Comparison of decomposition of belowground and aboveground plant litters in peatlands of boreal Alberta, Canada

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Abstract: Studies examining the decomposition rates of belowground plant tissues in peatlands are scarce despite the significant contribution these tissues make to total plant production. Therefore, we measured mass losses of *Carex aquatilis* Wahlenb. leaves and rhizomes and *Salix planifolia* Pursh leaves and roots in a rich, sedge-dominated fen and *Sphagnum fuscum* (Schimp.) Klinggr. plants in a forested bog using the litter bag technique over a 2-year period in southern boreal Alberta. After 2 years, mass losses of *C. aquatilis* rhizomes (75%) were significantly higher than those of *C. aquatilis* leaves and *Salix planifolia* leaves, which were similar to each other (54 and 48%, respectively). *Sphagnum fuscum* and *Salix planifolia* root mass losses also were similar to each other (21 and 29%, respectively), but they were significantly lower than those of the other three litter types. Different tissue nutrient concentrations as well as alkalinity- and phosphorus-related surface water chemistry variables correlated significantly with mass losses of different litter types; however, they alone did not explain all of the mass loss trends. The majority of sedge peat and carbon in the fen originates from *C. aquatilis* leaves (188 and 86 $g \cdot m^{-2}$, respectively), with the remainder originating from *C. aquatilis* rhizomes (102 and 47 $g \cdot m^{-2}$, respectively) after the first 2 years of decomposition. Conversely, the majority of *Salix planifolia* peat and carbon originates from its roots (33 and 16 $g \cdot m^{-2}$, respectively) and the remainder from its leaves (24 and 11 $g \cdot m^{-2}$, respectively) over the same period. After the first 2 years of decomposition, 150 $g \cdot m^{-2}$ of peat and 71 $g \cdot m^{-2}$ of carbon remained from the decomposing *Sphagnum fuscum* in the bog.

Key words: bog, fen, mass losses, *Carex aquatilis*, *Salix planifolia*, *Sphagnum fuscum*.

Résumé : Les études portant sur les taux de décomposition de tissus hypogés végétaux en tourbières sont rares, en dépit de l'importante contribution que ces tissus apportent à la production végétale totale. Conséquemment, les auteurs ont mesuré la perte en masse des feuilles et des rhizomes du *Carex aquatilis* Wahlenb. ainsi que des feuilles et des racines du *Salix planifolia* Pursh, dans une tourbière basse riche, dominée par les carex, et par des plants de *Sphagnum fuscum* (Schimp.) Klinggr. dans une tourbière boisée, de la région sud boréale de l'Alberta; ils ont utilisé la technique du sac à litière, au cours d'une période de deux ans. Après deux ans, les pertes de masse (75 %) des rhizomes du *C. aquatilis* sont significativement plus importantes que celles des feuilles du *C. aquatilis* et des feuilles du *Salix planifolia*, qui se ressemblent l'une l'autre (54 et 48 % respectivement). Les pertes de masse chez le *Sphagnum fuscum* et les racines du *Salix planifolia* sont également très similaires l'une l'autre (21 et 29 %, respectivement), mais sont significativement plus faibles que celles des trois autres types de litière. Des différences de teneurs en nutriments des tissus ainsi que des variables de l'eau de surface liées à l'alcalinité et au phosphore sont corrélées significativement avec les pertes de masse des différents types de litière; cependant, à elles seules, elles n'expliquent pas toutes les tendances de perte en masse. La majeure partie de la tourbe à carex et du carbone de la tourbière basse provient des feuilles du *C. aquatilis* (188 et 86 $g \cdot m^{-2}$, respectivement), le reste provenant des rhizomes du *C. aquatilis* (102 et 47 $g \cdot m^{-2}$, respectivement) après les deux premières années de décomposition. Réciproquement, la majeure partie de la tourbe et du carbone du *Salix planifolia* origine de ses racines (33 et 16 $g \cdot m^{-2}$, respectivement) et le reste de ses feuilles (24 et 11 $g \cdot m^{-2}$, respectivement), pour la même période. Après les deux premières années de décomposition, il reste 150 $g \cdot m^{-2}$ de tourbe et 71 $g \cdot m^{-2}$ de carbone à partir de la décomposition du *Sphagnum fuscum* dans la tourbière.

Mots clés : tourbière haute, tourbière basse, perte en masse, *Carex aquatilis, Salix planifolia, Sphagnum fuscum*.

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Introduction

Peatlands cover approximately 14% of Canada's (National Wetlands Working Group 1988) and 16% of Alberta's land base (Vitt et al. 1996). Specifically, bogs cover approximately 4.9% and fens approximately 11.4% of Alberta's land base (Vitt et al. 1996). These ecosystems are important to the global carbon cycle because of the accumulation of carbon in the form of peat (a heterogeneous assemblage of partially decomposed plant matter). Peat accumulates on an annual basis (Thormann et al. 1999*b*) and it has been suggested that

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peat accumulation is the result of slow rates of litter decomposition rather than high rates of net primary plant production (Clymo 1965; Malmer 1986; Farrish and Grigal 1988; Vitt 1990).

The rate of plant decomposition is affected by moisture, anoxia (acrotelm vs. catotelm), temperature, acidity, and the nutrient status of ecosystems (primarily nitrogen- and phosphorus-related water chemistry variables) (Brinson et al. 1981; Bartsch and Moore 1985; Farrish and Grigal 1988; Gorham 1991; Szumigalski and Bayley 1996*a*; Thormann and Bayley 1997*a*). Although litter quality also affects the rate of decomposition (total nitrogen (TN), total phosphorus (TP), and total carbon (TC) tissue concentrations, TC:TN quotients) (Brinson et al. 1981; Bridgham and Richardson 1992; Szumigalski and Bayley 1996*a*), Thormann et al. (1999*a*) suggested that water levels might be more important than surface water chemical and (or) litter quality variables affecting decomposition of plant litter in peatlands.

Most decomposition studies of vascular and non-vascular plant litter in peatlands have concentrated on aboveground plant material (Clymo 1965; Reader and Stewart 1972; Chamie and Richardson 1978; Bartsch and Moore 1985; Ohlson 1987; Verhoeven and Arts 1992; Szumigalski and Bayley 1996*a*; Thormann and Bayley 1997*a*; Arp et al. 1999). Decomposition rates of belowground tissues have been measured rarely in terrestrial ecosystems (McClaugherty et al. 1982; Robinson et al. 1999). In wetland ecosystems, the majority of these studies have been conducted in marshes (Puriveth 1980; Hackney and de la Cruz 1980; Buth 1987; Hemminga et al. 1988; Benner et al. 1991; Pozo and Colino 1992; Wrubleski et al. 1997) or anthropogenically manipulated wetlands (Hartmann 1999). To our knowledge, there are no decomposition studies of belowground plant litters in "natural" peatlands in North America and only one in Europe (Heal et al. 1978). This is surprising, because some studies have suggested that belowground production of some peatland plant species may account for up to 95% of the total production (Bernard and Fiala 1986; Wallén 1986; Backéus 1990; Saarinen 1996). Belowground production of sedges is primarily in the form of rhizomes and fibrous roots that may be long-lived, depending on the sedge species (Sjörs 1988). Similarly, belowground production of woody plant species, such as species of *Betula* and *Salix*, has not been determined in peatlands; however, it can account for up to 75% of the total net primary production in forest ecosystems (Persson 1978; Fogel 1983; Nadelhoffer and Raich 1992; Burke and Raynal 1994).

The greatest decomposition rates occur in the aerobic soil horizon, the acrotelm (Clymo 1965). As peat accumulates, the lower peat profile becomes the anaerobic catotelm and decomposition rates decrease significantly because of the absence of oxygen for decomposer communities. Thormann et al. (1999*a*) measured short-term peat and carbon accumulation potentials along a bog–fen–marsh wetland gradient in Alberta, Canada. Their results indicate an increasing potential for carbon and peat accumulation from marshes to fens to bogs. However, they only examined the contribution of aboveground plant tissues and excluded the contribution of belowground plant tissues in their study because of the scarcity of belowground plant production and decomposition data in the literature. It is useful to investigate the decay rates of the belowground plant tissues as well, owing to their large contribution to the total plant production in most wetlands. Much of the belowground plant tissues is located in the catotelm and remains alive via the transportation of oxygen through aerenchyma tissues to roots and rhizomes (Fagersted 1992; Jackson and Armstrong 1999). However, roots and rhizomes, which may be perennial, turn over periodically, thereby contributing to peat and carbon accumulation in wetlands, similar to the contribution of annual aboveground plant tissues.

Because sedge- and shrub-dominated fens constitute approximately 35 and 34%, respectively, of all peatlands in Alberta (Vitt et al. 1996), the focus of this study was to determine mass losses of *Carex aquatilis* Wahlenb. rhizomes and *Salix planifolia* Pursh roots in an open, rich fen and compare them with mass losses of aboveground plant tissues of other peatland plant species. We hypothesized that (*i*) *C. aquatilis* rhizomes would decompose faster than *C. aquatilis* leaves, *Salix planifolia* leaves and *Salix planifolia* roots in a fen, and *Sphagnum fuscum* (Schimp.) Klinggr. in a bog, because rhizomes are nutrient-storage tissues of the plant and thus may have higher concentrations of total nitrogen and total phosphorus and (*ii*) *Salix planifolia* roots would decompose more slowly than all other litter types across all species as a result of their woody tissues, which may be more resistant to decomposition than herbaceous tissues.

Materials and methods

Study areas and site descriptions

The riverine sedge fen and Perryvale bog lie within the Subhumid Low Boreal ecoclimatic region of Canada (Ecoregions Working Group 1989). The area has mild summers and cold, snowy winters with a long-term mean annual temperature of 1.7°C and a total mean annual precipitation of approximately 500 mm (Environment Canada 1982).

These sites have been described in detail in Thormann et al. (1999*b*). Briefly, the riverine sedge fen is dominated by *Carex aquatilis*, *Carex lasiocarpa* Ehrh., *Salix planifolia*, and *Equisetum fluviatile* L. The bryophyte stratum is sparse and discontinuous and consists primarily of *Brachythecium mildeanum* (Schimp.) Schimp. ex Milde and *Tomenthypnum nitens* (Hedw.) Loeske. The Perryvale bog is dominated by *Sphagnum fuscum*, *Sphagnum angustifolium* (C. Jens ex Russ.) C. Jens, *Picea mariana* (Mill.) BSP., and members of the Ericaceae, including *Rhododendron groenlandicum* (Oeder) Kron & Judd and *Andromeda polifolia* L.

Decomposition measurements

The methods used to set up the decomposition experiment follow those in Thormann and Bayley (1997*a*). Briefly, live aerial and belowground portions of the dominant plant species from each site were collected in early September 1997. These were *Sphagnum fuscum* in the bog and *Carex aquatilis* leaves and rhizomes and *Salix planifolia* leaves and roots in the sedge fen. Only senesced leaf litters were collected (yellow to pale-brown in colour) and used in this study. *Carex aquatilis* rhizomes were extracted by cutting the peat with a knife in a 30-cm-diameter circle around individual *C. aquatilis* plants. After these "cores" were carefully lifted, adhering peat and plant debris were washed free from the rhizomes with water from the fen. Rhizomes were separated from individual plants. Living *C. aquatilis* rhizomes (approximate diameter of 3–5 mm) are firm and light-brown, in contrast to dead ones, which are soft and dark-brown to black.

Roots of *Salix planifolia* were collected from carefully extracted whole plants (<1 m in height). The root material for this study was randomly selected from all roots with a diameter of approximately 2 mm or less. Of these, approximately half had secondary growth and was woody, while the remaining material lacked secondary growth and was non-woody (fine roots).

In the bog, the top 3 cm of living, healthy *Sphagnum fuscum* plants, including stems, branches, all associated leaves, and the capitulum, were collected for the decomposition study. All plant material was oven-dried to constant mass at 60°C and 1.8–2.5 g randomly selected material from each litter type was placed in individual nylon mesh bags (3 × 6 cm, 1-mm mesh gauge). The filled bags were weighed to the nearest 0.001 g, sewn shut, and placed either horizontally 3–10 cm beneath (*Sphagnum fuscum*, *Salix planifolia* roots, and *Carex aquatilis* rhizomes) or on top of the peat surface (*C. aquatilis* and *Salix planifolia* leaves) to mimic "natural" decomposition conditions. Buried bags were in the acrotelm in both sites, but they were below the water level in the fen and above the water level in the bog. Decomposition bags with the individual litters were placed in the site of the origin of the litter. Thus, fen litter decomposed only in the fen and bog litter decomposed only in the bog.

Twenty-four decomposition bags per litter type, each tied to a wooden stake to avoid losses, were deployed in mid-September 1997. Four decomposition bags from each litter type were retrieved from each site after 20 and 50 days (1997), 8 and 12 (1998), or 20 and 24 months (1999). Bags were cleaned immediately by removing coarse, intruding roots and other debris, such as leaves of other vascular and non-vascular plants that had grown into or through the leaf litter decomposition bags. Finer debris (soil, remaining "alien" plant parts, fungal mycelium, etc.) was removed carefully in the laboratory with forceps before drying to constant mass at 60°C. Each bag was then weighed, again to the nearest 0.001 g.

The percent masses remaining (MR) over the six incubation periods were determined using the following equation:

$$[1] \qquad MR = [(X_0 - X)/X_0] \times 100$$

where X_0 represents the initial dry litter mass (g) before decomposition and X represents the final dry litter mass (g) after incubation in the field. The 20-month decomposition bag set of *Sphagnum fuscum* in the bog was disturbed by animals but was still used for all subsequent analyses.

Environmental and litter quality variables

The litter quality was determined by analyzing dried and finely ground plant litter samples for TC and TN concentrations using a Model 440 Elemental Analyzer (Control Equipment Corp.). TP tissue concentrations were determined using the molybdophosphovanadate method with an Auto Analyzer as outlined by Prepas and Rigler (1982) and Parkinson and Allen (1975). Water samples were collected monthly from a depression within the peat during the ice-free season (May–November) and analyzed for nitrate (NO_3^-), ammonium (NH_4^+), total dissolved nitrogen (TDN), soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP), total phosphorus (TP), pH, conductivity, alkalinity, bicarbonate (HCO_3^-), dissolved organic carbon (DOC), calcium (Ca^{2+}), and potassium (K^+). Furthermore, water levels were monitored using meter sticks (attached to permanent wooden stakes driven into the mineral substrate) and the depth of the acrotelm was determined using steel welding rods inserted into the peat as described by Bridgham et al. (1991). These techniques and analyses followed Thormann and Bayley (1997*a*).

Peat and carbon accumulation potentials of the five litters

We did not measure above- and below-ground net primary production (NPP) of *Carex aquatilis* and *Salix planifolia* in the riverine sedge fen or that of *Sphagnum fuscum* in the bog in this study. Therefore, we adopted aboveground NPP values for *Salix* spp. (46 $g \cdot m^{-2} \cdot year^{-1}$, mean of aboveground NPP values of *Salix* spp. in moderate-rich and rich fens) and *C. aquatilis* (409 $g \cdot m^{-2} \cdot year^{-1}$) in the sedge fen from Thormann and Bayley (1997*b*). A NPP value of 190 $g \cdot m^{-2} \cdot year^{-1}$ was assumed for *Sphagnum fuscum* in the bog, which is the mean of NPP values reported by Thormann and Bayley (1997*b*) and Szumigalski and Bayley (1996*b*). Belowground NPP values for *C. aquatilis* and *Salix planifolia* were estimated from Campbell et al. (2000) as 50% of the total NPP. Thus, the total belowground NPP of *C. aquatilis* in the riverine sedge fen was estimated at 409 $g \cdot m^{-2} \cdot year^{-1}$ and that of *Salix planifolia* was estimated at 46 $g \cdot m^{-2} \cdot year^{-1}$. Using these values and the mass loss and TC tissue concentrations from this study, we calculated peat and carbon accumulation potentials of these five litter types after 1 and 2 years of decomposition.

Statistical analyses

Kruskal–Wallis tests (nonparametric, one-way analyses of variance) were used to examine differences in mass losses and litter qualities (TC, TN, TC:TN, and TP; dependent variables) of the individual litter types within these peatlands over time (after 0, 20, 50, 250, 365, 465, and 730 days of decomposition; independent variables). This test was used because of the small sample size of decomposition bags per sample period per litter type ($n = 4$). Transformation of data did not remove the heterogeneity of variance or normalize the data. Tukey-type post hoc tests were performed to determine where significant differences were present within each of the data sets following the indication of significance in the Kruskal–Wallis analyses.

Pearson's correlation coefficients indicated if any of the environmental variables correlated to each other. Pearson's correlation coefficients were also computed between mass losses of the individual litter types and litter quality (TC, TN, TC:TN, TP), environmental (surface water chemistry), and physical (peat and surface water temperature, depth of the acrotelm, water levels) variables in the bog and fen. Mean surface water chemistry, litter quality, and physical data at each sampling time were correlated with mass losses of the individual litters over each sampling period, i.e., means of these data from 0 to 20 days, 0 to 50 days, 0 to 8 months, etc., to reflect the mean conditions that the litters were exposed to during the varying incubation periods. Autocorrelations were performed on individual environmental variables to determine if successive data points within each site were related to each over time. Bonferroni tests ($p = 0.05$) provided probability values for all correlations. Two-tailed, paired *t*-tests were used to compare individual environmental variables between the bog and fen ($n = 21$ per variable).

Simple regressions were performed to develop statistical models for the masses remaining (dependent variable) of the litter types over the incubation periods in the field (independent variable). One day was added to each sample date to include the initial mass of each sample (day 1). Sample sizes were $n = 4$ for each of six sampling times ($n = 6$) for the five litter types over the 2-year decomposition period. All statistical analyses were performed on SYSTAT (SYSTAT Inc. 1992).

Results

Mass losses of decomposing belowground and aboveground plant tissues

Two-year mass losses of *C. aquatilis* rhizomes (75%) were significantly higher ($p < 0.05$) than those of *Salix planifolia* leaves and *C. aquatilis* leaves, which were similar to each other (48 and 54%, respectively) ($p > 0.05$) (Fig. 1). *Sphagnum fuscum* and *Salix planifolia* root mass losses were simi-

Fig. 1. Mass losses (% ± SE) of the dominant indigenous plant species over 20 and 50 days and 8, 12, 20, and 24 months from September 1997 to September 1999 in two peatlands in southern boreal Alberta. RSF, riverine sedge fen.

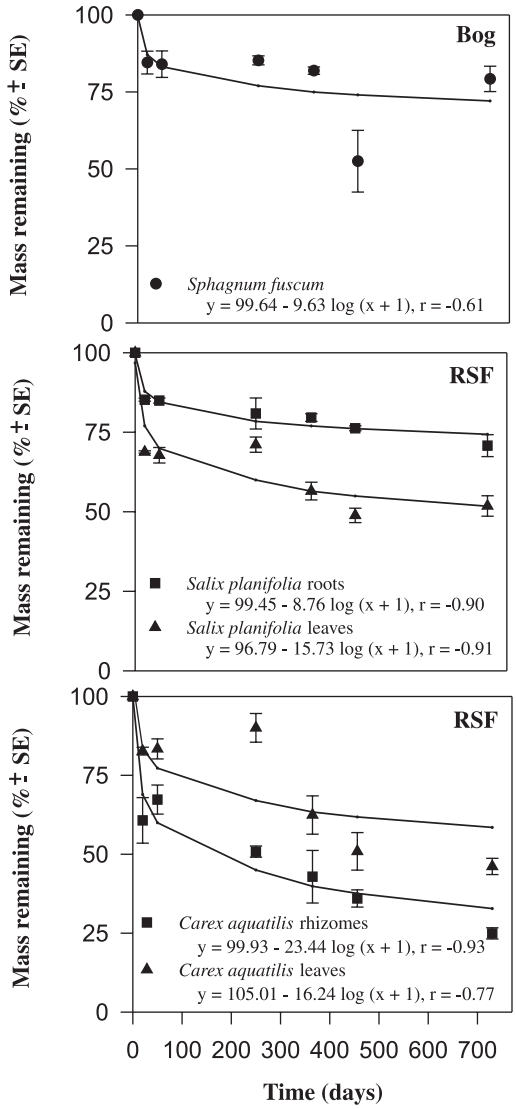

Fig. 2. Mean litter quality (mg·g^{-1} ± SE) of the plant litters in the bog (*Sphagnum fuscum*) and riverine sedge fen (*Carex aquatilis* leaves and rhizomes and *Salix planifolia* leaves and roots) from September 1997 to September 1999 in southern boreal Alberta, Canada. Note the different scales on the *y*-axes.

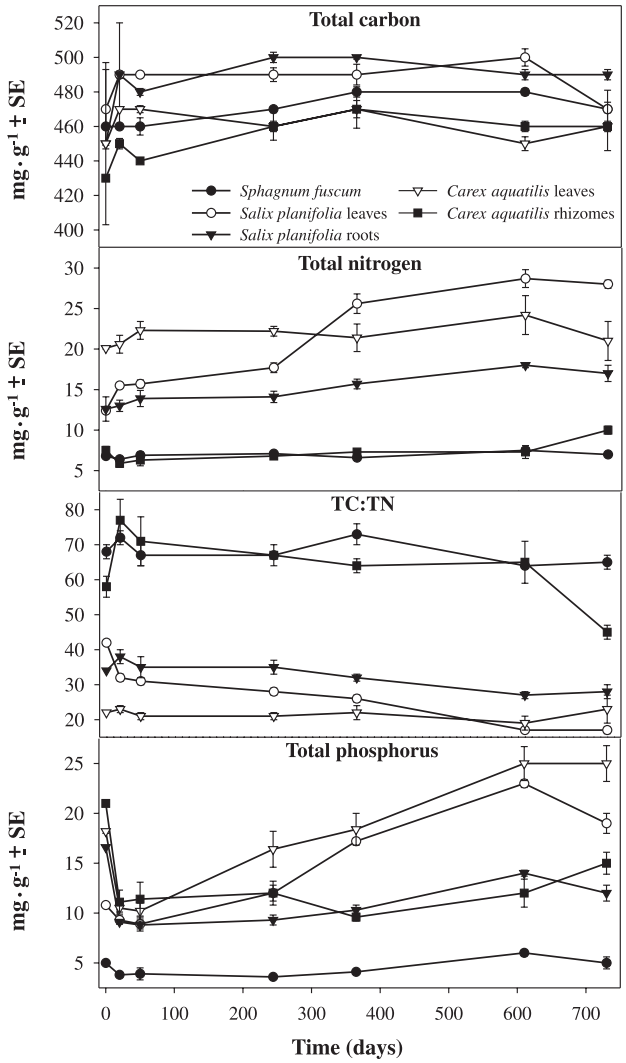

Table 1. Pearson's correlation coefficients for the 2-year mass losses of the dominant plant species in the bog and riverine sedge fen (RSF) and litter quality variables.

Sites	Litter types	TC	TN	TC:TN	TP
Bog	*Sphagnum fuscum* plants	0.32	0.46	–0.42	0.55
RSF	*Salix planifolia* leaves	0.50	0.87***	–0.91***	0.68**
	Salix planifolia roots	0.58*	0.73**	–0.57	–0.20
	Carex aquatilis leaves	–0.04	0.19	–0.08	0.70*
	Carex aquatilis rhizomes	0.81***	0.39	–0.20	–0.47

*$p < 0.05$.
**$p < 0.01$.
***$p < 0.001$.

lar to each other (21 and 29%, respectively) ($p > 0.05$), but they were significantly lower than those of the other three litter types over the same period ($p < 0.05$). Arith/log decomposition models (arithmetic/logarithmic, $y = \log(x) + b$) provided the best fit to the mass losses of the five litter types (Fig. 1).

Nutrient tissue concentrations of decomposing plant tissues

TN tissue concentrations increased significantly in *Salix planifolia* roots and leaves ($p < 0.05$), but they did not change significantly in *Carex aquatilis* rhizomes and leaves and *Sphagnum fuscum* over the 2-year decomposition period

Table 2. Litter masses and peat and carbon accumulation values from the five litter types in the bog and riverine sedge fen (RSF) prior to and after 1 and 2 years of decomposition.

		Initial			Year one			Year two		
Site	Litter type	Total NPP ($g \cdot m^{-2} \cdot year^{-1}$)	Carbon ($mg \cdot g^{-1}$)	Carbon ($g \cdot m^{-2}$)	Mass remaining ($g \cdot m^{-2}$)	Carbon ($mg \cdot g^{-1}$)	Carbon ($g \cdot m^{-2}$)	Mass remaining ($g \cdot m^{-2}$)	Carbon ($mg \cdot g^{-1}$)	Carbon ($g \cdot m^{-2}$)
Bog	*Sphagnum fuscum* plants	190[a]	460	87	160	480	77	150	470	71
RSF	*Salix planifolia* leaves	46[a]	470	22	26	490	13	24	470	11
	Salix planifolia roots	46[b]	450	21	36	500	18	33	490	16
	Carex aquatilis leaves	409	450	184	254	470	119	188	460	86
	Carex aquatilis rhizomes	409[b]	430	176	172	470	81	102	460	47

Note: RSF, riverine sedge fen.
[a]Mean estimates from bog and moderate-rich and rich fen NPP data in Thormann and Bayley (1997*b*).
[b]Estimate of the proportion of belowground NPP (50%) to the total NPP in boreal peatlands (Campbell et al. 2000).

($p > 0.05$) (Fig. 2). TP tissue concentrations showed a variable pattern, decreasing during the initial stages of decomposition before increasing in all litter types during the later stages of decomposition (Fig. 2). Generally, *Sphagnum fuscum* and *C. aquatilis* rhizomes had the lowest tissue concentrations of TN and TP throughout the entire decomposition period (Fig. 2). TC tissue concentrations did not change significantly throughout the 2-year decomposition process for any of the litter types ($p > 0.05$). TC:TN quotients did not show any clear patterns, decreasing significantly only in *Salix planifolia* leaves ($p < 0.05$), while remaining similar or fluctuating in the remaining four litter types over the 2-year decomposition period ($p > 0.05$) (Fig. 2). Specific values for the data presented in Fig. 2 are found in the Appendix.

TC tissue concentrations correlated with mass losses of both belowground litters over the first 2 years of decomposition (Table 1). TN tissue concentrations correlated with mass losses of *Salix planifolia* leaves and roots, while TP tissue concentrations were significantly correlated with mass losses of both leaf litters (Table 1). None of the litter quality variables significantly correlated with *Sphagnum fuscum* mass losses over the first 2 years of decay (Table 1).

Nearly two-thirds of all the short-term accumulated sedge peat and carbon originated from aboveground *C. aquatilis* tissues (Table 2). Conversely, both *Salix planifolia* litters had similar amounts of mass and carbon remaining after 1 and 2 years of decomposition (Table 2), despite significantly different mass losses over that period (Fig. 1). In the bog, 150 $g \cdot m^{-2}$ of the original *Sphagnum fuscum* litter remained after 2 years. With a carbon content of 470 $mg \cdot g^{-1}$, this amounts to an accumulation of 71 g $C \cdot m^{-2}$ within this period (Table 2). These peat and carbon accumulation potentials are similar to those of the *C. aquatilis* leaf litter in the riverine sedge fen (Table 2).

Relationship between environmental variables and mass losses of the decomposing plant tissues

The two peatlands differed significantly in most of their surface water chemistry from 1997 to 1999. Only nitrogen- and temperature-related variables did not differ significantly between these two peatlands ($p > 0.05$) (Table 3). Phosphorus-related surface water chemistry variables correlated significantly with mass losses of *Sphagnum fuscum* in the bog and *C. aquatilis* leaves and rhizomes in the fen (Table 4). Surface water concentrations of Ca^{2+} correlated significantly with mass losses of all four fen litter types (Table 4). In addition, NH_4^+ concentrations correlated significantly with mass losses of both leaf litters for *C. aquatilis* and *Salix planifolia* leaves (Table 4).

Discussion

Decomposition of *Salix planifolia* roots and leaves, *Carex aquatilis* rhizomes and leaves, and *Sphagnum fuscum*

Two-year mass losses of *Carex aquatilis* rhizomes were significantly higher than those of the other four litter types (Fig. 1). The leaf litters lost similar amounts of mass over the 2-year decomposition period but they significantly exceeded those of *Salix planifolia* roots and *Sphagnum fuscum* (Fig. 1).

Table 3. Mean environmental variables (surface water chemical and physical variables) of the bog and the riverine sedge fen in Alberta, Canada, from 1997 to 1999.

Variables	Perryvale Bog	Riverine sedge fen	*p*
pH	3.8 (0.03)	6.9 (0.10)	***
Conductivity ($\mu S \cdot cm^{-1}$)[a]	66 (7)	196 (19)	***
Alkalinity ($mg \cdot L^{-1}$ $CaCO_3$)	0 (—)	105 (10)	***
HCO_3^- ($mg \cdot L^{-1}$)	0 (—)	128 (12)	***
NO_3^- ($\mu g \cdot L^{-1}$)	8 (1)	9 (2)	ns
NH_4^+ ($\mu g \cdot L^{-1}$)	10 (4)	13 (4)	ns
Total dissolved nitrogen ($\mu g \cdot L^{-1}$)	1121 (62)	1040 (68)	ns
Soluble reactive phosphorus ($\mu g \cdot L^{-1}$)	9 (4)	96 (36)	*
Total phosphorus ($\mu g \cdot L^{-1}$)	140 (41)	970 (274)	**
Total dissolved phosphorus ($\mu g \cdot L^{-1}$)	36 (13)	125 (37)	*
Dissolved organic carbon ($mg \cdot L^{-1}$)	58 (2)	28 (2)	**
K^+ ($mg \cdot L^{-1}$)	0.4 (0.1)	1.5 (0.5)	*
Ca^{2+} ($mg \cdot L^{-1}$)	3 (0.3)	28 (3)	**
Peat temperature (°C)	7 (1)	8 (1)	ns
Water temperature (°C)	5 (1)	9 (1)	ns
Water level (cm)[b]	–37 (6)	1 (5)	***
Depth of acrotelm (cm)[b]	–47 (3)	–6 (3)	***

Note: Standard errors are given in parentheses. *, $p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ns, not significant.
[a]Conductivity was adjusted for temperature and pH.
[b]Water levels and depths of the acrotelm are with respect to the moss/peat surface.

Table 4. Pearson's correlation coefficients of 2-year mass losses of the dominant plant species in the bog and riverine sedge fen (RSF) and surface water chemistry variables.

Sites	Litter types	Surface water chemistry variables	*r*
Bog	*Sphagnum fuscum* plants	Total phosphorus	–0.826***
RSF	*Salix planifolia* leaves	Calcium	–0.871***
		Conductivity (adjusted)	–0.717*
		Ammonium	0.679*
	Salix planifolia roots	Calcium	–0.851***
	Carex aquatilis leaves	Total dissolved phosphorus	0.851***
		Soluble reactive phosphorus	0.840**
		Ammonium	0.838**
		Calcium	–0.712*
	Carex aquatilis rhizomes	Calcium	–0.846***
		Conductivity (adjusted)	–0.774**
		Total dissolved phosphorus	0.735*
		Alkalinity	–0.729*
		Bicarbonate	–0.729*

Note: Only significiant variables are shown. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

The arith/log model best described mass losses of the five litters types in this study (Fig. 1). This model was first introduced by Thormann and Bayley (1997*a*) and differs from the widely used log/arith (logarithmic/arithmetic, $\log(y) = x + b$) model developed by Jenny et al. (1949) and later adopted by Olson (1963) and Wieder and Lang (1982) to describe mass losses of plant litters under natural conditions in many ecosystems. Thormann and Bayley (1997*a*) suggested that the arith/log model might have provided a better fit to their data than the log/arith model because of the early sampling time of the vegetation used in their decomposition study (June). However, in this study, we collected the litters in early September and *Carex* and *Salix* leaves already had begun to senesce. Again, the arith/log model proved to describe mass losses of these litters better than the previously used log/arith model over the 2-year decomposition period.

Decomposition of belowground plant litters

Two-year mass losses of *C. aquatilis* rhizomes and *Salix planifolia* roots were 75 and 29%, respectively, and differed significantly (Fig. 1). Our first year mass loss of *C. aquatilis* rhizomes was 60% (Fig. 1). This value is substantially higher than those reported by Hackney and de la Cruz (1980), Buth (1987), Hemminga et al. (1988), Benner et al. (1991), and Pozo and Colino (1992) for salt marsh plant

Table 5. Mass losses of belowground plant tissues in wetland ecosystems after 1 year.

References	Location	Plant species and litter type	Mass loss (%)
This study	Riverine sedge fen, Alberta, Canada	*Carex aquatilis* rhizomes	60
		Salix planifolia roots	20
Tupacz and Day (1990)	Great Dismal Swamp, Virginia/North Carolina, U.S.A.	*Chamaecyparis thyoides* (L.) BSP. roots	26
		Quercus spp. roots	35
		Taxodium distichum (L.) Rich. roots	36
		Acer rubrum L., and *Nyssa* spp. roots	40
Wrubleski et al. (1997)	Freshwater marsh, Manitoba, Canada[a]	*Scolochloa festucacea* (Willd.) Link roots/rhizomes	60–67
		Phragmites australis (Cav.) Trin. ex Steud. roots/rhizomes	58–77
		Scirpus lacustris L. roots/rhizomes	38–58
		Typha glauca Godr. roots/rhizomes	48–54
Benner et al. (1991)	Salt marsh, Georgia, U.S.A.	*Spartina alterniflora* Loisel. roots/rhizomes	53
Hemminga et al. (1988)	Salt marsh, The Netherlands[b]	*Spartina anglica* Hubbard roots/rhizomes	37–55
Puriveth (1980)	Freshwater marsh, Wisconsin, U.S.A.	*Typha latifolia* L. roots/rhizomes	72
		Sparganium eurycarpum Engelm. ex Gray roots/rhizomes	58
		Scirpus fluviatilis (Torr.) Gary roots/rhizomes	40
Pozo and Colino (1992)	Salt marsh, Spain	*Spartina maritima* (Curt.) Fernald roots/rhizomes	42
Hartmann (1999)	Rewetted fen, Germany	*Carex riparia* Curtis roots	47
		Carex paniculata L. roots	31
		Phragmites australis roots	15
Buth (1987)	Salt marsh, The Netherlands[c]	*Puccinellia maritima* (Huds.) Parl. roots	32
		Halimione portulacoides (L.) Aellen roots	27
		Spartina anglica roots	18
Hackney and de la Cruz (1980)	Tidal marsh, Mississippi, U.S.A.	*Juncus roemerianus* Scheele roots	27
		Spartina cynosuroides (L.) Roth roots/rhizomes	21
		Juncus roemerianus rhizomes	16
Heal et al. (1978)	Bog, United Kingdom	*Eriophorum vaginatum* L. roots	12
		Calluna vulgaris (L.) Hull belowground stems	7
		Calluna vulgaris roots	5

[a]Different flooding regimes.
[b]Three different aquatic ecosystems, mass losses at a depth of 3 cm.
[c]30-week decomposition period, mass losses at a depth of 10 cm.

species, by Hartmann (1999) for freshwater wetland plant species, and by Heal et al. (1978) for bog plant species (Table 5).

It is interesting that few studies have examined decomposition rates of belowground tissues of wetland plant species, since a number of studies have suggested that the belowground biomass of some peatland plant species may significantly exceed that of the aboveground biomass (Bernard and Fiala 1986; Wallén 1986; Backéus 1990; Saarinen 1996). Rhizomes form most of the belowground biomass of *Carex* species in arctic ecosystems (59%) (Carlsson et al. 1990), while fine roots are more prevalent at more temperate latitudes (78–90%) (Bernard 1973; Saarinen 1996), a reflection of deeper soil horizons and greater water and nutrient availability at more southern latitudes. Fine roots appear to be the principal nutrient-absorptive organs and extend to great depths, often to the mineral soil horizon underlying the organic soil horizon (Saarinen 1996). However, Brooker et al. (1999) determined that rhizomes of *Carex bigelowii* Torr. ex Schwein. aid in the acquisition of N from the soil solution and fine roots are not the only nutrient-absorptive organs.

While rhizomes vary in longevity, depending on the species of *Carex* (Bernard and Fiala 1986), the fine roots of sedges and woody plant species are short-lived and have rapid turnover rates, thereby constituting a major component of carbon and nutrient cycles in many ecosystems (Saarinen 1996). Previous studies in forest ecosystems indicate that fine roots of woody plant species account for up to 75% of the total net primary production (Persson 1978; Fogel 1983; Nadelhoffer and Raich 1992; Burke and Raynal 1994) and lose between 12 and 25% of their mass within the first year of decomposition (Fogel and Hunt 1979; Berg 1981; McClaugherty et al. 1982). Those mass losses are similar to the mass losses we observed for *Salix planifolia* roots after 2 years (29%; Fig. 1). In contrast, mass losses of roots of woody plant species in the Great Dismal Swamp (Tupacz and Day 1990) generally exceeded those of *Salix planifolia*

in our study (Table 5), which can be attributed to differences in the plant litter and environmental conditions for those studies. These data further confirm the importance of examining belowground plant litters in the nutrient budget of peatlands.

Decomposition of aboveground plant litters

Carex aquatilis leaves lost 38 and 54% of their mass after 1 and 2 years, respectively (Fig. 1). First-year mass losses in our study are similar to those reported previously by Verhoeven and Arts (1992) (27–45%, floating fen, The Netherlands), Szumigalski and Bayley (1996*a*) (31–45%, boreal rich fens, Alberta), Thormann and Bayley (1997*a*) (50–59%, boreal rich fens, Alberta), and Arp et al. (1999) (58%, subalpine rich fens, Colorado) but are higher than those reported by Bartsch and Moore (1985) (6–27%, subarctic fen, Quebec).

Mass losses of *Salix planifolia* leaves were 43% after 1 year and 48% after 2 years and were similar to those of *C. aquatilis* leaves (Fig. 1). These results contradict those of Thormann and Bayley (1997*a*) who determined mass losses of *Salix pedicellaris* Pursh leaves to be significantly lower than those of *Carex lasiocarpa* leaves in a rich fen 1 km west of this sedge fen. These differences can be explained in part by the use of different species of *Carex* and *Salix* and significantly lower surface water phosphorus concentrations in their floating sedge fen compared with this riverine sedge fen (Table 3). Although decomposition rates of *Salix* litter are rarely measured, our data are within the range reported by Heal and French (1974) (33%, bog, Norway) and Thormann and Bayley (1997*a*) (42%, rich fen, Alberta). However, *Salix* spp. mass losses in a subarctic fen were substantially lower (Bartsch and Moore 1985) (17%, Quebec).

***Sphagnum fuscum* mass losses**

Sphagnum fuscum lost 16% and 21% of its mass after one and 2 years, respectively, with the majority of these mass losses occurring within the first 20 days of decomposition (16%) (Fig. 1). After 20 days, mass losses are nearly linear up to 2 years and only an additional 5% of mass was lost (Fig. 1). These mass loss values are similar to those reported in previous studies and are comparable to those of *Salix planifolia* roots (Fig. 1). Szumigalski and Bayley (1996*a*) reported first- and second-year mass losses of 14 and 15%, respectively, in a bog approximately 55 km north of our bog. S*phagnum* mass losses were just over 10% after 14 months in a bog in northwestern Ontario, Canada (Rochefort et al. 1990) and after 10 months in a bog in Sweden (Johnson and Damman 1991).

The difference in mass losses between this and other studies can, in part, be explained by species, surface water chemistry, environmental, and methodological differences inherent to these studies. For example, the use of different plant species and tissues (leaves, petioles, stems, and (or) mixtures thereof) will result in different mass losses because of inherently different tissue nutrient concentrations. Similarly, decomposition studies at higher latitudes indicate lower mass losses for similar litter types (Bartsch and Moore 1985). These may result from lower temperatures and soil and water nutrient concentrations at higher latitudes, factors that have been implicated previously in lower decomposition rates (Clymo 1965; Bridgham and Richardson 1992; Szumigalski and Bayley 1996*a*; Thormann and Bayley 1997*a*). Furthermore, the degree of senescence (Ohlson 1987), drying temperature (Clymo 1965), and placement of the plant litter within the peat horizon (Santelmann 1992) affect decomposition rates and result in differences among studies.

The role of litter quality on mass losses

Total carbon tissue concentrations

Initial TC tissue concentrations were similar for all five litter types, ranging from 430 (*C. aquatilis* rhizomes) to 470 $mg \cdot g^{-1}$ (*Salix planifolia* leaves) and did not change significantly over the 2-year decomposition period (Fig. 2). These values are similar to those reported previously from southern boreal and subalpine bog and fen vegetation (Szumigalski and Bayley 1996*a*; Thormann and Bayley 1997*a*; Hartmann 1999; Arp et al. 1999).

TC tissue concentrations correlated significantly with mass losses of *C. aquatilis* rhizomes and *Salix planifolia* roots (Table 1). Roots and rhizomes are the principal nutrient storage organs of many plant species during late fall, winter, and early spring, and many woody and herbaceous plant species translocate photosynthates and nutrients from aboveground tissues into roots and rhizomes prior to their senescence and death (Berendse and Jonasson 1992). This leaves more recalcitrant molecules in the leaves and increases the concentrations of more labile and smaller molecules in the belowground tissues. This may explain the significant correlation between mass losses and TC tissue concentrations of *Salix planifolia* roots and *C. aquatilis* rhizomes (Table 1).

Short-term peat and carbon accumulation potentials of these five litters were calculated using previously reported NPP values for species of *Carex* and *Salix* (Szumigalski and Bayley 1996*b*; Thormann and Bayley 1997*b*) and the estimated proportion of below- to above-ground plant production in western continental fens and bogs (1:1; Campbell et al. 2000). Using these data, almost two-thirds of the total accumulated sedge peat (61%) and carbon (65%) in the riverine sedge fen originated from *C. aquatilis* leaves, with the remainder originating from *C. aquatilis* rhizomes (Table 2) after the first 2 years of decomposition. This disparity resulted from the significantly higher rate of decomposition of the rhizomes (75%) compared with the leaves (54%) over the 2-year decomposition period (Fig. 1) and the use of a very conservative equal partitioning of above- and belowground NPP (Campbell et al. 2000). The ratio of the above- to below-ground plant tissue contribution to the peat and carbon accumulation potential would be more similar if a less conservative estimate of the contribution of the belowground plant tissues to the total plant production is used in the calculations. Most of the belowground plant tissues (rhizomes and roots, the latter were not measured as part of this study) are located in the catotelm and receive oxygen through aerenchyma tissues (Fagersted 1992; Jackson and Armstrong 1999). Therefore, the combination of high belowground NPP and significantly lower rates of decomposition in the catotelm (Damman 1996) results in a significant contribution of belowground plant tissues to the development of peatlands characterized by a significant presence of rhizomatous plant species, such as species of *Carex*.

Despite significantly different rates of decomposition (Fig. 1), *Salix planifolia* leaves and roots contribute similar amounts of peat and carbon to the fen (Table 2). However, owing to their low NPP, their contribution to the accumulation of peat and carbon in the riverine sedge fen is negligible compared with the contribution of the *Carex* litters (Table 2). The peat and carbon accumulation potentials of *Sphagnum fuscum* over the first 2 years of decomposition in the bog are similar to those reported by Thormann et al. (1999*a*). This suggests that rates of peat and carbon accumulation are similar among bogs in southern boreal Alberta.

Total nitrogen tissue concentrations

Initial TN concentrations ranged from 6.8 $mg \cdot g^{-1}$ in *Sphagnum fuscum* to 20 $mg \cdot g^{-1}$ in *C. aquatilis* leaves and they increased significantly over the 2-year decomposition period in the *Salix planifolia* litters but not in the sedge and bryophyte litters (Fig. 2). The TN tissue concentrations of the bryophyte litter were always lower than those of the fen vascular plant litters (Fig. 2). Our TN values are similar to those of Szumigalski and Bayley (1996*a*), Bartsch and Moore (1985), Ohlson (1987), Thormann and Bayley (1997*a*), and Arp et al. (1999). Nonsignificant changes in tissue TN concentrations have been reported previously (Szumigalski and Bayley 1996*a*) and may indicate similar rates of losses of N owing to leaching and microbial assimilation during the process of decomposition. Only the mass losses of the *Salix* litters were correlated significantly with TN tissue concentrations (Table 1). Both of these litters had similar initial TN tissue concentrations; however, they diverged during the decomposition process, with the leaf litter having significantly higher tissue concentrations of TN after 2 years (Fig. 2). This partially contributed to significantly higher mass losses for *Salix planifolia* leaves compared with roots over the 2-year decomposition period (29 vs. 48%, respectively) (Fig. 1).

TC:TN quotients

The initial TC:TN quotient of the litter is important in the decomposition process, because microbial populations (fungi and bacteria) accumulate nutrients, such as N, P, or K, during the early stages of decomposition (Verhoeven et al. 1990; Taylor et al. 1991) and low concentrations of these nutrients in the litter may lead to lower decomposition rates. In this study, TC:TN quotients decreased significantly only in *Salix planifolia* leaves, while remaining similar in the other four litter types (Fig. 2). Our TC:TN quotients are similar to those previously reported from bog and fen vegetation in North America (Szumigalski and Bayley 1996*a*; Thormann and Bayley 1997*a*; Arp et al. 1999). Initial TC:TN quotients ranged from 22 in *C. aquatilis* leaves to 68 in *Sphagnum fuscum* and decreased slightly, but not significantly, over the 2-year decomposition period (Fig. 2). These decreases are the result of increasing TN and constant TC tissue concentrations (Fig. 2). Although TC:TN quotients were negatively correlated with mass losses of all five litter types, the correlation was significant only for *Salix planifolia* leaves (Table 1).

Net immobilization of N occurs at TC:TN quotients above approximately 30 (Parnas 1974), resulting in decreases of the TC:TN quotient over time. Conversely, net mineralization occurs at lower TC:TN quotients owing to the equal utilization of N and C by microbial populations, resulting in insignificant changes in the TC:TN quotient (Verhoeven et al. 1990). The initial TC:TN quotients of four of the five litter types were above 30 (*Sphagnum fuscum*, *Salix planifolia* leaves and roots, *Carex aquatilis* rhizomes) and they all decreased during the decomposition process, albeit significantly only in *Salix planifolia* leaves (Fig. 2). This suggests that net immobilization, rather than mineralization, occurred. Conversely, the initial TC:TN quotient of *C. aquatilis* leaves was below 30 and it changed very little between sampling periods (Fig. 2).

Mass losses over the first 2 years of decomposition could not be predicted based on the TC:TN quotients. Neither the initial TN tissue concentrations, nor the initial TC:TN quotient of the litter is indicative of decomposition rates in this study, contradicting previous results by Taylor et al. (1991), Verhoeven et al. (1992), Szumigalski and Bayley (1996*a*), and Thormann and Bayley (1997*a*), who determined that litters with lower initial TC:TN quotients, and hence higher initial TN tissue concentrations, have higher decomposition rates.

Total phosphorus tissue concentrations

Initial TP tissue concentrations ranged from 5.0 (*Sphagnum fuscum*) to 21.0 $mg \cdot g^{-1}$ (*C. aquatilis* rhizomes) (Fig. 2). During the 2-year decomposition period, TP tissue concentrations showed a variable pattern, decreasing substantially during the early stages of decomposition before increasing during the later stages of decomposition (Fig. 2). Decreases in TP tissue concentrations of aboveground litter during the process of decomposition have been reported previously by Puriveth (1980), Verhoeven and Arts (1992), and Davis and van der Valk (1978). Decreases in P tissue concentrations in litter has been attributed to leaching during the early stages of decomposition. Subsequent increases in TP tissue concentrations have been attributed to assimilation by microbial populations from the surrounding water or soil solution and absorption by the decomposing plant materials (Puriveth 1980) during the later stages of decomposition.

TP concentrations were significantly correlated with the decay of both leaf litters (Table 1), indicating that higher concentrations of TP in *C. aquatilis* and *Salix planifolia* leaves resulted in increased mass losses. This trend does not apply to *C. aquatilis* rhizomes, which lost significantly more mass than the other four litter types (Fig. 1) and showed a negative correlation (not significant) between mass losses and TP tissue concentrations (Table 1). However, *C. aquatilis* rhizomes had significantly higher initial tissue concentrations of TP (21.0 $mg \cdot g^{-1}$) (Fig. 2), which may partially account for the large mass losses observed in this study.

Mass losses of *Salix planifolia* roots in the riverine sedge fen were similar to those of *Sphagnum fuscum* in the bog (29 and 21%, respectively) after 2 years (Fig. 1). These litter types differ significantly in TN and TP tissue concentrations, with the *Salix planifolia* roots having significantly higher tissue concentrations of both tissue nutrients (Fig. 2). Furthermore, surface water nutrient concentrations were significantly higher in the fen than the bog (Table 3) and should have contributed to higher mass losses of the root litter than the bryophyte litter. Despite the greater availability of nutrients to microbial communities in the fen, it is possible that the

root litter had higher concentrations of recalcitrant, structural carbohydrates, such as lignin and cellulose, than the bryophyte litter, thereby decreasing decomposition rates. Similarly, mass losses of *C. aquatilis* rhizomes significantly exceeded those of *C. aquatilis* leaves (74 vs. 54%, respectively) (Fig. 1), despite significantly lower tissue concentrations of TN and TP throughout the first 2 years of decomposition (Fig. 2). Hartmann (1999) determined that initial TN tissue concentrations of belowground tissues did not correlate with first year mass losses of her fen vegetation, indicating an inverse relationship between initial TN tissue concentrations and mass losses. Although neither she, nor we, measured cellulose and lignin tissue concentrations of our litters, Coulson and Butterfield (1978) suggested that the amount of cellulose associated with lignin (lignocellulose) affects mass losses of plant litters. Plant litters with high concentrations of lignocellulose are very resistant to decomposition (Benner et al. 1984).

Fungi

Physical characteristics of the litter types may significantly affect mass losses and may be more important than either environmental or litter quality variables. Litter that provides a large surface area for microbial (fungi and bacteria) attack may decompose faster than litter with a comparatively smaller surface area, despite a lower nutrient availability to microbial populations in the former litter type (Seliskar et al. 1977). Although *Salix planifolia* fine roots and *C. aquatilis* rhizomes may have similarly large surface areas for microbial attack, the root litter may have larger concentrations of decomposition-resistant materials, such as lignin and other phenolic compounds. For example, the presence of ectomycorrhizal fungal mycelium may increase cell wall lignification (Campbell and Ellis 1992) and phenolic (Horan et al. 1988) compound deposition by the host plant near the contact zone with the fungus as a defense mechanism. This may result in lower mass losses compared with non-mycorrhizal or non-ectomycorrhizal plant tissues, such as *C. aquatilis* rhizomes (Thormann et al. 1999*b*) or aboveground plant tissues. Thormann et al. (1999*b*) showed that roots of *Salix planifolia* were ectomycorrhizal in the riverine sedge fen. These fungi form a Hartig net and mantle in and around the roots of the host plant. Furthermore, the principal structural cell wall component of fungi is chitin and it is broken down poorly if at all through the saprophytic activities of other fungi (Carlile and Watkinson 1994). Thus, higher *C. aquatilis* rhizome mass losses could be the result of increased surface area for microbial attack due to aerenchyma tissue (oxygen-conducting tissues) (Fagersted 1992; Jackson and Armstrong 1999), significantly higher initial TP tissue concentrations (Table 1), and the absence of ectomycorrhizal fungal tissues (Thormann et al. 1999*b*).

The role of surface water chemistry variables on mass losses

Alkalinity-related surface water variables were negatively correlated with mass losses of the above- and below-ground litter types in the riverine sedge fen (Table 4). Similar negative correlations between the acidity–alkalinity gradient variables and mass losses in southern boreal poor and rich fens were previously reported by Szumigalski and Bayley (1996*a*), who suggested that the decomposition of litter in their study was inhibited by increased alkalinity, i.e., higher pH. In contrast, Tóth and Zlinszky (1989) and Verhoeven et al. (1990) found that decomposition of plant litter was inhibited at low pH. However, Farrish and Grigal (1988) and Bridgham and Richardson (1992) suggested that only anaerobic decay of plant litter is retarded at low pH and that aerobic decay may be unaffected or slightly enhanced by a decreasing pH. Our data support their hypothesis. Similarly, conductivity, alkalinity, and HCO_3^- surface water concentrations (Table 4) may have retarded mass losses of both *C. aquatilis* litters and *Salix planifolia* leaves. Also, most fungi are acidophiles and fungi constitute the dominant decomposer community in low pH ecosystems compared to bacteria (Latter et al. 1967). Therefore, a lower pH likely enhances their abilities to decompose plant litters.

TDP and NH_4^+ surface water concentrations correlated positively with mass losses of both *C. aquatilis* litter types and *Salix planifolia* leaves (Table 4). This suggests that their decomposition may be enhanced by a higher nutrient-availability to decomposer microbial populations, thereby supporting results by Coulson and Butterfield (1978), Slapokas and Granhall (1991), and Szumigalski and Bayley (1996*a*). Conversely, other studies suggest that wetlands richer in nutrients do not have higher decomposition rates (Bayley et al. 1985; Rochefort et al. 1990; Bridgham and Richardson 1992). Thormann and Bayley (1997*a*) determined that increased TDP surface water concentrations were negatively correlated with mass losses of *C. aquatilis* leaves in the same fen. In addition, mass losses of *Sphagnum fuscum* in the bog were negatively correlated with TP surface water concentrations (Table 4). These conflicting data suggest that other variables may be more important in the decomposition of plant litters in peatlands, such as water levels (Thormann et al. 1999*a*), litter quality and morphology, or the composition of microbial communities.

Conclusions

This is the first study that examined decomposition rates of belowground litter of the dominant sedge and shrub species and compared them with the aboveground plant litters in North American peatlands. Mass losses of *C. aquatilis* rhizomes (75%) significantly exceeded those of *C. aquatilis* leaves (54%), *Salix planifolia* leaves (48%), and *Salix planifolia* roots (29%) in a rich fen and *Sphagnum fuscum* (21%) in a bog after 2 years. Mass losses of the aboveground plant litters of the fen vegetation and the bog bryophyte were similar to those reported in previous studies in North America and Europe. Mass loss differences could only partially be explained by differences in litter quality or surface water chemistry and other variables, such as lignin, cellulose, chitin, and (or) other elemental nutrient concentrations, as well as litter morphology or different microbial populations, may influence decomposition rates.

Owing to the large contribution of belowground tissues of many wetland plant species to the total plant production, these tissues constitute a major component of carbon and nutrient cycles in wetlands. Decomposition rates of

C. aquatilis rhizomes are high in the acrotelm. These rates, however, may decrease significantly in the catotelm under anoxic conditions and, along with fine roots, rhizomes constitute a significant contribution to peat and carbon accumulation in sedge-dominated wetlands. Our data indicate that nearly one-third of all the sedge peat and carbon originates from rhizomatous plant tissues in this fen. We did not examine decomposition rates of *C. aquatilis* roots; however, they too constitute a significant portion of the total belowground production and would have increased the importance of belowground plant tissues relative to aboveground plant tissues in the development of peatlands in boreal Canada.

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Appendix. Mean litter quality (TC, TN, C:N, TP) ($mg \cdot g^{-1} \pm SE$) of decomposing plant material in the bog (*Sphagnum fuscum*) and riverine sedge fen (RSF, *Carex aquatilis* and *Salix planifolia*) from September 1997 to September 1999 in southern boreal Alberta, Canada.

		Initial				20 days				50 days			
Sites	Litter types	TC	TN	TC:TN	TP	TC	TN	TC:TN	TP	TC	TN	TC:TN	TP
Bog	*Sphagnum fuscum* plants	460	6.8	68	5.0	460	6.4	72	3.8	460	6.9	67	3.9
		(10)	(0.3)	(2)	(0.0)	(1)	(0.2)	(2)	(0.1)	(5)	(0.4)	(3)	(0.6)
RSF	*Salix planifolia* leaves	470	12.4	41	10.8	490	15.5	32	9.3	490	15.7	31	8.9
		(23)	(0.1)	(0)	(0.1)	(30)	(0.2)	(1)	(0.4)	(1)	(0.5)	(1)	(0.7)
	Salix planifolia roots	450	12.6	34	16.6	490	13.0	38	9.1	480	13.9	35	8.8
		(47)	(1.5)	(0)	(0.0)	(2)	(0.7)	(2)	(0.2)	(2)	(1.0)	(3)	(0.4)
	Carex aquatilis leaves	450	20.1	22	18.2	470	20.6	23	10.5	470	22.3	21	10.2
		(1)	(0.1)	(0)	(0.2)	(0)	(1.1)	(1)	(0.4)	(2)	(1.1)	(1)	(0.8)
	Carex aquatilis rhizomes	430	7.5	58	21.0	450	5.9	77	11.1	440	6.3	71	11.4
		(1)	(0.5)	(3)	(0.1)	(3)	(0.5)	(6)	(1.2)	(1)	(0.7)	(7)	(1.7)

Appendix. (*concluded*).

		8 months				12 months				20 months				24 months			
Sites	Litter types	TC	TN	TC:TN	TP	TC	TN	TC:TN	TP	TC	TN	TC:TN	TP	TC	TN	TC:TN	TP
Bog	*Sphagnum fuscum* plants	470	7.1	67	3.6	480	6.6	73	4.1	480	7.5	64	6.0	470	7.0	65	5.0
		(1)	(0.1)	(1)	(0.2)	(3)	(0.3)	(3)	(0.1)	(2)	(0.1)	(0)	(0.3)	(2)	(0.2)	(2)	(0.6)
RSF	*Salix planifolia* leaves	490	17.7	28	12.0	490	25.6	19	17.2	500	28.7	17	23.0	470	28.0	17	19.0
		(4)	(0.6)	(1)	(0.8)	(6)	(1.2)	(1)	(0.3)	(5)	(1.1)	(0)	(0.4)	(11)	(0.5)	(1)	(1.0)
	Salix planifolia roots	500	14.1	35	9.3	15.7	32	10.3	490	18.0	27	14.0	490	17.0	17.0	28	12.0
		(3)	(0.7)	(2)	(0.5)	(1)	(0.6)	(1)	(0.5)	(3)	(0.3)	(1)	(0.3)	(3)	(1.0)	(2)	(0.8)
	Carex aquatilis leaves	460	22.2	21	16.4	470	21.4	22	18.4	450	24.2	19	25.0	460	21.0	23	25.0
		(8)	(0.6)	(1)	(1.8)	(11)	(1.7)	(2)	(1.6)	(4)	(2.4)	(2)	(1.7)	(14)	(2.4)	(4)	(1.8)
	Carex aquatilis rhizomes	460	6.8	67	12.0	470	7.3	64	9.6	460	7.3	65	12.0	460	10.0	45	15.0
		(3)	(0.4)	(3)	(1.2)	(5)	(0.2)	(2)	(0.4)	(3)	(0.8)	(6)	(1.4)	(3)	(0.5)	(2)	(1.1)