Patterns of decomposition and carbon, nitrogen, and phosphorus dynamics of litter in upland forest and peatland sites in central Canada

T.R. Moore, J.A. Trofymow, M. Siltanen, C. Prescott, and CIDET Working Group

Abstract: We tested whether upland or peatland location affected rates of litter decomposition and nutrient dynamics. We examined the patterns of mass loss and carbon (C), nitrogen (N), and phosphorus (P) gain, retention, or loss in 11 forest tissues over 6 years at three upland and three peatland sites in the Low Boreal, High Boreal, and Low Subarctic zones of central Canada. After 6 years of decomposition, the average litter mass remaining ranged from 35% for fescue grass to 75% for western redcedar needles and 94% for wood blocks placed on the soil surface, with exponential decay coefficients (*k*) of –0.16, –0.05, and –0.01, respectively. At one pair of sites, the mass remaining and the *k* values indicated that faster decomposition occurred in the upland site than in the nearby peatland site. The reverse was the case in a second pair. No overall pattern was apparent in the third. In general, Douglas-fir needles decomposed significantly faster in peatland than upland sites, and the reverse pattern occurred for bracken fern. Most foliar litters retained their original N mass and lost P as they decomposed. There were few major differences between N and P dynamics in litters decomposing at upland and peatland sites, though N and P retention in some cases was greater at the peatland sites. These results suggest that longer term (>6 years) differences in decomposition rate and differences in litter quality account for larger C accumulation in peatland than in upland soils.

Résumé : Les auteurs ont vérifié si les milieux secs ou les tourbières affectent le taux de décomposition et la dynamique des nutriments. Ils ont examiné les patrons de perte de masse ainsi que le gain, la rétention ou la perte de carbone (C), d'azote (N) et de phosphore (P) dans 11 tissus de plantes forestières placés dans des sachets à décomposition. L'expérience a été réalisée sur une période de 6 ans dans trois milieux secs et trois tourbières jumelés dans les zones du Bas-Boréal, du Haut-Boréal et du Bas-Subarctique du centre du Canada. Après 6 ans de décomposition, la masse moyenne résiduelle de litière variait de 35 % pour la fétuque à 75 % pour les aiguilles de cèdre de l'ouest et 94 % pour les blocs de bois placés à la surface du sol, avec des coefficients exponentiels de décomposition (*k*) respectifs de –0,16, –0,05 et –0,01. Dans le cas d'une paire de sites, la masse résiduelle et les valeurs de *k* indiquaient une décomposition plus rapide dans le milieu sec que dans la tourbière. C'était l'inverse dans le cas d'une seconde paire alors qu'il n'y avait pas de différence dans le cas de la troisième paire. En général, les aiguilles de sapin Douglas se sont décomposées significativement plus rapidement dans les tourbières que dans les milieux secs et l'inverse a été observé pour la fougère aigle. La plupart des litières foliaires ont conservé leur masse originale de N mais ont perdu du P durant leur décomposition. Il y avait peu de différences majeures entre les dynamiques de N et P dans les litières se décomposant dans les milieux secs par rapport aux tourbières bien que dans certains cas, la rétention de N et P était plus importante dans les tourbières. Ces résultats suggèrent que des différences à plus long terme (>6 ans) dans le taux de décomposition ou que des différences dans la qualité de la litière sont responsables de la plus grande accumulation de C dans les tourbières que dans les milieux secs.

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Introduction

Organic matter accumulates in northern peatlands and other wetlands because the rates of net primary production of vegetation are faster than the rates at which dead plant tissues are decomposed in the soil profile. Net primary production rates in Canadian peatlands are small compared with those of other ecosystems (e.g., Campbell et al. 2000; Moore et al. 2002), so the organic matter accumulation has been linked to slow rates of litter decomposition. Several studies of short-term decomposition rates in peatlands have been made. In these, peat-forming plant tissues have been placed in litterbags, left

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for several years, and then retrieved. The mass remaining inside the bags is used as an indication of the rate of decomposition. These studies have shown that decomposition rates vary with overall climate (e.g., Hogg et al. 1994), tissue type (e.g., Rochefort et al. 1990; Johnson and Damman 1991), peatland type (e.g., Szumigalski and Bayley 1996; Thormann and Bayley 1997), and placement position within the soil profile (e.g., Belyea 1996).

The rate of decomposition of tissues has commonly been assumed to be slower in peatlands than in nearby well-drained upland sites having forest or grassland vegetation. One reason for this assumption is that many peatland litters, especially in bogs, have low nutrient concentrations, particularly nitrogen (N) and phosphorus (P) (e.g., Aerts et al. 1999). Some peat-forming plants, particularly *Sphagnum* moss, have very slow rates of decomposition (e.g., Clymo 1965) and produce compounds that may slow the rate of microbial activity and tissue decomposition as the peat forms (e.g., Painter 1991; van Breemen 1995). Furthermore, peatlands have a high water table, and the occurrence of flooding (e.g., Day 1983; Lockaby et al. 1996) and anoxic conditions may slow the rate of litter decomposition. The reduction in the rates of CO_2 production from peat during the conversion from oxic to anoxic conditions is well established (e.g., Bridgham et al. 1998; Scanlon and Moore 2000). However, in most peatlands, the water table is beneath the peat surface for most of the year, so aboveground litter initially decomposes under oxic conditions before entering the zone beneath the water table. Roots produced at or below the water table may decompose from the outset under anoxic conditions. Frolking et al. (2001) developed a simple peat decomposition model, based on prescribed decomposition rates, peat temperature, and reduction in decomposition upon passage from the oxic to anoxic zones. The authors were able to reasonably simulate organic matter accumulation in several eastern Canadian peatland profiles. Decomposition of litter under anoxic conditions may also affect the release or retention of N and P.

Because litter decomposition studies in peatlands and upland forests have usually been conducted separately, there is no clear evidence of whether the site (peatland or upland) is significant in controlling decomposition rates. To test and quantify this, we examined the rates of decomposition of 11 litters placed in three peatland and three nearby upland sites in central Canada, over a 6-year period. The pairs follow a climatic gradient that extends from near the forest–prairie border to the subarctic. We compared the mass remaining after 6 years and the exponential decay model parameter (k) calculated from annual collections over the 6 years. To test whether placement of litter in upland or peatland sites affects the dynamics of N and P during the early stages of decomposition, we also compared the retention, gain, or loss these two nutrients over the 6 years, as a function of the loss of carbon (C).

Materials and methods

The Canadian Intersite Decomposition Experiment (CIDET) study involved the placement of about 11 000 litterbags containing 12 material types (10 foliar litters, 1 surface wood block, and 1 buried wood block) at 21 locations (18 upland and 3 wetland sites) representing the major ecoclimatic provinces of Canada (Ecoregions Working Group 1989). Details on 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 wetland sites and 11 litter types examined in this paper are listed in Tables 1 and 2.

The 10 foliar litters were collected from litter traps or senescent tissues (Trofymow et al. 1995). Litters were air-dried, thoroughly mixed, and subsampled to determine air-dry to oven-dry conversion. Subsamples were milled to pass through 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. Litter C concentration was corrected for the presence of $CaCO_3$ at the Batoche site. Descriptions of the procedures (Trofymow and CIDET Working Group 1998) and results for the elemental and proximate analysis (Trofymow et al. 1995) and ^{13}C cross-polarization and magic-angle spinning NMR analysis (Preston et al. 1997, 2000) have been previously published. The chemical composition of the initial litter tissues varied considerably, in terms of C:N, C:P, and N:P ratios, as well as the acid-unhydrolyzable residue (AUR or "Klason lignin") content (Table 1).

Litterbags were made of 20 cm × 20 cm polypropylene fabric with 0.25 mm × 0.5 mm openings. They contained 10 g of litter per bag. Each litter 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 wetland sites. The wood blocks were placed either on the forest floor or moss surface, as were the other litters, and buried 10–30 cm beneath the surface of the soils. Sufficient bags were placed to allow for 10 collections. After collection, litterbags were oven-dried at 70 °C. The litter remaining was then weighed and the percent mass calculated. The residual material was milled and analyzed for C, N, and P concentration (as described previously), and those concentrations were combined with the mass remaining to estimate the change in mass of these three elements compared with the original tissue. The elemental data for wood blocks were not used.

Litterbags were retrieved annually at six sites (Table 2). Two represent a pair of upland forest (GI1) and nearby peatland (GI2) sites in the low subarctic ecoclimate province near Gillam. The second pair of upland (NH1) and peatland (NH2) sites was in the subhumid high boreal province near Nelson House. The final pair was an upland site (PAL) in the subhumid low boreal province near Prince Albert and a peatland site (BAT) 60 km south-southwest of Prince Albert, near Batoche, close to the boundary of the transitional grassland and subhumid low boreal provinces. Vegetation and forest floor or upper organic horizon properties of the six sites are listed in Table 3.

At the Batoche peatland, the water table has fluctuated near the soil surface, but the litterbags have remained above it, apart from the buried wood blocks. The Gillam peatland has a water table that is near the surface of the brown moss on which the litterbags were placed, so the bags there are subject to temporary waterlogging. The Nelson House peatland has accumulated *Sphagnum* rapidly, so most of the litterbags had been overlain by approximately 20 cm of moss by the sixth year and exposed to summer water table submergence from the fourth year.

Table 1. Initial composition of the 11 litter types (from Trofymow and CIDET Working Group 1998).

Litter type	Litter code	Initial litter composition									
		C (%)	N (%)	C:N ratio	P (%)	C:P ratio	N:P ratio	Ca (%)	AUR (%)	AUR:N ratio	AUR:P ratio
Trembling aspen(Populus tremuloides Michx.) leaves	Aspen	46.8	0.67	70:1	0.127	369:1	5.3:1	2.05	14.4	22:1	113:1
American beech (Fagus grandifolia Ehrh.) leaves	Beech	47.0	0.71	66:1	0.036	1306:1	19.7:1	0.99	28.0	39:1	778:1
White birch (Betula papyrifera Marsh.) leaves	Birch	48.0	0.72	67:1	0.038	1263:1	18.9:1	0.85	24.0	33:1	632:1
Western redcedar (Thuja plicata Don ex D. Don) needles	Cedar	49.7	0.64	78:1	0.047	1057:1	13.6:1	1.68	35.6	56:1	757:1
Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) needles	Fir	49.6	0.70	70:1	0.105	472:1	6.7:1	1.28	30.3	43:1	289:1
Fescue grass (Festuca halii (Vasey) Piper)	Fescue	43.8	0.71	62:1	0.058	755:1	12.2:1	0.37	11.2	16:1	272:1
Bracken fern (Pteridium aquilinum (L.) Kuhn)	Fern	46.3	0.88	53:1	0.066	702:1	13.3:1	0.77	32.9	37:1	498:1
Jack pine (Pinus banksiana Lamb.) needles	Pine	49.7	1.28	39:1	0.127	391:1	10.1:1	4.55	32.8	26:1	258:1
Black spruce (Picea mariana (Mill. B.S.P.) needles	Spruce	49.5	0.73	68:1	0.079	627:1	9.2:1	0.66	28.3	39:1	358:1
Tamarack (Larix laricina (Du Roi) K. Koch) needles	Tamarack	48.8	0.59	83:1	0.023	2122:1	25.7:1	0.66	24.0	41:1	1770:1
Western hemlock (Tsuga heterophylla) wood blocks	Wood	47.3	0.24	197:1	0.005	9460:1	48.0:1	0.11	29.4	123:1	5880:1

Note: AUR, acid-unhydrolyzable residue.

Table 2. Location and characteristics of the six upland and wetland sites (from Trofymow and CIDET Working Group 1998).

Site code and type	Location	Lat. (N)	Long. (W)	Ecoclimatic province	Soil type	Mean annual air temperature (°C)	Mean annual precipitation (mm)	Duff moisture code[a]	2-year mean soil temp. (°C)[b]	2-year mean soil degree-days[c]
PAL upland	Prince Albert, Sask.	53°13'	105°58'	Subhumid low boreal	Orthic Regosol	0.1	398	27	6.3	2299
BAT peatland	Batoche, Sask.	52°43'	106°07'	Transitional grassland	Limno Mesisol	0.1	398	27	5.8	2131
NH1 upland	Nelson House, Man.	55°55'	98°37'	Subhumid high boreal	Dystric Brunisol	–3.9	542	21	5.4	1983
NH2 peatland	Nelson House, Man.	55°55'	98°25'	Subhumid high boreal	Typic Fibrisol	–3.9	542	21	5	1823
GI1 upland	Gillam, Man.	56°19'	94°51'	Low subarctic	Brunisolic Cryosol	–5.2	485	18	3.7	1363
GI2 peatland	Gillam, Man.	56°19'	94°30'	Low subarctic	Typic Fibrisol	–5.2	485	18	4.9	1780

[a]Canadian Forest Fire Weather Index – duff moisture code.
[b]In situ soil temperature.
[c]Annual degree-days above 0 °C.

Table 3. Vegetation and surface soil chemistry at the six sites (from Trofymow and CIDET Working Group 1998).

Site[a]	Dominant vegetation	Soil horizon	Soil pH[b]	C (%)	N (%)	C:N ratio	P (%)	C:P ratio	N:P ratio	Ca (%)[c]
PAL	Picea banksiana, Arctostaphylos uva-ursi, Vaccinium myrtilloides, Symphoricarpos albus, Cladina mitis, Cladina rangiferina, Pleurozium schreberi, Aster laevis, Solidago spp.	LFH	—	28.1	0.60	47:1	0.057	492:1	10.5:1	0.226
		Ah	6.2	1.8	0.09	21:1	0.021	88:1	4.3:1	74.3
BAT	Betula glandulosa, Carex spp., Tomenthypnum nitens, Potentilla fruticosa, Triglochin maritima, Depanocladus spp.	FH–O	7.4	24.4	0.81	30:1	0.07	354:1	11.7:1	0.63
NH1	Pinus banksiana, Vaccinium myrtilloides, Arctostaphylos uva-ursi, Vaccinium vitis-idaea, Cladina rangiferina, Pleurozium schreberi	LFH	—	30.7	0.53	58:1	0.057	538:1	9.3:1	0.078
		Ae	4.8	0.6	0.03	21:1	0.009	60:1	3.3:1	13.0
NH2	Betula glandulosa, Carex spp., Sphagnum warnstorfi, Salix spp., Oxycoccus microcarpus, Tomenthypnum nitens	Of	4.5	43.4	0.85	51:1	0.105	413:1	8.1:1	0.3
GI1	Picea mariana, Larix laricina, Vaccinium uliginosum, Ledum groenlandicum, Hylocomium splendens, Cladina mitis, Petasites palmatus	LFHA	—	38.3	1.05	36:1	0.067	570:1	15.6:1	0.773
		Bm	6.6	4.6	0.21	22:1	0.053	87:1	4.0:1	70.6
GI2	Chamaedaphne calyculata, Rubus chamaemorus, Sphagnum angustifolium, Ledum groenlandicum, Smilacina trifolia, Mylia anomala	Of	4.3	42.1	1.04	40:1	0.06	658:1	0.667	0.34

[a]PAL, upland; BAT, peatland; NH1, upland; NH2, peatland; GI1, upland; GI2, peatland.
[b]Soil pH in water.
[c]Ca content in the upper horizon and percentage of cation exchange capacity in the lower horizon.

Site weather data and annual means (Table 2) were obtained from nearby Meteorological Services Canada weather stations at Prince Albert, Nelson House, and Gillam (Environment Canada 2000). Daily data for those stations were used to calculate the Canadian Forest Fire Weather Index (FWI) moisture variables (Van Wagner and Pickett 1985), specifically the duff moisture code for the snow-free period at each of three paired sites. In the FWI, the higher the duff moisture code the drier the surface organic layer. In situ daily mean soil temperatures for two 365-day periods (1997–1998 and 1999–2000) at each of the six sites were obtained using single-channel temperature dataloggers (Onset Stowaway, http://www.onsetcomp.com). The dataloggers were 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 was used to compare the microclimate at sites (Table 2).

The exponential decay model parameter k was calculated for each litter type at each location based on the logarithm of the mean mass remaining from years 0 to 6 (Trofymow et al. 2002). An analysis of variance (ANOVA) was performed in SYSTAT on the mass remaining in individual litterbags in year 6. The factors analyzed included the 12 litter types (10 foliar litters plus surface and buried wood blocks), the site type (three upland (PAL, NH1, and GI1) and three wetland (BAT, NH2, and GI2)), and the geographic region (low subarctic (GI1 and GI2), high boreal (NH1 and NH2), and low boreal (PAL and BAT)). To establish the patterns of N and P gain or loss within litter over the 6 years, a simple quadratic model was applied to the change in N or P mass in the litter (compared with the original mass) against the change in litter C mass, based on the mean value for years 0 to 6. This model allows for nonlinear relationships between C and N–P dynamics.

Results

Decomposition of litters

In general, the litters showed a rapid initial mass loss and then progressively slower losses through the remaining 5 years. For the buried and surface wood blocks at the upland sites, there was an increase in the rate of mass loss in the latter half of the 6-year period. For mass remaining after 6 years, the least average decomposition was observed in the surface and buried wood blocks and cedar needles (91%, 80%, and 73 % of original mass remaining, respectively) and the most in fescue, white birch leaves, and black spruce needles (34%, 45%, and 51%, respectively) (Table 4). For the 10 foliar litters, the greatest average mass loss occurred at the Gillam peatland sites (50% of original mass remaining) and the smallest mass loss at the Gillam upland site (61%).

At the Prince Albert – Batoche pair, buried wood blocks, cedar, fern and tamarack, pine and spruce needles had less mass remaining in the upland site than in the peatland site; and fescue, fir needles, and surface wood blocks had greater mass remaining in the upland than in the peatland site. At Nelson House, in contrast, aspen, beech, fescue, and fir had more mass remaining in the upland than the peatland sites; and the reverse occurred for fern, pine, and buried wood blocks. At Gillam, all litters had more mass remaining after

Table 4. Percent mass remaining after 6 years for each litter type at all six sites, expressed as mean (SE).

Tissue	PAL	BAT	NH1	NH2	GI1	GI2	Average
Aspen	55.1 (1.9)	54.3 (6.1)	55.7 (1.3)	46.3 (1.0)	59.6 (1.5)	48.6 (1.8)	53.3
Beech	66.7 (1.9)	69.4 (2.4)	70.8 (1.8)	54.7 (6.1)	72.0 (2.3)	48.7 (3.2)	63.7
Birch	48.9 (2.7)	45.9 (1.9)	40.7 (2.6)	44.9 (4.4)	52.5 (1.6)	41.9 (1.7)	45.8
Cedar	76.4 (1.4)	88.4 (1.9)	76.0 (1.4)	74.7 (1.3)	81.1 (1.3)	52.7 (2.0)	74.9
Fern	48.6 (3.0)	58.8 (3.3)	49.9 (0.9)	70.0 (3.8)	58.6 (2.2)	64.8 (1.4)	58.5
Fescue	34.9 (1.1)	23.3 (3.0)	39.5 (0.7)	34.7 (1.3)	38.3 (1.2)	40.7 (1.5)	35.2
Fir	69.6 (1.7)	55.1 (1.5)	61.1 (3.7)	48.5 (3.2)	65.5 (2.4)	46.8 (1.5)	57.8
Pine	53.5 (3.1)	61.5 (1.2)	50.0 (1.7)	63.7 (0.5)	57.8 (1.4)	51.6 (2.5)	56.4
Spruce	46.5 (3.1)	57.7 (2.0)	54.4 (1.2)	52.5 (0.4)	55.4 (1.2)	48.2 (2.0)	52.5
Tamarack	63.2 (2.9)	75.1 (1.8)	63.3 (3.0)	64.3 (1.2)	71.7 (0.2)	51.9 (3.9)	64.9
Foliar litter mean	56.6	59	56.4	56.1	61.3	49.6	—
Wood - surface	99.4 (1.5)	95.7 (0.8)	82.5 (6.4)	96.0 (0.5)	97.8 (0.1)	93.4 (0.9)	94.1
Wood - buried	52.7 (4.3)	100.5 (0.5)	61.2 (5.4)	99.6 (0.6)	99.3 (0.6)	97.3 (0.5)	85.1

Note: PAL, upland; BAT, peatland; NH1, upland; NH2, peatland; GI1, upland; GI2, peatland.

Fig. 1. Relationship between mass remaining after 6 years and exponential decay rate calculated over the 6 years.

$k = 0.153\text{Ln(mass)} - 0.705$
$r^2 = 0.975$
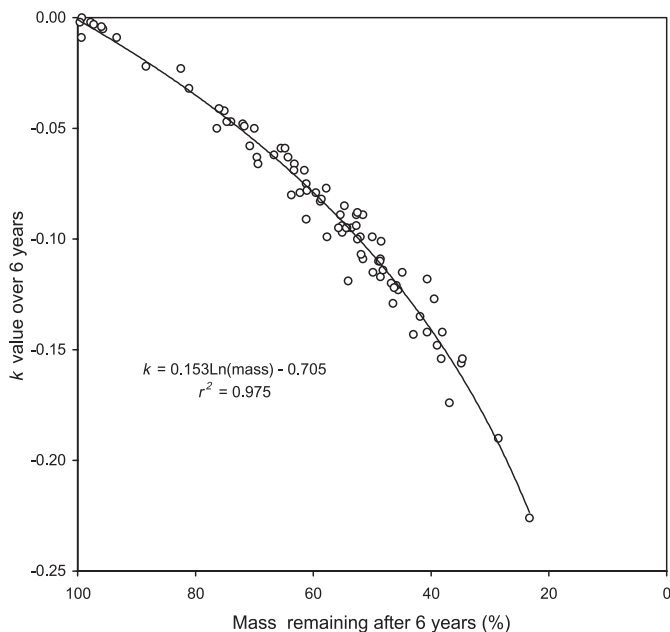
6 years at the upland site than those at the peatland site, except for fern and fescue.

The ANOVA, using the individual litterbag mass remaining after 6 years, revealed that there was no significant difference between the uplands and peatlands ($N = 286$, $F = 0.252$, $P = 0.616$). The analysis also failed to reveal significant differences among the three ecoclimatic provinces ($F = 1.003$, $P = 0.368$), but there was a strong difference among the 12 litter types ($F = 39.313$, $P < 0.001$).

Individual exponential k decomposition values ranged from –0.00 to –0.23, with averages of –0.16 for fescue grass to –0.05 for western redcedar needles, and –0.01 for wood blocks. The mass remaining after 6 years and the exponential k values were strongly related, providing similar relationships among pairs of sites to those obtained for mass remaining (Fig. 1). At the Prince Albert – Batoche pair, fir and fescue had more negative k values in the peatland than in the upland site; and the reverse was true for buried wood

blocks, cedar, fern, and pine, spruce, and tamarack needles (Fig. 2). At the Gillam pair, only the fern had a more negative k value at the upland than at the peatland site, and at the Nelson House pair, only fern and surface wood blocks had more negative k values in the upland site. Thus, of the 36 comparisons between upland and peatland decomposition for the three pairs of sites, about one-third showed a faster decomposition in the upland than in the peatland, one-third showed the reverse, and the remainder were indeterminate. A two-tailed Student's t test with assumed unequal variance was applied to the k values of the 12 litters, which were separated into uplands and peatlands ($n = 3$ for each), and showed that only fern and fir had a significant difference ($P < 0.05$). Fern decomposed faster (more negative k values) in upland than in peatland sites, and the reverse was the case for fir.

Decomposition rates of foliar litters at upland sites generally follow the regional climate, as shown by the mean annual air temperature, decreasing from 0.1 °C at Prince Albert to –3.9 °C and –5.2 °C at Nelson House and Gillam, respectively (Table 2). This was not the pattern for the peatland foliar litters, where decomposition was fastest at Gillam.

In addition to differences in soil water regime, microsite thermal regime at the pairs may partially account for differences between upland and peatland sites. The Prince Albert upland had a warmer mean annual temperature (by 0.5 °C) and 168 more degree-days than the Batoche peatland. A similar difference was recorded at the two Nelson House sites. At Gillam, however, the pattern was reversed with the peatland 1.2 °C warmer and having 417 more degree-days than the upland site. Thus, the distinctly faster decomposition rates at the Gillam peatland may, in part, be attributed to a warmer microclimate where the litterbags were placed. Despite a warmer location, therefore, the upland sites at Prince Albert and Nelson House did not show overall faster rates of decomposition.

Decomposition of surface-placed materials in the peatlands did not follow the latitudinal gradient, with decay being more rapid at high latitude (mean foliar k, –0.109) and similar at the mid- (mean foliar k, –0.091) and low-latitude (mean foliar k, –0.092) peatlands. The confounding effects of varying surface water table levels and degree of moss overgrowth may have accounted for some of the differences. However, within in each pair, for most litter types and for the foliar
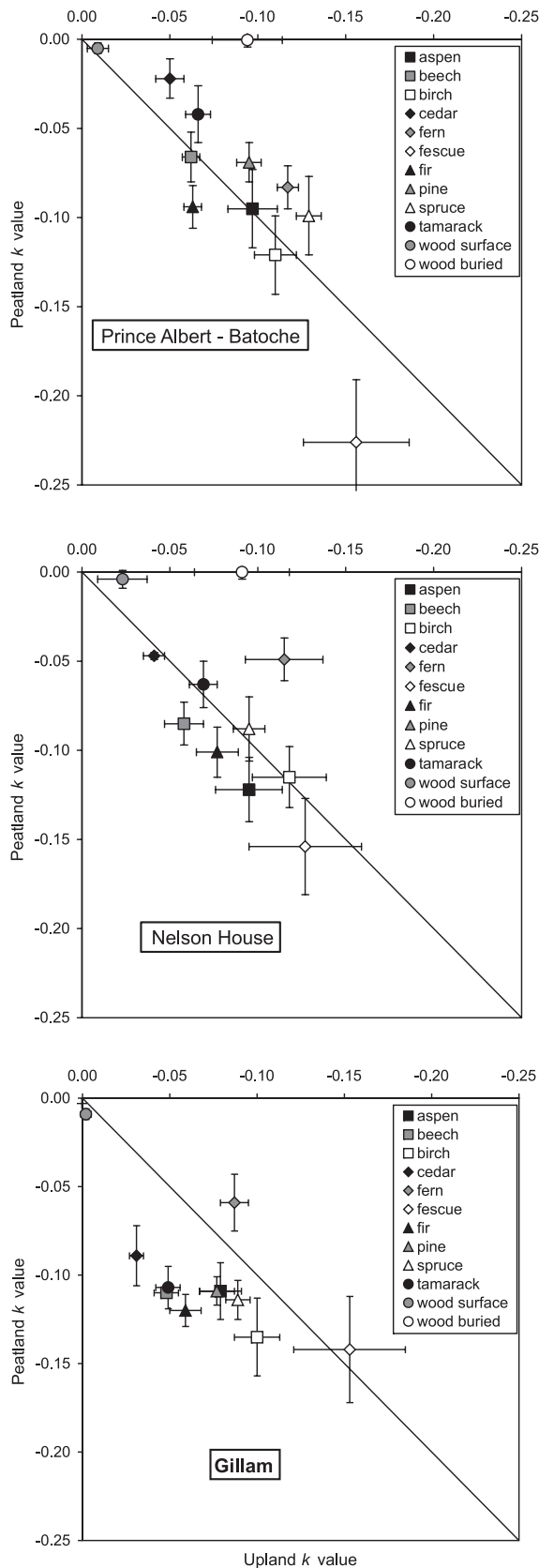
Fig. 2. Relationship between exponential decay constant k after 6 years of the 12 litters at the three pairs of sites: Prince Albert upland – Batoche peatland, Nelson House 1 upland – Nelson House 2 peatland, and Gillam 1 upland – Gillam 2 peatland. Solid line represents 1:1 relationship.

N and P dynamics in foliar litter

We looked for differences among the sites by comparing the proportion of the original N and P mass in the retrieved litter with the original C mass remaining. We fitted a polynomial regression to this relationship over the 6 years and found that, in general, litters retained most of their original N mass as they decomposed, but showed a substantial loss of original P. That loss of P was greatest (to 30%–40% of the original litter P mass after 6 years) in the aspen leaves and least (70%–120%) in the birch and beech leaves and tamarack needles. This was generally inversely correlated with the C:P quotient in the original litter. We illustrate these patterns with three examples — for spruce needles, aspen leaves, and fern — to represent needle, broad-leaved, and shrub litter types (Figs. 3 and 4).

The spruce needles retained most of their original N over the 6 years, though about half of the original C was lost. There was no significant difference between the upland and peatland sites in the three pairs (Fig. 3). The aspen leaves showed a more variable pattern, with some evidence of an initial gain in N at the Prince Albert and Nelson House peatland sites, and Batoche in the later stages of decomposition. The peatland member of the three pairs all showed a greater retention or gain of N than did the upland member, which lost about half of the original C. The fern showed a similar pattern to the aspen, with some initial N gain and a larger N content after 6 years in the peatland sites than in the upland sites.

The spruce needles lost about half of their original P content over the 6 years, but no consistent difference was apparent between the upland and peatland sites (Fig. 4). The aspen leaves also lost about half of their original P mass, and for Prince Albert – Batoche and Nelson House, the loss was smaller at the peatland than at the upland sites. The fern also lost P, with the peatland sites retaining a larger proportion than the upland sites.

Discussion

The results of this study suggest that, over the first 6 years, there are relatively small differences in the rates of decomposition or dynamics of N and P between litters decomposing at well-drained forest sites and those in nearby peatlands. Although the effects of microtopography and moss species on decomposition within a peatland have been examined (e.g., Johnson and Damman 1991), few studies have examined the effect of drainage class on decomposition rates. At a well-drained deciduous forest site and a nearby swamp (with Brunisol and Mesisol soils, respectively), T.R. Moore (personal communication) observed decomposition (k) coefficients over 6 years for beech, maple, and birch leaves of –0.33, –0.75, and –0.67, respectively, in the forest and –0.12, –0.54, and –0.45, respectively, in the swamp. Using a variety of techniques, Trumbore and Harden (1997) estimated that long-

mean, initial mass loss (exponential regression intercept or year 1 mass remaining) was always 1%–2% greater in the wetland than in the upland site.

Fig. 3. Relationship between C and N mass remaining in spruce needles, aspen leaves, and fern at the six sites. Lines represent quadratic relationship, with R^2 indicated in the diagram.
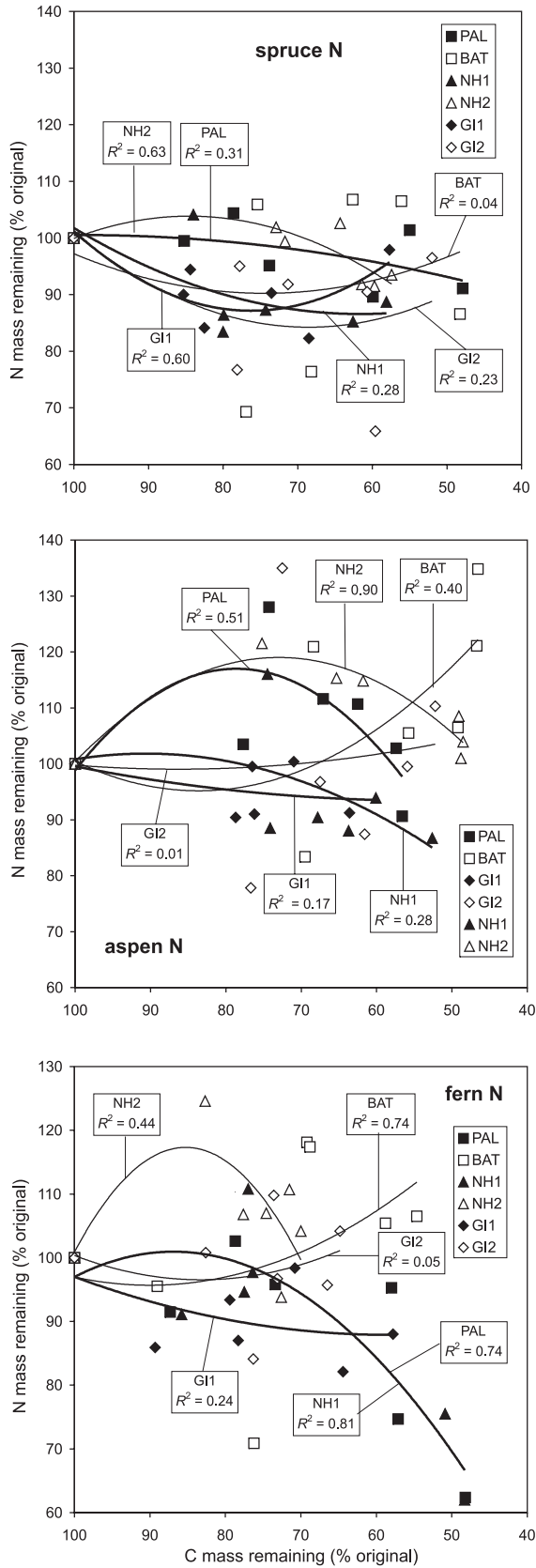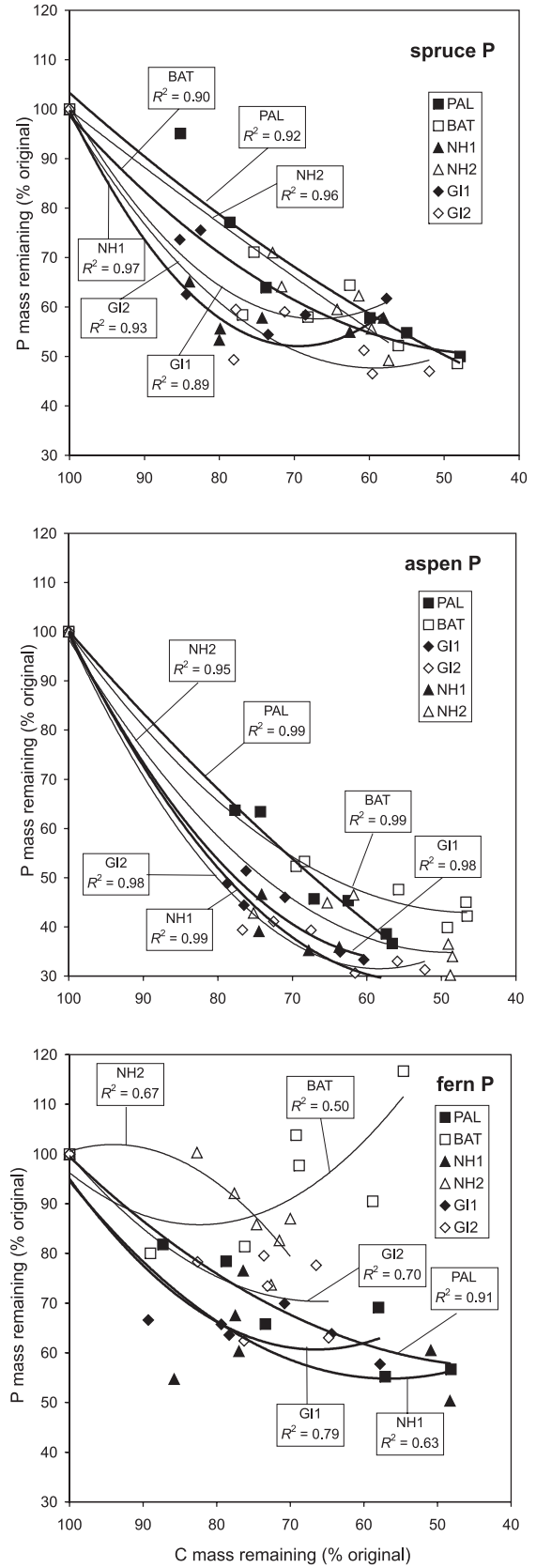
Fig. 4. Relationship between C and P mass remaining in spruce needles, aspen leaves, and fern at the six sites. Lines represent quadratic relationship, with R^2 indicated in the diagram.

term decomposition rates (*k*) of surficial organic matter in northern Manitoba, close to the Nelson House sites, ranged from –0.12 in well-drained upland jack pine soils to –0.02 to –0.03 in poorly drained *Sphagnum* – black spruce and wetland fen sites. These *k* values, however, indicate the decomposition rate of the native litter in the soils rather than comparing the same litter under different drainage classes.

The lack of a pronounced difference in decomposition rates at the CIDET sites reported here may be the result, in part, of the low water table at most of the peatland sites and of the surface emplacement of the litters, except for the buried wood blocks. The water table, and thus the development of anoxic conditions, is beneath the zone of litterbags in the peatland sites for most of the year, though flooding may occur in the spring. Only at the Nelson House peatland sites have the litterbags been overgrown by mosses and the water table risen so that the bags have been submerged for most of the year from the fourth year. Examination of the mass loss data for this site shows that there is little evidence for a distinct slowing of decomposition in the last 3 years. The buried wood blocks show slower rates of decomposition in the peatland sites than in the upland sites, except for Gillam, where decomposition was also very slow in the upland soil.

The effect of flooding on litter decomposition rates has been examined in several studies with variable results depending on duration, litter type, and influence of water chemistry (e.g., Baker et al. 2001; Day 1983; Lockaby et al. 1996; Wylie 1987). Short periods of flooding may stimulate decomposition, while prolonged flooding may slow rates. In a laboratory incubation study over 60 days at 22 °C, Moore and Dalva (2001) found that CO_2 production under oxic conditions in old and fresh maple leaves and *Sphagnum* was, respectively, 4, 19, and 22 times that under anoxic conditions. Peat samples incubated in the laboratory for varying periods show oxic:anoxic CO_2 production ratios ranging from 2.5:1 to 16:1 (e.g., Bridgham et al. 1998; Moore and Dalva 1997; Scanlon and Moore 2000; Updegraff et al. 1995). Field studies of peat soils (e.g., Bubier et al. 1998; Silvola et al. 1996) suggest a ratio of between 4:1 and 6:1. Thus, the development of anoxic conditions can slow the rate of decomposition, but litter has to be submerged before this occurs.

The differences in microclimate temperature between the pairs of sites confound the importance of hydrologic regime in controlling decomposition rates. Among upland sites, the decomposition of surface-placed materials followed the latitudinal and mean annual temperature gradient. Decomposition declined with increasing latitude (mean foliar *k* values: BAT, –0.097; NH1, –0.091; GI1, –0.076) as did mean annual air and in situ soil temperature. In an analysis of all 18 upland sites in CIDET, including the three upland sites in this study, Trofymow et al. (2002) found that the most important climatic variable accounting for the variance in the 6-year mass remaining and *k* values was mean annual air temperature. Initial mass loss (intercept) showed the reverse trend, being smallest at low latitude and largest at high latitude, corresponding to the increasing precipitation and decreasing predicted duff moisture content with increasing latitude (Table 2). Trofymow et al. (2002) also found that the most important climate variable accounting for initial mass loss (intercept of decay equation or year 1 mass remaining) was precipita-

tion, particularly winter precipitation, and differences in air temperature accounted for little of the variance.

The CIDET study used litters derived from upland forests, though spruce and tamarack needles can contribute litter to peatlands, and fern and fescue are similar in character to shrub leaves and sedges. Comparing decomposition rates using different litterbag experiments is difficult because of differences in litter collection and treatment, the mesh size of the litterbag, the place of emplacement, and the frequency and duration of sampling. T.R. Moore (personal communication) has used litterbags with a mesh size of 1.5 mm × 2 mm to determine decomposition rates of various peat-forming litters at bog and fen sites in temperate, boreal, and subarctic eastern Canada. Over 6 years, average exponential decay coefficients (*k* values) ranged from –0.15 to –0.21 for evergreen and deciduous shrub leaves, –0.15 to –0.22 for tree needles and leaves, –0.20 to –0.37 for sedges, and –0.02 to –0.08 for hummock and hollow-lawn *Sphagnum* species, respectively. These values are similar to most of the litter *k* values found in the present study. The exception is that for *Sphagnum*, a very common genus in many northern peatlands. A survey of the literature for *Sphagnum* decomposition reveals that decomposition rates are slow, even under well-drained conditions (e.g., Clymo 1965; Hogg et al. 1994; Johnson and Damman 1991, 1993; Rochefort et al. 1990), with similar *k* values to those shown previously.

Of importance to the amount of organic matter accumulating in soil is the proportion of the original litter that reaches stability in the soil. In upland soils, this "limit of maximum decomposition" (Berg et al. 1996) may not be strongly related to the early rate of decomposition, as shown here over 6 years. Critical to the accumulation of organic matter in peatlands is the point at which the decomposing tissue enters the anoxic zone of the soil, a point at which the rate of decomposition is reduced, as shown previously. At the Nelson House site, this point is being reached, but in many peatlands with low water tables it may be decades before the decomposing litter enters the anoxic zone. This means that accumulation rates are more a function of litter substrate quality than of hydrology.

The general retention of original litter N and loss of P over the first 6 years of decomposition is similar to that noted in a range of upland sites where rates are slow (Moore et al., in press). This study showed that over the range of litters at sites from the subarctic to temperate forests, decomposing litters progress to a C:N ratio of about 30:1 as the C mass was reduced to 20%–30 % of the original litter. An average C:N ratio of <55:1 in decomposing litter appeared to be critical for the loss of N. The C:P ratio progressed to about 500:1 over this degree of decomposition, and P loss from decomposing litters appeared at average C:P ratios of between 700:1 and 900:1. At the upland and peatland sites studied here, the mass or C loss after 6 years is still small, between 25% and 65% of the original, so that the litters are in the early stages of decomposition, in which N tends to be retained and P lost.

The relatively minor effect of site on N and P dynamics in decomposing litter reported in this study may be associated with the similarity in surface properties between the pairs of upland and peatland soils. In a study of N and P dynamics of

litters decomposing at the 18 upland CIDET sites, a weak negative relationship was found between the retention of N and P, standardized to 60% of original C remaining, and the C:N and C:P ratios of the uppermost organic layer of the soil on which the litterbags lay (Moore et al., in press). A large C:N or C:P ratio was correlated with relatively weak N and P retention by the litter. There are small differences in surface soil C:N ratio between the upland and peatland soils at Gillam and Nelson House, but the differences are larger between Batoche (30:1) and Prince Albert (47:1) (Table 3). This pattern may be able to explain some of the differences in N dynamics for the aspen leaves (Fig. 3). Forest floor or surface organic soil C:P ratios are smaller at Batoche (354:1) than at Prince Albert (492:1), and Nelson House peatland (413:1) site than upland (538:1) site, but larger at Gillam House peatland site (658:1) than upland site (570:1) (Table 3). Two litters at the Batoche and Nelson House peatland sites retained more P than at the upland sites, whereas there was no consistent pattern at the Gillam pair of sites (Fig. 4).

Acknowledgements

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