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Organic matter accumulation, peat chemistry, and permafrost melting in peatlands of boreal Alberta[1]

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Abstract: In the discontinuous permafrost zone of boreal western continental Canada, permafrost is limited almost exclusively to ombrotrophic peatlands. Permafrost in peatlands recently has been degrading and continues to degrade at its southern limit across western Canada, with no evidence of regeneration. The melting of permafrost could have dramatic effects on organic matter accumulation, organochemical properties, and nutrient status in peatlands. Our objectives are to quantify differences in peat chemistry (*i.e.*, concentrations of organic fractions, N, P, and S) and rates of organic matter accumulation over the past 200 years between a site with permafrost, a site with degraded permafrost (internal lawn), and three sites with no evidence of permafrost since the last glaciation (continental peatlands: two bogs and one poor fen). Results indicate that peat chemistry may differ according to the presence, absence, or degradation of permafrost. Recent rates of organic matter accumulation follow similar trends over the past 100-200 years in the permafrost and continental bogs; however, net rates of organic matter accumulation are accelerated by 60% in the internal lawn. As decomposition in peatlands is influenced by nutrient limitations and organic matter quality, peat chemistry is likely to be a critical factor in the carbon balance response of boreal peatlands to climate change.
Keywords: peatlands, permafrost, discontinuous permafrost zone, carbon, global climate change, nutrients, carbon quality, ^{210}Pb-dating, boreal forest, Alberta.

Résumé : Dans la zone de pergélisol discontinu de la partie boréale de l'Ouest canadien, le pergélisol se trouve exclusivement dans les tourbières ombrotrophes. À la limite sud de cette zone, le sol des tourbières dégèle depuis plusieurs années. Le dégel du pergélisol pourrait avoir des conséquences sérieuses sur l'accumulation de matière organique dans les tourbières et sur les propriétés organochimiques et les éléments nutritifs des sols. Les objectifs de ce travail sont de comparer l'évolution, au cours des 200 dernières années, de la chimie de la tourbe (c'est-à-dire de la concentration des fractions organiques et celle de l'azote, du phosphore et du soufre) et des taux d'accumulation de matière organique de plusieurs tourbières : une tourbière avec pergélisol, une tourbière avec pergélisol en voie de dégradation et trois tourbières où il n'y a aucune preuve de la présence de pergélisol depuis la dernière époque glaciaire (deux tourbières ombrotrophes et une tourbière minérotrophe). Les résultats indiquent que la chimie de la tourbe diffère selon la présence ou l'absence de pergélisol, ou selon que ce dernier est en voie de dégradation. Les taux récents d'accumulation de matière organique des tourbières continentales à pergélisol sont similaires à ceux des 100-200 dernières années. Toutefois, les taux nets d'accumulation de matière organique sont 60 % plus rapides dans le site de pelouse. Puisque le taux de décomposition dans les tourbières est influencé par la faible quantité d'éléments nutritifs et par la qualité de la matière organique, la chimie de la tourbe est probablement un facteur déterminant qui influence le bilan du carbone dans les tourbières boréales surtout dans un contexte de changements climatiques.
Mots-clés : tourbières, pergélisol, zone de pergélisol discontinu, carbone, changement climatique planétaire, nutriments, qualité du carbone, datation au ^{210}Pb, forêt boréale, Alberta.

Introduction

Peatlands are a key component of Canada's landscape, occupying approximately 21% of the total landbase of Alberta, Manitoba, and Saskatchewan (Vitt *et al.*, in press). Near its southern limit in boreal western continental Canada, permafrost (*i.e.*, earth materials having a temperature below 0°C for two or more years) is restricted mostly to ombrotrophic peatlands (Thie, 1974; Vitt, Halsey & Zoltai, 1994; Halsey, Vitt & Zoltai, 1995). Permafrost landforms existing south of the 0°C isotherm represent relict features of the Little Ice Age that have been preserved by insulating peat (Thie, 1974; Gavrilova, 1993; Halsey, Vitt & Zoltai, 1995).

Permafrost aggradation and degradation lead to major changes in the hydrology, insolation, and topography of a landscape, and therefore have the potential to affect biological and chemical processes in peatlands. The soil surface of permafrost landforms is elevated above that of the surrounding soil surface (Zoltai, 1972; 1993; Vitt, Halsey & Zoltai, 1994; Williams & Burn, 1996), as permafrost formation causes volume expansion of freezing soil water. Species thriving well above the water table dominate permafrost systems, including *Cladina* spp., *Hylocomium splendens*, *Picea mariana*, *Pleurozium schreberi*, and *Sphagnum fuscum* (Zoltai, 1993; Bubier *et al.*, 1995). Although mosses cover much of the soil surface on permafrost features, the underlying peat is sylvic in nature with much of the organic matter input appearing to come from *P. mariana* needle litter and fine root production. Permafrost features typically have a thick fine root mat at the top of the peat (pers. observ.). Permafrost degradation, resulting in nearly circular or oval-shaped thermokarst pools, causes the soil surface to subside and creates wet, fen-like depressions

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that are suitable for wet-adapted *Sphagnum* and/or *Carex* species (Zoltai, 1993; Vitt, Halsey & Zoltai, 1994). Such depressions in the southern portions of the discontinuous permafrost zone are typically surrounded by nonpermafrost (*i.e.*, continental) peatlands as the dominant landscape feature and are called internal lawns (Vitt, Halsey & Zoltai, 1994). Surface peat in internal lawns clearly is *Sphagnum*-derived. At some depth, transition to the sylvic peat that characterized the former permafrost feature always is present. Further north in the discontinuous permafrost zone, nearly circular, wet features known as collapse scars are surrounded by larger matrices of permafrost (Zoltai, 1993; Vitt, Halsey & Zoltai, 1994; Halsey, Vitt & Zoltai, 1995). It is unclear, however, whether collapse scars necessarily represent areas in which permafrost has degraded or alternatively, whether permafrost simply never accumulated in these areas.

Permafrost in peatlands recently has been degrading and continues to degrade at its southern limit across boreal western continental Canada, with no evidence of regeneration (Halsey, Vitt & Zoltai, 1995). Permafrost degradation could have dramatic effects on thermokarst development and hydraulic regimes, as well as carbon storage in peatlands (Gorham, 1991; Woo, Lewkowicz & Rouse, 1992; Koster, 1995; Camill & Clark, 1998).

Canada's discontinuous permafrost zone represents a region adjusting to recent and ongoing climate change, and is ideal for examining the influence of climate on peat accumulation, which is the manifestation of the balance between peatland CO_2 fixation and dissolved or gaseous C releases. Currently, peatlands function as a net sink for atmospheric CO_2, sequestering approximately 76 Tg yr^{-1} of C from the atmosphere, and contain about 1/3 of the world's soil C pool (Gorham, 1991). Because of the magnitude of C stored in peatlands globally, and given predictions that climatic warming will be most pronounced in northern latitudes (Raisanen, 1997; Moore, Roulet & Waddington, 1998), how peatland C cycling is controlled by climate has emerged as an important question (Gorham, 1994).

Previous studies in the discontinuous permafrost region of Canada have focused on direct measurements of C gas fluxes across the peatland/atmosphere interface (Bubier *et al.*, 1995; Liblik *et al.*, 1997; Bellisario & Moore, 1998; Waddington, Griffis & Rouse, 1998; Bubier *et al.*, 1999; Trumbore *et al.*, 1999). There is little information, however, on the chemical nature of recently accumulated peat in sites underlain by permafrost or in sites where permafrost has degraded. Decomposition of peat, which drives C gas fluxes, is likely to respond not only to abiotic climate variables, but also to various aspects of organic matter quality and nutrient availability (Yavitt & Lang, 1990; Updegraff *et al.*, 1995; Yavitt, Williams & Wieder, 1997).

We selected five peatland sites as representative examples of the various peatland features common to the landscape at the southern limit of permafrost in western continental Canada. This includes a bog underlain with permafrost (permafrost bog), a bog in which permafrost has degraded (internal lawn), and three continental peatlands (two bogs and one poor fen) in which there is no discernible evidence of permafrost over the past few thousand years. We address the following question: how do sites with permafrost present, absent, or degraded differ in organic matter chemistry, nutrient status, and rates of organic matter accumulation of near-surface peat?

Material and methods

SITE DESCRIPTIONS AND CORE COLLECTION

We collected cores from three peatlands in north-central Alberta: one permafrost bog (55° 59' N, 112° 32' W), one internal lawn (56° 00' N, 112° 32' W), and one continental bog (referred to as Sylvie's Bog; 56° 03' N, 112° 31' W; Figure 1). Ground cover in the permafrost bog is dominated by *Pleurozium schreberi,* while the canopy is closed and exclusively comprised of *Picea mariana*. The permafrost table in this site at the time of sampling was located at approximately 34 cm depth. The adjacent internal lawn is dominated by *Sphagnum angustifolium* and *S. riparium* as well as *Carex limosa, Ledum groenlandicum, Smilacina trifolia*, and *Vaccinium oxycoccos*. Live trees are sparse, whereas pitching, fallen, or buried *P. mariana* snags are abundant. Vegetation of Sylvie's Bog is characterized by *Chamaedaphne calyculata, Ledum groenlandicum, Rubus chamaemorus, Sphagnum angustifolium, S. fuscum, Vaccinium oxycoccus*, *V. vitis-idaea*, and intermittent live *P. mariana* (S. Mauser, pers. comm.). Cores also were collected from a bog and fen in the Bleak Lake peatland complex (54° 41' N, 113° 28' W) in central Alberta (Figure 1). Bleak Lake Bog is an ombro-trophic forested bog dominated by a nearly continuous *Sphagnum* moss ground layer of mostly *S. fuscum*, with a mixture of shrubs and trees, including *L. groenlandicum, V. oxycoccos, Smilacina trifolia, R. chamaemorus,* and scattered *P. mariana* (Vitt, Bayley & Jin, 1995). Bleak Lake Fen is a non-forested poor fen water track dominated by *Carex tenuiflora, Spha-gnum angustifolium,* and *S. teres* (Vitt, Bayley & Jin, 1995).

Two intact peat cores were collected from each site using 10-cm diameter, 40-cm long PVC cylinders with sharpened bottom edges. Peat within each core was minimally compacted (less than 5 cm). Cores were frozen and

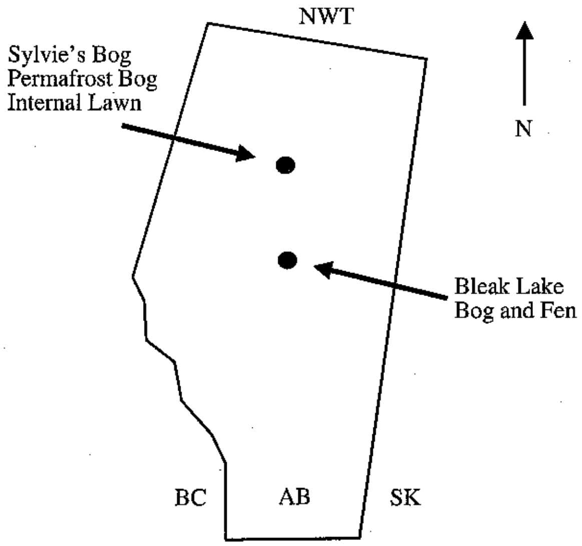

FIGURE 1. Map showing locations of field sites in northern Alberta, Canada.

sectioned into 2-cm depth intervals on a band saw. Individual 2-cm depth intervals of each peat core were dried and weighed for bulk density measurements prior to homogenization by grinding with a Tecator Cyclotec sample mill.

RATES OF PEAT ACCUMULATION

Rates of organic matter accumulation as peat were determined via ^{210}Pb dating of cores by acid digestion and application of the constant rate of supply model (Appleby & Oldfield, 1978). A 2-3 g subsample from each peat core section, along with 15 dpm (250 mBq) of ^{209}Po as a chemical yield tracer, was digested with concentrated HCl, concentrated HNO_3, and H_2O_2. The Pb and Po isotopes were passively plated onto silver disks for activity measurement on an EG&G ORTEC 576A alpha spectrometer (Wieder *et al.,* 1994). The method of ^{210}Pb-dating assumes that all of the ^{210}Pb deposited as particulate matter from the atmosphere is immobile within the peat substrate (Vile, Wieder & Novák, 1999; Turetsky & Wieder, in review). Numerous studies have concluded that Pb remains immobile after deposition onto a peat surface, through both direct investigation of Pb behaviour in peat and corroboration with other dating tools (Benninger, Lewis & Turekian, 1975; Livett, Lee & Tallis, 1979; El-Daoushy, Tolonen & Rosenberg, 1982; Clymo *et al.,* 1990; Cole *et al.,* 1990; Mitchell *et al.,* 1992; Belyea & Warner 1994a; Wieder *et al.,* 1994; Vile *et al.,* 1995; Appleby, Shotyk & Fankhauser, 1997; Farmer *et al.,* 1997; Shotyk *et al.,* 1997; Vile, Wieder & Novák, 1999). Others, however, have questioned the mobility of Pb in peat in interpreting vertical distributions of Pb in peat chronologies (Damman, 1978, Clymo & Hayward 1982, Pakarinen *et al.,* 1983, Pakarinen & Gorham, 1983; Urban *et al.,* 1990, Oldfield, Richardson & Appleby, 1995; Sanders, Jones & Hamilton-Taylor, 1995). ^{210}Pb concentrations in peat are expected to decrease exponentially with depth, approaching a low constant value taken to represent the supported ^{210}Pb fraction formed within soil as opposed to that deposited from the atmosphere (the unsupported ^{210}Pb fraction). This pattern was not observed in one internal lawn core and both Bleak Lake Fen cores; therefore, we were not able to construct ^{210}Pb-based chronologies for these cores.

NUTRIENT STATUS AND ORGANIC MATTER CHEMISTRY

Subsamples were analyzed for N and P by Kjeldahl digestion and colorimetric determination on a Technicon AutoAnalyzer II, and for S using a LECO SC-32 total S analyzer. Analysis of organic matter quality involved sequential extractions to separate the various organic fractions in bulk peat: soluble nonpolars (fats, oils, and waxes), hot-water-soluble carbohydrates, hot-water-soluble phenolics, total hot-water solubles, holocellulose, α-cellulose, hemicellulose, lignin, and acid-soluble carbohydrates, as well as ash concentration (Wieder & Starr, 1998). All organic fraction and nutrient concentration data are expressed on an ash-free, dry mass basis.

For each of the 16 measured and derived variables, we performed a one-way analysis of variance, using site (permafrost bog, internal lawn, Sylvie's Bog, Bleak Lake Bog, Bleak Lake Fen) as a main effect with *a posteriori* comparisons of site means using Duncan's Multiple Range Tests (SAS, 1990). In addition, we performed a canonical discriminant analysis to assess differences between peatland landform types (site) using all of the 16 measured and derived variables simultaneously (SAS, 1990).

Results

RATES OF PEAT ACCUMULATION

Depth-age relationships, established via ^{210}Pb-dating of peat, reveal differences between sites in net vertical accumulation of near surface peat over time. Bleak Lake Bog, Sylvie's Bog and the internal lawn all have accumulated approximately 26 cm of peat in the past 100 years (Table I; Figure 2). On the other hand, the permafrost bog has had substantially less vertical accumulation over time, accumulating only 12-13 cm of peat in the past 100 years.

By quantifying the dry mass and ash concentrations of each peat core depth interval and by knowing the bulk density of each depth interval as well as the age-depth relationships within each core, we were able to construct cumulative organic matter (ash-free mass) accumulation beneath a given peat surface area over time (Figure 3). Cores from Sylvie's Bog and Bleak Lake Bog exhibit similar accumulation of organic matter over the past 100 years (average of both cores 11.1 and 10.0 kg m^{-2} 100 yr^{-1}, respectively) (Table I, Figure 3). The two permafrost cores exhibit rather different patterns of organic matter accumulation over the last 50 years, with sharp discontinuities in the organic matter accumulation curves (Figure 3), such that individual 2-cm peat sections represent very minimal organic matter accumulation over time intervals of 50-100 years. For example, at a depth of 12 cm in both permafrost cores, a single 2-cm peat section represents approximately 109 years of accumulation. However, the permafrost site has accumulated 11.8 kg m^{-2} in the past 100 years (average of both cores), which is comparable to the rates measured for Sylvie's Bog and Bleak Lake Bog. Over the past 100 years, the internal lawn peat demonstrates a much higher rate of organic matter accumulation (18.4 kg m^{-2} 100 yr^{-1};Table I, Figure 3) compared to the permafrost or continental peatlands.

NUTRIENT STATUS AND ORGANIC MATTER CHEMISTRY

All of the 16 measured and derived variables exhibit significant site effects (Table II; $p \leq 0.002$). Sylvie's Bog peat has the lowest concentrations of P, the highest concentrations of soluble nonpolars and hemicellulose, as well as the highest mean C:N ratio (Table II). Bleak Lake Bog peat is similar to Sylvie's Bog peat for 8 of the 16 variables. However, peat from Bleak Lake Bog has greater concentrations of ash, N, P, and hot-water-solubles and lower concentrations of soluble nonpolars and hemicellulose, as well as lower C:N and lignin:N ratios compared to Sylvie's Bog. Permafrost bog peat has the highest bulk density, the highest concentrations of ash, S, and lignin, and the lowest concentrations of hot-water-soluble carbohydrates, α-cellulose, and hemicellulose. Internal lawn peat is characterized as having the highest lignin:N ratio, while Bleak Lake Fen peat has the highest N concentrations and the lowest lignin:N ratio.

TABLE I. Vertical height growth and net organic matter accumulation (ash-free, dry mass) in peatland sites over 50- and 100-year periods, based on ^{210}Pb-dated chronologies. Only chronologies dated with the CRS (constant rate of supply) model are included. When tabulated net values for vertical height accumulation and/or organic matter accumulation over the 50- and 100-year periods were not included within sources, quantities were estimated from presented graphical materials.

Site and Location	Site description (Microtopography at core collection)	Vertical height accumulation (cm		Organic matter (kg m^{-2}) accumulation)	
		50 years	100 years	50 years	100 years
NORTH AMERICAN SITES					
Permafrost Bog, northern Alberta (55° 59' N, 112° 32' W)[1]	Permafrost mound - core #1	7.1	12.4	5.8	13.4
	core #2	12.3	13.3	8.7	10.1
Sylvie's Bog, northern Alberta (56° 03' N, 112° 31' W)[1]	Bog (Lawn)- core #1	22	28	8.4	11.6
	core #2	18.6	23.2	6.9	10.7
Internal Lawn, northern Alberta (55° 60' N, 112° 32' W)[1]	Internal lawn (lawn)	19.1	26.1	11.5	18.4
Bleak Lake Bog, central Alberta[1]	Bog (Lawn) - core #1	22.2	28	9.1	11.2
	core #2	19	26.4	7.7	10.7
Rainy River Bog, northwest Ontario (48° 47'N, 94° 33' W)[2]	Bog (Hummock)	36.9			
	Bog (Hummock)	55.3			
	Bog (Hollow)	21.5			
	Bog (Hollow)	6.9	9.5		
Marcell S-2 Bog, Manitoba (47° 32 ' N, 93° 28' W)[3]	Bog (Hollows or lawns)	15.8	22.5	10.1	14.8
Tivoli South Bay Marsh, New York (42° 2' N, 73° 55' W)[4]	Marsh (Away from hummocks)	13.5	25		
Black Rock Forest Bog, New York (41° 23' N, 74° 02' W)[4]	Bog (Away from hummocks)	7	13		
Stockport Marsh, New York (42° 17' N, 73° 45' W)[4]	Marsh (Away from hummocks)	14.5	22		
Lefgrens Bog, New York (42° 19' N, 75° W)[4]	Bog (Away from hummocks)	12	17		
Spruce Flats Bog, Pennsylvania (40° 07' N, 79° 11' W)[4]	Bog (Away from hummocks)	16	23.5		
Spruce Flats Bog, Pennsylvania (40° 07' N, 79° 11' W)[5]	Bog (Hollow)	20.5	25.3	17.7	28.2
Manns Bog, Virginia (37° 19' N, 80° 30' W)[4]	Bog (Away from hummocks)	13	20		
Big Run Bog, West Virginia (39° 07' N, 79° 35' W)[3]	Bog (Hollows or lawns)	19.9	30.1	9	14
Tub Run Bog, West Virginia (39° 07' N, 79° 33' W)[3]	Bog (Hollows or lawns)	18.2	21.9	12.9	16.9
Cranseville Swamp, Maryland (39° 26' N, 79° 31' W)[3]	Swamp (Hollows or lawns)	12.1	22.2	9.5	17.9
Tamarack Swamp, Pennsylvania (41° 15' N, 75° 38' W)[3]	Swamp (Hollows or lawns)	9.8	15	9.5	15.4
Cowles Bog, Indiana[6]	Calcareous fen (*Sphagnum* mound)	8.1	20	11.9*	19.4*
EUROPEAN SITES					
Ellergower Moss, southwest Scotland (National Grid reference NX 482795)[7]	Bog (Hollow)	15	19.6		
Ringinglow Bog[8]	Bog (Hollow)	3.5	5.9		
Heathwaite Moss[8]	Bog (Hollow)	4.7	6.9		
Bloak Moss[8]	Bog (Hollow)	9	12		
Øverbygd, north Norway[9]	Bog (Hummock)	23.5	30.5		
Vindein, northcentral Sweden[9]	Bog (Hummock)	17	22.5		
Kårvatn, southcentral Norway[9]	Bog (Hummock)	12	20		
Aspvreten, south Sweden[9]	Bog (Hummock)	29.1	38.7		
Birkenes, south Norway[9]	Bog (Hummock)	14			
Rörvik, south Sweden[9]	Bog (Hummock)	22	25.5		
Etang de la Gruère, Jura region, Switzerland (47° 13' N, 7° 6' E)[10]	Bog (*Sphagnum* Lawn)	17.3	30.3		
La Tourbière des Genevez, Jura region, Switzerland (47° 13' N, 7° 6' E)[10]	Bog (*Sphagnum* Lawn)	23	36		
Praz Rodet, Switzerland (46° 46' N, 7° 14' E)[10]	Bog (*Sphagnum* Lawn)	24.6	44.1		
Kärpänsuo Bog, Kuhmoinen, Finland (61° 35' N, 25° 20' E)[11]	Bog (Hummock) *Sphagnum fuscum* core	26.7	41.5		
Kunonniemensuo Bog, Kitte, Finland (62° 05' N, 30° 10' E)[11]	Bog (Hummock) *Sphagnum fuscum* core	27.7	35.4		
Bozí Dar Bog, north Bohemia (50° 24'N, 12∞ 54' E)[12]	Bog	4.5	8.9		
Jezerní slať, south Bohemi (49° 03' N, 13° 36' E)[12]	Floating Bog	6	8.7		
Puscizna Rekowianska Bog, south Poland (49° 29' N, 19° 48' E)[13]	Bog	15.8	22.1		

*values not expressed on an ash-free basis

[1]this publication; [2]Belyea & Warner, 1994; [3]Wieder *et al.* 1994; [4]Schell, Tobin & Massey, 1989; [5]Schell, 1986; [6]Cole *et al.*, 1990; [7]Clymo *et al.*, 1990; [8]Oldfield, Richardson & Appleby, 1995; [9]Jensen, 1997; [10]Appleby, Shotyk & Fenkhauser, 1997; [11]El-Daoushy, Tolonen & Rosenberg, 1982; [12]Vile *et al.*, 1995; [13]Holynska *et al.*, 1998.

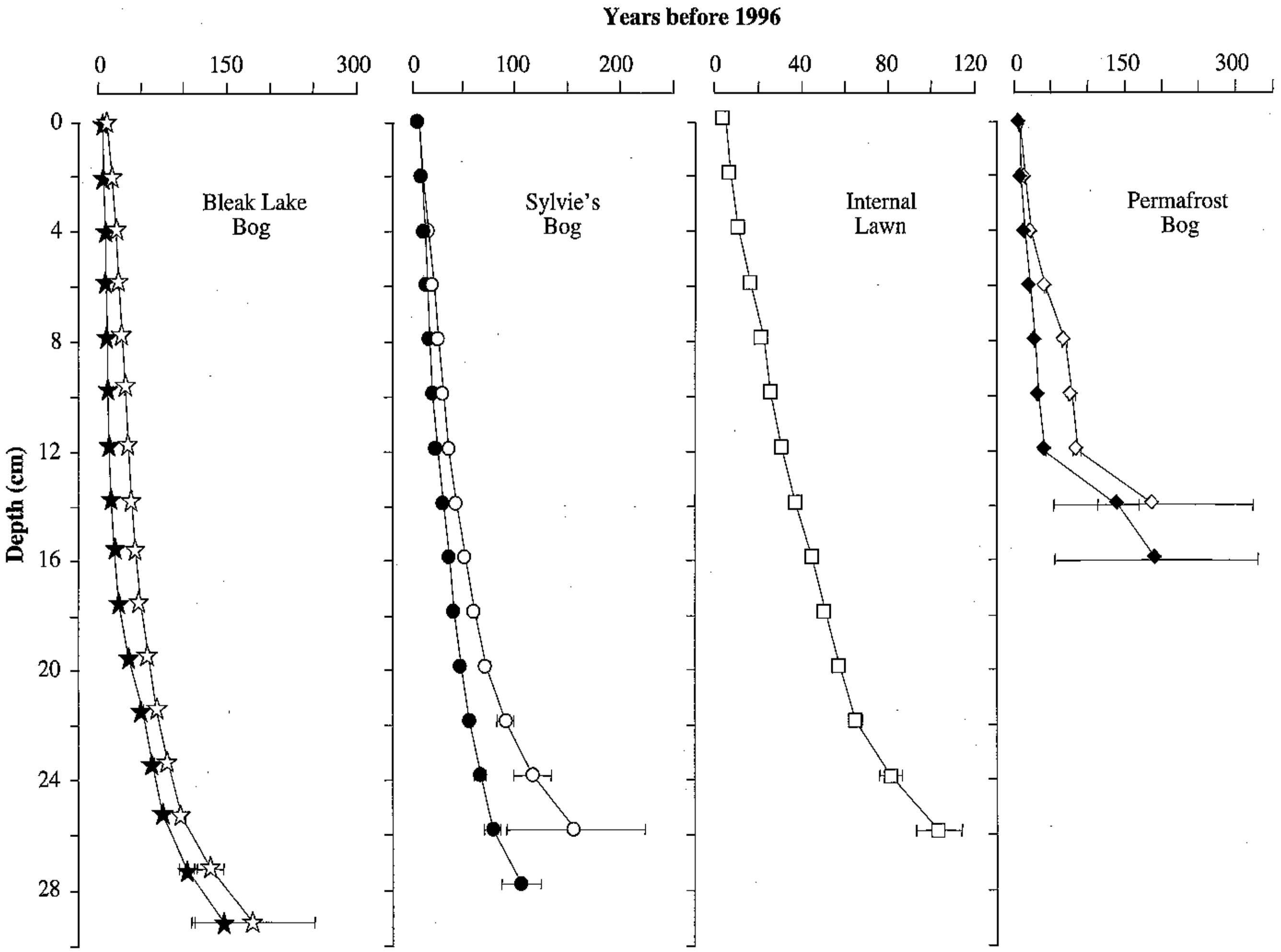

FIGURE 2. Peat age/depth depictions of the ^{210}Pb-based chronologies for duplicate cores from Bleak Lake Bog, Sylvie's Bog, and the permafrost bog, as well as one internal lawn core. Error bars represent counting errors (from α spectroscopy), propagated with increasing depth in a core.

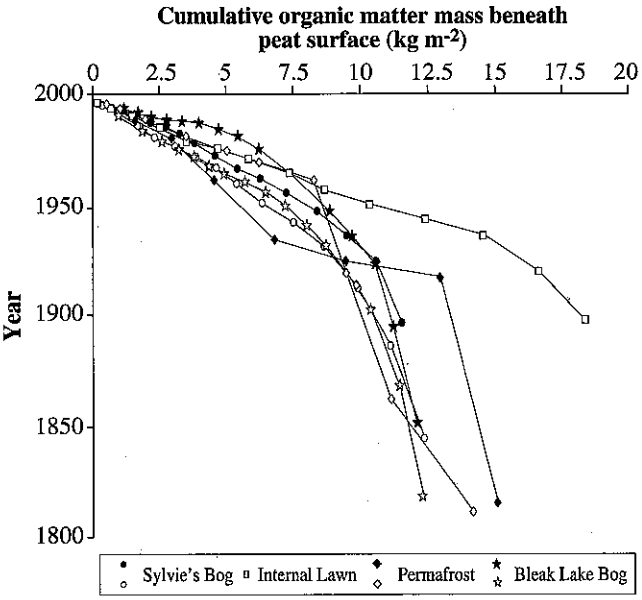

FIGURE 3. Cumulative organic matter mass beneath the peat surface (kg m^{-2}) *versus* year, for each of the seven dated cores. Each plotted point represents a single 2-cm section from an intact peat core.

Physical and chemical characteristics of peat may change with depth as a result of botanical composition, compaction and/or decomposition. N concentrations are fairly uniform with depth except in the Bleak Lake Bog and Bleak Lake Fen cores, where they increase with depth beginning at 12-14 cm, a pattern evident to a lesser extent for P concentrations as well (Figure 4). Permafrost peat exhibits an unusual depth profile for P concentrations, with high concentrations near the surface decreasing to fairly constant concentrations of 0.5-0.6 mg g^{-1} beneath 18 cm. The most striking pattern is for S concentrations in permafrost peat, which increase substantially in a nearly linear manner from the peat surface to the permafrost table (Figure 4).

Various organic matter fractions in peat will decompose both to differing degrees and at different rates. In all sites, changes in the concentrations of the recalcitrant organic matter fraction, lignin, and the more labile holocellulose fraction tend to be inversely correlated with depth; higher holocellulose concentrations are associated with lower proportions of lignin, and *vice versa* (Figure 5). Both lignin and holocellulose profiles remain fairly constant with depth in Sylvie's Bog, while profiles from Bleak Lake Fen

TABLE II. Means ± SE (averaged across all depths and two replicate cores) for 16 chemical variables for peat from five peatlands. Means with the same letter superscript do not differ significantly, $p < 0.002$.

Variable	Sylvie's bog	Permafrost bog	Internal lawn Means ± SE	Bleak Lake bog	Bleak Lake Fen
Bulk density (mg cm^{-3})	$47.2 \pm 3.1^{b,c}$	132.3 ± 9.1^{a}	59.2 ± 4.5^{b}	40.8 ± 1.8^{c}	57.7 ± 5.0^{b}
Ash (% of dry moss)	1.8 ± 0.1^{d}	7.5 ± 0.5^{a}	2.5 ± 0.2^{cd}	2.7 ± 0.1^{c}	3.9 ± 0.2^{b}
N (mg g^{-1} ash-free mass)	5.0 ± 0.2^{d}	10.5 ± 0.3^{b}	$6.1 \pm 0.3^{c,d}$	7.2 ± 0.4^{c}	13.2 ± 0.9^{a}
P (mg g^{-1} ash-free mass)	0.5 ± 0.0^{d}	1.0 ± 0.1^{a}	$0.8 \pm 0.1^{b,c}$	0.7 ± 0.0^{c}	$0.9 \pm 0.0^{a,b}$
S (mg g^{-1} ash-free mass)	0.8 ± 0.1^{b}	7.0 ± 0.8^{a}	1.0 ± 0.0^{b}	0.8 ± 0.0^{b}	1.4 ± 0.1^{b}
Soluble nonpolars (mg g^{-1} ash-free mass)	90.0 ± 1.9^{a}	$63.5 \pm 3.2^{c,d}$	73.9 ± 2.7^{b}	$68.5 \pm 2.7^{b,c}$	58.1 ± 2.8^{d}
Hot-water-soluble carbohydrates (mg g^{-1} ash-free mass)	52.8 ± 2.4^{a}	27.0 ± 2.9^{c}	41.5 ± 1.8^{b}	$47.5 \pm 1.3^{a,b}$	45.9 ± 1.8^{b}
Hot-water soluble phenolics (mg g^{-1} ash-free mass)	5.5 ± 0.3^{b}	$6.5 \pm 0.5^{a,b}$	7.3 ± 0.4^{a}	6.0 ± 0.7^{b}	5.7 ± 0.2^{b}
Total hot-water solubles (mg g^{-1} ash-free mass)	95.5 ± 4.4^{b}	102.7 ± 5.8^{b}	101.9 ± 2.8^{b}	127.3 ± 2.8^{a}	118.6 ± 3.8^{a}
Holocellulose (mg g^{-1} ash-free mass)	$543,1 \pm 6.2^{a}$	286 ± 11.3^{c}	327.6 ± 23.7^{c}	508.6 ± 12.2^{a}	390.6 ± 15.0^{b}
α-cellulose (mg g^{-1} ash-free mass)	383.6 ± 7.8^{a}	129.7 ± 7.8^{c}	171.6 ± 18.5^{d}	357.3 ± 13.2^{a}	243.2 ± 15.8^{b}
Hemicellulose (mg g^{-1} ash-free mass)	113.7 ± 2.9^{a}	71.7 ± 3.1^{c}	95.4 ± 8.1^{b}	93.7 ± 1.8^{b}	95.2 ± 2.1^{b}
Lignin (mg g^{-1} ash-free mass)	271.4 ± 7.3^{d}	551.5 ± 14.0^{a}	496.6 ± 22.5^{b}	295.6 ± 12.0^{d}	432.7 ± 17.4^{c}
Acid-soluble carbohydrates (mg g^{-1} ash-free mass)	556.8 ± 58.8^{a}	251.0 ± 15.9^{c}	198.3 ± 27.6^{c}	523.3 ± 9.5^{a}	412.9 ± 17.9^{b}
C/N	$12.3. \pm .2^{a}$	57.9 ± 2.4^{c}	102.5 ± 5.4^{b}	$100.0 \pm .3^{b}$	52.2 ± 3.8^{c}
Lignin/N	57.0 ± 1.9^{b}	53.6 ± 2.4^{b}	84.7 ± 4.8^{a}	44.3 ± 2.1^{c}	36.0 ± 1.8^{d}

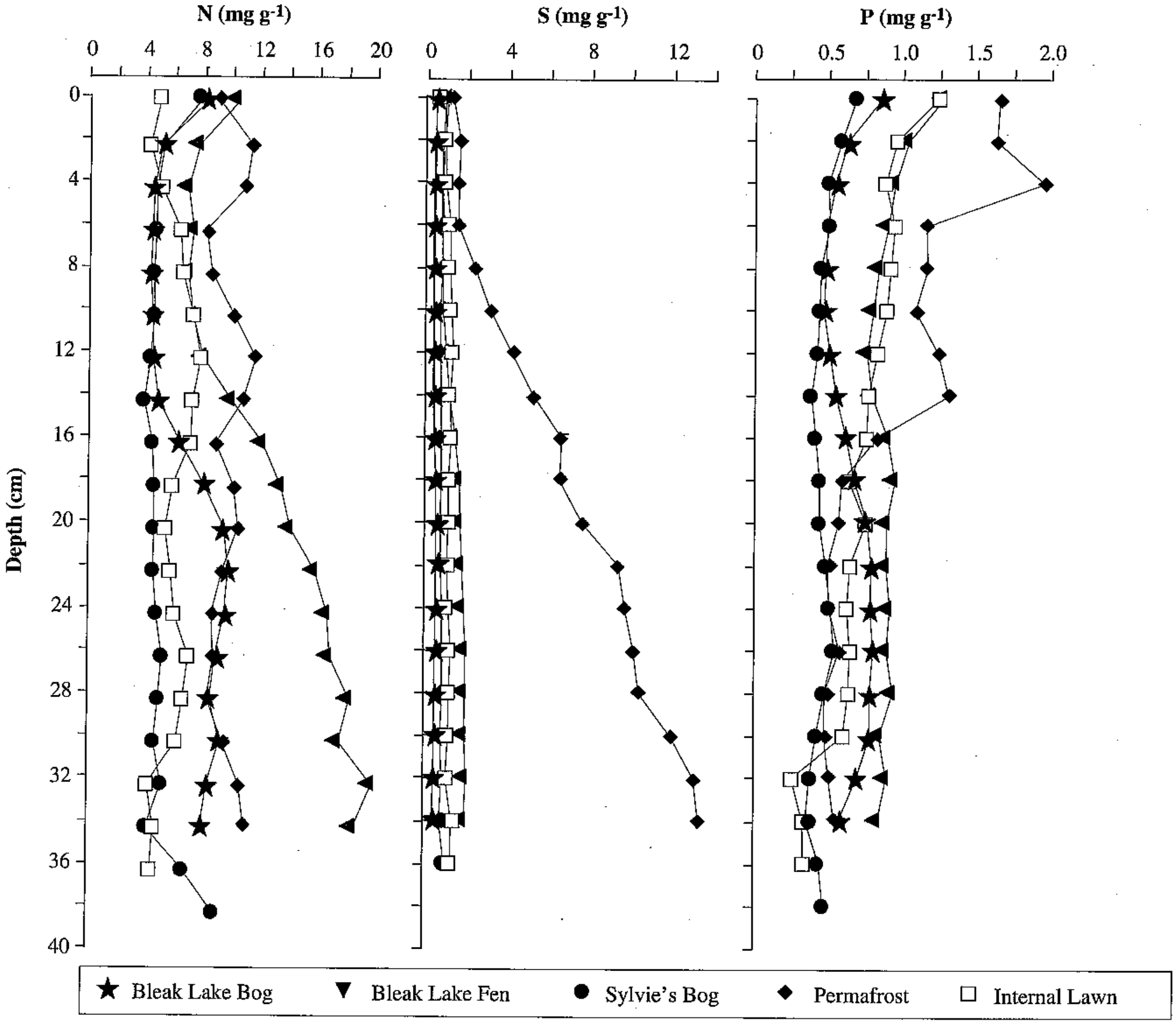

FIGURE 4. Total N, S, and P concentrations (mg g^{-1}; averaged across two replicate cores) *versus* depth (cm) in peat collected in intact cores from each of five peatland sites in Alberta.

and the permafrost bog depict generally decreasing holocellulose and increasing lignin concentrations to a depth of about 34 cm. Peat from the internal lawn and Bleak Lake Bog have a tendency for holocellulose concentrations to decrease and lignin concentrations to increase near the middle of the depth profiles, with concentrations deep in the core resembling surface values (Figure 5).

Plotting chemical data as a function of depth provides only a general perspective on chemical changes occuring over time, as depth-age relationships in peat are not linear (Figure 2). However, plotting chemical concentrations as a function of time, here using ^{210}Pb-dated chronologies, allows for a more direct assessment of temporal changes in peat chemistry. This approach is particularly useful for constituents that are produced primarily at the peat surface, are subsequently affected by decomposition, and are immobile in the peat column. For our boreal sites, both holocellulose and lignin profiles through time show similar trends for Bleak Lake Bog and Sylvie's Bog cores, while the internal lawn and permafrost cores are similar over the past 150-200 years (Figure 5). We note, however, that a drawback to this approach is that core sections deeper than the oldest, datable depth interval necessarily are excluded.

While univariate statistical methods indicate differences between our sites, a definitive separation of peat from the five peatland sites is obtained when all variables are combined into a multivariate canonical discriminant analysis (Figure 6). Peat collected from the permafrost site separate well from the three sites without permafrost (Sylvie's Bog, Bleak Lake Bog, Bleak Lake Fen) along the first canonical axis. Internal lawn peat tends to have intermediate values along the first canonical axis compared to peat collected from the permafrost and continental peatlands. The second canonical axis separates the two continental bogs, Bleak Lake Bog peat from Sylvie's Bog peat, and also separates the internal lawn peat from Bleak Lake Bog and Fen peats. Although univariate statistics show that Bleak Lake Bog and Fen peats differ for 11 of the 16 variables, they are not distinguished strongly by the multivariate analysis (Figure 6).

Discussion

RATES OF PEAT ACCUMULATION

Peatlands vary considerably in their vegetation type as well as water and soil chemistry, which are controlled largely by differences in hydrological regimes. Ombrogenous bogs

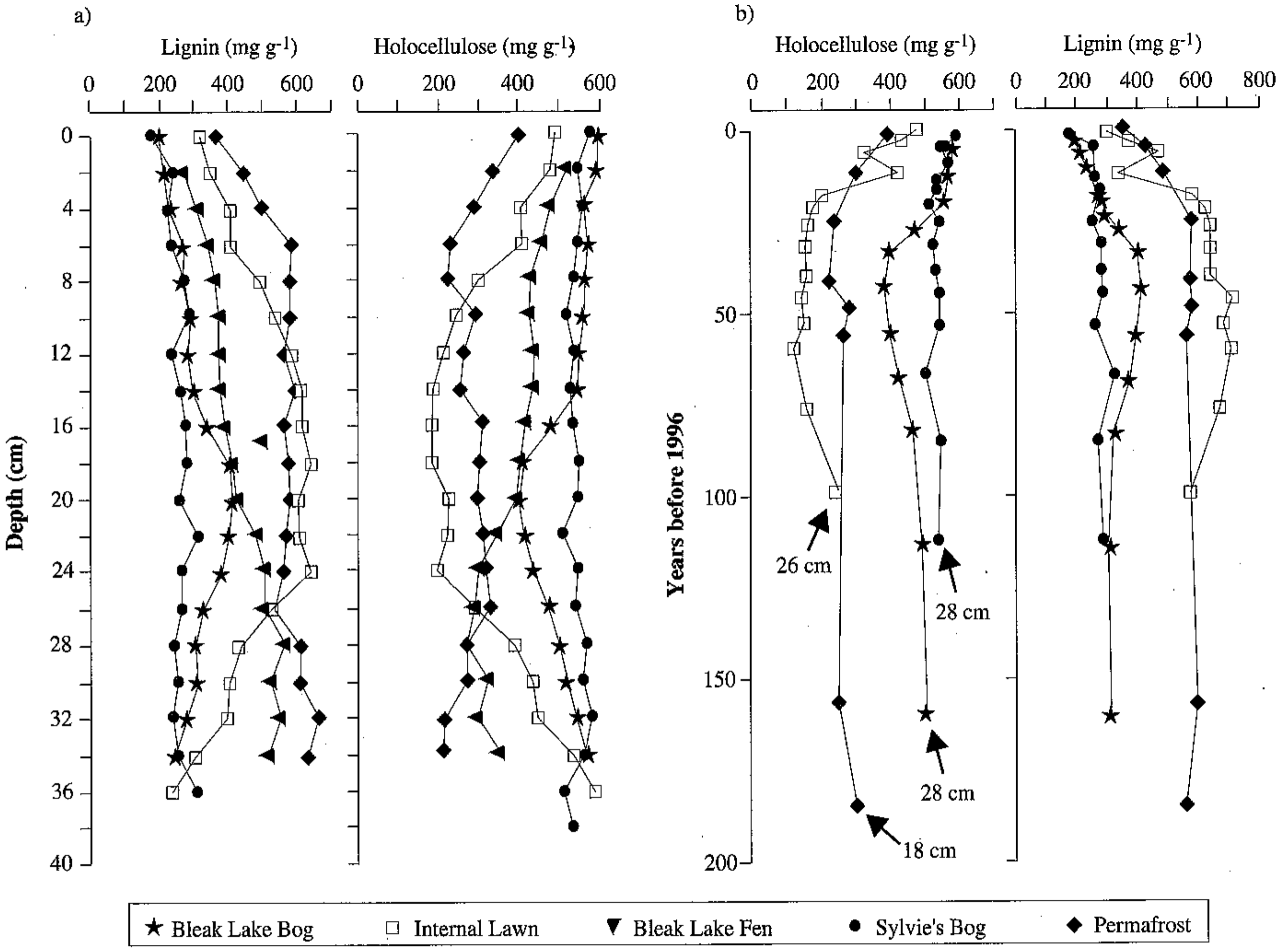

FIGURE 5. Concentrations of holocellulose and lignin (mg g^{-1}; averaged across two replicate cores) as a function of (a) depth and (b) age based on ^{210}Pb-dated chronologies, in peat cores from five Alberta peatlands. Depths (cm) corresponding to the oldest, dateable depth sections of each core are labeled on the holocellulose profile in b.

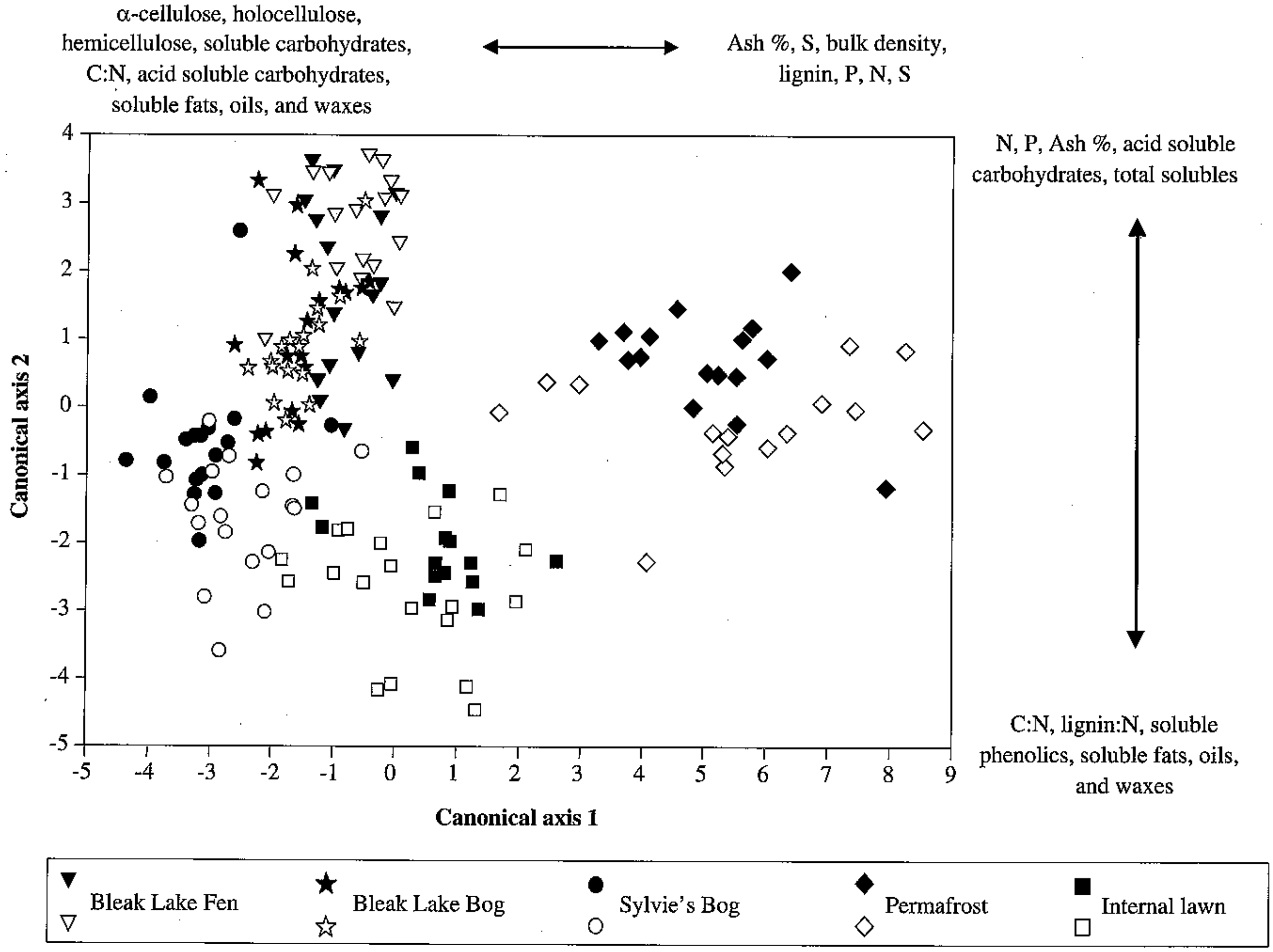

FIGURE 6. Graphical presentation of results of a canonical discriminant analysis of 16 measured and derived chemical variables (see Table II) indicating that the five sites were distinguishable based on peat chemistry. Each plotted point represents a single 2-cm peat core section. There are two cores per peatland site, denoted by open *versus* closed symbols. The first and second canonical axes explained 59.6 and 21.2% of the total variation, respectively. Significant positive or negative ($p < 0.05$) Pearson correlations between the canonical axes and the original 16 variables are indicated above and to the right of the graph.

receive nutrients via precipitation only, while geogenous fens are influenced by groundwater and/or surface water inputs. Peatland studies in boreal western continental Canada have focused on either bogs or fens or have studied sites along acidity-alkalinity gradients (Gignac *et al.*, 1991; Vitt, Bayley & Jin, 1995; Szumigalski & Bayley, 1996; Szumigalski & Bayley, 1997; Thormann & Bayley, 1997a, b; Thormann, Szumugalski, & Bayley, 1999). However, near the southern limit of permafrost in continental western Canada, two additional peat-accumulating features are present on the landscape, *i.e.*, permafrost bogs and internal lawns, which represent the ongoing melting of relict permafrost features (Halsey, Vitt & Zoltai, 1995). By characterizing how peatlands with permafrost, without permafrost, and with degraded permafrost differ in rates of organic matter accumulation and/or peat chemistry, we hope to gain insights into how the landscape of boreal, continental western Canada may respond to ongoing climate change.

Within the discontinuous permafrost zone of boreal, western continental Canada, permafrost melting is likely to play a critical role in the response of peatlands to climate change. While the timing of permafrost degradation remains unkown, it seems likely that permafrost melting will influence water availability and temperature relations both locally and regionally (Woo, 1990; Gavrilova, 1993). Net primary production and decomposition, and hence peat accumulation and peatland C cycling, are influenced by both water availability and temperature, although the nature of these dependencies remains obscure particularly for permafrost bogs and internals lawns.

Peat accumulation can be investigated using ^{210}Pb-dated chronologies to estimate net vertical peat growth or net organic matter accumulation over the past 100-200 years. For North American and European sites, a large variation in rates of net vertical peat growth, established via ^{210}Pb-dating, has been reported (Table I). Values range from 3.5 - 55.3 cm and 5.9 - 44.1 cm of net vertical growth over a 50 and 100 year period, respectively, and average 17 and 22 cm, respectively (Table I). For our two continental bog sites, Bleak Lake Bog and Sylvie's Bog, net vertical peat growth averaged 20.5 and 26.4 cm over 50 and 100 years, respectively (Table I, Figure 2). Net vertical peat growth was similar in the internal lawn (19.1 and 26.1 cm over 50 and 100 years, respectively), but was much slower in the permafrost bog, averaging only 9.7 and 12.9 cm, respectively over 50 and 100 years.

From a climate change and C cycling perspective, net organic matter accumulation is arguably more important than net vertical growth of a peat deposit. We are aware of organic matter accumulation data only for a few temperate zone sites, which average 11.5 and 17.9 kg m^{-2} over a 50 and 100 year period, respectively (Table I). Our boreal bog sites had much lower net organic matter accumulation than the temperate zone sites, averaging 8.0 and 11.2 kg m^{-2} over 50 and 100 years, respectively (Table I, Figure 3). Similar rates of organic matter accumulation were obtained for permafrost peat (averaging 7.2 and 11.8 kg m^{-2} over 50 and 100 years, respectively). In contrast, net organic matter accumulation as peat was much greater in the internal lawn, which accumulated approximately 1.6 times the amount of organic matter compared to our other boreal sites. Rates of organic matter accumulation in the internal lawn (averaging 11.5 and 18.4 kg m^{-2} over 50 and 100 years, respectively) were more similar to sites situated further south in the temperate zone than to our boreal sites (Table I).

Peatlands are a dominant landscape feature in boreal, continental Canada (Zoltai, 1988). In this region, permafrost is dominant in the Subarctic and becomes discontinuous and exclusive to peatlands in the Mid- to High-Boreal wetland regions (Ecological Stratification Working Group, 1995; Vitt *et al.*, in press). The distribution of permafrost may have reached its maximum extent in western continental Canada during the Little Ice Age (A.D. 1550-1850), extending further south and east than today (Vitt, Halsey & Zoltai, 1994). Permafrost, near its southern limit in the discontinuous permafrost zone, is limited to peatlands where ice is insulated by the thick deposits of organic matter (Thie, 1974; Halsey, Vitt & Zoltai, 1995). Despite the landscape changes in topography and species composition associated with permafrost aggradation, our results reveal no differences in net rates of organic matter accumulation between a permafrost bog and two continental (nonpermafrost) bogs. From a carbon cycling perspective, then, the presence of permafrost at the southern limit of discontinuous permafrost may not influence the accumulation of organic matter as peat in either a positive or negative manner. Working further north in the discontinuous permafrost zone near Fort Simpson, Northwest Territories, Robinson & Moore (1999; in press) report decreased rates of carbon accumulation over a 1200 year period in mature permafrost plateaus compared to unfrozen bogs.

Permafrost degradation, without subsequent signs of permafrost aggradation, has been documented in boreal, continental Canada (Thie, 1974; Vitt, Halsey & Zoltai, 1994; Halsey, Vitt & Zoltai, 1995; Vitt *et al.*, in press). Degradation at the southern limit of permafrost is a relatively recent phenomenon, and may be related to the effects of fire (Thie, 1974; Zoltai, 1993) or to an ongoing recent warming of the southern boreal region (Vitt, Halsey & Zoltai, 1994; Halsey, Vitt & Zoltai, 1995). Internal lawns, representing the degradation of relict permafrost features, are open, wet lawns dominated by *Sphagnum* and/or *Carex* (Vitt, Halsey & Zoltai, 1994). Our results indicate that the internal lawn is characterized by higher rates of organic matter accumulation over the past 100 years compared to the permafrost or continental bogs. The internal lawn accumulated organic matter at rates similar to peatlands situated further south in the temperate zone (Table I). In a global change context, accelerated rates of permafrost degradation may enhance carbon sequestration in boreal peatlands. However, the high rate of peat accumulation observed in the internal lawn may become less important over time following the degradation of permafrost. Eventually, peat will accumulate well above the water table in internal lawns and aerobic decomposition may begin to limit the accumulation of peat (Figure 7). Given sufficient time, rates of peat accumulation in internal lawns and continental bogs should converge. The age of internal lawns (*i.e.*, time since permafrost degradation), then, or the rate of succession to dry *Sphagna*, may be an important consideration in determining the carbon balance in sites affected by permafrost melting.

NUTRIENT STATUS AND ORGANIC MATTER CHEMISTRY

Ongoing climate change is likely to influence peat accumulation and carbon cycling of the various peatland features in boreal, western Canada, yet the nature of these responses almost certainly will be constrained by the nutrient status and organic matter quality of near-surface peat (Valentine, Holland & Schimel, 1994; Updegraff *et al.*,

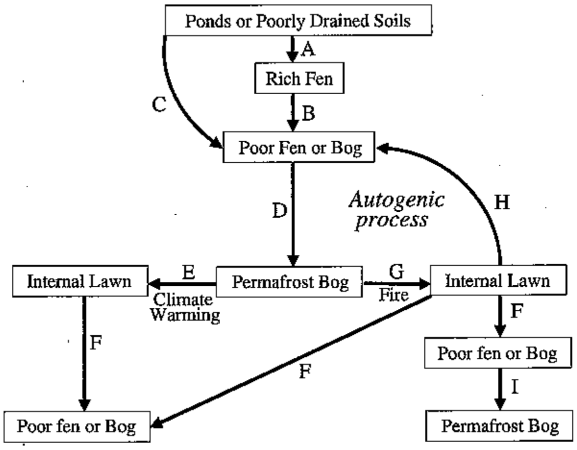

FIGURE 7. Historical development of peatlands in the discontinuous permafrost zone of boreal, western Canada. A. After the retreat of the Laurentide ice sheet, peatlands in continental, western Canada developed as fens on areas of poor drainage through paludification or over small water bodies through terrestrialization (Zoltai, 1995; Kuhry *et al.*, 1993; Nicholson & Vitt, 1994). Shallow ponds were filled in with gyttja and/or marsh peat. Open or forested wet rich fens developed. B. Peat accumulation continued leading to drier local conditions. *Sphagnum* spp. replace the brown moss communities and pH declines (Kuhry *et al.*, 1993). C. *Sphagnum* spp. may encroach upon forested or poorly drained sites through terrestrialization (Kubiw, Hickman & Vitt, 1989). D. Following the Hypsithermal warm period in western Canada (beginning approximately 10 000 before present), permafrost aggradation may have been a direct response to climatic cooling or to the development of *Sphagnum*-dominant peatlands caused by the cooler and moister conditions. Insulation caused by surface peat and/or interception of snow by dense black spruce canopies may have initiated permafrost development in western Canadian peatlands (Zoltai, 1995). E. Melting of discontinuous permafrost may be triggered by a recent, ongoing warming of the southern boreal region of Canada (Vitt, Halsey & Zoltai, 1994; Halsey, Vitt & Zoltai, 1995). F. Peat accumulation isolates the vegetation surface from the water table and more dry-loving *Sphagnum* spp. dominate. If relict permafrost features situated south of the 0°C isotherm are degraded, temperatures are not cold enough to support permafrost aggradation. G. Melting of permafrost may be related to fire activity (Thie, 1974; Zoltai, 1993). H. Peat accumulates above the water table and more dry-loving *Sphagnum* spp. invade. I. Temperatures are cold enough to support permafrost aggradation (Zoltai, 1993).

1995; Yavitt, Williams & Wieder, 1997; Bridgham, Updegraff & Pastor, 1998). In a general sense, the nutrient status of peatlands is affected by the chemical composition of precipitation (both wet and dry deposition), the chemical composition of surface water or groundwater entering a peatland (fens only), disturbances that may cause the release of nutrients such as fire and erosion, as well as decomposition, which also will release nutrients for subsequent plant or microbial uptake (Damman, 1990). Peat organic matter quality, in contrast, is influenced by the initial organic composition of the vegetation from which peat is derived, and the subsequent alteration via differential susceptibility of different organic components to decomposition (Williams & Yavitt, in press; Williams *et al.*, 1998).

Most of the published data on nutrient concentrations in *Sphagnum*-derived peats has focused on bogs and fens; less information is available for peat overlying permafrost or for the peat in internal lawns. Damman (1988) reports that N concentrations of *Sphagnum* moss litter are usually less than 6 mg g^{-1}, and are expected to increase with depth as a function of decomposition. In general, N concentrations in surface peat range from 4-29 mg g^{-1} for temperate and boreal peatlands (Waughman, 1980; Lowe & Bustin, 1985; Wieder, 1985; Malmer & Wallén, 1996; Bridgham, Updegraff & Pastor, 1998). Total P and S concentrations of surface peat range from 0.18-1.7 and 0.342-5.6 mg g^{-1}, respectively for boreal and temperate sites (Waughman, 1980; Lowe & Bustin, 1985; Wieder, 1985; National Wetlands Working Group, 1988; Nicholson, 1989; Vitt & Chee, 1990; Novák & Wieder, 1992; Bottrell & Novák, 1997; Bridgham, Updegraff & Pastor, 1998).

Although comparatively little data exist for peat organic matter quality, published information generally has been presented within the context of relationships with organic matter mineralization. In this context, three indices (C:N ratio, lignin:N ratio, cellulose:lignin ratio) have been used as predictors of mineralization, with varying degrees of success (Valentine, Holland & Schimel, 1994; Updegraff *et al.*, 1995; Yavitt, Williams and Wieder, 1997; Bridgham, Updegraff, & Pastor, 1998). In addition, changes in peat C:N ratios with depth in individual peat cores have been used as an indirect approach to quantifying carbon losses over time, assuming that C is lost during mineralization, while N is conserved (Malmer & Holm, 1984; Malmer & Wallén, 1993; Kuhry & Vitt, 1996). Reported C:N ratios in a variety of bog sites have ranged from 27 to 200 (Malmer & Holm, 1984; Malmer & Wallén, 1993; Belyea & Warner, 1994b; Kuhry & Vitt, 1996). Bridgham, Updegraff & Pastor (1998) report mean lignin:N ratios of 25 and 16 for northern Minnesota bogs and acidic fens, respectively. Across 12 North American sites (all of which are temperate zone sites except for Bleak Lake Bog), Yavitt, Williams & Wieder (1997) report a wide range in the relative abundance of cellulose (acid-soluble fraction) *versus* lignin (acid-insoluble fraction) in *Sphagnum*-derived surface peat, with lignin:cellulose ratios of about 0.5 for Bleak Lake Bog peat, but of about 3 for peat from a site in central New York, U.S.A. Bridgham, Updegraff & Pastor (1998) report mean lignin:cellulose ratios of 0.36 and 0.30 for surface peat of northern Minnesota bogs and poor fens, respectively.

From this survey of nutrient concentrations and organic matter quality in peat from bogs and poor fens we draw several conclusions. First, the peat from our five sites, including peat from the permafrost bog and the internal lawn, can be regarded as generally similar to other bog and fen peats. Second, although we report some significant differences in mean nutrient concentrations between sites, and hence between peatland features, these differences are not large given the range of concentrations reported as typical for bog and poor fen peats. Moreover, it is sometimes the case that variation in the concentration of a nutrient within a peat profile (Figures 4 and 5) is at least as great as differences in mean concentrations between sites.

Although the theme of using peat inorganic and organic chemistry to predict past, present, or future carbon or nutrient mineralization is common, the focus of such efforts often is quite different. On one extreme, peat chemical characteristics have been used as predictors of mineralization across quite different peat types, that may differ widely in vegetation, pH, and hydrology (Yavitt, Williams & Wieder, 1997; Bridgham, Updegraff & Pastor, 1998). Whereas such an approach may lead to an ability to predict differences in mineralization between peat types, within-peat-type predictions are much less likely to emerge. A different approach uses peat chemical characteristics to describe peat mineralization over time within a single peat type (Malmer & Holm, 1984; Malmer & Wallén, 1993; Belyea & Warner, 1994b; Kuhry & Vitt, 1996), where initial vegetation and site chemical characteristics are more similar. This approach may lead to an ability to predict differences in mineralization within a single peat type, but will be less useful in making comparisons between peat types. A combination of both approaches may be needed in efforts relating peat chemical characteristics to mineralization within the broader context of permafrost degradation in boreal western continental Canada in a continually changing climate.

Both between-site and within-site peat chemistry, however, is taken into consideration when all variables are included in canonical discriminant analysis (Figure 6). A clear distinction between sites is evident, indicating that between-site differences far outweigh changes in nutrient status and/or organic matter quality as a function of depth within a peat core. Of particular note is the clear separation of permafrost peat from the other peat types. As we have mentioned before, permafrost peat appears to be derived more from fine vascular plant roots than from mosses, which alone could lead to major differences in organic matter quality. Indeed, the high concentrations of N, P, and S in permafrost peat are surprising (Table II, Figure 4). High concentrations could result from efficient retention of atmospherically deposited nutrients (documented to be especially true in bogs for N and P; *e.g.*, Malmer & Nihlgård, 1980; Malmer, 1988) coupled with slow net organic matter accumulation, although organic matter accumulation in the permafrost peat is similar to that of the bog sites (Figure 3). An alternative explanation is that the dense, often lichen-covered canopy of *Picea mariana* is an effective scavenger of dry deposition from the atmosphere, especially as compared to the bogs and internal lawns of our study, for which *P. mariana* cover is sparse. The total inventory of N and P in the uppermost 100 years of permafrost peat accumulation is 5.5 and 9.5 times, respectively, that which could have been delivered to the peat surface by wet deposition alone (applying 1996 wet deposition values and assuming that N, P, and S wet deposition has not changed over the past 100 years; Table III).

The canonical discriminant analysis somewhat separates out Sylvie's Bog peat from Bleak Lake Bog peat (Figure 6). Although both are representative of continental bogs, Sylvie's Bog appears to be somewhat less susceptible to future decomposition than Bleak Lake Bog, as the second axis is negatively correlated with both C:N and lignin:N ratios. As with the permafrost peat, both of our bog sites have greater inventories of N and P in the top 100 cm of accumulated peat than can be explained by wet deposition inputs alone, as has been reported for other bog sites as well (Malmer & Nihlgård, 1980; Malmer, 1988).

Finally, we expected internal lawn peat to be chemically similar to Bleak Lake Fen peat, given what we perceive as similarities between these sites in surface wetness and a predominance of *Sphagnum* species that prefer wet sites. The canonical discriminant analysis, however, clearly distinguishes Bleak Lake Fen peat from the internal lawn peat. Notably peat from the internal lawn peat has higher C:N and lignin:N ratios than Bleak Lake Fen peat, and hence is possibly more resistant to further decomposition (Figure 6).

The internal lawn peat clusters between the permafrost peat and Sylvie's Bog peat along the first canonical axis (Figure 6). This position could be interpreted as reflecting a progressive shift in the accumulating surface peat of the internal lawn, away from the chemistry of the underlying and increasingly buried permafrost peat, toward the chemistry of a continental bog. We also note that in terms of nutrient stock in the past 100 years of accumulated peat, internal lawns stand out as having much more N, P, and S than can be explained by wet depositional inputs (Table III). As a result of permafrost degradation, internal lawns occupy the lowest position on the local landscape. Hence, during especially wet periods, internal lawns may receive "runoff" from adjacent continental bogs and/or permafrost features, some of which may be undergoing active degradation. As internal lawns accumulate organic matter at greater rates than either continental or permafrost bogs, increasing distance from the peat surface to the mean water table may drive a succession from the hydrophilic *Sphagnum* species currently found in internal lawns to the more mesic to xeric *Sphagnum* species that are characteristic of continental bogs (Figure 7; Vitt, Halsey & Zoltai, 1994).

Conclusion

The mosiac of continental bogs, relict permafrost features, internal lawns, and poor fens in boreal, western continental Canada offers a unique opportunity to investigate abiotic and biotic controls on peat accumulation, as well as to monitor effects of global climate change on a sensitive region of boreal forest, the discontinuous permafrost zone. Changes in peatland water table and thermal regimes caused by permafrost degradation will trigger changes in net primary production and decomposition.

Using a descriptive approach, we have documented both similarities and differences between continental bogs, a relict permafrost feature, an internal lawn, and a poor fen with regard to vertical peat growth and organic matter accumulation over the past 100-150 years (excluding the poor fen), as well as in the nutrient status and organic chemistry of near-surface peat. We acknowledge that our sampling and chemical analyses, although intensive, are limited; our results and interpretations should be regarded as preliminary. Nonetheless, it does appear that the various recognizable peatland features that are spatially intermixed at scales of hundreds of meters to tens of kilometers within the landscape of boreal continental western Canada are functioning quite individually in terms of peat accumulation and organic chemistry, at least in the short-term. Peat chemical composition may differ according to the presence, absence, or degradation of permafrost, and is likely to be a critical, moderating factor in the regional carbon balance response of peatlands to climate change. The spatial heterogeneity that characterizes the landscape of the discontinuous permafrost zone of western Canada adds considerable complexity to the already challenging question of the future role of peatlands as providing either positive or negative feedback on global climate change.

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TABLE III. Precipitation chemistry and net accumulation values for N, P, and S over a 100 year period. Cumulative inputs of wet deposition are based on 1996 data (Myrick & Hunt, 1998) for 11 sampling sites across Alberta, assuming no change in precipitation chemistry over the 100 year interval.

	Inputs via wet deposition*			Net nutrient accumulation		
	Range	Mean	Sylvie's Bog	Bleak Lake Bog	Permafrost Bog	Internal Lawn
	mg.m^{-2}.100 years^{-1}			mg.m^{-2}.100 years^{-1}		
N	7700-20 700	14 275	41 129	71 248	77 834	92 103
P	436-1491^{+}	931^{+}	4133	6477	8862	9080
S	6000-14 700	10 708	6146	7561	8136	16 501

*Values based on 1996 data (Myrick & Hunt, 1998).

+Due to limited available data, wet deposition values for PO_4^3 -P were estimated by linear regression against measured NH_4^+ -N values. PO_4^{3-} -P = 0.113525*NH_4^+ -N - 0.00722 ($R^2 = 0.45, p = 0.007, n = 15$).

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