

Litter decomposition and nitrogen and phosphorus dynamics in peatlands and uplands over 12 years in central Canada

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Abstract The large accumulation of organic matter in peatlands has been partially attributed to litter decomposition rates, which are slowed by a high water table. To test this, we examined whether there were significant differences in the decomposition and N and P dynamics of ten foliar litters and wood blocks at three pairs of upland forest and peatland sites in the transitional grassland, high boreal and low subarctic regions of central Canada, using litterbags collected over a 12-year period. At two of the three pairs, the decomposition rate, as determined by proportion of the original mass remaining after 12 years and by the exponential decay coefficient (k), was faster overall at the upland than at the peatland. In the third pair, there was no significant difference, despite the water table being close to the peat surface; warmer soil temperatures in the peatland than the upland may be the cause. In general, there were small losses or gains of N in the litters after 12 years, compared to the original litter, though there were some

differences among litter types and sites, net gains in N likely reflecting the higher exogenous N availability. P was lost from most litters at the two northern pairs of sites, but at the transitional grassland pair, there were large net gains in P and greater variation among litters. The N:P ratio in the original litters ranged from 5 to 26 and after 12 years the ratio narrowed, with the site average of the ten litters ranging from 13 to 22, varying with the soil ratio. Decomposition rates and N and P dynamics after 12 years are different between upland and peatland sites: although the water table is a primary control on these differences, other factors such as temperature and soil nutrient status are also important.

Keywords Water table · Forests · Wetlands · Carbon · Nitrogen

Introduction

Peatlands contain larger amounts of organic matter than adjacent upland forest soils, and much of this difference has been ascribed to slower rates of decomposition attributed to litter with slow inherent decomposition rates, a high water table and cooler temperatures within peatland soils (see Moore and Basiliko 2006). In warm temperate ecosystems, several studies have examined the effects of flooding on litter decomposition, but the results have been variable, dependent on duration of flooding and litter type (e.g. Day 1983; Lockaby et al. 1996; Baker et al. 2001). Laboratory studies of decomposition of soil organic matter, such as peat, has shown that rates of decomposition are slower under anaerobic than aerobic conditions and under low temperatures (e.g. Scanlon and Moore 2000). However, Moore et al. (2005) showed that there was little difference after 6 years in decomposition of foliar litters placed at

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three pairs of upland forest and nearby peatland in central Canada. Moore et al. (2007) determined litter decomposition rates at five sites varying in their water table position within peatlands in southern Quebec and New Hampshire and found little difference in decomposition rate over 4–5 years.

These litter bag studies in northern environments are limited by determining decomposition rates over only a few years. The exception to this is the study reported by Latter et al. (1998) in which *Calluna* and *Eriophorum* litter was collected after 23 years of decomposition in a blanket bog. The small differences in decomposition rates observed between litter placed in northern upland and peatland soils, or at sites of varying wetness with peatlands, raises the question of whether organic matter accumulation in peatlands is primarily a function of the types of litter entering peatlands and their inherent decomposability, or whether 6 years or less is too short a period to determine significant differences in decomposition rates.

N and P are two important macro-nutrients whose concentrations and stoichiometry have been examined in leaves (e.g. McGroddy et al. 2004), affect rates of litter decomposition (e.g. Enriquez et al. 1993; Güsewell and Freeman 2005; Güsewell and Verhoeven 2006) and comprise an important part of nutrient cycling in peatlands (Aerts et al. 1999). N and P are retained by decomposing litter until critical ratios of C:N and C:P are reached, after which they are lost and the N:P ratios of decomposing litter converge to about 16:1 by mass (Moore et al. 2006), similar to that observed as critical in wetland plant growth (e.g. Güsewell et al. 2003). We have previously shown that litters decomposing in peatlands have higher N and P retention rates than those decomposing in upland soils, but this was based on decomposition over 6 years (Moore et al. 2005).

Here we test the hypothesis that decomposition rates of surface-placed litters are slower in northern peatlands than nearby upland soils, by determining loss of mass and the exponential decay constant (k) over 12 years. We also examine whether the transformation of N and P in the decomposing litters varies as a function of varying water regime and N and P content of the initial litter and of the peatland and upland soils. The Canadian Intersite Decomposition Experiment (CIDET) (Trofymow et al. 2002; Trofymow and CIDET Working Group 1998) placed litter bags representing ten foliar litters and surface- and subsurface-placed wood blocks at 21 sites in Canada, of which six sites were three pairs of upland forest and nearby peatland sites in central Canada. The 6-year results from these three pairs have been reported previously (Moore et al. 2005). Litterbags were retrieved yearly over the first 8 years and again after 10 and 12 years, providing an unusually long record of decomposition and N and P gain or loss.

Materials and methods

Litter bags and nutrient analyses

Details on CIDET and its litter collection, field methods, sample processing, and sites have been published previously (Trofymow and CIDET Working Group 1998). The salient characteristics of the three upland and three peatland sites examined in this paper are listed in Tables 1 and 2. The ten foliar litters were trembling aspen (*Populus tremuloides*), american beech (*Fagus grandifolia*), Douglas-fir (*Pseudotsuga menziesii*), white birch (*Betula papyrifera*), jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), tamarack (*Larix laricina*), western red cedar (*Thuja plicata*), bracken fern (*Pteridium aquilinum*) and plains rough fescue (*Festuca hallii*). They were collected from litter traps or senescent tissues, air-dried, thoroughly mixed and sub-sampled to determine air-dry to oven dry conversion. Western hemlock (*Tsuga heterophylla*) wood blocks were 2.5 cm thick cut from rough 5 × 10-cm planks custom sawn from the heartwood of a single 1-m-diameter log and oven-dried at 70°C. Sub-samples of each substrate type were milled to pass a 0.2-mm mesh prior to chemical characterization, which included total elemental analysis (C, N, P, S, Ca, Mg, K) and analysis of C fractions by wet chemical proximate analysis (Trofymow et al. 1995).

Litterbags were made of 20 × 20-cm polypropylene shade cloth with 0.25 × 0.5-mm openings and contained 10 g of litter. Each substrate type was placed at all sites, in four replicate plots per site. Bags were placed so they were in contact with the forest floor at upland sites and on the moss surface at the peatland sites. The ca. 50-g wood blocks were placed both on the forest floor or moss surface, as were the other litters. Additional wood blocks were buried at the forest floor/mineral soil interface (10–30 cm) and at ~20 cm beneath the surface at the peatland sites. After collection, litterbags were oven-dried at 70°C, the litter remaining weighed and percentage mass remaining calculated. The residual material was milled and analysed for N and P concentration as above, and concentration was combined with mass remaining to estimate the change in mass of these elements, compared to the original tissue, after 12 years of decomposition. The elemental concentrations for wood blocks were very low, in many cases below detection, and hence only the mass remaining data are reported in this paper.

Position of the litterbags relative to water table and moss and vascular plants was noted at each sampling time. To provide an estimate of the water table during the growing season, copper rods were installed at each site and the depth to oxidation noted as an approximation of the water table position.

We calculated k , and its SE, for each foliar litter type at each location, based on the natural logarithm of the mean

Table 1 Location and characteristics of the six upland and peatland sites. *na* Not applicable for wetland sites as Canadian fire weather index developed for upland forests

Site and code	Location	Latitude (N)	Longitude (W)	Ecoclimatic province	Soil type	13-year mean annual air temperature (°C)	13-year mean annual precipitation (mm)	2-year duff moisture code ^a	2-year mean soil temperature (°C) ^b	2-year mean soil degree-days ^c
Termundee upland (TER)	Termundee, SK	51°50'	104°55'	Transitional grassland	Orthic Black Chernozem	3.7	370	27	6.3	2,285
Batoche peatland (BAT)	Batoche, SK	52°43'	106°07'	Transitional grassland	Limno Mesisol	2.0	403	na	5.8	2,131
Nelson House upland (NH1)	Nelson House, MB	55°55'	98°37'	Subhumid high boreal	Dystric Brunisol	-2.9	471	21	5.4	1,983
Nelson House peatland (NH2)	Nelson House, MB	55°55'	98°25'	Subhumid high boreal	Typic Fibrisol	-2.9	471	na	5.0	1,823
Gillam upland (G11)	Gillam, MB	56°19'	94°51'	Low subarctic	Brunisolic Cryosol	-3.8	482	18	3.7	1,363
Gillam peatland (G12)	Gillam, MB	56°19'	94°30'	Low subarctic	Typic Fibrisol	-3.8	482	na	4.9	1,780

^a Canadian fire weather index

^b In situ soil temperature

^c Annual soil temperature degree-days above 0°C

Table 2 Vegetation and surface soil chemistry at the six sites (from Trofymow and CIDET Working Group 1998). For site codes, see Table 1

Site code	Dominant vegetation	Soil horizon	pH (CaCl ₂) ^a	C (%)	N (%)	C:N ratio	P (%)	C:P ratio	N:P ratio	Ca (%)
TER	<i>Populus tremuloides</i> , <i>Symphoricarpos occidentalis</i> , <i>Rosa woodsii</i> , <i>Bromus anomalous</i> , <i>Anemone canadensis</i>	LFH	6.4	15.0	0.90	16.6	0.097	155:1	9.3:1	0.379
BAT	<i>Betula glandulosa</i> , <i>Carex</i> spp., <i>Tomenthyppnum nitens</i> , <i>Potentilla fruticosa</i> , <i>Triglochin maritima</i> , <i>Drepanocladus</i> spp.	Ah FH/O	6.0 7.4	4.1 24.4	0.33 0.81	12.5 30:1	0.051 0.069	81:1 354:1	6.5:1 11.7:1	52.1 0.630
NH1	<i>Pinus banksiana</i> , <i>Vaccinium myrtilloides</i> , <i>Arctostaphylos uva-ursi</i> , <i>Vaccinium vitis-idaea</i> , <i>Cladina mitis</i> , <i>Cladina rangiferina</i> , <i>P. schreberi</i>	LFH Ae	4.0 4.5	30.7 0.6	0.53 0.03	58:1 21:1	0.057 0.009	538:1 60:1	9.3:1 3.3:1	0.078 13.0
NH2	<i>B. glandulosa</i> , <i>Carex</i> spp., <i>Sphagnum warnstorffii</i> , <i>Salix</i> spp., <i>Oxycoccus microcarpus</i> , <i>T. nitens</i>	Of	4.8	43.4	0.85	51:1	0.105	413:1	8.1:1	0.30
G11	<i>Picea mariana</i> , <i>Larix laricina</i> , <i>Vaccinium uliginosum</i> , <i>Ledum groenlandicum</i> , <i>Hylocomium splendens</i> , <i>Cladina mitis</i> , <i>Petasites palmatus</i>	LFH Ah and Bm	5.9 6.5	38.3 4.6	1.05 0.21	36:1 22:1	0.067 0.053	570:1 87:1	15.6:1 4.0:1	0.773 70.6
G12	<i>Chamaedaphne calyculata</i> , <i>Rubus chamaemorus</i> , <i>Sphagnum angustifolium</i> , <i>L. groenlandicum</i> , <i>Smilacina trifoliata</i> , <i>Mylia anomala</i>	Of	3.6	42.1	1.04	40:1	0.064	658:1	16:1	0.34

^a Soil pH in 0.01 M CaCl₂

^b Ca content in the upper horizon and percentage of cation exchange capacity in the lower horizon

mass remaining of quadruplicate litterbags collected at each sampling time from years 0 to 12 (Trofymow et al. 2002). We calculated the mass and initial amount of N and P remaining for each litter type at each location after 12 years, as the mean and SD of quadruplicate litter bags collected. Using mass, N and P remaining and k -value for the ten foliar litters at each site, we performed an ANOVA between the peatland and upland pair at each location to test whether there was a significant difference between the pairs.

Site characteristics

Two sites represent a pair of upland forest (Gillam upland; GI1) and nearby peatland (Gillam peatland; GI2) sites in the low subarctic ecoclimate province near Gillam. The second pair of upland (Nelson House upland; NH1) and peatland (Nelson House peatland; NH2) sites was in the subhumid high boreal province near Nelson House. The final pair was an upland site (Termundee upland; TER) in the transitional grassland province near Termundee and a peatland site (Batoche peatland; BAT) near Batoche, 160 km northwest of Termundee (Table 1).

The GI1 soil, a Cryosol underlain by permafrost in a *palsa*, was in a spruce-shrub forest with a high pH in the forest floor (5.9 in 0.01 M CaCl_2) and upper mineral soil (6.5) (Table 2). GI2 was a poor fen in a collapse scar, free of permafrost, with shrubs and mosses and a Fibrisol soil with a low pH (3.6). At GI2 the litterbags became covered by a small amount of the brown moss *Tomenthypnum nitens*, without any *Sphagnum* spp. Some litterbags were occasionally under water, and at the 12-year collection, the water table was very close to the surface, as shown by the oxidation of the copper wire (Fig. 1).

The NH1 soil, a sandy Brunisol, was located in a jack pine–lichen woodland with a low pH (4.0 and 4.5). The NH2 site was a poor fen located within a collapse scar, free of permafrost, with shrub, sedges and a moss layer, a Fibrisol with a low pH (4.8). At the NH2 site, there was fast growth of *Sphagnum* moss (*Sphagnum warnstorffii*) and a rising water table, so that after 12 years there was about 20–30 cm of *Sphagnum* and water over the bags. This is shown by the decreasing thickness of an oxidation layer in the copper wire (Fig. 1).

The TER soil was a Chernozem located in a trembling aspen stand with a shrub understory and a high pH (6.4 and 6.0). At the BAT site, brown mosses underlay the shrubs and sedges and the soil was a Mesisol with a high pH (7.4). At BAT there was a significant seasonal variation in the water table position, high in the spring and lower in the summer. The depth of oxidation of the copper wire suggests that the water table fell to 30–40 cm beneath the surface during the summer; after 12 years, a few of the

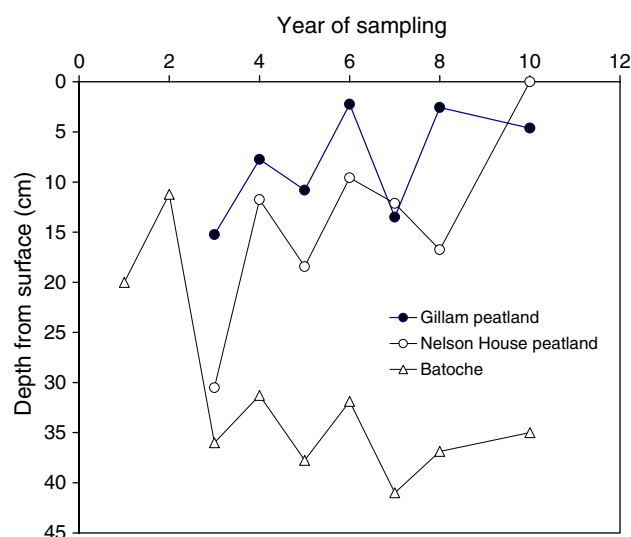


Fig. 1 Depth of oxidation of copper wires installed at the three peatland sites, indicating approximate position of water table

litterbags were covered with *T. nitens*, but very few were buried.

Site weather data for the 13 years encompassing the study period were obtained from nearby Meteorological Services Canada (MSC) weather stations at Saskatoon, Prince Albert, Nelson House and Gillam (Environment Canada 2006) and annual means calculated (Table 1). Mean weather data for BAT and TER are ANNUCLIM interpolated values derived from the MSC station data (McKenney et al. 2001). In situ daily mean soil temperatures for two 365-day periods (1997–1998, 1999–2000) at each of the six sites were obtained using single-channel temperature dataloggers (Onset Stowaway <http://www.onsetcomp.com>) placed in watertight enclosures within litterbags identical to those used in the litter decay study (Trofymow and CIDET Working Group 1998). Mean annual soil temperature and degree-days above 0°C were calculated for the six sites for each year and the average of the 2 years used to compare the microclimate at sites (Table 1). Daily weather data for those stations were used to calculate the Canada Fire Weather Index (FWI) moisture variables (Van Wagner and Pickett 1985), specifically the duff moisture code for the snow-free period at the upland site at each of the three paired sites for the same 2 years in which soil temperature was measured. In the FWI, the higher the duff moisture code the drier the surface organic layer and its calculation is generally only appropriate for upland sites without high water tables. The snow-free period was determined as the period from the last spring snow-fall and first autumn snow-fall shortened by the period of snow-on days in the spring. Snow-on days were determined to be when the mean daily soil temperature was less than or equal to 0°C, or when the mean daily air

temperature was less than 0°C and the range in soil temperature was less than or equal to 0.75°C.

Results

Litter decomposition

The general patterns of decomposition for trembling aspen (representing deciduous leaf litter), fescue (representing sedges) and black spruce (representing evergreen needle litter) at the six sites are illustrated in Fig. 2. In general, mass remaining became more variable within quadruplicate litterbags with increasing time of decomposition. Overall, excluding the wood blocks, there was an increase in the

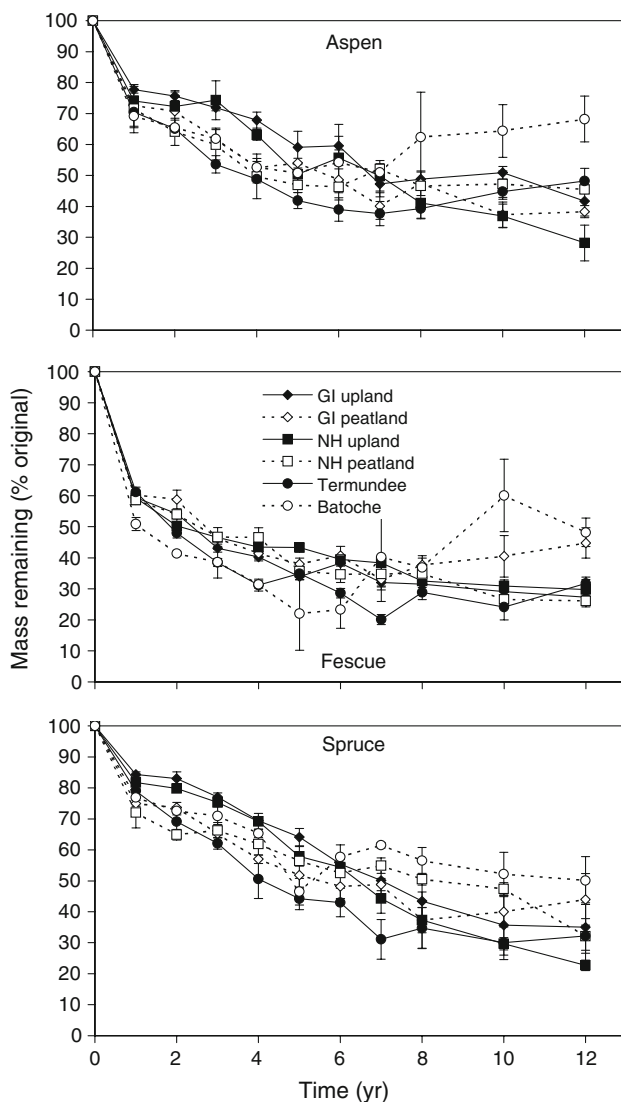


Fig. 2 Mass remaining using aspen leaves, fescue shoots and spruce needles. Error bars are the SD by mass of quadruplicate litterbags collected at each sampling date. GI Gillam, NH Nelson House, yr year

average SD from 1.8% in year 1 to 5.6% in year 12, representing an increase in the coefficient of variation of mass remaining from 0.024 to 0.122. In general, the variability in mass remaining among litterbags collected from the peatlands was greater than that in the upland litterbags, suggesting greater spatial variation in decomposer environments within the peatlands, though this pattern was less pronounced when expressed as the coefficient of variation. The increasing variability in mass remaining makes it more difficult to detect significant differences in decomposition over the longer 12-year period.

The aspen leaves revealed a steady decline in mass remaining, with 12-year mass remaining ranging from 28 to 68% of the original; the Batoche litterbags showed little average mass loss after 6 years and an increasing mass in the last 6 years. The fescue showed a more rapid initial mass loss than the aspen leaves and a 12-year mass remaining of 26–42%, with some evidence of increasing mass in the litterbags at GI2 and BAT in the final 4 years of decomposition. The black spruce needles revealed a slow decrease in mass remaining over the 12 years, with a final mass remaining of between 23 and 50% of the original, but with no evidence of increasing mass in the later stages of decomposition at any site.

Comparison of mass remaining after 12 years for the ten foliar litters and wood blocks placed at the surface and buried beneath the surface at the three pairs of upland and peatland sites revealed significant differences among the litters and sites (Fig. 3). At the Gillam sites, there were few differences in mass remaining between the upland and peatland sites, the exception being fescue (peatland > upland) and western red-cedar (peatland < upland) (Fig. 3a). The mean mass remaining of the ten foliar litters at the Gillam sites were not significantly different. At the other two pairs of sites, nearly all the litters exhibited a larger mass remaining in the peatland than the upland, the exceptions being fescue, white birch leaves and black spruce needles. The mean mass remaining of the ten foliar litters at the upland and peatland sites at Nelson House and Batoche–Termundee were significantly different at the $P < 0.01$ and $P < 0.001$ levels, respectively.

Comparison of mass remaining after 12 years for the wood blocks placed at the surface and buried beneath the surface at the three pairs of upland and peatland sites revealed significant differences among sites and placement (Fig. 3b). The differences were pronounced for both the buried and surface wood blocks, with generally <10% mass loss at the peatland sites and up to 75% mass loss in the upland sites, resulting in significant ($P < 0.01$) differences at the Batoche–Termundee and Nelson House pairs, but not at the Gillam pair ($P > 0.05$).

For the ten foliar litters, k gave a reasonable representation of the mass remaining over the 12 years for each of the

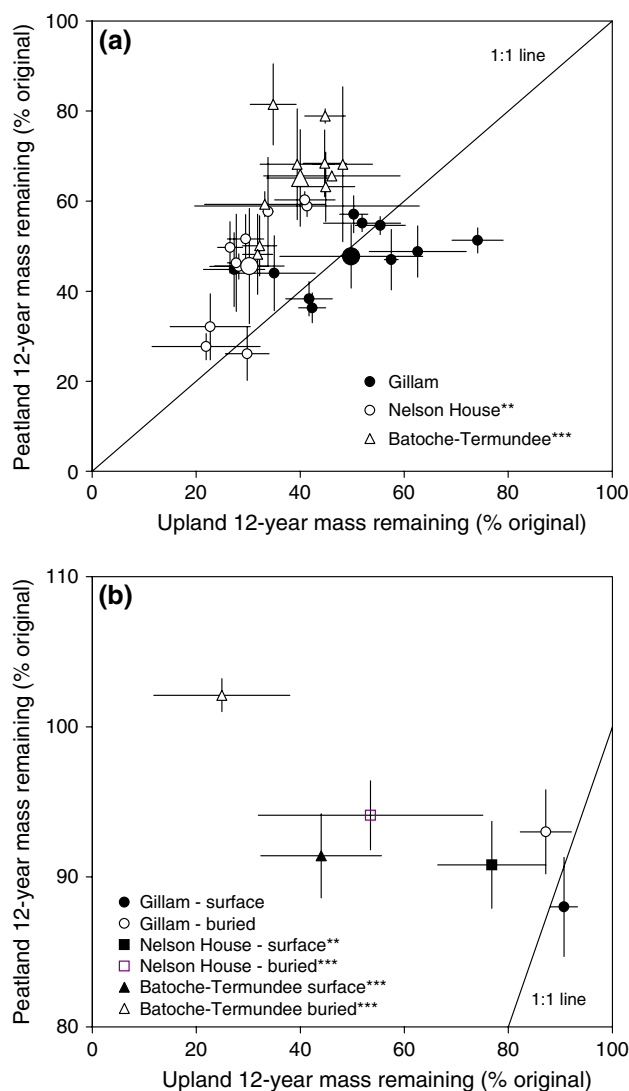


Fig. 3 Comparison of mass remaining (as percentage of original) after 12 years for **a** ten foliar litters and **b** surface and buried wood blocks at Gillam and Nelson House upland and peatland sites and Termundee upland and Batoche peatland sites. Error bars are the SD of quadruplicate litterbags. Large circles represent the mean and SD of the mass remaining of the ten foliar litters and significant differences between upland and peatland sites by ANOVA are indicated as * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

litter types, with r^2 -values ranging from 0.03 to 0.97 with an average of 0.80. All regressions were significant at $P < 0.05$, except for the fescue litter at Batoche, which showed a rapid initial mass loss and an increase in mass in the latter stages of decomposition (Fig. 2). Comparison of k -values for upland and peatland pairs revealed significantly larger values for all litters at the NH1 and Batoche-Termundee pairs, except fescue (Fig. 4). At the Gillam pair, however, there was no consistent pattern, with most litters being similar in their upland and peatland k -values, except black spruce needles, fescue and bracken fern, where the upland

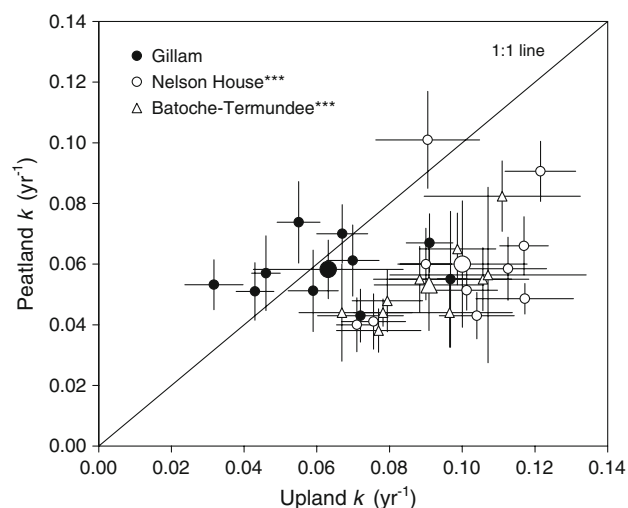


Fig. 4 Comparison of exponential decay value (k) over 12 years for ten litter types (excluding wood blocks) at Gillam and Nelson House upland and peatland sites and Termundee upland and Batoche peatland sites. Error bars represent SE of estimate of k . Symbols as in Fig. 3

value was significantly larger than the peatland value. Decomposition dynamics of the wood blocks deviated significantly from a simple exponential decay and so k -values could not be calculated.

N and P dynamics

After 12 years, there was little loss or gain of N in the litters placed at the GI1 and GI2 sites, with average values (expressed as percentage of the original N remaining) of 99 and 103%, respectively, and no significant difference between the average values for upland and peatland (Fig. 5a). In general, the litters placed at the Nelson House sites lost N, with an average of 72 and 83% of the original N remaining after 12 years at the upland and peatland site, respectively, though the range was greater than for the Gillam litters, with aspen and beech leaves retaining >100% at the peatland site and black spruce and jack pine needles having a N mass remaining of 55 to 60%. In general, the N remaining in the NH2 litters was larger than in upland litters, the exception being fescue, which had more N mass remaining in the upland than peatland litter. There was no significant difference ($P > 0.05$) between the average of N remaining in the ten foliar litters between upland and peatland sites.

The average N remaining at Termundee and Batoche sites after 12 years was 108 and 135%, respectively, significantly different at $P < 0.05$ (Fig. 5a). N gain was most pronounced in the aspen and beech leaves, Douglas-fir and tamarack needles and the bracken fern litters. In the latter three litters, the N increase in the peatland was significantly greater than that in the upland.

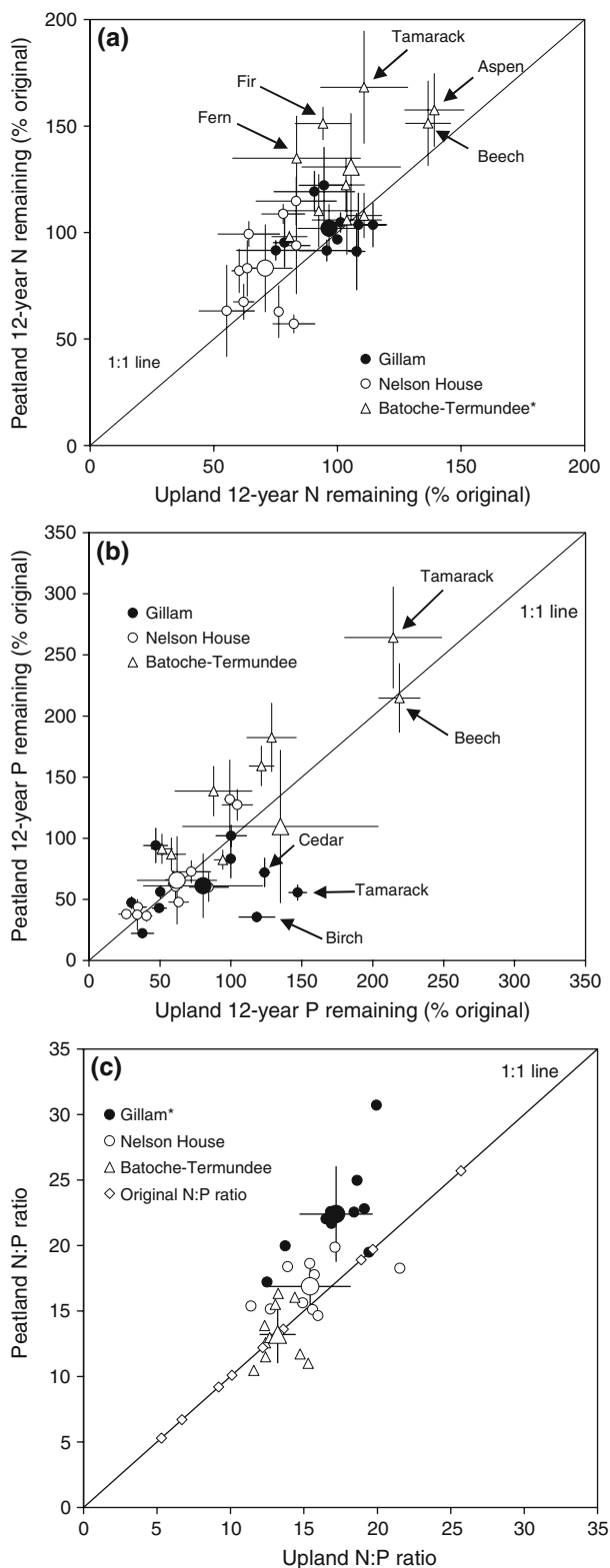


Fig. 5 Comparison of nutrient remaining (as percentage of original) after 12 years for ten foliar litter types at Gillam and Nelson House upland and peatland sites and Termundee upland and Batoche peatland sites: **a** N remaining, **b** P remaining, **c** N:P ratio (diamonds represent the original N:P ratio in the litters). Error bars are the SD by mass of quadruplicate litterbags. Symbols as in Fig. 3

At the Gillam and Nelson House sites, most litters lost P over the 12 years of decomposition, with average P mass remaining of 84 and 62% and 62 and 66%, for upland and peatland sites, respectively (Fig. 5b). The P remaining in the upland and peatland sites were similar, except for white birch leaves, western red-cedar and tamarack needles which had more P remaining (>100% of original) at the upland than wetland site at Gillam. There was no significant difference in the average P remaining in the ten foliar litters between the peatland and upland sites at Gillam and Nelson House.

The greatest variation in P dynamics occurred at the Batoche and Termundee sites, though there was no significant difference between the sites for the average of the ten litters. The average P remaining in litters after 12 years at Batoche and Termundee was 110 and 135%, respectively, with individual litters ranging from 51 to 264% of the original P remaining. While trembling aspen leaves and jack pine needles retained only about 60% of their original P, beech leaves and tamarack needles increased their P mass by over 200%.

The N:P ratio (mass basis) of the original litters varied widely, from 5.3 and 6.7 for aspen leaves and Douglas-fir needles to 19.7 and 25.7 for beech leaves and tamarack needles, respectively (Fig. 5c). The relative losses and gains of N and P during decomposition over 12 years resulted in N:P ratios narrowing to 10.5 to 30.7. Average N:P ratios for the ten foliar litters at each site were 13.2, 13.2, 15.4, 16.9, 17.2 and 22.4 at Termundee, Batoche, NH1 and NH2 and GI1 and GI2, respectively. Thus, the mean N:P ratio was smallest in the Batoche-Termundee litters and largest in the Gillam litters and in most cases the ratio is larger in the peatland than upland, though this pattern was significant ($P < 0.05$) at Gillam. This follows the trend in N:P ratio in the surface forest floor/organic layers, which are largest at the Gillam sites (Table 2). Decomposition over 12 years has resulted in a general narrowing of the N:P ratio in the ten litters, with an overall average of 16.4 and a SD of 3.9. This reflects a lowering of the ratio in litters with a high initial ratio and a raising of the ratio in those with a low initial ratio.

Discussion

In upland forest soils, surface litter decomposes under aerobic conditions, whereas in wetlands initial decomposition may be under aerobic conditions, but when litter enters the waterlogged catotelm, decomposition proceeds under anaerobic conditions. Incubation of soil organic matter under aerobic and anaerobic conditions has shown that decomposition rates, expressed as CO_2 production, are faster under aerobic than anaerobic conditions, though there is a great variability with aerobic:anaerobic ratios ranging from 1:1 to >20:1 (see Moore and Basiliko 2006). Thus,

decomposition rates should decrease when litter enters the water table zone. The period for this to occur varies with the rate of peat growth and the position of the water table, ranging from a few years when the water table is close to the surface to several centuries when the water table is low. In fast-decomposing litters, little mass may be left when this transfer from aerobic to anaerobic condition occurs. The occurrence of fires in upland soils may also contribute to their smaller accumulation of organic matter compared to peatlands, where fires are less frequent.

The litterbag technique allows an examination of decomposition rates of specific litters, though results are constrained by the mono-specific litter, the influence of mesh size on decomposer organisms and the micro-environment created within the bag. In addition, most litterbag studies are limited by a short duration, compared to the time taken as litter transforms to soil organic matter, particularly in cold soils. Furthermore, the relative variability in mass remaining appears to increase with time, as shown by the study of Latter et al. (1998), the current study and the larger CIDET data set (J. A. Trofymow, unpublished data).

After 12 years, there were significant differences in mass remaining and exponential k -value between the upland and peatland for two of the three pairs of sites in this study. At the Batoche-Termundee and Nelson House pairs, decomposition rates were slower in the peatland, except for the litters at Nelson House that decomposed at faster rates (e.g. birch leaves, fescue and black spruce needles). The differences at Nelson House were greater than those found there after 6 years (Moore et al. 2005) and may be explained by the rapid transfer of the litter into that part of the peat profile which was waterlogged, as shown by the oxidation of the copper wires and observations when the bags were retrieved.

At the Batoche-Termundee pair of sites, there appeared to be an increase in mass for some litter types from 8 to 12 years, with the increase more pronounced in the peatland than upland litters. This is despite the water table being low (<30 cm) during the summer in the peatland. The most likely cause of this pattern is the accumulation of CaCO_3 in the zone in which the litterbags are located, near the soil surface. Both upland and peatland soils have a high pH (6.4–7.4) and a high Ca content (Table 1).

At the Gillam pair of sites, however, this pattern is not repeated, even though the peatland has a water table near the surface, as does NH2. The average annual air temperature at the Gillam pair of sites is colder than those at Nelson House, by about 1°C, though surface soil temperature at the GI2 is the same as at the NH2 and 1.2°C warmer than at the GI1, which is underlain by permafrost. Thus, part of the reason for the lack of difference between the Gillam sites may be associated with the warmer peatland surface. A second reason may be associated with the ground flora. At the Nelson House sites, the peatland litterbags were rapidly overgrown by *Sphagnum*

mosses, which have been shown to produce a leachate that can retard decomposition rates of vascular litter (Verhoeven and Toth 1995; Verhoeven and Liefveld 1997; Van Breemen 1995). At the GI2 site, *Sphagnum* mosses were less extensive and brown mosses overgrew the litterbags, possibly resulting in less inhibition of decomposition.

One may conclude, then, that litters may decompose slower in peatland sites than adjacent upland forest sites, but the reasons may be different, deriving from a mixture of hydrological, thermal and chemical regime differences. The larger accumulation of organic matter in peatlands is associated primarily with the inherent slow decomposability of litter types found in peatlands, such as *Sphagnum* and other mosses and vascular litters with low concentrations of N and other nutrients (see Moore et al. 2007). In a series of floodplain communities in the southern United States, Baker et al. (2001) also noted that while frequency of flooding was a primary control on decomposition rates over 2 years, initial litter quality and soil properties were also important.

During decomposition, the fate of N and P depends on the initial concentration in litter. Based on 6 years of decomposition at the 21 CIDET sites, Moore et al. (2006) suggested that, overall, there is a net gain in N and then as decomposition proceeds N begins to be lost from the litter at C:N ratios of between 37:1 to 71:1, when about 40% of the original litter mass remains. P begins to be lost at C:P ratios of <682:1 to 904:1. At the Gillam pair of sites, there was little differentiation in the N left after 12 years. At the Nelson House sites, there was a larger differentiation, with less N lost in the peatland than upland litters, consistent with the faster decomposition in the upland litters. Substantial N net gain occurred in decomposing litters in TER and even more so at the BAT, and must be associated with N being immobilized from the surrounding soil, perhaps even from the groundwater system. Baker et al. (2001) also noted that there can be early retention, or gain, of N in litter decomposing on floodplains, but that the overall pattern was similar to loss of C.

As the original litters had a large range in C:P ratios (from 369:1 to 2122:1, Moore et al. 2006) the patterns of P loss or retention are more variable than for N. At Gillam and Nelson House, the litters that lost the most P (aspen, black spruce, and pine) are those with the smallest C:P ratios in the original litter (369:1 to 627:1), whereas those with high initial C:P ratios (beech, tamarack) generally gained or retained the most P. At the Batoche and Termundee sites, the range of P dynamics was greater than at the other two pairs of sites, with litters with low initial C:P ratios losing P and large gains in P in litters with high initial C:P ratios (beech and tamarack). Both Batoche and Termundee sites have low C:P ratios in the surface soils suggesting that exogenous P availability was high (Table 2).

The evolution of decomposing litter towards a common N:P ratio, approaching 16:1, has been noted across Cana-

dian forest sites by Moore et al. (2006). This pattern is repeated in the six sites reported here, from 5:1 to 26:1 to 10:1 to 25:1, though the progress is dependent on the site. The smallest ratios are found at the Batoche and Termundee, with the greatest decomposition, and least at the Gilham sites with the least decomposition. The results suggest that, in upland and peatland sites, litters converge to N:P ratios of between 12:1 and 16:1 as they decompose. The initial N:P ratio of litters in the floodplain study by Baker et al. (2001) did not vary greatly (from 11:1 to 21:1) but there was also a convergence, resulting in a range from 13:1 to 18:1 after 2 years of decomposition.

Conclusion

Our results suggest that, over 12 years, the decomposition of surface litter in northern peatlands is slower than in nearby upland forest soils. Although this reflects differences in water table position, this difference is small compared to the natural variability in decomposition rates among litters, based on their initial litter quality, and can also be affected by differences in the soil temperature regime of the peatland and upland. Of the three pairs of uplands and peatlands that we investigated, only two showed significantly slower decomposition rates in the peatland than the upland. In these northern ecosystems, N and P dynamics are tied to decomposition rates, with gain, retention and loss of these elements in the decomposing litter being dependent on the initial N and P concentration and on the availability of N and P in the surrounding soil. Overall, there is a convergence of the N:P ratio to 12:1 to 16:1, which appears independent of hydrologic regime and dependent on initial litter chemistry and soil characteristics.

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