NOTE

Carbon-isotope ratios and carbon, nitrogen and sulfur abundances in flora and soil organic matter from a temperate-zone bog and marsh

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Stable carbon-isotope ratios (^{13}C/^{12}C) and the abundance of carbon, nitrogen and sulfur were measured in flora and soil organic matter from the Sifton Bog and Point Pelee Marsh, which are located in the temperate climatic zone of southwestern, Ontario, Canada. Characteristic bog vegetation contains less N and S than marsh flora; however, invasive species (e.g., *Typha*) at the Sifton Bog have N and S contents that are similar to vegetation from the Point Pelee Marsh. Flora from both wetlands have δ^{13}C values that are similar and characteristic of vegetation possessing the C_3 photosynthetic pathway. The only exception is *Utricularia vulgaris* L. at the Point Pelee Marsh, which is ^{13}C-enriched (average δ^{13}C = –18.4‰; range –18.8 to –17.6‰) probably because of CO_2 limitation during growth. Organic matter from peat soils at each wetland exhibits a similar depth distribution of C:N ratios and δ^{13}C values. The C:N ratio of soil organic matter decreases with depth, consistent with consumption of labile carbohydrates and fixation of nitrogen by soil microorganisms. Both C:N ratios and δ^{13}C values stabilize at a shallow depth in soils at the Point Pelee Marsh, consistent with greater decay efficiency and less recalcitrant vegetation in marsh than in bog environments. Paleovegetational changes associated with a fen to bog succession also may have contributed to the more gradual and larger change in δ^{13}C values and C:N ratios observed for soil organic matter at the Sifton Bog.

INTRODUCTION

Stable carbon-isotope ratios (^{13}C/^{12}C) are particularly useful in the study of carbon-cycling in wetlands because they provide a means to trace sources of organic detritus (Chmura and Aharon, 1995; Keough *et al.*, 1998) and to investigate metabolic pathways associated with microbial decay (Whiticar *et al.*, 1986; Lansdown *et al.*, 1992; Sugimoto and Wada, 1993; Hornibrook *et al.*, 1997; Middelburg *et al.*, 1997). Stable carbon-isotope compositions and C, N, S abundances of organic matter gradually evolve during degradation because different biochemical constituents are preferentially consumed, produced or sequestered

(Benner *et al.*, 1987). Accordingly, isotopic and elemental characterization of flora in wetlands is necessary to provide a baseline for recognition of changes in organic detritus as decay proceeds. We present δ^{13}C values and C, N, S compositions of flora and soil organic matter from a bog and marsh in southwestern Ontario, Canada. We briefly discuss the differences that exist in the composition of organic matter between the two wetlands.

EXPERIMENTAL

Study sites

The Sifton Bog and Point Pelee Marsh are located within the Eastern Temperate climatic zone

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Fig. 1. Location map for the Sifton Bog and Point Pelee Marsh in southwestern, Ontario, Canada.

of southwestern Ontario, Canada (Fig. 1). The zone is characterized by mild winters (mean daily January temperature –9°C), warm summers (mean daily July temperature 20°C) and a high annual input of precipitation (~35 cm/yr as rainfall and ~210 cm/yr as snowfall; Glooschenko *et al.*, 1993).

The Sifton Bog (43°00′00″N) is an acidic *Sphagnum* peat bog (pH ~3.8) located within the City of London, Ontario, Canada. The bog covers an area of ~28 hectares and was formed by lakefill of a small kettle depression created at the end of the last glaciation. The site consists of a small central open pond surrounded by a floating *Sphagnum*-mat that gradually changes at its periphery into lower damp woods and eventually upland wooded slopes. Judd (1957) and McLeod (1991) have described the flora within each of the vegetation zones. The central portion of the bog contains as much as 10 m accumulation of peat (Warner, 1989). The organic soils overlie deltaic deposits of sand and gravel, which in turn overlie glacial tills of a terminal moraine. Peat samples were collected from a hollow on the floating-mat at a site located approximately midway between the pond and the edge of the lower damp woods. The mat thickness was ~1.5 m at the site. With the exception of vegetation and peat that occur on

hummocks, the surface of the floating-mat remains moist throughout the year because the mat rises and falls with fluctuations in water levels.

The Point Pelee Marsh (41°58′00″N) is a freshwater wetland (pH ~6.9) located within Point Pelee National Park, near Leamington, Ontario, Canada. It exists within a quasi-symmetrical cuspate foreland that projects ~15 km into Lake Erie. Sand ridges enclosing the marsh formed ~4000 years B.P from remnants of the Pelee-Lorain moraine during a progressive rise of lake levels in the western and central basins of Lake Erie (Coakley, 1976; Coakley *et al.*, 1998). Marsh waters are considered to be isolated from those of Lake Erie, except during major storm events (Bayly and O'Neill, 1971; Huddart *et al.*, 1999). The present marsh covers an area of ~1,050 hectares or ~70% of the park area. It consists primarily of extensive floating-mats bearing monocultures of the Common Cattail (hybrid *Typha × glauca* Godr.) with minor subpopulations of *Typha angustifolia* (L.) and *T. latifolia* existing in restricted areas (Bayly and O'Neill, 1971). The *Typha*-bearing mats are interspersed with large, shallow open ponds and channels that contain an abundance of aquatic vegetation during summer months.

Sample analysis

Peat and plant samples were oven-dried at 60°C to constant weight prior to elemental and isotopic analysis. Dried samples and standards were ground to a powder and homogenized. A Carlo Erba 1108 elemental analyzer was used to determine C, N and S abundances in plant and soil organic matter and to convert organic carbon to CO_2 for stable carbon-isotope analyses. Reproducibility of standards was ±1% of elemental abundance for C and N, and ±2% for S. The analytical precision was similar for C and N analyses of samples. However, because of the low abundance of S in organic matter, especially bog vegetation, the relative precision of S analyses ranged from ±2 to ±10% for sample weights of 3 to 10 mg.

Collection of CO_2 for stable carbon-isotope analysis was achieved by diverting the gas stream

Table 1. C, N, S and stable carbon-isotope compositions of plant matter from the Sifton Bog

Plant	Sample Description	n[1]	C (wt%)	N (wt%)	S (wt%)	C:N	$\delta^{13}C$ (‰)
Sphagnum magellanicum Brid.	whole plant	2	44.3[2] (44.0/44.6)[3]	0.84 (0.69/0.98)	<0.08 (bdl[4]/0.08)	55 (46/64)	-31.3 (-31.7/-30.9)
S. capillaceum (Weiss) Schrank	whole plant	1	42.8	0.60	bdl	71	-27.6
S. centrale C. Jens.	whole plant	1	45.6	0.80	0.13	57	-27.0
S. fimbriatum Wils. ex Hook.	whole plant	1	46.8	0.90	0.11	52	-26.9
S. riparium Ångstr.	whole plant	1	47.4	0.77	0.15	62	-27.2
S. recurvum P.-Beauv.	whole plant	1	47.1	0.98	0.08	48	-27.4
Drosera rotundifolia L.	roots	1	46.9	0.92	0.06	51	-29.1
D. rotundifolia	stem + seeds	1	43.6	1.65	0.10	26	-25.1
D. rotundifolia	leaf + resin	1	58.4	1.42	0.04	41	-28.1
Sarracenia purpurea L.	leaf	1	44.4	0.85	0.03	52	-25.7
Galerina sphagnicola (Atk.) Smith and Singer	pileus + stem	1	47.9	5.91	0.35	8	-25.0
Dryopteris spinulosa (O.F. Muell.) Watt	leaf	7	48.3 (39.9/61.6)	2.07 (1.24/3.04)	0.29 (0.15/0.77)	25 (18/38)	-30.7 (-31.8/-28.8)
Eriophorum virginicum L.	flower	1	44.3	0.74	0.79	60	-24.9
E. virginicum	stem + leaf	1	46.3	0.35	bdl	132	-26.6
Dulichium arundinaceum (L.) Britton	leaf	1	47.6	1.04	0.33	46	-28.0
Andromeda glaucophylla Link.	leaf	1	54.8	1.26	0.16	44	-28.7
A. glaucophylla	stem	1	50.8	0.57	bdl	89	-25.7
Chamaedaphne calyculata (L.) Moench	leaf	2	52.1 (51.5/52.6)	1.40 (1.39/1.40)	0.20 (0.16/0.23)	38 (37/38)	-28.8 (-29.0/-28.6)
C. calyculata	stem	1	49.2	0.42	bdl	117	-27.9
Kalmia polifolia Wang.	leaf	5	46.7 (42.0/51.7)	1.68 (1.42/2.23)	0.21 (0.16/0.27)	28 (23/31)	-29.8 (-30.8/-28.7)
Vaccinium oxycoccus L.	stem + leaf	1	50.4	0.89	bdl	57	-28.6
V. oxycoccus	berry	1	47.5	0.26	bdl	183	-26.9
Vaccinium macrocarpon Ait.	stem + leaf	4	46.3 (41.2/49.0)	0.83 (0.54/1.09)	0.48 (0.13/0.94)	59 (43/76)	-29.9 (-30.2/-29.5)
Nuphar advena (Ait.)	leaf	2	47.4 (45.0/49.7)	3.66 (3.37/3.95)	0.27 (0.21/0.32)	13 (13/13)	-24.8 (-25.0/-24.5)
Typha latifolia (L.)	leaf (living)	1	43.0	2.21	bdl	19	-27.6
Cornus obliqua Raf.	leaf	4	46.1 (42.7/48.2)	2.46 (1.58/3.50)	0.39 (0.14/0.57)	19 (14/27)	-31.1 (-31.8/-30.7)
Cornus racemosa Lam.	leaf	3	40.8 (36.5/43.8)	3.02 (2.56/3.50)	0.36 (0.26/0.52)	14 (13/14)	-29.7
Rhamnus frangula L.	leaf	1	45.4	3.47	0.32	13	-27.3
Larix laricina (DuRoi) K. Koch	twig	1	55.1	0.49	bdl	112	-30.1
L. laricina	needles	4	53.0 (46.8/62.4)	1.30 (1.09/1.50)	0.27 (0.18/0.35)	41 (32/47)	-29.8 (-30.3/-29.1)
Picea mariana (Miller) BSP	twig	1	52.2	0.58	0.08	90	-26.3
P. mariana	needles	7	48.5 (42.7/53.7)	1.03 (0.83/1.34)	0.13 (0.11/0.16)	48 (40/58)	-28.0 (-29.0/-27.4)
Pinus strobus L.	needles	3	47.2 (46.1/49.1)	1.94 (1.73/2.17)	0.19 (0.13/0.23)	24 (23/27)	-27.7
Acer saccharum Marsh.	leaf	13	45.4 (39.0/54.8)	1.16 (0.63/2.40)	0.18 (0.02/0.56)	45 (21/66)	-29.7 (-30.8/-27.8)
Acer negundo L.	leaf	2	44.4 (40.7/48.0)	0.65 (0.62/0.67)	0.09 (0.05/0.13)	69 (61/77)	-29.9
Betula populifolia Marsh.	leaf	6	43.9 (37.3/55.0)	1.21 (0.73/1.85)	0.14 (0.02/0.30)	42 (22/64)	-29.3 (-29.9/-27.7)

[1] Number of samples.
[2] Average value.
[3] Range of values.
[4] Abundance below detection limit.

Table 2. C, N, S and stable carbon-isotope compositions of plant matter from the Point Pelee Marsh

Plant	Sample description	n[1]	C (wt%)	N (wt%)	S (wt%)	C:N	δ^{13}C (‰)
Typha × glauca Godr.	leaf (living)	2	49.3[2] (48.1/50.5)[3]	2.67 (2.42/2.92)	1.18 (0.93/1.42)	19 (17/20)	−27.7 (−27.7/−27.6)
T. glauca	leaf (dead)	1	45.8	1.45	0.99	32	−27.6
Impatiens biflora Walt.	leaf	1	46.5	2.72	0.79	17	−27.4
Nuphar advena (Ait.)	leaf	1	46.2	3.99	1.47	12	−25.5
Anacharis canadensis (Michx.) Planch.	leaf	2	38.4 (38.2/38.5)	1.83 (1.77/1.89)	0.85 (0.83/0.87)	21 (20/22)	−24.6 (−24.6/−24.5)
Utricularia vulgaris (L.)	leaf	3	41.8 (40.1/43.7)	2.48 (1.87/3.04)	0.32 (0.04/0.76)	17 (14/21)	−18.4 (−18.8/−17.6)
Brown moss (unidentified)	whole plant	2	43.6 (42.5/44.7)	2.68 (2.03/3.32)	0.78 (0.14/1.42)	17 (13/21)	−29.3 (−29.3/−29.2)
Algae (unidentified)	whole plant	2	41.9 (34.2/49.5)	5.80 (5.18/6.42)	1.09 (0.59/1.58)	8 (7/8)	−26.9 (−27.3/−26.4)

[1] *Number of samples.*
[2] *Average value.*
[3] *Range of values.*

from the vent of the thermal conductivity detector on the elemental analyzer into a vacuum extraction-line containing coils immersed in liquid nitrogen. Yield of CO_2 from combustion of organic matter was measured by manometer. Stable carbon-isotope ratios (^{13}C/^{12}C) were measured using a VG-Optima mass-spectrometer, and are reported in the standard δ-notation after Craig (1953), relative to VPDB (Coplen, 1994). The precision of δ^{13}C results was normally better than ±0.1‰.

RESULTS

The C, N and S contents and δ^{13}C values for plants collected at the Sifton Bog and Point Pelee Marsh are presented in Tables 1 and 2, respectively. Sample collection at the two sites was focused primarily on prominent plant species that provide litter to the soil carbon pool. The C, N and S abundances and δ^{13}C values for soil organic matter from the two wetlands are presented in Table 3.

Table 3. C, N, S and stable carbon-isotope compositions of soil organic matter from the Sifton Bog and Point Pelee Marsh

Depth (cm)	C (wt%)	N (wt%)	S (wt%)	C:N	δ^{13}C (‰)
Sifton Bog					
20	41.9	1.73	0.19	24.3	−28.0
30	37.8	2.15	0.63	17.6	−27.6
40	37.6	2.37	0.69	15.9	−27.8
50	40.2	2.53	0.27	15.9	−27.4
60	38.4	3.04	0.82	12.6	−26.9
75	35.3	2.92	0.48	12.1	−27.1
90	32.7	2.26	0.12	14.5	−25.8
110	46.4	4.05	0.23	11.5	−25.0
Point Pelee Marsh					
3	46.0	2.71	1.75	16.9	−29.7
8	47.2	2.81	0.69	16.8	−28.5
10	46.1	3.30	0.85	14.0	−28.3
13	45.1	3.00	0.89	15.0	−28.1
18	46.0	3.52	0.62	13.1	−27.5
23	46.0	3.64	0.83	12.6	−27.9
30	44.4	3.51	0.64	12.7	−28.1
50	48.5	3.82	0.92	12.7	−28.1
65	44.5	3.59	1.26	12.4	−28.3
80	40.3	3.24	1.30	12.4	−28.1
105	43.6	3.64	1.12	12.0	−28.2

DISCUSSION

Flora

Bog and marsh flora have a similar carbon content; however, in general, marsh vegetation contains a greater quantity of both sulfur and nitrogen (Fig. 2). Marsh flora also exhibit a much smaller range of C:N ratios (8 to 32) compared to bog vegetation (8 to 183) (Fig. 3), consistent with marsh environments having higher rates of decay and nutrient turnover (e.g., Farrish and Grigal, 1988; Thormann *et al.*, 1999). The sulfur content of bog flora was low and exhibited a minor positive-correlation with nitrogen content ($r^2 = 0.38$). Sulfur rarely is a limiting nutrient in wetlands since plant requirements for growth and reproduction generally are met by sulphate in rainwater.

The high C:N ratios determined for Sifton Bog flora are similar to values reported for other peatlands (~26 to 150; Malmer and Holm, 1984; Damman, 1988; Verhoeven *et al.*, 1990; Hayati

and Proctor, 1991; Schindler and Bayley, 1993; Bartsch and Schwintzer, 1994). The low abundance of N in bog plants is consistent with limited nutrient inputs to ombrotrophic environments (Vitousek and Howarth, 1991), albeit ombrotrophic conditions in bogs do not necessary coincide with oligotrophy (Bridgham *et al.*, 1996, 1998). The higher C:N ratio in bog flora also may reflect a greater efficiency in the use of nutrients by vegetation adapted to ombrotrophic conditions.

Several species of plants within the open bog have an unusually high N-content. The low C:N (~8) ratio in *G. sphagnicola* (a fungi) likely results from the ability of obligate saprophytes to decompose and acquire nutrients from plant litter efficiently (Weier *et al.*, 1982). Although litter derived from *Sphagnum* and other common bog species has a high C:N ratio (e.g., >50), the small fraction of this material that is labile and easily biodegradeable tends to be N-enriched (Van Breemen, 1995).

Spatterdock (*N. advena*) and the Common Cattail (*T. latifolia*) also exhibit a low C:N ratio. Generally, the presence of these plants is indicative of nutrient enrichment (Crum, 1988). McLeod (1991) has classified the area within the Sifton Bog that contains extensive growth of *Typha* as being a marsh subenvironment. In recent years, there has been concern that the trophic status of the Sifton Bog is changing, not naturally, but as a result of
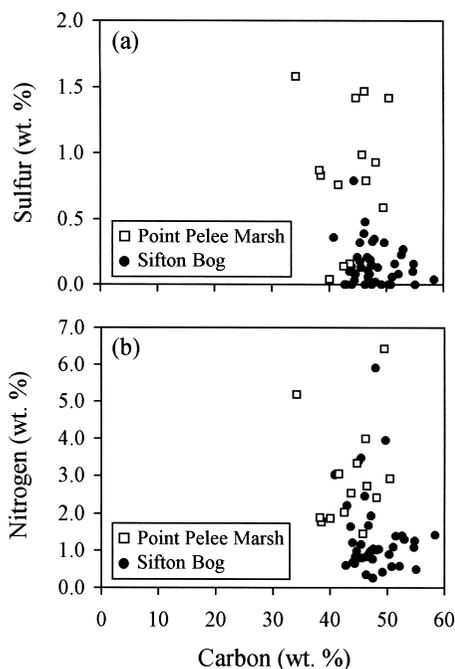

Fig. 2. (a) Sulfur versus carbon, and (b) nitrogen versus carbon contents of dried plant matter collected at the Sifton Bog (●) and Point Pelee Marsh (□).
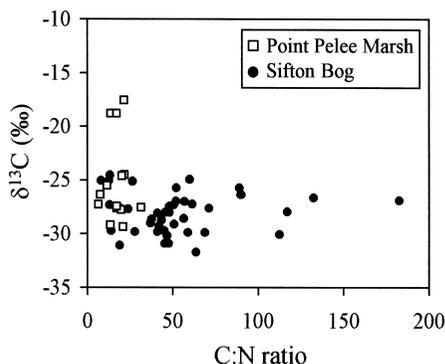

Fig. 3. $\delta^{13}C$ value versus C:N ratio of dried plant matter collected at the Sifton Bog (●) and Point Pelee Marsh (□).

nutrient-loading *via* atmospheric deposition of pollutants or possibly, runoff from the surrounding urban environment. Characteristic bog flora (e.g., *Sphagnum* sp., *C. calyculata*, *D. rotundifolia*, etc.) growing in close proximity to Spatterdock and the Common Cattail have much higher C:N ratios, which supports the suggestion that bog vegetation has a lower requirement for nitrogen. The lower C:N ratios of Spatterdock and the Common Cattail suggests that these invasive species may possess a physiological advantage for nutrient uptake.

Plants from both wetlands have $\delta^{13}C$ values that are similar (marsh, range $\delta^{13}C$ = –29.3 to –24.5‰ (excluding *U. vulgaris*); bog, range –31.8 to –24.5‰) and characteristic of vegetation utilizing the C_3 photosynthetic pathway. One exception occurs at the Point Pelee Marsh where Bladderwort (*U. vulgaris*) possesses significantly higher $\delta^{13}C$-values (average $\delta^{13}C$ = –18.4‰; range –18.8 to –17.6‰). Aquatic macrophytes often exhibit variable $\delta^{13}C$-values that can range between –50 to –10‰ (Boutton, 1991). Under conditions of low CO_2 availability, ^{13}C-enrichment can result from reduced expression of the kinetic isotope effect associated with CO_2 fixation by ribulose biphosphate (RuBP) carboxylase (O'Leary, 1993). In habitats with slow-moving water, poor-mixing results in the development of thin unstirred layers around submersed objects, which causes a boundary-layer effect at the leaf-water interface (Osmond *et al.*, 1981). The effect can limit carbon uptake by submersed aquatic vegetation because CO_2 diffuses ~10^4 times more slowly in water than in air (Smith and Walker, 1980). In addition, Maberly and Spence (1983) reported that *U. purpurea* Walt. had the lowest ability for ΣCO_2 uptake among fourteen different species of aquatic macrophytes. *U. purpurea* relied solely upon $CO_{2(aq)}$ as a carbon source and was unable to utilize HCO_3^-. At the Point Pelee Marsh, water in channels and ponds has a pH of ~6.9, which results in carbonate equilibria being shifted to favor HCO_3^-. Consequently, ^{13}C-enrichment in Bladderwort at the Point Pelee Marsh may result from a combination of an intrinsically high

CO_2-compensation point (i.e., a poor capacity for CO_2 uptake) coupled with a restricted supply of $CO_{2(aq)}$ because of boundary layer effects and the neutral pH of marsh water.

In general, the degree to which different plants are CO_2-limited will contribute to individual $\delta^{13}C$ variations. At the Point Pelee Marsh, $\delta^{13}C$-values were higher for submerged aquatic plants (–25.6 ± 1.2‰) than for subaerial vegetation on the floating mats (–28.1 ± 0.9‰), suggesting that aquatic flora may have been more carbon-limited. Amongst the submerged aquatic vegetation, algae had the lowest $\delta^{13}C$-values (average –26.9‰), consistent with the report by Maberly and Spence (1983) that phytoplankton possess a superior ability for CO_2 uptake relative to aquatic macrophytes.

Living and dead leaves from Common Cattail at the Point Pelee Marsh have essentially the same $\delta^{13}C$ value (–27.7‰ (average) and –27.6‰, respectively; Table 2); however, their C:N ratios differ significantly (19 (average) and 32, respectively; Table 2). The lower abundance of nitrogen in dead leaves of *Typha* may result from nutrient translocation prior to the onset of winter dormancy (Crum, 1988) or possibly, the early effects of aerobic decomposition. Living tissue from marsh *Typha* has C:N ratios and $\delta^{13}C$ values that are similar to samples from living *Typha* at the Sifton Bog (C:N = 19, $\delta^{13}C$ = –27.6‰, Table 1).

Soil Organic Matter (SOM)

Changes with depth in C:N ratios and $\delta^{13}C$ values are illustrated in Fig. 4. In both wetlands, C:N ratios decrease while SOM becomes more ^{13}C-rich with increasing depth. Microbial consumption of carbon- and hydrogen-rich organic substances (e.g., sugars, starches, cellulose and hemicellulose) results in a decreased abundance of carbon relative to nitrogen. In addition, nitrogen abundance may increase in plant litter during degradation because mineralized nitrogen is retained within microbial biomass (Damman, 1988).

Organic matter in shallow soils at the Point Pelee Marsh has a low $\delta^{13}C$-value (–29.7‰ at 3 cm depth, Table 3) compared with *Typha* (–27.7‰, Table 2), the dominant source of organic detritus.

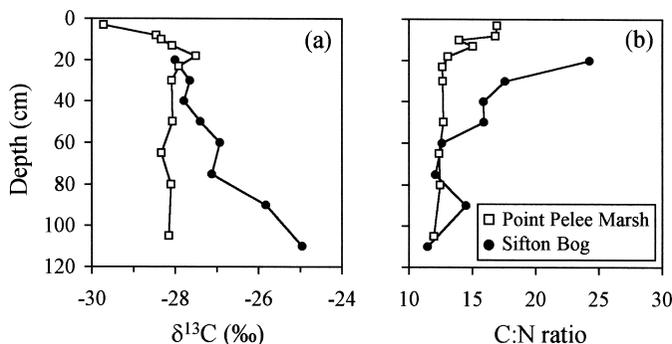*Fig. 4. Depth distribution of (a) $\delta^{13}C$ values, and (b) C:N ratios for organic matter in peat soils at the Sifton Bog (●) and the Point Pelee Marsh (□).*

The ubiquitous brown moss growing on the surface of the floating mats may contribute to the low $\delta^{13}C$-values since it is ^{12}C-enriched (average $\delta^{13}C = -29.3‰$, Table 2) relative to *Typha*. However, the shorter half-life for anaerobic decay of ^{13}C-enriched cellulose and hemicellulose compared to ^{13}C-depleted lignin also can result in a short-term decrease in the $\delta^{13}C$ value of soil organic matter (Benner *et al.*, 1987). Such an effect is unlikely to be observed in bog environments because *Sphagnum* spp. do not contain lignin (Van Breemen, 1995).

Wieder and Yavitt (1994) have also reported a trend of ^{13}C-enrichment in SOM with increasing depth for peatlands situated in West Virginia and Minnesota, USA, and northern Ontario, Canada. In contrast, Waldron *et al.* (1999) measured a decrease in $\delta^{13}C$ values with depth of ~1.5‰ for peat collected from Ellergower Moss, Scotland. From the sparse data that are currently available, it is unclear whether the changes are related to selective decay of biochemical constitutents in plant debris or variable input of plant detritus as wetlands mature and develop different assemblages of flora.

At the Point Pelee Marsh, the C:N ratio and $\delta^{13}C$ value of SOM stabilize at soil depths of ~20 cm (Fig. 4), suggesting that the labile carbon fraction is readily removed from organic detritus derived from *Typha* and other marsh vegetation. In contrast, the C:N ratio and $\delta^{13}C$ value of SOM at the Sifton Bog exhibit a continuous and gradual

change with increasing depth (Fig. 4). Farrish and Grigal (1988) and Thormann *et al.* (1999) have reported differences in the rate of SOM decay between different types of wetlands. In general, anaerobic decay of organic matter is more efficient in minerotrophic than ombrotrophic wetlands, with the result that bogs have a greater potential to accumulate peat than fens or marshes. Van Breemen (1995) suggests that peat accumulation in bogs is primarily the result of the refractory nature of *Sphagnum* litter rather than differences in environmental conditions. The recalcitrance of *Sphagnum* litter is considered to result from chemical protection of cell wall polysaccharides by polymer networks of polyphenolic substances and lipid surface-coatings (Van Breemen, 1995). Sugimoto and Fujita (1997) reported that CH_4 flux was lowest in portions of a temperate-zone wetland dominated by *Sphagnum* moss because the underlying SOM was more recalcitrant than within areas containing predominately marsh vegetation. To eliminate the effects of root exudates on CH_4 production, they used anaerobic incubations of aboveground biomass to demonstrate that decay of *Sphagnum* debris was much slower than that of marsh trefoil and reed material. Although rates of CH_4 production in wetlands can vary as a result of differences in organic substrate, Thormann *et al.* (1999) note that the potential for peat accumulation also depends upon rates of productivity. For example, Vitt (1990) suggests that hummocks generally are

formed in bogs because of low rates of decay while they are maintained in fens largely because of high rates of production.

Finally, the C:N ratio of organic matter below 40 cm of depth at the Sifton Bog is low (<16) for *Sphagnum* peat. Crum (1988) reported that *Sphagnum* peat can have a C:N ratio as high as 60 compared to values of ~20 for peat derived from sedge because the former usually contains a much lower abundance of nitrogen (*Sphagnum* peat ~0.5% N, sedge peat ~5% N). In addition, Warner (1989) reported that *Sphagnum*-dominated peat comprised only the upper 20 cm of a core from the Sifton Bog. Peat from greater depths was mixed in composition, consisting of *Sphagnum*, *Pterocorpus* mosses, and sedge peat. Consequently, the decrease in C:N ratio with depth in soils at the Sifton Bog probably arises in part from paleovegetation changes. Conceivably, the increase in $\delta^{13}C$ values with depth also may result in part from species-dependent changes in plant detritus. Certain flora belonging to the families Cyperaceae and Gramineae utilize the C_4 photosynthetic pathway (Downton, 1975; Raghavendra and Das, 1978), which can lead to higher $\delta^{13}C$ values for soil organic matter.

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