ECOSYSTEMS

Decomposition and Peat Accumulation in Rich Fens of Boreal Alberta, Canada

Dale H. Vitt,[1]* R. Kelman Wieder,[2] Kimberli D. Scott,[2] and Susan Faller[1]

[1]Department of Plant Biology and Center for Ecology, Southern Illinois University Carbondale, Carbondale, Illinois 62901, USA;
[2]Department of Biology, Villanova University, Villanova, Pennsylvania 19085, USA

ABSTRACT

Fens are important components of Canada's western boreal forests, occupying about 63% of the total peatland area and storing about 65% of the peatland carbon. Rich fens, dominated by true moss-dominated ground layers, make up more than half of the fens in the region. We studied organic matter accumulation in three rich fens that represent the diversity in structural types. We used in situ decomposition socks, a new method that examines actual decomposition throughout the upper peat profile over an extended period of time. We coupled our carbon loss data with macrofossil analyses and dated peat profiles using ^{210}Pb. Across the three rich fens and in the top 39 cm of the peat column, dry mass increases on average 3.1 times. From our dry mass loss measurements, we calculate that annual mass loss from the top 39 cm varies from 0.52 to 1.08 kg m^2. Vertical accumulation during the past 50 years has varied from 16 to 32 cm and during these 50 years, organic matter accumulation has averaged 174 g m^{-2} y^{-1} compared to 527 g m^2 y^{-1} dry mass loss, with additional mass losses of 306 g m^2 y^{-1} from peat between 50 and 150 years of age. Organic matter accumulation from our rich fens compares well with literature values from boreal bogs, whereas peat bulk densities increase about three times within the uppermost 40 cm, much more than in bogs. Hence, rich fens accumulate peat not because the plant material is especially hard to decompose, is acidic, or has the catotelm especially close to the surface, but because dense, rapidly produced inputs outweigh the relatively rapid decomposition process of the upper peat column.

Key words: Boreal; bulk density; carbon; decomposition; fen; moss; peat; peat accumulation; peatland.

INTRODUCTION

Fens are peat-forming wetlands that are influenced by both atmospheric and groundwater inputs of water and nutrients (inorganic cations and anions). Atmospheric inputs are from both precipitation and dry deposition and reflect the regional climatic and pollution regimes, whereas groundwater inputs are much more locally variable, depending on the surficial geology, localized soil development, and elevational position of the peatland in the watershed (Vitt 2006).

In continental western Canada (the provinces of Alberta, Saskatchewan, and Manitoba), peatlands occupy 365,157 km^2 or about 21% of the landscape. These peatlands have a modal maximum depth from 250 to 300 cm and store about 48 Pg of carbon (C) as peat and aboveground vegetation

(Vitt and others 2000). Both fens and bogs develop deep deposits of peat, with maximum depths for fens somewhat higher than for bogs (Vitt and Wieder 2008). Although peatlands in this region represent 10% of the world's boreal peatland area, they contain about 17% of the boreal peatland C stock (Wieder and others 2006), thus reflecting a high carbon density on an area basis of about 115 kg C m^{-2}.

Fens in continental western Canada occupy 231,155 km^2 or 63% of the total peatland area (Vitt and others 2000). Carbon density of fens on a volume basis ranges from 0.049 to 0.054 g C cm^{-3}; about 31.2 Pg (65%) of the region's peatland C is found in fen peat (Vitt and others 2000). Thus, compared to bogs, fens are more abundant on the landscape, have higher C densities, and have as deep or deeper peat deposits. Although the importance of fens in long-term C accumulation in this region is evident, accumulation of peat in fens has rarely been addressed in the literature and we know little about how peat accumulates in this wetland type.

Fens, or geogenous peatlands, can be separated into two fundamentally different types based on floristic and chemical criteria (DuReitz 1949; Sjörs 1950, 1952). Floristically, fens can have a ground layer dominated by *Sphagnum* (poor fens), or a ground layer dominated by true mosses (rich fens), generally termed brown mosses because the typical species usually have a reddish-brown color. Additionally, there are major differences between fen types in the vascular plant species (see Chee and Vitt 1989 for list of species defining fen types). In general, both poor fens and rich fens are structurally variable and can be sedge-dominated, shrub-dominated, or wooded (Vitt and others 1996). Across continental boreal Canada, rich fens are the most abundant fen type occupying about 60% of the total fen area (estimated from Vitt and others 1997).

Sphagnum-dominated poor fens and true moss-dominated rich fens differ in the chemistries of their surface and interstitial pore waters. Poor fen waters have pH values ranging from around 4.5 to 5.5, whereas rich fen waters have pH values from about 6.0 to 8.5 or higher (Vitt and Chee 1990). Thus, poor fens are acidic ecosystems, whereas rich fens are generally basic (or neutral). Associated with the pH differences are differences in base cation concentrations and alkalinity, with poor fen waters having less then 5 mg l^{-1} of Ca^{2+}; low concentrations of Mg^{2+}, K^+, and Na^+; and little or no bicarbonate alkalinity, whereas rich fen waters have higher concentrations of base cations, especially Ca^{2+}, and appreciable alkalinity. Concentrations of key nutrients (soluble inorganic forms of N and P) in fen pore waters are generally similar in poor and rich fens and always are low (Vitt and others 1995).

Peat chemistry has also been used to differentiate between peatland types. Zoltai and Johnson (1987) provided a detailed study of elemental chemistry of 230 peatlands across western Canada. They proposed four 'nutrient classes' for the peatlands based on the total Ca concentrations within the upper 50 cm of peat. Calcium concentrations ranged from less than 5,000 mg kg^{-1} (oligotrophic) to more than 30,000 mg kg^{-1} (macrotrophic). Their values for Ca in the upper 50 cm of peat for poor fens (oligotrophic and dystrophic nutrient classes) varied from 3,300 to 7,900 mg kg^{-1}, whereas their values for mesotrophic and macrotrophic nutrient classes (=rich fens) ranged from 15,700 to 49,900 mg kg^{-1}. Magnesium and S concentrations also increased along the Ca gradient, however, concentrations of other elements (Fe, P, K, Pb, and Na) varied, but not in relation to the four nutrient classes. Although these authors defined 'nutrient' broadly and included Ca, Mg, and Na in their concept, others have limited the term 'nutrients' to only N, P, and K. Zoltai and Johnson's values for P concentrations in peat range are 694–928 for poor fens and 567–1,192 for rich fens; their values for K are 1,276–2,462 for poor fens and 421–1257 for rich fens (all values mg kg^{-1}) (they did not provide data for N). In the synthesis by Walbridge and Navaratnam (2006), peatland types could not be distinguished based on N and P concentrations in peat. Two conclusions can be drawn from these findings: rich fens are more variable in their chemistries then poor fens, and these two fen types cannot be distinguished based on concentrations of critical potential limiting nutrients (N, P, K).

Peat accumulates because plant production is greater than the combination of decomposition and dissolved organic C (DOC) losses. The scarce data for fen net primary production (NPP) reveal considerable variability. Bartsch and Moore (1985) reported aboveground NPP for several species of *Carex* occurring in rich and poor fens of northern Québec; NPP of the rich fen species ranged from 164 to 233 g m^{-2}. In Alberta, *Carex aquatilus* was reported to have aboveground NPP of 340 g m^{-2}, whereas graminoid-dominated peatlands elsewhere vary from 25 g m^{-2} in Alaska to 1,181 g m^{-2} in Wisconsin and 1,492 g m^{-2} in New Jersey (reviewed in Bartsch and Moore 1985). Belowground NPP data are also sparse, but Conlin and Lieffers (1993) reported root growth for peatland trees to be

about 200–340 g m^{-2}. Finér and Laine (1998) reported *Pinus sylvestris* root production in a meso-oligotrophic tall sedge fen in Finland of 396 g m^{-2}, whereas Saarinen (1996) reported NPP for a Finnish tall sedge fen of 1,100 g m^{-2} y^{-1}. Ground layer (bryophytes) production for wet boreal rich fens varies from around 100 to 160 g m^{-2} y^{-1} (Vitt 1990). A review of plant production for Canadian peatlands (Campbell and others 2000; Vitt and others 2001) provided a summary of NPP for a variety of fen types in western Canada. Values for aboveground NPP ranged from 246 to 358 g m^{-2} y^{-1} (organic matter) for fens in general, including at least one site each from open, shrubby, and wooded structural types. Thormann and Bayley (1997) reported that aboveground fen production across boreal North America ranged from 114 to 710 g m^{-2} y^{-1} (organic matter), averaging 319 g m^{-2} y^{-1}. Although fen NPP appears to be highly variable, rich fen NPP might easily exceed 1,000 g m^{-2} based on 150–200 g m^{-2} for the ground layer, 300–350 g m^{-2} for aboveground vascular plant production, and about 500 g m^{-2} for belowground vascular plant production.

The peat column receives C inputs from aboveground vascular plant litter, from belowground vascular plant roots, and from the bryophytic ground layer. Bryophytes lack roots and do not synthesize true lignin. In a review of peatland species decomposition, in general, moss tissues decompose more slowly than do vascular plant litter and roots (Turetsky 2003). Among bryophytes, decomposition differs significantly among species (Rochefort and others 1990; Johnson and Damman 1991) and in a reciprocal transplant study, Turetsky and others (2008) found that after three years, decay rates differed among species and between surface microtopographic positions (hummock vs. hollow) within a peatland, but did not differ among peatland types (bog, poor fen, rich fen). Over the three-year period, exponential decay constants (k values) varied from 0.022 (*Sphagnum fuscum*—a bog species) to 0.149 (*Sphagnum riparium*—a poor fen species); for the remaining six species in their transplant study k values averaged 0.062. Thus, it appears that rates of decomposition in the upper peat profile may largely depend on both the sources of the plant material deposited at the surface of the peat column and the surface microtopographic position. In light of these findings, it seems that higher proportions of vascular plant material litter input should lead to overall faster decomposition rates, whereas higher proportions of *Sphagnum* input should lead to overall slower

rates, and higher proportions of true moss input should lead to intermediate decomposition rates. Most decomposition studies to date typically have been based on fresh species-specific plant material being placed near the surface of the peat column (see review by Moore and Basiliko 2006) and therefore give only a partial picture of decomposition within the upper peat column. Nonetheless, a few studies have examined the decomposition as a function of depth within peat profiles (for example, Clymo 1965; Johnson and Damman 1991; Belyea 1996).

Ivanov (1957) proposed that the entire peat column could be divided into two parts, the lower, water saturated, mostly anaerobic portion, the catotelm; and the upper unsaturated, aerobic portion, the acrotelm. Rates of organic matter decomposition are presumed to be high in acrotelms and extremely low in catotelm environments (Clymo 1984; Belyea and Warner 1996). Continental bogs differ from most continental fens in that in bogs the water table may fall to at least 60-cm below the peat surface during mid-summer whereas in fens the water table fluctuates less and remains within 10–20 cm of the growing moss surface. As a result, continental bogs possess a well-developed aerobic layer, especially within hummocks composed of several species of *Sphagnum* and in hollows that, except sometimes in early spring, are also above the saturated zone. Bogs with well-developed aerobic layers are considerably different from fens of the region wherein the water table is just below the peat surface throughout the year and aerobic hummocks are rare, or restricted to strings in patterned fens or to scattered, loosely composed hummocks dominated by several species of true mosses.

A general model of peat accumulation might predict that peat accumulates in bogs (with well-developed acrotelms) and poor fens (with poorly developed acrotelms) due to the presence of a ground layer of moss species (*Sphagnum*) that have high resistance to decomposition. However, rich fens that have ground layer species (with an abundance of true mosses) with relatively little resistance to decomposition, abundant vascular plants, and poorly developed acrotelms might be expected to have low rates of peat accumulation. Additionally, disturbances that lead to changes in the acrotelm–catotelm boundary may have an influence on peat accumulation.

In this paper, we examine the upper peat profiles of three rich fens in boreal, continental Alberta to answer the following questions: (1) what are the biological, chemical, and physical properties of the

upper peat column of rich fens; (2) how variable are the rates of organic matter loss in the upper peat column; and (3) how do rates of peat accumulation in rich fens compare with those from bogs?

SITE SELECTION AND METHODOLOGY

Study Area

In June of 2003, three fens (Edson, Hondo, and Saulteaux) were selected using aerial photography and road reconnaissance (Figure 1). We chose three rich fens to take into account the vegetational diversity of these fen types in northern Alberta. Rich fens are varied in structure ranging from open, sedge-dominated peatlands to rather open, shrubby peatlands to wooded peatlands. Wooded rich fens are dominated by *Larix laricina*. General descriptions of rich fens in Alberta are given in Chee and Vitt (1989) and Slack and others (1980).

Figure 1. Map of Alberta, Canada (inset) showing location of three rich fen study sites.

Edson Rich Fen (53°35′N, 116°45′W, 976 m elev.) is a sparsely wooded rich fen dominated by *Larix laricina*, *Betula glandulosa*, *Carex* species (including *C. diandra*, *C. chordorrhiza*, and *C. lasiocarpa*), *Muhlenbergia glomerata*, *Aulacomnium palustre*, *Tomenthypnum nitens*, *Hamatocaulis vernicosus*, and sporadic occurrences of *Sphagnum warnstorfii* and *Sphagnum teres*. The hummock-hollow topography is well developed, with low hummocks 20–30 cm above moist depressions.

Hondo Rich Fen (55°07′N, 114°07′W, 589 m elev.) is a shrubby fen dominated by several species of *Salix*, *Betula glandulosa*, *Carex lasiocarpa*, and *Potentilla fruticosa* along with hollows with sporadic populations of *Hamatocaulis vernicosus* and *Drepanocladus aduncus*.

Low hummocks rise 10–15 cm above water filled depressions. Recent oil-well roads in the local area may have affected fen water levels in the vicinity of our plots.

Saulteaux Rich Fen (55°07′N, 114°10′W, 600 m elev.) is an open fen dominated by *Carex lasiocarpa*, *C. aquatilus*, *Triglochin maritima*, *Menyanthes trifoliata*, *Hamatocaulis vernicosus*, *Brachythecium mildeanum*, and *Campylium stellatum*. No hummocks are present.

Experimental Design

At each of the three sites along a randomly placed transect running more or less through the center of the fen, we located five plots approximately 20 m apart. In each plot, we installed a 1-m long, 10-cm diameter slotted PVC pipe capped at the top except for when sampling for water chemistry. Peat depths are greater than 1 m at all three sites. From randomly selected locations within a 25 m^2 plot, we extracted six 10-cm 0.5-m long cores using a 1-m long sharpened PVC pipe or a stove pipe. Care was used to ensure that the extracted cores were not compacted. A 10-cm diameter, empty, PVC pipe was placed in two of the extraction columns for later placement of decomposition socks.

The Decomposition Sock Approach

From each plot, two of the 10-cm diameter cores were taken to the laboratory, frozen, removed from the PVC pipes, cut into 3-cm slices (=pucks) using a band saw, labeled with its position in the core, and dried at 60–70°C until a constant weight was achieved (generally 48 h). Each dried puck was placed in a 3-cm × 10-cm diameter 'sandwich bag' sewn from tulle with 1-mm diameter mesh. Individual pucks in these sandwich bags were then stacked in original depth order within a
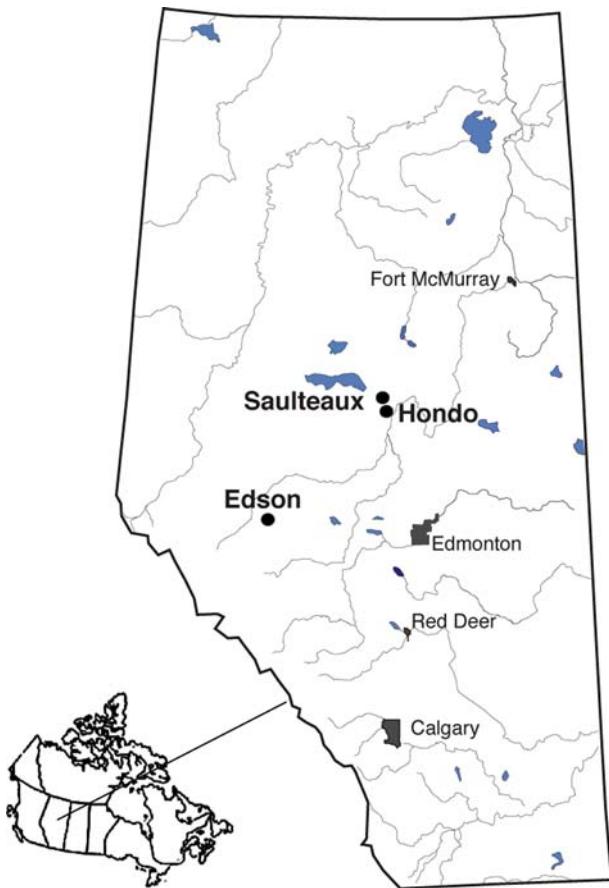
10-cm diameter 'decomposition sock' (ca. 50-cm long tube closed at one end that was sewn from tulle with 3-mm diameter mesh) to reconstruct the original peat profile. Each 'decomposition sock' with its reassembled pucks was returned to its original location in the field after removal of the empty PVC pipe and was covered by 2-cm of living moss. Socks were replaced in the peatland between July 26 and October 6, 2003. Half ($n = 5$ from each of the three fens) of the decomposition socks were then extracted on October 5–6, 2005 (all socks were in place for 24–26 months) and returned to the laboratory. Each puck was removed from the tulle mesh bags and living roots greater than 1-mm in diameter that had grown into the pucks (inside of the netting) were manually separated out. The pucks and the removed roots were dried separately and weighed. Initial extraction of the initial 10-cm diameter cores killed all living roots. When the decomposition socks were placed back into the field, these dead roots cannot grow, but begin decomposing while new roots grow into the decomposition sock pucks. The combination of decomposing dead roots and root ingrowth was used to approximate changes in root biomass within the peat via natural root turnover. We calculated net dry mass loss as the change in total puck mass from over the course of incubation in the field that resulted from decomposition of peat and initially killed roots and the dry mass added by the ingrowth of new roots.

Macrofossil and Biophysical Analyses

From each plot, two of the 10-cm diameter cores were sectioned into 3-cm slices ($n = 10$ from each fen). From each core section, two 1-cm^3 plugs were extracted using a 1-cm diameter cork corer. One plug was used for bulk density analysis and the second for macrofossil analysis. Bulk density was determined after oven drying for 8 h at 80°C. Ash was determined by heating in a muffle furnace at 500°C for 8 h and then at 900°C for 8 h; ash-free bulk density was calculated by dividing the total organic mass by the sample volume.

Macrofossil analysis was carried out by placing the second 1-cm^3 plug from each core section into a Plexiglas s-shaped channel template (1-cm wide × 25-cm long) and wetting with distilled water. Macrofossil identifications were done without chemical treatment or sieving. The wetted material was then evenly distributed along the s-shaped channel and inspected under a dissecting microscope at 20–25× magnification. Peat botanical

composition (% *Sphagnum*, true moss, above ground litter, roots), charcoal presence, and % debris were estimated following Bauer and others (2003). Because the samples were not pre-sieved, organic debris was included in the analysis and used as a proxy for the extent of organic matter decomposition and/or changes in peat type within the peat column.

^{210}Pb Dating

From each plot, two of the 10-cm diameter cores were returned to the laboratory where they were frozen and sectioned on a band saw into 3-cm depth intervals. Each depth section was dried and weighed for bulk density measurements prior to grinding with a Tecator Cyclotec sample mill. To assign a date to the bottom of each 3-cm depth interval, cores were ^{210}Pb-dated by acid digestion of a subsample from each core section (adding a known amount of ^{209}Po as a chemical yield tracer) and alpha spectrometry. Dates were calculated using the constant rate of supply model (Appleby and Oldfield 1978; Wieder and others 1994; Turetsky and others 2004; Brenner and others 2004). Overall efficiencies of the digestion and counting procedure (recovery of the ^{209}Po chemical yield tracer) averaged $5.2 \pm 0.2\%$ (mean ± one standard error; $n = 217$). Several of the cores were not considered dateable because unsupported ^{210}Pb concentrations did not decline to low and constant values; apparently the cores were not collected to a sufficient depth. For the 16 cores that were considered dateable, total unsupported ^{210}Pb inventories (8.7 ± 1.3 pCi cm^{-2}; $n = 16$) and corresponding atmospheric ^{210}Pb deposition rates (0.27 ± 0.04 pCi cm^{-2} y^{-1}; $n = 16$) were at the lower end of the range of values given in Appleby and Oldfield (1978).

Water Chemistry

At each site, we installed 50-cm tall 1-m deep wells (10-cm diameter PVC pipes, with slots cut at 5-cm intervals), which were capped at the top except during sampling. Water samples were collected from the top of the water table of each well periodically during the growing season for the two year field life of the project except at Edson (where they were collected less frequently), and returned to the laboratory where pH was determined prior to filtering (Whatman 42 filter paper). Samples were frozen and shipped to Villanova University for analysis of concentrations of Ca^{2+}, Mg^{2+}, Na$^+$, K$^+$ (atomic absorption spectrometry), NH$_4^+$-N (phenate method), NO$_3^-$-N (hydrazine reduction

method), and ortho-P (stannous chloride method) (APHA 2006). In addition, at similar intervals at the Hondo and Saulteaux sites, dissolved O_2 and temperature were measured at 10-cm intervals by lowering a probe (YSI 556; Yellow Springs, Ohio) down the well to a depth of 40 cm.

Statistical Analyses

Differences between the three fens were analyzed using a one-way analysis of variance. When examining patterns between sites and with depth, we used a repeated measures analysis of variance with depth within core treated as the repeated effect. Post hoc comparisons were carried out using the Tukey–Kramer test. All statistical analyses were done using SAS 9.1 software (SAS 2003). All statements of significance are based on $P \leq 0.05$.

RESULTS

Surface Water Chemistry

The only two water chemical parameters that differed between the three sites were pH and Mg^{2+} concentrations; values for each parameter were highest at Saulteaux and lowest at Edson (Figure 2). Ca^{2+} concentrations were higher at Saulteaux than at the other two sites and NO_3^--N concentrations were higher at Hondo than at the other two sites. Concentrations of Na^+, K^+, NH_4^+-N, and ortho-P did not differ significantly between the three rich fen sites. In comparison to Saulteaux, Hondo fen waters had higher dissolved O_2 concentrations and warmer waters, although neither site had strictly anoxic water throughout the 30-cm immediately below the water table surface (Figure 2).
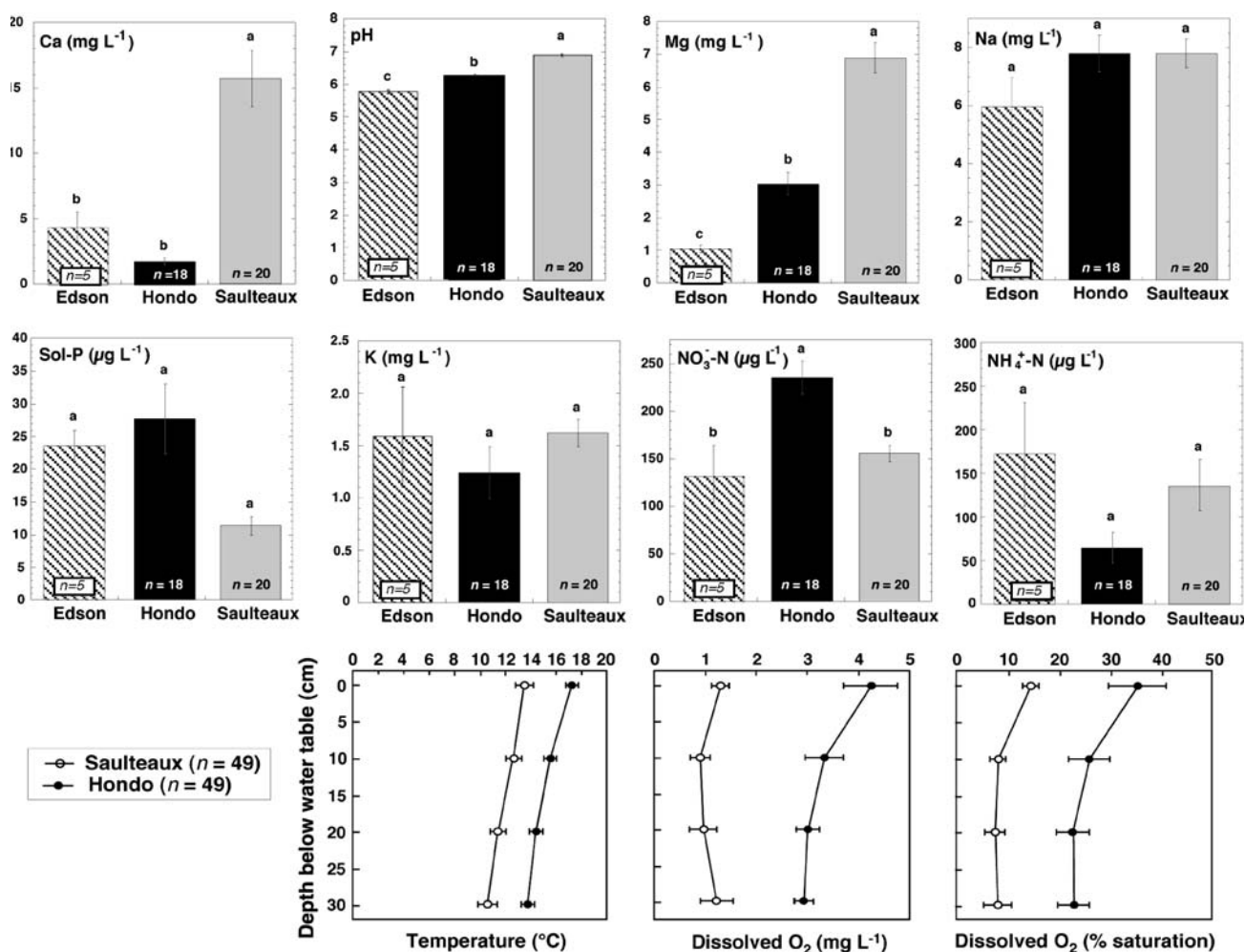

Figure 2. Comparison of water chemistry parameters for the three rich fens. Nonsignificant differences are shown by same letters above the bars as determined by post hoc comparison of means. Lines are S.E.M.

Physical and Botanical Characterization of the Upper Peat Column

Ash-free Bulk Density

Ash-free bulk density exhibited a significant site by depth interaction ($P < 0.0001$). Mean values at all sites generally increased with depth throughout the upper 41 cm, with maximum values varying from about 0.09 g cm^{-3} at Edson to 0.12 g cm^{-3} at Hondo (Figure 3).

Macrofossil Composition

Each of the three macrofossil categories exhibited a significant site by depth interaction ($P < 0.0001$). Debris percentage did not differ significantly between the Edson and Saulteaux sites or between the upper 32 cm of the Edson and Hondo sites (Figure 3). In general, debris percentage increased with depth from near-surface values of about 1–4% to 40–71% at 35–41 cm. Bryophyte remains are those of true mosses, except for some *Sphagnum*
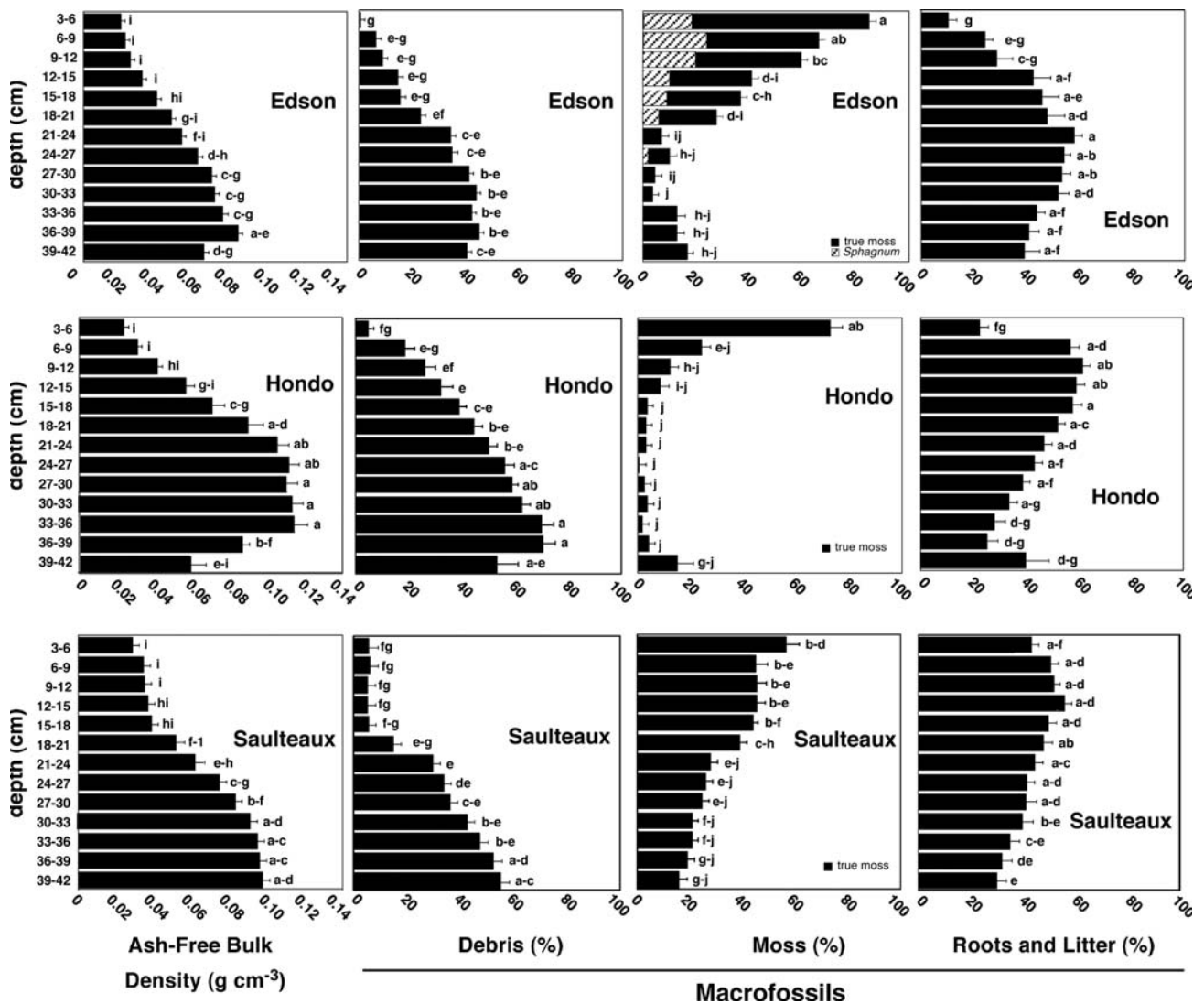

Figure 3. Ash free bulk density (*left*) and botanical composition (% macrofossils) of upper peat columns for the three rich fens. Bars are means of 3-cm thick slices from ten cores for each site. Nonsignificant differences for depth increments are shown by same letters beside the bars and in parentheses for the sites as determined by post hoc comparison of means. Lines are S.E.M.

remains (up to 20%) in the top portion of the peat profile at Edson. Total bryophyte abundance is high at the surface (56–89%) and decreases with depth with no differences between sites at depths below 20 cm where mosses average 12% of the macrofossil assemblage (Figure 3). Root/litter biomass was generally similar between the three sites, with the only differences at depths of 2–11 cm where the root/litter biomass percentage was slightly lower at Edson than at the other two sites.

Dry Mass Content

The three fens in our study differ significantly in total dry mass content of the top 39 cm of the peat profile with mean values ranging from 19.3 kg m^{-2} (Edson) to 31.2 kg m^{-2} (Hondo), averaging 25.4 kg m^{-2} across the three rich fens (Table 1). For the 3–9 cm interval, across the three rich fens, dry mass ranges from 1.4 to 2.3 kg m^{-2}, compared to a range of 5.1–7.3 kg m^{-2} for the 33–39 cm depth interval. Across the three rich fens, dry mass increases with depth from an average of 2.0 kg m^{-2} (3–9 cm) to 6.4 kg m^{-2} (33–39 cm), an increase of 3.1 times. For the top half (3–21 cm) of the peat profiles, dry mass at Hondo is about twice that for peat at either Saulteaux and Edson; for the bottom half (21–39 cm) of the profiles Edson peat mass is less than at either Saulteaux or Hondo. Overall, the upper half of the profiles average 8.0 kg m^{-2} of dry mass, compared to 17.4 kg m^{-2} for the lower half (Table 1).

Dry Mass Loss in the Upper Peat Column

Annual total mass loss for the top 39 cm of the peat profile varied from 0.52 to 1.08 kg m^{-2}, representing a mean annual mass loss of between 3.3 and 5.0% (Table 1). Annual mass losses from the top 21 cm of the peat column were lower at Edson and at Saulteaux (0.28–0.41 kg m^{-2}, respectively) than at Hondo (0.83 kg m^{-2}). However, mass losses in the lower half of the profiles (21–39 cm) were not significantly different, ranging from 0.24 to 0.37 kg m^{-2} y^{-1}. In summary, on a mass basis, upper peat profiles of rich fens annually lose 6.4%, compared to lower peat profiles that lose 1.7%. Annual average mass loss from the upper peat profile was 1.8 times as great as the lower part of the peat profile (0.51 g m^{-2} compared to 0.28 g m^{-2} for the lower part of the profile).

Peat mass loss, whether expressed as a percent of initial mass per year or on a kg m^{-2} basis exhibited a significant site by depth interaction ($P < 0.0003$). When decompositional losses are considered on a percentage basis, there is a general pattern of a

Table 1. Total Dry Mass (DM), Total Mass Loss, Root Production (> 1 mm diameter) (all kg m^{-2}), and Percent Mass Loss from Various Parts of Upper Peat Profiles of the Three Rich Fens

Site	DM at 3–9 cm depth (kg m^{-2}) (S.E.)	DM at 33–39 cm depth (kg m^{-2})	DM at 3–21 cm depth (kg m^{-2}) (S.E.)	DM at 21–39 cm depth (kg m^{-2}) (S.E.)	DM at 3–39 cm depth (kg m^{-2}) (S.E.)	Net dry total mass loss at 3–21 cm depth (kg m^{-2})	Net dry total mass loss at 21–39 cm depth (kg m^{-2})	Net dry total mass loss at 3–39 cm depth (kg m^{-2})	Annual root production at 3–39 cm depth (kg m^{-2})	Percent dry mass loss at 3–21 cm depth (S.E.)	Percent dry mass loss at 21–39 cm depth (S.E.)	Percent dry mass loss at 3–39 cm depth (S.E.)
Edson wooded	1.41^b (0.20)	5.13^b (0.54)	5.95^b (0.69)	13.32^b (1.28)	19.28^c (1.30)	0.28^b (0.06)	0.24^a (0.06)	0.52^b (0.08)	0.29^a (0.12)	4.59 (0.45)	1.94^a (0.29)	3.27 (0.32)
Hondo shrubby	2.27^a (0.23)	7.28^a (0.40)	10.78^a (0.30)	20.38^a (1.24)	31.16^a (1.24)	0.83^a (0.13)	0.25^a (0.04)	1.08^a (0.14)	0.06^a (0.02)	8.77 (0.98)	1.25^a (0.11)	5.01 (0.69)
Saulteaux open	2.36^a (0.13)	6.88^a (0.26)	7.20^b (0.71)	18.65^a (0.65)	25.85^b (0.84)	0.41^b (0.05)	0.37^a (0.07)	0.78^{ab} (0.12)	0.05^a (0.01)	5.78 (0.68)	2.04^a (0.18)	3.91 (0.44)
Mean for rich fens	1.99 (0.16)	6.40 (0.35)	8.03 (0.66)	17.36 (1.05)	25.40 (1.53)	0.51 (0.08)	0.28 (0.03)	0.79 (0.09)	0.14 (0.05)	6.43 (0.47)	1.73 (0.13)	4.08 (0.30)

Nonsignificant differences are shown as superscript letters that were determined by post hoc comparison of means. Edson site (wooded); Hondo site (shrub-dominated); Saulteaux site (open, sedge-dominated).
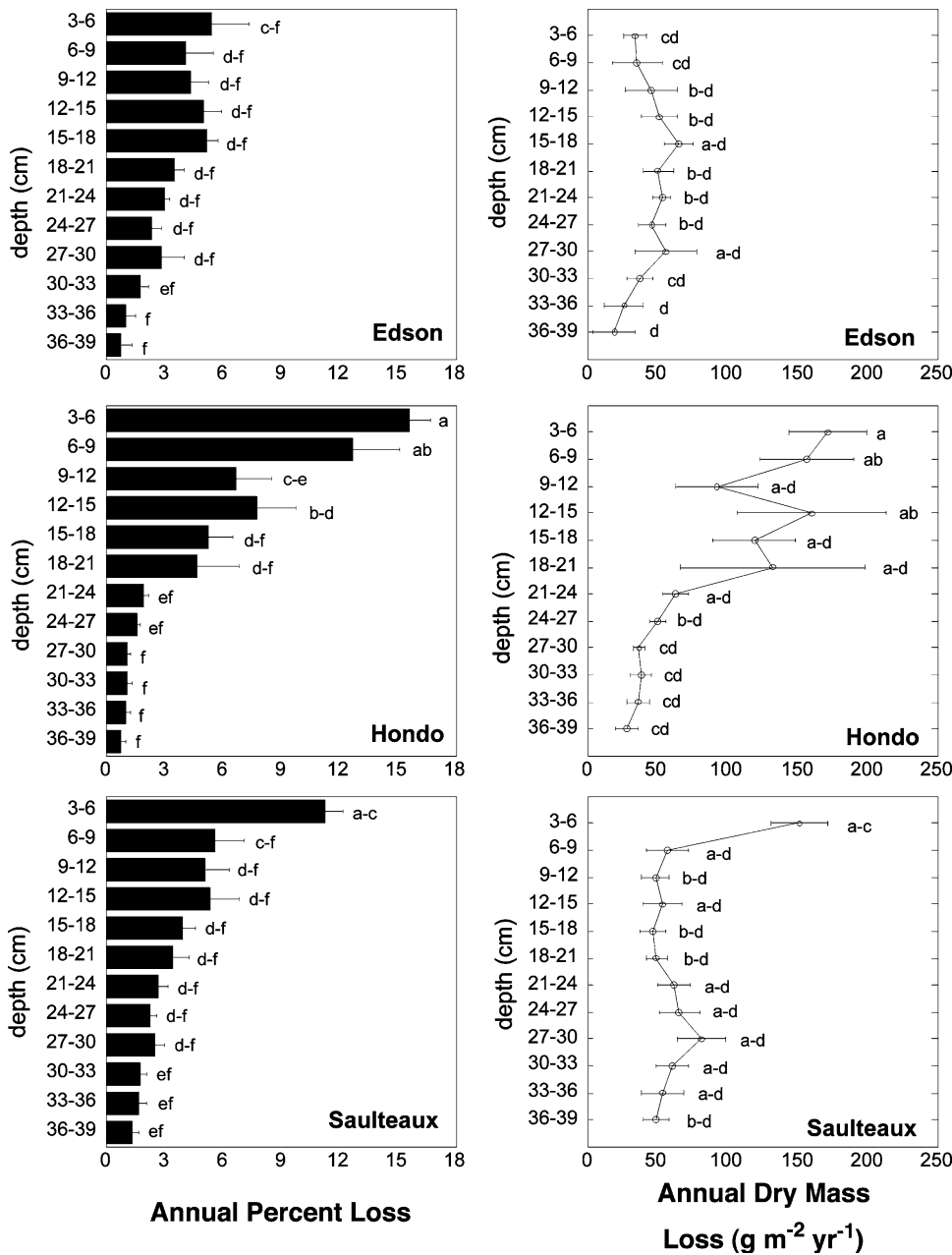
Figure 4. Dry matter mass loss profiles for the upper peat columns of the three rich fens. Bars (*left*) are annual % loss; lines and circles (*right*) are actual annual mass loss in g m². Nonsignificant differences for depth increments are shown by same letters beside the bars and in parentheses for the sites as determined by post hoc comparison of means. Lines are S.E.M.

decrease with depth, although there are no depth differences within a site below 15 cm and no site differences at depths below 9 cm (Figure 4). A somewhat different pattern emerges when decomposition losses are calculated on a kg m^{-2} basis with differences with depth within a site evident at Hondo, but not at Edson or Saulteaux.

Root Production

Root production (kg m^{-2} y^{-1} at each 3-cm depth interval) did not differ between sites ($P = 0.0685$) or with depth ($P = 0.9765$) (site by depth interaction not significant, $P = 0.4803$), averaging 11.7 $\pm$ 1.5 g m^{-2} y^{-1}. Similarly, total root production integrated over the 3–39 cm peat profile was not significantly different between the three rich fen sites ($P = 0.0685$), averaging 0.14 $\pm$ 0.5 kg m^{-2} y^{-1} (Table 1). Roots were variously produced throughout the top 39 cm of peat (Figure 5).

Organic Matter Accumulation and Loss in Rich Fens

Age–depth relationships (Figure 6) allow the determination of vertical peat accumulation. Over the past 25 years, net vertical peat accumulation
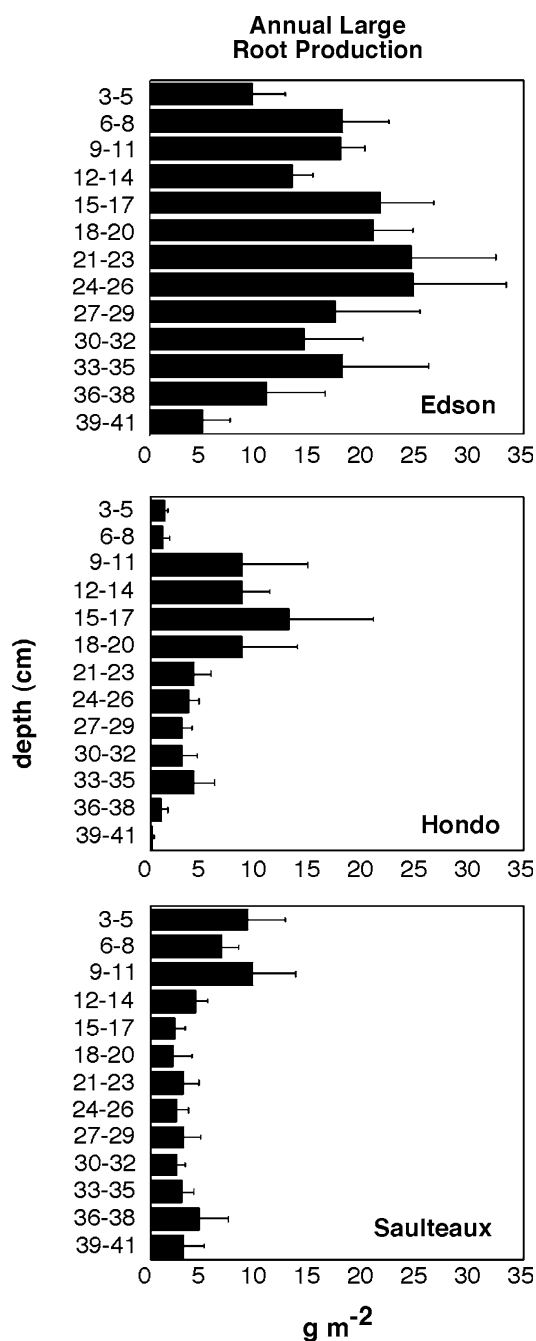
Annual Large Root Production

Figure 5. Large root production (>1 mm diameter) for the upper 41 cm profiles of the three rich fens. Bars are means of 3-cm thick slices from five decomposition socks for each site. Lines are S.E.M.

rates have varied from about 12 to 25 cm, whereas over the past 50 years they have varied from 16 to nearly 33 cm. Net vertical accumulation rates are significantly higher at Edson than at either Hondo or Saulteaux (Figure 7A).

Utilizing relationships of depth to age along with ash-free bulk density profiles, rates of net organic matter accumulation were quantified over 25- and
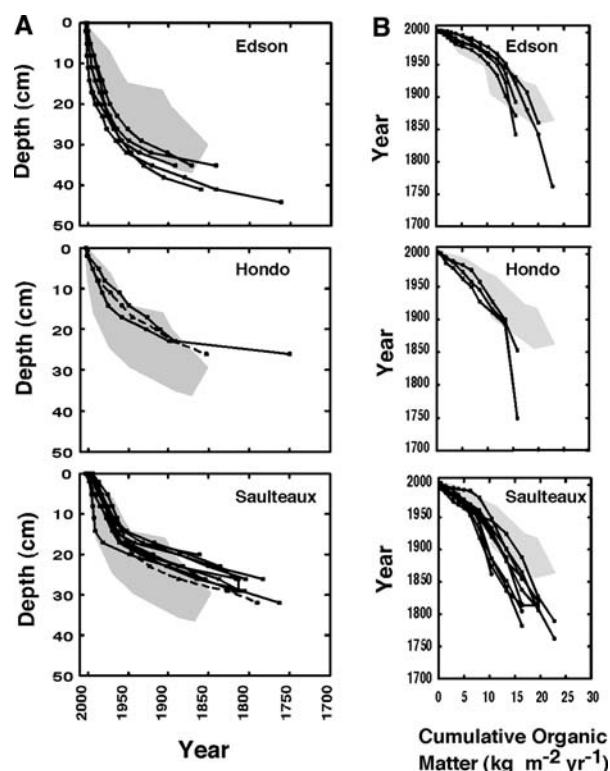

Figure 6. A Depth age relationships and **B** Cumulative organic matter accumulation rates for the most recent 300 years (*left*) and 300 years (*right*) as determined by $^{Pb}210$ dating of peat cores from the three rich fens. Lines are S.E.M. Shaded areas show range of variation in accumulation for bogs as given in Turetsky and others (2007).

50-years horizons (Figure 6). Over the 25-year horizon, the three rich fens have accumulated between 4.3 and 7.6 kg m^{-2}; over the past 50 years accumulation has been 7.7 and 6.8 kg m^{-2} at Hondo and Saulteaux, respectively, versus 12.6 kg m^{-2} at Edson (Figure 7B). Across the three rich fens, organic matter accumulation over the most recent 25 years has averaged 208 g m^{-2} y^{-1} and over the past 50 years it has averaged 174 g m^{-2} y^{-1}.

Estimating Decompositional Losses Over the Past 50 Years

Our ^{210}Pb dating allows us to predict both vertical peat accumulation and net accumulation of organic matter over the past 50 years (Figure 7). Extrapolating the 50-year vertical accumulation values (32, 16, and 18 cm for Edson, Hondo, and Saulteaux, respectively) on to the mass loss profiles (Figure 4) provides us with a mechanism to estimate annual dry mass losses for the three fens and compare these values to net organic matter accumulation. For Edson, over the past 50 years, decomposition
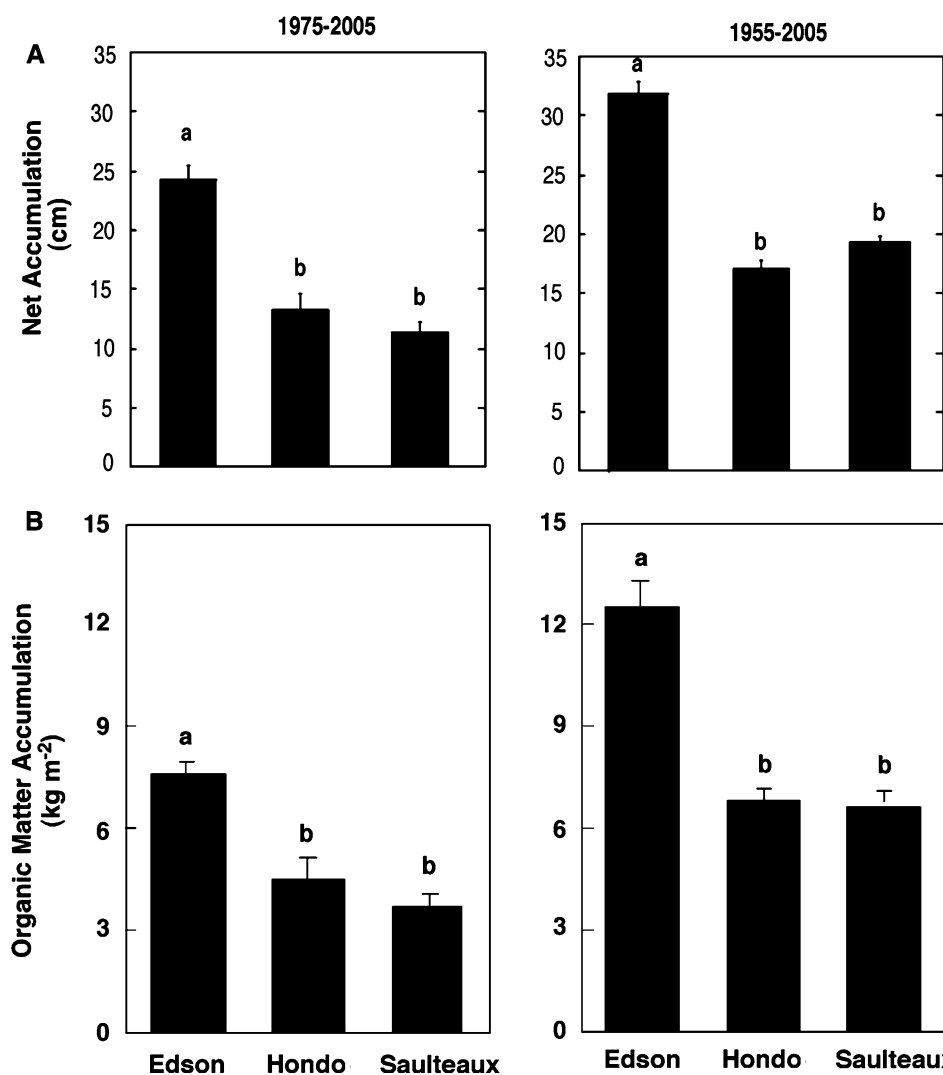
Figure 7. **A** Net vertical accumulation rates and **B** Cumulative organic matter accumulation rates over the past 30 (*left*) and 50 year (*right*) intervals for the three rich fens. Nonsignificant differences are shown by same letters as determined by post hoc comparison of means. Lines are S.E.M.

losses are estimated to total 25.7 kg m^{-2} compared to an accumulation of 12.7 kg m^{-2} (dry mass accumulation of 13.4 kg m^{-2}; ash concentration of Edson peat averages 5.2% of dry mass). For Hondo losses are 32.9 kg m^{-2} compared to an accumulation of about 6.5 kg m^{-2} (dry mass accumulation of 7.1 kg m^{-2}; ash concentration of Hondo peat averages 8.5% of dry mass), and for Saulteaux losses are 20.4 kg m^{-2} compared to about 6.3 kg m^{-2} accumulation (dry mass accumulation of 7.6 kg m^{-2}; ash concentration of Saulteaux peat averages 16.6% of dry mass). Over the past 50 years, Edson, Hondo, and Saulteaux have annual dry mass losses of 515, 658, and 408 g m^{-2} y^{-1}, respectively, and 268, 142, and 152 g m^2 of dry matter accumulation, respectively. There are also additional decomposition losses within the upper 39 cm of the peat profile, from peat older than 50 years that occurs within the peat lower then 32, 16, and 18 cm depths in each of these sites, and for Hondo and Saulteaux, in particular, these are substantial. Dry mass losses from peat older than 50 years range from 92 g m^{-2} y^{-1} for Edson to 423 and 403 g m^{-2} y^{-1} for Hondo and Saulteaux.

DISCUSSION

Rich fens of boreal Canada are abundant and accumulate peat to depths equal or greater than *Sphagnum*-dominated poor fens and bogs (Vitt and others 2005). Rich fens across the western boreal region of Canada are highly variable in chemistry, structure, and flora.

Structurally, the three fens span a vegetation gradient from open (Saulteaux) without hummocks, to shrubby (Hondo) with only poorly developed hummock-hollow topography, to sparsely wooded (Edson) with well-developed hummock-hollow topography. The ground layer is well developed at both Saulteaux and Edson, but less so

at Hondo, and Edson has *Sphagnum* present in some abundance. Despite these structural differences, based on water chemistry and flora, all three sites are characterized as moderate rich fens (compare Vitt and Chee 1990). Our three fens represent a cross-section of moderate-rich fen variability found in western continental Canada with Edson the most acidic and Saulteaux the most basic.

The Upper Peat Profile of Rich Fens

As decomposition takes place in fens, intact plant material is broken down into smaller parts until the individual plant parts are no longer recognizable and debris results. In our rich fens, this debris from moss plants, vascular plant roots, and aboveground litter increased to between 40 and 60% within the upper 41 cm of the peat profile. Whereas moss input to accumulating peat occurs only at the surface, vascular plant input is derived both from the surface (litter) and from root production within the profile. Root production is evident along the entire upper peat profile (Figure 5). Death and subsequent decomposition of roots contributes a substantial root/litter component of the peat within the profile (Figure 3).

Ash-free bulk densities generally increased with depth (Figure 3). Across the three sites, ash-free bulk density was strongly positively correlated with debris percentage ($r = 0.82$, $P < 0.0001$, $n = 377$), negatively correlated with moss percentage ($r = -0.60$, $P < 0.0001$, $n = 375$), and not correlated with root/litter percentage ($r = -0.01$, $P = 0.8635$, $n = 375$). Ash-free bulk density seems to provide a reasonable proxy of the extent of decomposition within the peat profile.

Overall, the three fens differ significantly in the total dry masses of the peat in the 3–39 cm profile (from 19 (Edson) to 26 (Saulteaux) to 31 kg m^{-2} (Hondo)). How can this be? The Edson fen begins with relatively light peat (1.4 kg m^{-2}) at the surface (3–9 cm) with a relatively slow decomposition rate (4.6% y^{-1} compared to 5.8–8.8% y^{-1} for the other two fens—Table 1). The relatively slow decomposition rate at Edson may be related to the greater proportional input of moss (especially *Sphagnum*) at this site. Comparatively, Saulteaux has greater mass to begin and loses more to decomposition, resulting in denser peat and a heavier overall profile mass. The result is that Edson has a net organic matter accumulation rate that is nearly twice that of Saulteaux (Figure 7). Although the Hondo profile begins with dense largely moss-free peat near the surface (3–9 cm) decomposition proceeds relatively rapidly (5.0% y^{-1}

throughout the profile), which may be attributable in part to more oxic, warmer water with elevated NO_3^- concentrations (Figure 2). The result is a relatively dense peat throughout the profile.

Mass Losses and Organic Matter Accumulation in Rich Fen Upper Peat Columns

In evaluating mass losses throughout the upper column using original in situ material, our three fens show strikingly different decomposition profiles and accumulation patterns. Net organic accumulation varies from 126 (Saulteaux) to 130 (Hondo) to 254 g m^{-2} y^{-1} (Edson) (152, 142, and 268 g dry mass m^{-2} y^{-1}, respectively) over the past 50 years. Decomposition dry mass losses over that same time period vary from 408 (Saulteaux) to 515 (Edson) to 659 g m^{-2} y^{-1} (Hondo). For the upper 50 year portion of the peat to be neither accumulating nor losing peat, dry mass inputs via NPP must equal the sum of net accumulation and decomposition, that is, NPP must be 560 (Saulteaux), 783 (Edson), and 800 g m^{-2} y^{-1} (Hondo). Additionally the upper 39 cm of the peat profiles are very different in ages ranging from 150 to over 300 years in age (Figure 7). The result is that in the older profiles, considerable decomposition losses continue to occur beyond 50 years (Figure 4). These additional losses are again variable ranging from 92 (Edson) to 403 (Saulteaux) to 423 g dry mass m^{-2} y^{-1} (Hondo). When these decompositional losses in the upper 39 cm of the peat profile that are older than 50 years are included, the NPP inputs required for these fens to be neither accumulating nor losing peat range from 875 (Edson) to 963 (Saulteaux) to 1,229 g dry mass m^{-2} y^{-1} (Hondo).

We did not measure NPP at these three rich fen sites. However, as reviewed in the introduction, it seems reasonable that total rich fen production may be in the range of 950–1,050 g m^{-2} y^{-1}. Using this NPP range, two of our fens, Edson and Saulteaux, would appear to be accumulating dry mass, and hence carbon. The peat accumulation status of the Hondo fen, however, is tenuous. Comparatively large decomposition losses in the upper profile of the Hondo fen, reflected in only 16 cm of vertical accumulation over 50 years, along with large decomposition losses in peat older than 50 years, have produced a relatively dense peat column. We note that at Hondo, our decomposition socks were placed about 50 m downslope from a gravel road that transects the fen. Although a culvert channels horizontal water flow under the road, a noticeably higher water table upslope of the

road suggests some impedance of water flow. It may be that this recent lowering of the water table at the Hondo fen site has enhanced decomposition, compromising ecosystem performance with respect to the carbon sink function.

Comparisons to Bogs

During the most recent 25-years, vertical organic matter accumulation in our three rich fens varied between 11 and 24 cm comparing well to the mean value of 16 cm for continental bogs given by Turetsky and others (2007). Likewise, net organic matter accumulation for the three rich fens over the past 25 years of 3.5–7.6 kg m^{-2} (140–304 g dry mass m^{-2} y^{-1}) bracketed the 6.3–7.3 kg m^{-2} organic matter accumulation values for continental bogs given by Turetsky and others (2007). On an annual basis and over a 25-year interval Turetsky and others (2007) reported that continental bogs accumulate 270 g m^{-2} y^{-1} compared to an average of 208 g m^{-2} y^{-1} in our rich fens. For 23 bogs in eastern Canada, Turunen and others (2004) reported carbon accumulation rates of 77–178 g m^{-2} y^{-1} (assuming organic matter is 47% C, 164–379 g organic matter m^{-2} y^{-1}). Recent rates of organic matter, or carbon, accumulation are similar in bogs and our rich fens.

The processes that lead to peat accumulation, however, differ between bogs and rich fens. Ombrotrophic bogs are dominated by *Sphagnum* mosses, and the dominant peat former, *S. fuscum*, is exceptionally resistant to decay (Turetsky and others 2008). Most of the decomposition in bog peat profiles occurs within the upper 10-cm or so; decomposition rates decrease markedly with increasing depth even before peat enters the catotelm (Clymo and others 1998; Wieder 2001). In contrast, rich fens have higher NPP with substantial aboveground and belowground contributions from vascular plants, and our results show that decomposition is considerable throughout the upper 39 cm of the peat column that may include peat that is 150–300 years old. Although both bogs and rich fens have accumulated substantial peat and carbon, historically, bogs have much slower organic matter turnover rates (proportion of NPP that ends up as stored peat) than bogs.

SUMMARY AND CONCLUSIONS

Rich fens in Canada's western boreal forest have accumulated large stores of peat over the past millennia. This carbon storage has occurred despite these systems not being highly acidic, not being dominated by *Sphagnum*, and not being particularly nutrient rich. These rich fens are highly variable in structure—from open sedge-dominated systems to shrubby and wooded sites. They all have water at or near the peat surface yet the upper water columns appear to have low amounts of O_2 present—thus they do not appear to have upper peat profiles that are strictly anaerobic. The surface material (largely true mosses) that has contributed to the decomposing peat column in rich fens has a relatively high density when compared to *Sphagnum*-derived peat in bogs and poor fens. Relatively large inputs of roots within the peat column also contribute high quality material to the decomposing peat column in rich fens. Peat bulk densities increase about three times within the uppermost 40 cm, much more so than in bogs and poor fens. Thus, initially dense surface inputs and additional high quality internal inputs all lead to exceptionally dense peat at 40 cm depth. As a result, rich fens accumulate peat not because the plant material is especially hard to decompose, is acidic, or the catotelm is especially close to the surface; but because dense and rapidly produced inputs outweigh the relatively rapid decomposition processes of the upper peat column.

REFERENCES

APHA. 2006. Standard methods for the analysis of water and wastewater, 4500-P phosphorus, American Public Health Association.

Appleby PG, Oldfield FR. 1978. The calculation of ^{210}Pb dates assuming a constant rate of supply of unsupported ^{210}Pb to the sediment. Catena (Supplement) 5:1–8.

Bartsch I, Moore TR. 1985. Preliminary investigation of primary production and decomposition in four peatlands near Schefferville, Quebec. Can J Bot 63:1241–8.

Bauer I, Gignac LD, Vitt DH. 2003. Development of a peatland complex in boreal western Canada: lateral site expansion and local variability in vegetation succession and long-term peat accumulation. Can J Bot 81:833–47.

Belyea LR. 1996. Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland. Oikos 77:529–39.

Belyea LR, Warner BG. 1996. Temporal scale and the accumulation of peat in a *Sphagnum* bog. Can J Bot 74:366–77.

Brenner M, Schelske CL, Kenney WF. 2004. Inputs of dissolved and particulate ^{226}Ra to lakes and implications for ^{210}Pb dating recent sediments. J Paleolimnol 32:53–66.

Campbell C, Vitt DH, Halsey LA, Campbell ID, Thormann MN, Bayley SE. 2000. Net primary production and standing biomass in northern continental wetlands. Northern Forestry Centre Information Report NOR-X-369. Ottawa, ON: Canadian Forest Service. 57 p.

Chee W-L, Vitt DH. 1989. The vegetation, surface water chemistry, and peat chemistry of moderate-rich fens in central Alberta, Canada. Wetlands 9:227–62.

Clymo RS. 1965. Experiments on the breakdown of *Sphagnum* in two bogs. J Ecol 53:747–58.

Clymo RS. 1984. The limits to peat growth. Philos Trans R Soc Lond B 303:605–54.

Clymo RS, Turunen J, Tolonen K. 1998. Carbon accumulation in peatland. Oikos 81:368–88.

Conlin TS, Lieffers VJ. 1993. Seasonal growth of black spruce and tamarack roots in an Alberta peatland. Can J Bot 71:359–36.

DuReitz GE. 1949. Huvidenheter och huvidgranser i Svensk myrvegetation. Summary: main units and main limits in Swedish mire vegetation. Sven Bot Tidskr 43:274–309.

Finér L, Laine J. 1998. Root dynamics at drained peatland sites of different fertility in southern Finland. Plant Soil 201:27–36.

Ivanov KE. 1957. Osnovy gidrologii bolot lesnoi zony. St Petersburg: Gidrometizdat.

Johnson LC, Damman AWH. 1991. Species controlled *Sphagnum* decay on a south Swedish raised bog. Oikos 61:234–42.

Moore TR, Basiliko N. 2006. Decomposition in boreal peatlands. In: Wieder RK, Vitt DH, Eds. Boreal peatland ecosystems. Berlin/Heidelburg/New York: Springer. p 125–43.

Rochefort L, Vitt DH, Bayley SE. 1990. Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. Ecology 71:1986–2000.

Saarinen T. 1996. Biomass and production of two vascular plants in a boreal mesotrophic fen. Can J Bot 74:934–8.

SAS. 2003. SAS, Version 9.1. Cary, NC: SAS Institute.

Sjörs H. 1950. Regional studies in north Swedish mire vegetation. Bot Notiser 1950:174–221.

Sjörs H. 1952. On the relation between vegetation and electrolytes in north Swedish mire waters. Oikos 2:242–58.

Slack NG, Vitt DH, Horton DG. 1980. Vegetation gradients of minerotrophically rich fens in western Alberta. Can J Bot 58:330–50.

Thormann MN, Bayley SE. 1997. Above ground net primary production along a bog-fen-marsh gradient in southern boreal Alberta, Canada. Écoscience 4:374–84.

Turetsky MR. 2003. Bryophytes in carbon and nitrogen cycling. Invited essay for New Frontiers in Bryology and Lichenology. Bryologist 106:395–409.

Turetsky MR, Manning S, Wieder RK. 2004. Dating recent peat deposits. Wetlands 24:324–56.

Turetsky MR, Wieder RK, Vitt DH, Evans RJ, Scott KD. 2007. The disappearance of relict permafrost in boreal North America: effects on peatland carbon storage and fluxes. Global Change Biol 13:1922–34.

Turetsky MR, Crow S, Evans RJ, Vitt DH, Wieder RK. 2008. Tradeoffs in resource allocation among moss species control decomposition in boreal peatlands. J Ecol 96:1297–305.

Turunen J, Roulet NT, Moore TR, Richard JPH. 2004. Nitrogen deposition and increased carbon accumulation in ombrotrophic peatlands in eastern Canada. Global Biogeochem Cycles 18: GB3002. doi: 10.1029/2003GB002154.

Vitt DH. 1990. Growth and production dynamics of boreal mosses over climatic, chemical and topographic gradients. Bot J Linn Soc 104:35–59.

Vitt DH. 2006. Functional characteristics and indicators of boreal peatlands. In: Wieder RK, Vitt DH, Eds. Boreal peatland ecosystems. Berlin/Heidelburg/New York: Springer. p 9–24.

Vitt DH, Chee W-L. 1990. The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. Vegetatio 89:87–106.

Vitt DH, Wieder RK. 2008. The structure and function of bryophyte-dominated peatlands. In: Shaw JA, Goffinet B, Eds. Bryophyte biology. 2nd edition. Cambridge: Cambridge University Press. p 357–92.

Vitt DH, Bayley SE, Jin T-L. 1995. Seasonal variation in water chemistry over a bog-rich fen gradient in continental western Canada. Can J Fish Aquat Sci 52:587–606.

Vitt DH, Halsey LA, Thormann MN, Martin T. 1996. Peatland Inventory of Alberta. Edmonton, AB: Alberta Peat Task Force, University of Alberta.

Vitt DH, Halsey L, Thormann MN. 1997. The Wetlands of Alberta: A 1:1,000,000 summary map. 2nd edition with revisions. Edmonton, AB: Alberta Environmental Protection Agency.

Vitt DH, Halsey LA, Bauer IE, Campbell C. 2000. Spatial and temporal trends of carbon sequestration in peatlands of continental western Canada through the Holocene. Can J Earth Sci 37:683–93.

Vitt DH, Halsey LA, Campbell C, Bayley SE, Thormann MN. 2001. Spatial patterning of net primary production in wetlands of continental western Canada. Écoscience 8:499–505.

Vitt DH, Halsey LA, Nicholson BJ. 2005. The Mackenzie River basin wetland complex. In: Fraser LH, Keddy PA, Eds. The World's largest wetlands: their ecology and conservation. Cambridge: Cambridge University Press. p 218–54.

Walbridge MR, Navaratnam JA. 2006. Phosphorus in boreal peatlands. In: Wieder RK, Vitt DH, Eds. Boreal peatland ecosystems. Berlin: Springer. p 231–58.

Wieder RK. 2001. Past, present, and future peatland carbon balance: an empirical model based on ^{210}Pb-dated cores. Ecol Appl 11:327–42.

Wieder RK, Novak M, Schell WR, Rhodes T. 1994. Rates of peat accumulation over the past 200 years in five *Sphagnum* dominated peatlands in the United States. J Paleolimnol 12:35–47.

Wieder RK, Vitt DH, Benscoter B. 2006. Peatlands and the boreal forest. In: Wieder RK, Vitt DH, Eds. Boreal peatland ecosystems. Berlin/Heidelberg/New York: Springer. p 1–8.

Zoltai SC, Johnson JD. 1987. Relationships between nutrients and vegetation in peatlands of the Prairie Provinces. In: Rubec CDA, Overend RP (compilers) Proceedings, Symposium 1987: Wetlands/Peatlands. Edmonton, AB, 23–27 August 1987. p 535–42.