{11} u_0 q_0^\beta t)^{\frac{1-e_0}{\eta_{11} e_0 \beta}}} \quad (1)$$

where m_0 is the initial litter mass; f_c is the constant carbon concentration in the decomposer biomass; β is needed to transform the data into a linear form; η_{11} describes the rate of quality change during decomposition; u_0 is a basic metabolic rate parameter and as such responds to temperature and humidity (site characteristics); q_0 is the initial litter (substrate) quality; t is time (years); e_0 is the decomposer efficiency. We ran the model for each litter at each location to estimate the parameters q_0 and u_0 , setting the other parameters at $f_c = 0.5$, $\beta = 7$, $\eta_{11} = 0.36$ and $e_0 = 0.28$. The parameter q_0 was arbitrarily set at one for *Typha* for each site and depth, the u_0 was calculated and then used to estimate the q_0 for the other tissues. Thus, we have estimated one u_0 for each site or depth, based on *Typha*, and the estimates of q_0 for each tissue at that site, relative to q_0 *Typha* = 1. The u_0 was estimated for all species using the previous estimates of q_0 within specific site. We report the standard error (SE) of each estimate of q_0 and u_0 and the mean square error for the whole model. To run the model, the script was written for JMP IN 5.1 (SAS) statistical software.

Litter Analyses

We analyzed initial tissues for concentrations of C and N using a Carlo Erba NC–2500 elemental analyzer. Proximate analysis into ash, non-polar extractables, hot-water soluble substances, cellulose and lignin fractions was performed using the method developed for peat soils by Wieder and Starr (1998); not all the fractions in the original method were determined.

Environmental Characteristics

Air temperature and temperature at depths of 10, 30 and 60 cm were determined from continuous

measurements made at an eddy-covariance tower at MB, and continuous water table measurements were recorded at a hummock at this location (Table 1). The hummock temperature and water table position is taken to be similar to the bog site at MB.

At SF, the meteorological station continuously sampled air and peat temperature at several depths (every 2 cm below the peat surface to –20 cm, then at –25, –30, –50, –70, and –90 cm), water table position and precipitation.

RESULTS

Patterns of decomposition are illustrated in Figure 1. We tested the single-exponential linear regression model to derive the decay constant k and the intercept a . There was a generally good fit of the exponential model, using individual litterbag data ($n = 18–21$) with r^2 values ranging from 0.04 to 0.91, with an average of 0.55, and only seven of the 75 data sets having a P value greater than 0.05 (Tables 2, 3). The r^2 values increased with k values ($r^2 = 0.46$, $P < 0.001$), suggesting that errors in analysis of litter, particularly in *Sphagnum* samples that decompose slowly, constrain the efficiency of the regression model in these systems. The intercept of mass remaining at time zero ranged from ln 4.172 to 4.691 (equivalent to 65–109%), with a mean of ln 4.542 (equivalent to 94%), suggesting a double-exponential decay, the first representing rapid leaching losses and the second decomposition. This pattern has been noted in other decomposition studies (for example, Hobbie and Gough 2004); but to simplify comparison of decomposition rates among our litters and with those in the literature, we have used a single-exponential model. The continuous-quality non-linear regression model performed well with mean standard errors of about 0.02 (that is, 2% mass), the exceptions being the *Sphagnum* samples (Tables 2, 3).

Decomposition Among Surface Litters

The rate of decomposition, as the k value, ranged from –0.04 to 0.37 y^{-1} and was in the general se-

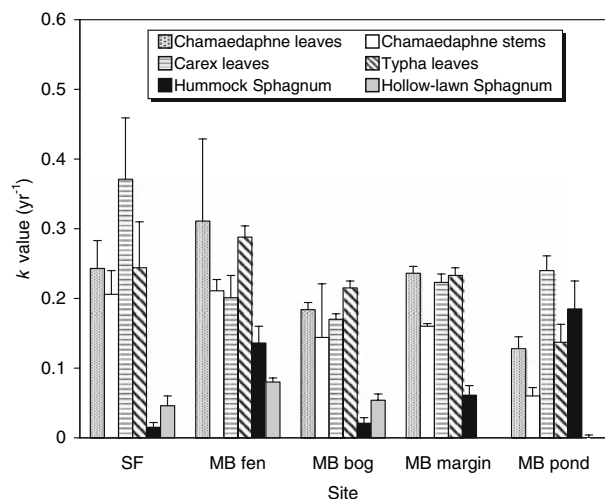


Figure 1. Exponential decay values (k) among sites by litter type. Bars indicate standard error of value.

quence *Typha* leaves = *Chamaedaphne* leaves = *Carex* leaves > *Chamaedaphne* stems > hummock *Sphagnum* = hollow/lawn *Sphagnum* (Table 2; Figure 1). The same pattern is produced when comparing the mass remaining at the end of the study. There were, however, some differences in litter decomposition rates within specific sites (Table 2). At the SF fen, the dominant sedge, *C. rostrata*, decomposed rapidly ($k = 0.37 \text{ yr}^{-1}$) compared to other litters at the site and much faster than the *C. oligosperma* at the other four sites ($k = 0.17\text{--}0.22 \text{ yr}^{-1}$). At the MB bog, the *Typha* leaves decomposed quickly compared to the sedge and shrub leaves ($k = 0.22$ vs. 0.17 and 0.18 yr^{-1}) and at the MB fen site, the *C. oligosperma* leaves decomposed more slowly than the shrub and *Typha* leaves ($k = 0.20$ vs. 0.31 and 0.29 yr^{-1}). At the MB beaver pond margin, the sedge, shrub and cat-tail leaves decomposed at a similar rate ($k = 0.22\text{--}0.24 \text{ yr}^{-1}$) and faster than the shrub stems (0.16 yr^{-1}). In the MB pond, the sedge leaves decomposed more quickly than the shrub and cat-tail leaves ($k = 0.24$, and 0.13 and 0.14 yr^{-1}), the shrub stems decomposed slowly ($k = 0.06 \text{ yr}^{-1}$) and the pattern of moss decomposition was erratic with *S. capillifolium* decomposing relatively quickly ($k = 0.19 \text{ yr}^{-1}$) and *S. angustifolium* showing no significant mass loss over the 3.3 years ($k = -0.02 \text{ yr}^{-1}$).

The continuous-quality non-linear regression model estimated initial quality (q_0) ranging from 1.04 to 0.59, where *Typha* leaves at each site were set at 1.00 (Table 2). As with the exponential k values, there was some variability in q_0 among sites, but the general sequence was *Typha*

leaves = *Chamaedaphne* leaves > *Carex* leaves > *Chamaedaphne* stems > hummock *Sphagnum* = hollow/lawn *Sphagnum*.

Analysis of the original litters showed that C:N quotients driven primarily by variations in N concentrations (Table 4) fell in a narrow range (47–63) for the leaves at SF and MB, with larger quotients for the stems (87 and 113). The *Sphagnum* used at MB had C:N quotients of 51 and 53, substantially smaller than those used at SF (87 and 105). Proximate analyses showed a small ash content (generally <2%) and varying concentrations of lignin with the mosses greater than 20% (Table 5).

There were few strong relationships between litter chemistry and decomposition rates derived as the k or q_0 values. The C:N quotient and lignin:N quotient were not significantly related to decomposition rate at any of the five sites, using the six litters (Figure 2). But there were significant ($P < 0.05$) negative correlations between the lignin concentration and decomposition rate at four of the five sites, driven by the high lignin concentration and slow decomposition rate of the two *Sphagnum* litters. There is a strong correlation between the k and q_0 values for surface litters, so that a very similar series of relationships is demonstrated for q_0 .

Decomposition Among Sites

When the mean k value of the six surface litters is calculated, the sequence is MB fen > SF > MB margin > MB bog = MB pond (values are 0.21, 0.19, 0.15, 0.13 and 0.12 yr^{-1} , respectively). The *Typha* leaves were placed at all sites and show the same overall sequence of k values (Figure 3). The continuous-quality model site values (u_0) showed a similar pattern, but with the SF site having a much larger value (0.80) than the MB sites (0.17–0.37). Thus, it appears that the decomposition rates are fastest at those sites with an intermediate wetness (water table generally 10–20 cm beneath the peat surface), with slower rates at the dry bog and inundated pond sites. Note that subsurface temperatures at SF are colder than those at MB, despite warmer air temperatures (Table 1).

Decomposition with Depth

At each site, there was a pronounced decrease in decomposition rate from the 10 to 60 cm depths: the k values fell from an overall average of 0.15 yr^{-1} at 10 cm to 0.08 and 0.05 yr^{-1} at 30 and 60 cm, respectively (Table 3; Figure 4). The *Typha* leaves were placed on the peat surface and at the three depths and showed a decrease in average k value

Table 2. Decomposition Rates of Litters placed on the Peat Surface at Sallie’s Fen (SF) and Mer Bleue (MB) Sites, Expressed as Single-exponential Linear and Continuous-quality Models

Litter	a	k	kSE	r ²	P	q ₀	q ₀ SE	u ₀	u ₀ SE	MSE
SF										
<i>C. calyculata</i> leaves	4.343	0.243	0.040	0.706	<0.001	0.938	0.011	0.798	0.063	0.011
<i>C. calyculata</i> stems	4.487	0.206	0.034	0.681	<0.001	0.863	0.011	0.798	0.068	0.011
<i>C. rostrata</i> leaves	4.492	0.371	0.088	0.714	<0.001	0.935	0.011	0.798	0.069	0.013
<i>T. latifolia</i> leaves	4.172	0.244	0.066	0.42	<0.001	1	n/a	0.798	0.093	0.020
<i>S. magellanicum</i>	4.487	0.015	0.007	0.064	0.163	0.678	0.016	0.798	0.129	0.008
<i>S. fallax</i>	4.428	0.046	0.014	0.203	0.006	0.76	0.013	0.798	0.093	0.012
MB fen										
<i>C. calyculata</i> leaves	4.531	0.311	0.118	0.71	<0.001	1.026	0.019	0.333	0.043	0.125
<i>C. calyculata</i> stems	4.618	0.211	0.016	0.892	<0.001	0.936	0.013	0.333	0.032	0.007
<i>C. oligosperma</i> leaves	4.525	0.201	0.032	0.798	<0.001	0.979	0.013	0.333	0.031	0.007
<i>T. latifolia</i> leaves	4.583	0.288	0.016	0.94	<0.001	1	n/a	0.333	0.022	0.004
<i>S. capillifolium</i>	4.602	0.136	0.024	0.693	<0.001	0.873	0.02	0.333	0.052	0.015
<i>S. angustifolium</i>	4.555	0.080	0.006	0.765	<0.001	0.836	0.012	0.333	0.032	0.004
MB bog										
<i>C. calyculata</i> leaves	4.517	0.184	0.01	0.914	<0.001	0.968	0.008	0.323	0.018	0.003
<i>C. calyculata</i> stems	4.594	0.144	0.077	0.431	<0.001	0.91	0.019	0.323	0.047	0.015
<i>C. oligosperma</i> leaves	4.59	0.170	0.008	0.915	<0.001	0.925	0.009	0.323	0.021	0.003
<i>T. latifolia</i> leaves	4.5	0.215	0.010	0.935	<0.001	1	n/a	0.323	0.016	0.002
<i>S. capillifolium</i>	4.539	0.021	0.008	0.15	0.061	0.735	0.022	0.323	0.067	0.007
<i>S. angustifolium</i>	4.573	0.054	0.009	0.483	<0.001	0.785	0.018	0.323	0.05	0.007
MB margin										
<i>C. calyculata</i> leaves	4.543	0.236	0.010	0.87	<0.001	0.965	0.009	0.368	0.025	0.003
<i>C. calyculata</i> stems	4.589	0.160	0.004	0.83	<0.001	0.889	0.009	0.368	0.026	0.002
<i>C. oligosperma</i> leaves	4.589	0.223	0.012	0.843	<0.001	0.935	0.012	0.368	0.033	0.005
<i>T. latifolia</i> leaves	4.478	0.233	0.011	0.862	<0.001	1	n/a	0.368	0.027	0.004
<i>S. capillifolium</i>	4.567	0.061	0.014	0.231	0.044	0.785	0.032	0.368	0.105	0.011
<i>S. angustifolium</i>	4.536	-0.038	0.019	0.077	0.25	0.745	*	0.368	*	0.018
MB pond										
<i>C. calyculata</i> leaves	4.486	0.128	0.017	0.745	<0.001	1.022	0.014	0.174	0.017	0.006
<i>C. calyculata</i> stems	4.586	0.060	0.012	0.59	<0.001	0.857	0.015	0.174	0.022	0.002
<i>C. oligosperma</i> leaves	4.609	0.240	0.021	0.87	<0.001	1.044	0.015	0.174	0.018	0.007
<i>T. latifolia</i> leaves	4.526	0.137	0.026	0.596	<0.001	1	n/a	0.174	0.023	0.009
<i>S. capillifolium</i>	4.62	0.185	0.040	0.56	<0.001	0.966	0.025	0.174	0.032	0.011
<i>S. angustifolium</i>	4.606	-0.023	0.027	0.004	0.4	0.585	*	0.174	*	0.016

The single-exponential linear regression model has $\ln y = a - kt$, using the percentage of mass remaining and t in years where a = intercept, k = decay constant, SE = standard error of the k estimate for the regression model, r^2 = coefficient of determination and P = P value. The continuous-quality model has q_0 as an estimate of the initial litter (substrate) setting *Typha* leaves as 1.00 and u_0 is a basic metabolic rate parameter responding to site characteristics, with their standard errors (SE). MSE is the continuous-quality mean standard error. * Unable to estimate SE.

from 0.25 y^{-1} at the surface to 0.18, 0.11 and 0.06 y^{-1} at 10, 30 and 60 cm, respectively. Similarly, the average site u_0 value fell from 0.25 at 10 cm to 0.13 and 0.07 at 30 and 60 cm, respectively.

Within each site, there was some variability in the decomposition rates among litters. At the SF site, the roots of *C. rostrata* decomposed most quickly, followed by the *Typha* leaves and the roots of *Chamaedaphne*. At the MB sites, the fastest decomposition was shown by the *Typha* leaves; this was followed by the *Chamaedaphne* roots at the MB bog site and *C. oligosperma* roots at the MB margin

site, with no difference in rates in the two root litters at the MB fen site. At the MB pond, the *Typha* leaves decomposed most rapidly, followed by the *Carex* roots and the *Chamaedaphne* roots. The mean of q_0 for all sites and depths was 1.00 for *Typha* leaves, 0.87 for *Carex* roots and 0.94 for *Chamaedaphne* roots

Differences among sites were small compared to those among depths, with the general sequence MB bog > SF > MB margin = MB fen = MB pond primarily related to differences in decomposition at the 10 cm depth, as those at 30 and 60 cm were similar among the five sites. This differentiation is

Table 3. Decomposition Rates of Litters Placed at Depths of 10, 30 and 60 cm at SF and MB Sites, Using the Single-exponential Linear and Continuous-quality Models Described in Table 2

Species	Depth	a	k	kSE	r ²	P	q ₀	q ₀ SE	u ₀	u ₀ SE	MSE
SF											
<i>C. rostrata</i> roots	10	4.350	0.214	0.031	0.738	<0.0001	0.973	0.037	0.212	0.057	0.073
	30	4.385	0.161	0.029	0.600	<0.0001	0.908	0.025	0.150	0.029	0.017
	60	4.376	0.077	0.065	0.041	<0.0001	0.922	0.02	0.139	0.021	0.012
<i>C. calyculata</i> roots	10	4.549	0.144	0.023	0.636	<0.0001	0.911	0.028	0.212	0.046	0.033
	30	4.515	0.039	0.013	0.035	<0.0001	1.087	0.035	0.150	0.034	0.058
	60	4.551	0.012	0.001	0.184	0.026	1.099	0.035	0.139	0.031	0.057
<i>T. latifolia</i> leaves	10	4.376	0.191	0.187	0.257	0.004	1	n/a	0.212	0.044	0.054
	30	4.510	0.077	0.014	0.416	<0.0001	1	n/a	0.150	0.035	0.045
	60	4.550	0.048	0.007	0.406	<0.0001	1	n/a	0.139	0.029	0.035
<i>T. latifolia</i> transplant	10	4.415	0.146	0.068	0.355	0.001	0.801	0.025	0.212	0.046	0.013
	30	4.519	0.075	0.013	0.456	<0.0001	0.958	0.022	0.150	0.024	0.020
	60	4.553	0.051	0.007	0.443	<0.0001	0.89	0.044	0.139	0.048	0.043
MB fen											
<i>C. oligosperma</i> roots	10	4.534	0.073	0.01	0.625	<0.001	0.856	0.015	0.294	0.037	0.006
	30	4.635	0.05	0.011	0.406	0.001	0.912	0.037	0.059	0.017	0.010
	60	4.662	0.032	0.025	0.115	0.114	0.831	0.163	0.031	0.043	0.026
<i>C. calyculata</i> roots	10	4.559	0.073	0.012	0.618	<0.001	0.838	0.015	0.294	0.036	0.005
	30	4.587	0.036	0.002	0.587	<0.001	0.933	0.016	0.059	0.007	0.002
	60	4.597	0.029	0.002	0.556	<0.001	0.978	0.018	0.031	0.004	0.002
<i>T. latifolia</i> leaves	10	4.448	0.164	0.06	0.573	<0.001	1	n/a	0.294	0.038	0.015
	30	4.553	0.047	0.003	0.653	<0.001	1	n/a	0.059	0.006	0.003
	60	4.600	0.035	0.002	0.578	<0.001	1	n/a	0.031	0.004	0.002
MB bog											
<i>C. oligosperma</i> roots	10	4.648	0.133	0.016	0.765	<0.001	0.845	0.015	0.321	0.040	0.008
	30	4.544	0.04	0.009	0.341	0.003	0.823	0.019	0.219	0.035	0.007
	60	4.651	0.041	0.013	0.277	0.008	0.818	0.055	0.075	0.035	0.012
<i>C. calyculata</i> roots	10	4.610	0.206	0.038	0.769	<0.001	0.936	0.018	0.321	0.044	0.014
	30	4.590	0.074	0.006	0.759	<0.001	0.855	0.011	0.219	0.020	0.003
	60	4.622	0.078	0.031	0.375	0.002	0.957	0.031	0.075	0.017	0.013
<i>T. latifolia</i> leaves	10	4.513	0.238	0.057	0.748	<0.001	1	n/a	0.321	0.044	0.017
	30	4.533	0.167	0.016	0.838	<0.001	1	n/a	0.219	0.019	0.006
	60	4.542	0.064	0.056	0.184	0.041	1	n/a	0.075	0.018	0.021
MB margin											
<i>C. oligosperma</i> roots	10	4.654	0.168	0.027	0.759	<0.001	0.912	0.02	0.247	0.038	0.015
	30	4.683	0.042	0.015	0.255	0.012	0.783	0.118	0.092	0.098	0.016
	60	4.691	0.004	0.013	0.400	0.756	0.528		0.044	0.021	0.021
<i>C. calyculata</i> roots	10	4.543	0.086	0.014	0.620	<0.001	0.887	0.015	0.247	0.023	0.007
	30	4.584	0.037	0.007	0.365	0.002	0.873	0.026	0.092	0.019	0.007
	60	4.672	0.067	0.021	0.411	0.001	0.977	0.055	0.044	0.017	0.016
<i>T. latifolia</i> leaves	10	4.529	0.184	0.012	0.904	<0.001	1	n/a	0.247	0.018	0.004
	30	4.622	0.12	0.059	0.418	0.001	1	n/a	0.092	0.017	0.015
	60	4.577	0.047	0.065	0.081	0.189	1	n/a	0.044	0.021	0.038
MB pond											
<i>C. oligosperma</i> roots	10	4.600	0.132	0.017	0.73	<0.001	0.958	0.019	0.176	0.025	0.012
	30	4.645	0.155	0.021	0.717	<0.001	0.978	0.021	0.137	0.020	0.012
	60	4.685	0.009	0.029	0.345	0.005	0.934	0.081	0.057	0.035	0.035
<i>C. calyculata</i> roots	10	4.548	0.064	0.064	0.735	<0.001	0.89	0.012	0.176	0.017	0.003
	30	4.547	0.078	0.015	0.555	<0.001	0.933	0.014	0.137	0.015	0.005
	60	4.642	0.078	0.013	0.626	<0.001	0.98	0.029	0.057	0.012	0.008
<i>T. latifolia</i> leaves	10	4.521	0.127	0.012	0.843	<0.001	1	n/a	0.176	0.012	0.003
	30	4.556	0.123	0.012	0.834	<0.001	1	n/a	0.137	0.014	0.006
	60	4.661	0.104	0.014	0.743	<0.001	1	n/a	0.057	0.010	0.004

Table 4. Carbon and N Concentrations and C:N Quotient in Original Litters and Other Plant Tissues at SF and MB Sites

Litter	C (%)	N (%)	C:N quotient
SF			
<i>C. calyculata</i> leaves	53.5	1.11	48
<i>C. calyculata</i> stems	50.7	0.59	87
<i>C. calyculata</i> roots	48.8	0.25	194
<i>C. rostrata</i> leaves	45.8	0.82	56
<i>C. rostrata</i> roots	45.5	0.56	82
<i>T. latifolia</i> leaves	47.2	1.01	47
<i>S. fallax</i>	43.9	0.42	105
<i>S. magellanicum</i>	45.3	0.52	87
MB			
<i>C. calyculata</i> leaves	50.6	1.08	47
<i>C. calyculata</i> stems	46.3	0.41	113
<i>C. calyculata</i> roots	45.9	0.27	170
<i>C. oligosperma</i> leaves	43.8	0.75	58
<i>C. oligosperma</i> roots	46.5	0.40	116
<i>T. latifolia</i> leaves	45.5	0.72	63
<i>S. capillifolium</i>	43.1	0.81	53
<i>S. magellanicum</i>	43.2	0.85	51
<i>S. papillosum</i>	41.8	1.18	35
<i>S. majus</i>	44.0	0.77	57
<i>P. strictum</i>	43.2	0.94	46

probably related to water table position and thus exposure to aerobic or anaerobic conditions. At the MB bog, the 10 cm depth samples were above the water table throughout the year, and those at 30 cm depth would be at the water table in the spring and late autumn and be above the water table during the summer. For the *Chamaedaphne* roots and *Typha* leaves, there is little difference in decomposition rates between samples placed on the peat surface ($k = 0.14$ and 0.22 y^{-1}) and those at 10 cm depth ($k = 0.21$ and 0.24 y^{-1}). At the 30 cm depth, the *Typha* leaves retained a high k value (0.17 y^{-1}) but the other two litters have slowed decomposition to 0.04 – 0.07 y^{-1} , similar to that observed at a depth of 60 cm, which is beneath the water table year-round. *Typha* leaves' k value also fell to 0.06 y^{-1} at 60 cm.

At the SF, MB fen and MB margin sites, 10 cm depth samples were initially close to the water table in the spring and autumn and above it during the summer, whereas litterbags at 30 and 60 cm would be nearly always beneath the water table. At the two fen sites, the rapid growth of the vegetation and the rise in water table position meant that in the later stages of decomposition, the litter bags were infrequently above the water table. *Typha* leaves placed at 10 cm decomposed more slowly

than those placed on the surface (k values of 0.19, 0.16 and 0.18 y^{-1} vs. 0.24, 0.29 and 0.23 y^{-1} at SF, MB fen and MB margin, respectively), but were faster than those at either 30 or 60 cm depths (Figure 5). With the two root litters, decomposition rates were relatively fast ($k = 0.07$ – 0.24 y^{-1}) at the 10 cm depths and decreased at the 30 and 60 cm depths ($k = 0.03$ – 0.16 y^{-1}). Decomposition of *Carex* roots at SF was faster than the other litters.

The litterbags at the MB pond site were permanently under water, and generally showed the slowest decomposition rate at 10 cm depth. There was only a small decrease in decomposition rate with increasing depth in the MB pond, u_0 ranging from 0.17 at the sediment surface to 0.18 at 10 cm and 0.07 at 60 cm, compared to the other sites.

Temperature at these depths also influences rates of decomposition. The mean annual temperature from the surface to 60 cm at the SF and MB bog sites does not vary greatly (5.8 – 7.8°C , Table 1). But during the growing season, from May to October, air temperatures averaged 15.6 and 14.9°C at the SF and MB sites, respectively, whereas temperatures fell with depth. At SF, the May to October mean temperature decreased from 15.6°C in the air, to 12.1 , 10.6 and 10.5°C at depths of 10, 30 and 60 cm, respectively. At MB bog, the decreases were from 14.9 to 15.3 , 12.8 and 10.5°C . Note that the MB bog was slightly warmer than the SF fen, perhaps because of the lower water table.

DISCUSSION

The litterbag technique is simple, inexpensive and commonly used, but there are caveats. We used litterbags containing only one type of litter, whereas litter naturally decomposes in mixtures and this may affect the decomposition rates (see review by Gartner and Cardon 2004). Although we measured decomposition over 3–5 years, this is a relatively short time compared to the rate at which litter is incorporated into soil organic matter in peatlands and measurements over longer periods may reveal different patterns of decomposition (for example, Latter and others 1998). Our data, and nearly all short-term (<5 years) litter bag studies in environments with slow decomposition rates, preclude the development of double exponential decay models. Data from Heal and others (1978), as analyzed by Yu and others (2001), show that a simple exponential model tends to underestimate mass remaining in the later stages of decomposition. The mesh size we used ($1.5 \times 2 \text{ mm}$) allowed sedges and mosses to grow in and through the bags

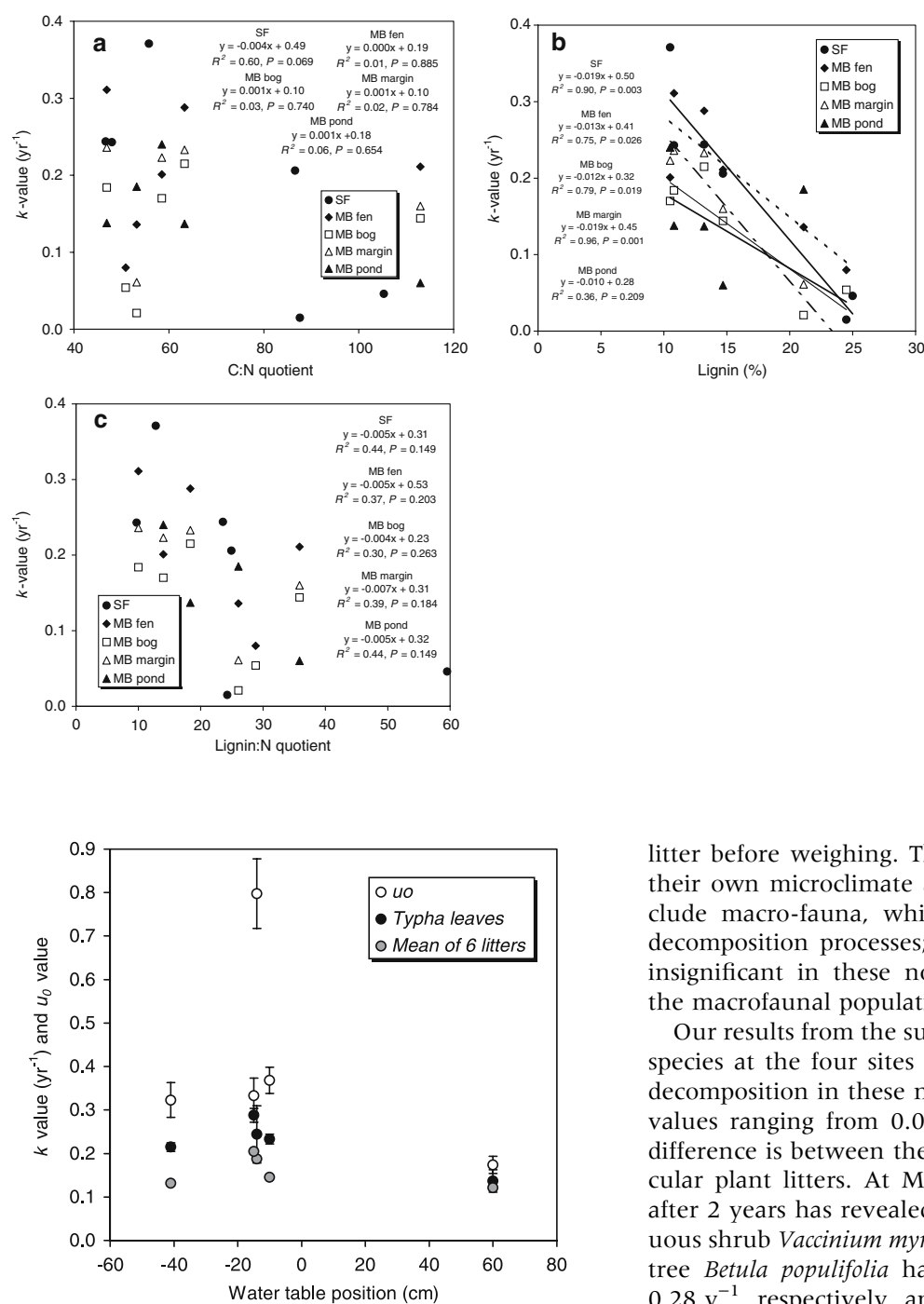


Figure 3. Exponential k values of *Typha* leaves placed at the surface of the five peatland sites and estimated site decomposition parameter u_0 , as a function of average water table depth during the growing season. Bars indicate standard error.

placed on the peat surface, thus maintaining the position that litter would normally occupy as it decomposed; however, this growth into the bag of fresh tissues required careful sorting of the original

Figure 2. Relationship between exponential decay constant k and C:N quotient (A), lignin (B) and lignin:N quotient (C) of surface litters at SF and MB sites.

litter before weighing. The mesh bags may create their own microclimate and fine meshes may exclude macro-fauna, which may be important in decomposition processes; the latter is likely to be insignificant in these northern peatlands, where the macrofaunal population is small.

Our results from the surface litters of major plant species at the four sites confirm the slow rates of decomposition in these northern peatlands, with k values ranging from 0.05 to 0.37 yr^{-1} . The major difference is between the *Sphagnum* moss and vascular plant litters. At Mer Bleue, a second study after 2 years has revealed that leaves of the deciduous shrub *Vaccinium myrtilloides* and the deciduous tree *Betula populifolia* have k values of 0.14 and 0.28 yr^{-1} , respectively, and the herb *Maianthemum trifoliata* decomposes very rapidly, with a k value of 0.94 yr^{-1} (T. Moore, unpublished data).

A collation of data on decomposition rates of surface litters in northern peatlands and wetlands confirms that the range of k values is generally between 0.05 and 0.35 yr^{-1} (Table 5). Despite the range of species and sites, the range of k values for the vascular plant litters is narrow and not very different from the decomposition rates of foliar litters in northern forests (for example, 0.10–0.25 yr^{-1} in Canadian forests reported by Trofymow and

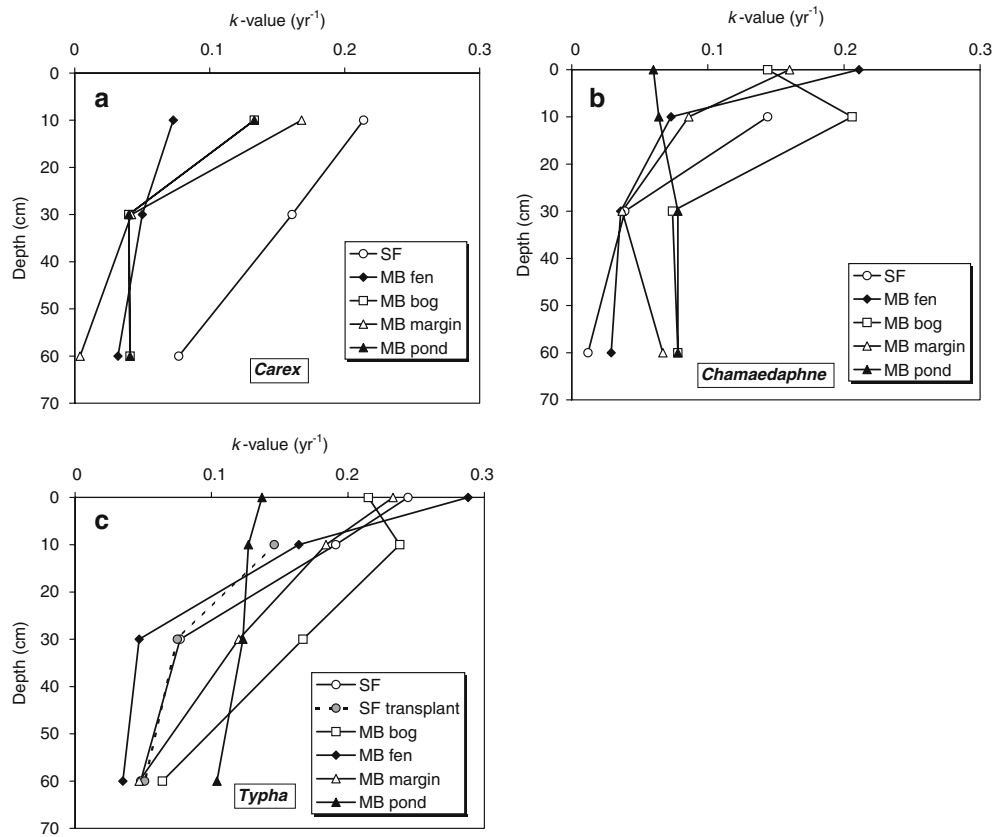


Figure 4. Decomposition rates of *Carex* roots (A), *Chamaedaphne* roots (B) and *Typha* leaves (C) at the SF and MB sites at three depths (10, 30 and 60 cm, plus 0 cm for the *Typha*) expressed as the exponential decay constant k . Average May to September water table position at the SF, MB bog, MB fen, MB margin and MB pond sites were -14 , -44 , -18 , -15 and $+50$ cm, respectively.

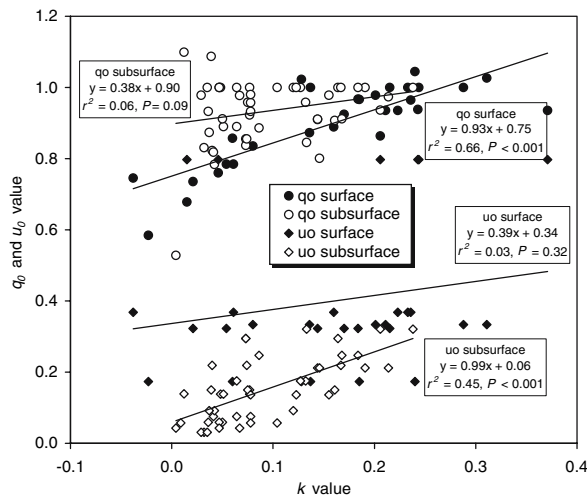


Figure 5. Comparison of estimated k and u_0 and q_0 parameters from the exponential and continuous-quality models for surface and subsurface litters.

others 2002). In general, it appears that sedge litter decomposes at a faster rate than shrub leaves, though the difference is not great (Table 6).

There are few studies of the decomposition of non-foliar litters in peatlands, even though woody biomass is an important part of the above-ground fraction in many peatlands: at MB, shrubs stems comprise 54 and 44% of the total aboveground vascular biomass, or 148 and 90 g m⁻², at the MB bog and fen sites, respectively (Bubier and others 2006). Our k values of 0.14–0.22 y⁻¹ for shrub stems are similar to shrub and sedge leaves at SF and MB. Hobbie and Gough (2004) reported k values of 0.03 and 0.05 y⁻¹ for the stems of the shrub *Betula nana* in Alaskan tundra, considerably slower than 0.07–0.19 y⁻¹ observed in sedge and shrub leaves. The tundra shrubs had 39% lignin, compared to 15% in our study.

Our study and many others have identified the slow rate of decomposition of *Sphagnum* mosses in peatlands, though the range of reported k values is

Table 5. Proximate Analysis (following Wieder and Starr 1998) of Litters and Other Plant Tissues from Mer Bleue

Litter	Ash	NPE	HWS	Cell	Lig
<i>C. calyculata</i> leaves	1.9	17.2	7.9	18.9	10.8
<i>C. calyculata</i> stems	0.9	7.5	14.7	18.7	14.7
<i>C. calyculata</i> roots	0.8	8.1	15.2	21.2	14.7
<i>C. oligosperma</i> leaves	3.6	8.2	6.2	17.8	10.5
<i>C. oligosperma</i> roots	0.8	7.1	12.8	21.5	10.5
<i>T. latifolia</i> leaves	1.4	8.2	8.0	25.2	13.2
<i>S. capillifolium</i>	2.0	36.8	7.9	19.7	21.1
<i>S. magellanicum</i>	1.2	10.5	10.5	20.7	24.5
<i>S. majus</i>	2.0	9.9	18.6	15.1	20.9
<i>S. papillosum</i>	1.4	10.0	9.1	16.8	25.0
<i>P. strictum</i>	0.8	9.6	10.2	28.4	18.1

Ash = ash concentration, NPE = non-polar extractables, HWS = hot-water solubles, Cell = cellulose, Lig = lignin, all values in %.

large, from 0.00 to 0.22 y^{-1} (Table 6). In part, this variation is related to species, with cuspidata *Sphagnum*, growing in wetter lawns and hollows, decomposing at generally faster rates than the acutifolia *Sphagnum* occupying the drier hummocks (see Johnson and Damman 1993). Our study failed to consistently confirm this difference, though the hummock-forming *S. capillifolium* decomposed generally slower than the other *Sphagnum* species. It must also be noted that part of the variability may be related to variations in the section of *Sphagnum* stem used and its chemistry, and the position of emplacement of the *Sphagnum* litter. Furthermore, a wide range of pre-treatments has been applied to *Sphagnum* litters, ranging from air drying at 20°C to oven drying at temperatures between 30 and 70°C and even autoclaving. Nevertheless, it is clear that the slow rate of decomposition of surface *Sphagnum* is a major contributor to the accumulation of organic matter in peatlands.

The continuous-quality model was developed including a microbial decomposer component and a shift on the quality of the tissue, as decomposition proceeds. It has been applied to a range of decomposing litters from forests (for example, Ågren and Bosatta 1996; Joffre and others 2001) and more recently to the temperature sensitivity of organic matter decomposition (Hyvönen and others 2005). This is the first time, to our knowledge, that it has been applied to peatlands and allowed a separation into the initial litter quality (q_0) and site (u_0) parameters. When the exponential decay k and q_0 and u_0 parameters are compared, there was a strong correlation between k and q_0 in the surface litters ($r^2 = 0.66$, $P < 0.001$) because site plays a minor role in determining decomposition rates, compared to the broad range in decomposability of

the litters (Figure 5). On the other hand, the strong correlation ($r^2 = 0.45$, $P < 0.001$) between k and u_0 in the subsurface litters is anticipated, because of the importance of position, relative to the water table, compared to litter quality between the two roots and *Typha* leaves. In general, the standard error of the continuous-quality model was smaller than that of the exponential decay model (Tables 2, 3).

Although the number and range of litters used in this study is small (six), there was not as good a relationship between decomposition rate and litter chemistry as has been found for foliar material in upland forests (for example, Trofymow and others 2002). At four of the five sites, the exception being the sediment at the base of the beaver pond, a significant relationship was found between decomposition rate and lignin concentration, but not with either C:N ratio or lignin:N ratio. In three central Canadian peatlands, lignin:N ratio provided a modest explanation of decomposition rate after 6 years (r^2 of 0.21–0.59) among ten foliar litters (Moore and others 2005; Moore and Basiliko 2006). Both the peat substrate and the leachate of *Sphagnum* may affect decomposition rates (for example, Aerts and others (1999); Verhoeven and Toth 1995; Verhoeven and Liefveld 1997) and N content can have varying effects on *Sphagnum* decomposition rate (for example, Limpens and Berendse 2003). In moist tundra sites, Hobbie and Gough (2004) also found that chemical analyses were not strong predictors of litter decomposition rates.

There are some differences in decomposition rates of the surface litters at the four MB sites in our study, with the wetter fen and beaver pond margin sites showing slightly faster decomposition rates

Table 6. Exponential Decay Constants (k) for Different Litter Types in Northern Peatlands, Based on the Literature

Litter type and position	k value		Locations	Source
	Range	Mean		
Surface				
Wood	0.00 to 0.01	0.01	Bogs and pothole peatland	Moore and others (2005)
Tree foliage				
Needles	0.08–0.23	0.15	Bogs and swamp	Moore (unpublished)
Needles	0.04–0.12	0.09	Bogs and pothole peatland	Moore and others (2005)
Leaves	0.07–0.38	0.22	Bogs and swamp	Moore (unpublished)
Leaves	0.09–0.12	0.11	Bogs and pothole peatland	Moore and others (2005)
Shrub stems	0.14–0.22	0.18	Temperate bog and fen	This study
	0.03–0.05	0.04	Arctic moist tundra	Hobbie and Gough (2004)
Shrub leaves				
Evergreen	0.12–0.19	0.15	Bogs and swamp	Moore (unpublished)
	0.18–0.31	0.25	Temperate bog and fen	This study
Deciduous	0.19–0.23	0.21	Bogs and swamp	Moore (unpublished)
		0.33	Boreal bog, fen and marsh	Thormann and others (2001)
Sedges	0.16–0.44	0.28	Subarctic fens and boreal bogs	Moore (unpublished)
	0.17–0.37	0.25	Temperate bog and fen	This study
	0.29–0.37	0.33	Temperate bogs and fens	Limpens and Berendse (2003)
	0.36–0.70	0.53	Boreal bog, fen and marsh	Thormann and Bayley (1997)
		0.39	Boreal bog, fen and marsh	Thormann and others (2001)
Grass	0.15–0.22	0.17	Bogs and pothole peatland	Moore and others (2005)
Herbs (for example, <i>Rubus chamaemorus</i> , <i>S. trifoliata</i>)	0.32–0.94	0.63	Boreal bog and temperate fen	Moore (unpublished)
Typha	0.22–0.29	0.25	Temperate bog and fen	This study
		0.52	Boreal bog, fen and marsh	Thormann and Bayley (1997)
<i>Sphagnum</i> moss				
Acutifolia (hummocks)	0.01–0.03	0.02	Subarctic, boreal and temperate bogs and fens	Moore (unpublished)
	0.07–0.12	0.1	Subarctic fens	Bartsch and Moore (1985)
	0.02–0.14	0.06	Temperate bog and fen	This study
	0.09–0.09	0.09	Boreal bog	Rocheffort and others (1990)
	0.07–0.15	0.08	Subarctic, boreal and temperate bogs and fens	Moore (unpublished)
		0.12	Boreal bog, fen and marsh	Thormann and others (2001)
	0.03–0.08	0.07	Temperate bogs and fens	Limpens and Berendse (2003)
		0.17	Temperate bog	Clymo (1965)
		0.08	Temperate bog	Johnson and Damman (1991)
Cuspidata (hollows-lawns)	–0.03–0.08	0.06	Temperate bog and fen	This study
	0.08–0.12	0.10	Subarctic fens	Bartsch and Moore (1985)
	0.02–0.03	0.03	Arctic moist tundra	Hobbie and Gough (2004)
		0.11	Boreal bog	Rocheffort and others (1990)
	0.04–0.22	0.11	Temperate bogs and fens	Limpens and Berendse (2003)
		0.17	Temperate bog	Clymo (1965)
		0.12	Temperate bog	Johnson and Damman (1991)
Lichen		0.08	Boreal bog	Moore (unpublished)
Below-ground				
Sedge roots	0.00–0.21	0.09	Temperate bog and fen	This study
		0.69	Boreal bog, fen and marsh	Thormann and others (2001)
Shrub roots	0.01–0.21	0.07	Temperate bog and fen	This study
		0.16	Boreal bog, fen and marsh	Thormann and others (2001)

Litter treatments, litterbag mesh size and length of exposure vary considerably.

than the dry bog and inundated beaver pond sites (Figure 2). In a 6-year study of decomposition of ten foliar litters at three pairs of well-drained upland and peatland sites in central Canada, Moore and others (2005) found minor differences in decomposition rates between paired sites, expressed as the mass remaining or k values. After 12 years of decomposition, the differentiation between upland and peatland decomposition rates was greater with only eight of the 36 litter upland-peatland pairs showing a decomposition rate slower in the upland, or at the same rate as the peatland, based on k values and mass remaining after 12 years (T. Moore and J.A. Trofymow, personal communication).

This follows from the initial decomposition of aboveground litters in aerobic environments at or close to the peat surface. As noted earlier, short periods of inundation may stimulate decomposition, whereas dry conditions on hummocks, or permanently inundated sediments in ponds, may slow decomposition. However, our data suggest that over the initial period of decomposition (3–5 years), the effect of surface emplacement is minor. With water tables at 10–30 cm beneath the peat surface, it may take decades to centuries for the surface litter to enter the anaerobic section of the peat. At the MB bog site, peat in hollows at a depth of 30–40 cm has been shown to be about 200 years old (Richard, personal communication). This is the depth of the summer water table. The time taken to reach this anaerobic zone would be longer in hummocks and shorter in sites with a rapid growth in *Sphagnum* and water table, such as the MB and SF fens.

Our results, however, have revealed the importance of position in the peat profile in determining decomposition rates, using two root litters and the *Typha* leaf control. Plant material entering the peat profile below 50 cm (beneath the water table) has a similar rate of decomposition as *Sphagnum*, placed on the peat surface. Others have also shown the importance of position on decomposition rates (for example, Belyea 1996; Johnson and Damman 1991, 1993) though few studies have used root materials (for example, Thormann and others 2001). Although root material may have the same potential for decomposition as litter from surface tissues, the rate of decomposition is strongly dependent on position within the profile, decreasing up to tenfold from 10 to 60 cm. At Mer Bleue, we have shown that most of the roots of shrubs at the bog are located above the position of the summer water table, thus are likely to decompose fairly quickly, whereas in the fen, the roots of

sedges can penetrate beneath the water table, slowing their rate of decomposition (Moore and others 2002).

The primary control on slowing decomposition rates with depth is the occurrence of anaerobic conditions brought about by the water table. Very variable results of the effect of anaerobism on decomposition rate of peat materials have been reported but Scanlon and Moore (2000) showed that at Mer Bleue conversion from aerobic to anaerobic conditions resulted in a decrease in CO₂ production rate from peat samples by 7–16 times. Although there are minor differences in mean annual temperature from the surface to a depth of 60 cm at the MB and SF sites, the surface temperature from May to October is about 5°C warmer than that at 60 cm (Table 1). Assuming a Q₁₀ value of about two for the temperature dependence of decomposition of peat and litter (Scanlon and Moore 2000; Trofymow and others 2002), the warmer conditions near the surface could increase decomposition rates by about half, compared to those at 60 cm depth. The cooler May to October subsurface (by 2–3°C at 10 and 30 cm depth) at SF, compared to MB, may explain why rates of decomposition were faster at the surface, but slower beneath the surface at SF than MB.

These decomposition rates can be used in models of C cycling in peatlands. For example, Frohking and others (2001) developed a peat decomposition model based on prescribed rates of plant production and rates of decomposition of litter, derived from general litter type and temperature and time at which the litter passed from the aerobic to anaerobic sequence of decomposition, at the water table. It was able to simulate accumulation rates observed in several peatlands of eastern Canada. Of critical importance to modelling are the rates of below-ground plant production, such as roots, how fast they decompose and their position relative to the water table. Where the roots decompose in an aerobic environment, above the water table, they are unlikely to contribute to long-term organic matter accumulation, compared to the very slowly decomposing *Sphagnum* input from the surface. But in fens, where sedge roots are able to grow beneath the water table, their contribution to long-term accumulation may be significant.

This study examines part of the continuum from plant tissues to peat that occurs in these wetland ecosystems. Initial decomposition rates (k value) in the surface litters range from 0.05 to 0.25 y⁻¹ and litters entering in the peat profile have decomposition rates ranging from 0.05 to 0.15 y⁻¹. Based on the measurement of carbon dioxide emitted from

intact soil cores obtained from the MB bog, fen and margin sites, estimated k values range from 0.06 y^{-1} in the aerobic 10 cm layer to $0.001\text{--}0.005 \text{ y}^{-1}$ under anaerobic conditions at 30–40 cm (Scanlon and Moore 2000). The modelling efforts of Clymo and others (1998) suggest that these decomposition rates fall to 0.0005 y^{-1} when the whole of the anaerobic catotelm is considered. Clearly, the dominant controls on rates of decomposition in these peatlands are the type of litter (vascular material vs. *Sphagnum*) and the position of the water table in controlling how fast the decomposing tissues enter the catotelm and what proportion of belowground production is subject to anaerobic decomposition. Changes in climate, or other disturbances, may be expected to affect plant production and decomposition rates and thus C accumulation in peatlands. Vegetation structure strongly influences the C sink capacity of peatlands (Belyea and Malmer 2004). A change from *Sphagnum* to vascular plants, such as associated with increased rates of N deposition (Bubier and others 2007), will result in faster overall rates of decomposition. Warmer temperatures will increase decomposition rates of litter and a lowered water table under drier climates will also accelerate the decomposition of plant litters introduced within the peat profile.

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REFERENCES

- Aerts R. 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79:439–49.
- Aerts R, Verhoeven JTA, Whigham DF. 1999. Plant-mediated controls on nutrient cycling in temperate fens and bogs. *Ecology* 80:2170–81.
- ågren G, Bosatta E. 1996. Quality: a bridge between theory and experiment in soil organic matter studies. *Oikos* 76:522–8.
- Backéus I. 1990. Production and depth distribution of fine roots in a boreal open bog. *Ann Bot Fenn* 27:261–5.
- Baker TT, Lockaby BG, Conner WH, Meier CE, Stanturf JA, Burke MK. 2001. Leaf litter decomposition and nutrient dynamics in four southern forested floodplain communities. *Soil Sci Soc Am J* 65:1334–47.
- Banerjee RD, Sen SP. 1979. Antibiotic activity of bryophytes. *Bryologist* 82:141–53.
- Bartsch I, Moore TR. 1985. A preliminary investigation of primary production and decomposition in subarctic peatlands. *Can J Bot* 63:1241–8.
- Belyea LR. 1996. Separating the effects of litter quality and macroenvironment on decomposition rates in a patterned peatland. *Oikos* 77:529–39.
- Belyea LR, Malmer N. 2004. Carbon sequestration in peatland: patterns and mechanisms of response to climate change. *Glob Change Biol* 10:1043–52.
- Bubier J, Crill P, Mosedale A, Froelking S, Linder E. 2003a. Peatland responses to varying interannual moisture conditions as measured by automatic CO₂ chambers. *Glob Biogeochem Cycles* 17(2). doi:10.1029/2002GB001946.
- Bubier JL, Bhatia G, Moore TR, Roulet NT, Lafleur PM. 2003b. Spatial and temporal variability in growing season net ecosystem CO₂ exchange at a large peatland, Ontario, Canada. *Ecosystems* 6:353–67. doi:10.1007/s1002-003-0125-0.
- Bubier JL, Moore TR, Bledzki LA. 2007. Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog. *Glob Change Biol* 13:1168–1186.
- Bubier JL, Moore TR, Crosby G. 2006. Fine-scale vegetation distribution in a cool temperate bog. *Can J Bot* 84:910–23.
- Campbell C, Vitt DH, Halsey LA, Campbell ID, Thormann MN, Bayley SE. 2000. Net primary production and standing biomass in northern continental wetlands. Canadian forestry service information report NOR-X-369. Edmonton: Canadian Forestry Service.
- Clymo RS. 1965. Experiments on breakdown of *Sphagnum* in two bogs. *J Ecol* 53:737–57.
- Clymo RS, Turunen J, Tolonen K. 1998. Carbon accumulation in peatland. *Oikos* 81:368–88.
- Day FP. 1983. Effects of flooding on leaf litter decomposition in microcosms. *Oecologia* 56:180–84.
- Froelking S, Bubier JL, Moore TR, Ball T, Bellisario LM, Bhardwaj A, Carroll P, Crill PM, Lafleur PM, McCaughey JH, Roulet NT, Suyker AE, Verma SB, Waddington JM, Whiting GJ. 1998. The relationship between ecosystem productivity and photosynthetically active radiation for northern peatlands. *Glob Biogeochem Cycles* 12:115–26.
- Froelking S, Roulet NT, Moore TR, Richard PJH, Lavoie M, Muller SD. 2001. Modelling northern peatland decomposition and peat accumulation. *Ecosystems* 4:479–98.
- Gartner TB, Cardon ZG. 2004. Decomposition dynamics in mixed-species leaf litter. *Oikos* 104:230–46.
- Gorham E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecol Appl* 1:182–95.
- Heal OW, Latter PM, Howson G. 1978. A study of the rates of decomposition of organic matter. In: Heal Perkins OW DF, Ed. *Production ecology of British Moors and Montane Grasslands*. New York: Springer. pp 136–59.
- Hobbie SE, Gough L. 2004. Litter decomposition in moist acidic and non-acidic tundra with different glacial histories. *Oecologia* 140:113–24.

- Hyvönen R, ågren GI, Dalias P. 2005. Analysing temperature response of decomposition of organic matter. *Glob Change Biol* 11:770–8.
- Joffre R, ågren GI, Gillon D, Bosatta E. 2001. Organic matter quality in ecological studies: theory meets experiment. *Oikos* 93:451–8.
- Johnson LC, Damman AWH. 1991. Species controlled *Sphagnum* decay on a south Swedish raised bog. *Oikos* 61:234–42.
- Johnson LC, Damman AWH. 1993. Decay and its regulation in *Sphagnum* peatlands. *Adv Bryology* 5:249–96.
- Laiho R, Finér L. 1996. Changes in root biomass after water-level drawdown on pine mires in southern Finland. *Scan J For Res* 11:251–60.
- Latter PM, Howson G, Howard DM, Scott WA. 1998. Long-term study of litter decomposition on a Pennine peat bog: which regression?. *Oecologia* 113:94–103.
- Limpens J, Berendse F. 2003. How litter quality affects mass loss and N loss from decomposing *Sphagnum*. *Oikos* 103:537–47.
- Lockaby BG, Wheat RS, Clawson RG. 1996. Influence of hydroperiod on litter conversion to soil organic matter in a floodplain forest. *Soil Sci Soc Am J* 60:1989–93.
- Melloh RA, Crill PM. 1996. Winter methane dynamics in a temperate peatland. *Glob Biogeochem Cycles* 10:247–54.
- Mitsch WJ, Gosselink JG. 2000. *Wetlands*. New York: Wiley.
- Moore TR, Basiliko N. 2006. Decomposition. In: Wieder RK, Vitt DH, Eds. *Boreal peatland ecosystems, ecological studies*, vol 188. Heidelberg: Springer. pp 126–43.
- Moore TR, Bubier JL, Lafleur PM, Froking S, Roulet NT. 2002. Plant biomass, production and CO₂ exchange in an ombrotrophic bog. *J Ecol* 90:25–36.
- Moore TR, Trofymow AJ, Siltonen M, Prescott C, CIDET Working Group. 2005. Litter decomposition and C, N and P dynamics in upland forest and peatland sites, central Canada. *Can J For Res* 35:133–42.
- Painter TJ. 1991. Lindow Man, Tollund Man and other peat-bog bodies: the preservative and antimicrobial action of Sphanan, a reactive glycurnoglycan with tanning and sequestering properties. *Carbohydr Polym* 15:123–42.
- Rochefort Vitt L DH, Bayley SE. 1990. Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. *Ecology* 71:1986–2000.
- Roulet NT, Lafleur PM, Richard PJH, Moore TR, Humphreys E, Bubier JL. 2007. Comparison of a six year contemporary carbon balance and the carbon accumulation for the last 3,000 years for a northern peatland. *Glob Change Biol* 13:397–411.
- Saarinen T. 1996. Biomass and production of two vascular plants in a boreal mesotrophic fen. *Can J Bot* 74:934–8.
- Scanlon D, Moore T. 2000. CO₂ production from peatland soil profiles: the influence of temperature, oxic/anoxic conditions and substrate. *Soil Sci* 165:153–60.
- Sjörs H. 1991. Phyto- and necromass above and below ground in a fen. *Holarctic Ecol* 14:208–18.
- Thormann MN, Bayley SE. 1997. Decomposition along a moderate-rich fen-marsh peatland gradient in boreal Alberta, Canada. *Wetlands* 17:123–37.
- Thormann MN, Bayley SE, Currah RS. 2001. Comparison of decomposition of belowground and aboveground plant litters in peatlands of boreal Alberta. *Can J Bot* 79:9–22.
- Trofymow JA, Moore TR, Titus B, Prescott C, Morrison I, Siltonen M, Smith S, Fyles J, Wein R, Camiré C, Duschene L, Kozak L, Kranabetter M, Visser S. 2002. Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. *Can J For Res* 32:789–804.
- Turetsky MR. 2003. The role of bryophytes in carbon and nitrogen cycling. *Bryologist* 106:395–409.
- Verhoeven JTA, Liefveld WM. 1997. The ecological significance of organochemical compounds in *Sphagnum*. *Acta Bot Neerl* 46:117–30.
- Verhoeven JTA, Toth E. 1995. Decomposition of *Carex* and *Sphagnum* litter in fens: effect of litter quality and inhibition by living tissue homogenates. *Soil Biol Biochem* 27:271–5.
- Wallén B. 1986. Above and belowground dry mass of three main vascular plants on hummocks on a subarctic peat bog. *Oikos* 46:51–6.
- Wieder RK, Starr ST. 1998. Quantitative determination of organic fractions in highly organic, *Sphagnum* peat soils. *Commun Soil Sci Plant Anal* 29:847–57.
- Wylie GD. 1987. Decomposition and nutrient dynamics of litter of *Quercus palustris* and *Nelumbo lutea* in a wetland complex of Southeast Missouri, U.S.A. *Arch für Hydrobiol* 111:95–106.
- Yu ZC, Turetsky MR, Campbell ID, Vitt DH. 2001. Modelling long-term peatland dynamics. II Processes as inferred from litter and peat-core data. *Ecol Model* 144:159–73.