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Modern *Sphagnum* $\delta^{13}C$ signatures follow a surface moisture gradient in two boreal peat bogs, James Bay lowlands, Québec

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ABSTRACT: Carbon isotopic composition of *Sphagnum* macrofossils can potentially be used as a palaeohydrological tool for peat-based climatic studies since a relationship between *Sphagnum* $\delta^{13}C$ values and peatland surface moisture has been presented in previous studies. In order to verify this hypothesis, modern *Sphagnum* $\delta^{13}C$ values were measured along a moisture (microtopographic) gradient in two boreal peat bogs. Isotopic measurements were performed on bulk material of *S. fuscum*, *S. magellanicum*, *S. capillifolium* and S. *pulchrum*. Isotopic variations found within and between *Sphagnum* species along the microtopographic gradient were compared using analysis of variance. A significant positive correlation ($P < 0.0001$) was found between *Sphagnum* $\delta^{13}C$ values and their position along the surface moisture gradient. Results show that ^{13}C-depleted values are related to low water table depths (WTD), while ^{13}C-enriched values correspond to a water table that is close to the peat surface. Although the mechanisms underlying carbon fractionation processes in mosses are not well understood, we demonstrate that water resistance to CO_2 diffusion is an important fractionation process that is observed in bulk *Sphagnum* $\delta^{13}C$ measurements, since drier and wetter samples exhibit consistent and very different isotopic signatures. Copyright © 2008 John Wiley & Sons, Ltd.

KEYWORDS: stable carbon isotopes; ombrotrophic peatland; *Sphagnum*; microtopographic gradient; boreal Quebec.

Introduction

In the boreal region, *Sphagnum* mosses account for about 50% of peatland biomass (Rydin and Jeglum, 2006). Because each species possesses a well-defined ecological range that is primarily based on peatland surface moisture conditions (Gignac, 1994; Bastien and Garneau, 1997), *Sphagnum* macrofossils have been extensively used as eco-hydrological proxy indicators in peat-based hydroclimatic reconstructions (e.g. Barber *et al.*, 1994). However, shortcomings regarding this method have been highlighted and concern, for example, the diversity found within assemblages (Barber *et al.*, 1998), the different decomposition rates between species (Rochefort *et al.*, 1990) or the microhabitat specificities (Lavoie and Richard, 2000).

Owing to the anoxic conditions that prevail in the waterlogged peat masses and to the specific chemical composition of *Sphagnum* mosses, these non-vascular plants exhibit a relatively high resistance to decay (Rochefort *et al.*, 1990; Blodau, 2002). The stable carbon isotopic composition ($\delta^{13}C$) of *Sphagnum* mosses can therefore be preserved within the *Sphagnum* tissues. It then potentially yields information on environmental parameters during moss growth, thus providing datasets that can be corroborated with other peat-based palaeoenvironmental indicators. A few studies have used stable isotope analysis of peat sequences in order to reconstruct Holocene climatic changes (e.g. Aucour and Hillaire-Marcel, 1994; Aucour *et al.*, 1999; White *et al.*, 1994), but a better understanding of processes influencing fractionation in mosses is required to evaluate the potential of *Sphagnum* $\delta^{13}C$[1] values as proxy indicators.

During moss photosynthesis, which follows the C_3 photosynthetic pathway, a primary fractionation occurs through a reaction that involves carbon dioxide from the atmosphere and the Rubisco carboxylation enzyme, since the latter preferentially uses $^{12}CO_2$ (Farquhar *et al.*, 1989). Due to a kinetic effect, a diffusional fractionation that discriminates against heavier CO_2 molecules also occurs.

Because they lack stomata, mosses are unable to regulate their carbon and water uptakes. A superficial water film can

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[1] $\delta^{13}C\ (‰) = ((^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{standard} - 1)1000$, where the standard is V-PDB (Coplen, 1995).

therefore play a key role in moss carbon assimilation by creating an additional resistance to CO_2 diffusion (Rice and Giles, 1996; Rice, 2000; Ménot and Burns, 2001). For example, as the water film increases the resistance to CO_2 uptake, a decline in the carbon isotope discrimination is recorded by plant tissues, leading to higher (less negative) $\delta^{13}C$ values (Farquhar *et al.*, 1989; Rice and Giles, 1994; Price *et al.*, 1997; Ménot and Burns, 2001). Similarly, Rice (2000) suggested that moss CO_2 uptake is reduced when the water content is above a certain optimal value. Inversely, as mosses dry, discrimination against $^{13}CO_2$ increases, leading to lower $\delta^{13}C$ values (Price *et al.*, 1997; Rice, 2000). Other processes leading to carbon isotopic fractionation include (i) moss physiology (Rice and Giles, 1996), (ii) light and temperature regime (Titus and Wagner, 1984; Jedrysek and Skrzypek, 2005), (iii) changes in atmospheric CO_2 concentration (White *et al.*, 1994) and (iv) changes in carbon sources (Farquhar *et al.*, 1989).

Previous studies have shown wide ranges (6–8 ‰) of carbon isotope values for modern *Sphagnum* mosses. Since discrimination against $^{13}CO_2$ during photosynthesis is believed to affect all *Sphagnum* mosses the same way, a narrow range of isotopic signatures across a peatland's surface is expected. The measured wide range of values must then either relate to environmental parameters (light intensity, mean temperature or peat surface moisture level), to species-specific features (photosynthetic cells arrangement) or to both. For example, *Sphagnum fuscum*, *S. capillifolium* (Acutifolia type) and *S. pulchrum* (Cuspidata type) possess triangle-shaped photosynthetic cells that are exposed at the leaf surface (Fig. 1). In contrast, photosynthetic cells of *S. magellanicum* (Sphagnum type) are completely enclosed within water-filled hyaline cells (Fig. 1). It may be assumed that the latter pattern leads to a higher diffusional resistance to CO_2 uptake within the leaves because of the aqueous barrier created by the hyaline cells. However, Rice and Giles (1996) demonstrated that surface water film variations lead to a greater difference in carbon isotope discrimination than species-specific leaf anatomy.

In order to evaluate the potential use of *Sphagnum* $\delta^{13}C$ in palaeohydrological studies, the present study aims to assess the relationship between $\delta^{13}C$ variations within and between *Sphagnum* species along a surface moisture (microtopographic) gradient, since an empirical link was reported between changes in peat bog surface moisture and *Sphagnum* $\delta^{13}C$ by Price *et al.* (1997). The response of modern species-specific mosses to different moisture levels could then be used to interpret $\delta^{13}C$ values obtained from peat bog cores.

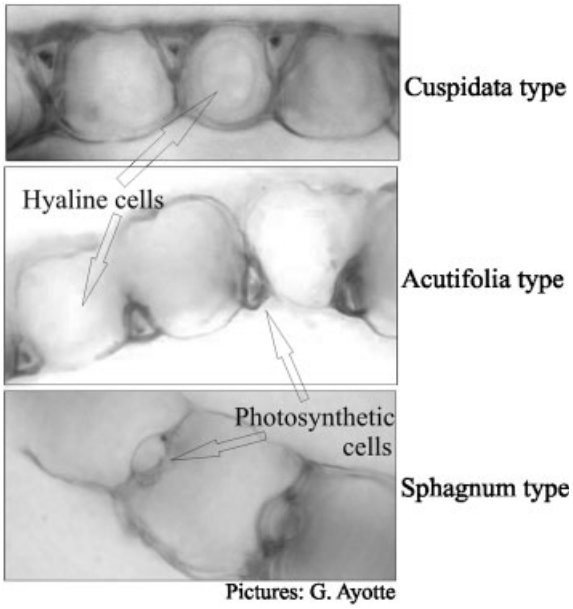

Figure 1 Leaf structure of *Sphagnum* Acutifolia, Cuspidata and Sphagnum types. Photosynthetic and hyaline cells are shown

Methodology

Study sites

Samples were collected in July 2006 in two boreal peat bogs in the James Bay lowlands region of Quebec (Fig. 2). Mean monthly temperature ranges from −23.2°C in January to 13.7°C in July, and mean annual precipitation is 684 mm, of which 267 mm fall as snow (30-year (1971–2000) mean; Environment Canada, 2007). Both Lac Le Caron Bog (52° 17′ N, 75° 50′ W, 248 m above mean sea level (a.m.s.l.)) and Mosaik Bog (51° 58′ N, 75° 24′ W, 297 m a.m.s.l.) cover approximately 2.5 km^2. They have a well-developed hummock–hollow patterned surface, where hummock height ranges between 25 and 50 cm above the peat surface. Vegetation is dominated by ericaceous shrubs such as *Chamaedaphne calyculata*, *Kalmia angustifolia*, *Ledum groenlandicum* and *Andromeda glaucophylla*. The ground layer is largely covered by the following Sphagnaceae: *Sphagnum fuscum*, *S. capillifolium*, *S. magellanicum*, *S. rubellum*, *S. pulchrum*, *S. teres*, *S. majus* and *S. lindbergii*, following the microtopographic gradient. Water table depth (WTD) measurements were performed every 2 weeks throughout the 2006 and 2007 growing seasons (Pelletier, unpublished data), and the measurements used in this paper approximately reflect mean summer WTD.

Field sampling and *Sphagnum* $\delta^{13}C$ analyses

In order to assess the relationship between *Sphagnum* $\delta^{13}C$ values and WTD, four sampling sites with similar light were chosen within each peatland. At each of these sites, the three following microforms were sampled and replicated: a hummock (U), a hollow (O) and a lawn (L), which represents an intermediate microtopographic form. In total, 12 microforms were sampled within each of the two peatlands. Because they constitute the most representative *Sphagnum* species within the studied region, *S. capillifolium* (U), *S. fuscum* (U and L), *S. magellanicum* (L and O) and *S. pulchrum* (O) were chosen. All sites had ambient surface temperature regimes.

For each sampled microform (24 in total), WTD measurements and 1 m^2 vegetation relevés were processed. Peat samples (~950 cm^3) were carefully removed from the surface and stored at 4°C in cylindrical plastic containers. *Sphagnum* mosses were picked out of the peat samples, and the top 3–4 cm of the specimens (including the capitulum) were separated, washed with deionised water, freeze dried and ground. Isotopic measurements were performed with a Carlo Erba NC 1500™ elemental analyser coupled to a Micromass Isoprime™ infrared mass spectrometer in continuous-flow mode (GEOTOP, Montreal). The resulting carbon isotope ratios were calibrated against V-PDB and duplicates were processed at 10 sample increments. The analytical error was ±0.1‰ and reproducibility was better than ± 0.04‰. A one-way analysis of variance (ANOVA) was conducted to compare *Sphagnum* isotopic signature differences found within and between species along the microtopographic gradient. r^2 values were obtained for each of the two groups of variables (species and

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Figure 2 James Bay lowlands region and peatlands location

microform) through ANOVA by dividing the sum of the squares (SS) of each group by the total SS ($r^2 = \text{SS(group)/SS(total)}$).

Results and discussion

Sphagnum δ^{13}C values

Table 1 and Figure 3 present *Sphagnum* δ^{13}C values and their relative position along the hummock–hollow gradient for both studied peatlands. The average δ^{13}C value recorded was −26.3‰, and the results together conform to the C_3 fractionation pathway. There is no significant difference in the values for both peatlands, where results ranged from −30.2‰ to −25.2‰ for the Lac Le Caron Bog, and from −30.4‰ to −24.0‰ for the Mosaik Bog (Table 1). For both sites, mean δ^{13}C values obtained for hummock, lawn and hollow species are respectively −28.5‰, −26.8‰ and −26.6‰, with average standard deviations of 0.9 for hummocks, 0.7 for lawns and 1.5 for hollows (Table 2). Tables 1 and 2 present additional information regarding the number of samples that were analysed as well as WTD measurements.

Variations found along the microtopographic gradient

ANOVA were based on a combination of total data from both peatlands and revealed that hummock *Sphagnum* δ^{13}C values were significantly lower than those found within the other microforms ($P < 0.0001$). Hummock mosses were characterised by WTD that ranged between −40 and −21 cm (lowest recorded value = 15 cm), meaning that they photosynthesised with a low external diffusion resistance. The isotopic signatures recorded for lawn and hollow species were significantly heavier than those from hummock species ($P < 0.0001$), which is consistent with the hypothesis that less discrimination against ^{13}C occurs in *Sphagnum* under a thicker water film. WTD values ranged from −12 to −3 cm for lawns (highest and lowest recorded values = 15 and 0 cm, respectively), while at the peat surface (−1 to 0 cm, with a maximum of +4 cm) in hollows. However, differences in the isotopic signature of lawn and hollow mosses were not statistically significant. In fact, results show that hollow species experienced a very wide range of values (5.5‰) and a large standard deviation (1.48) when compared to lawn species (3.2 ‰ and 0.68, respectively).

A few studies have suggested that carbon isotopic signatures measured for hollow mosses can be influenced by a combination of the following mechanisms: (1) Bryophyte canopy structure – hollow mosses are more sensitive to water table changes than hummock and lawn mosses since they are directly surrounded by water, have less developed capillary water transport systems, have a smaller water-holding capacity and reside in a more open carpet (Titus and Wagner, 1984; Rice, 2000; Gauthier, 2001). The δ^{13}C signature of hollow species is hence likely to fluctuate more often, leading to a wider range of δ^{13}C values. (2) *Sphagnum* carbon sources – although mosses primarily take up their carbon from the atmosphere, hollow species are likely to take up dissolved inorganic carbon forms (DIC) from the surrounding water (Price *et al.*, 1997; Raghoebarsing *et al.*, 2005). The highly varying isotopic signature of the dissolved inorganic carbon can hence impact on δ^{13}C values of partially submerged mosses (Dever *et al.*, 1982; Proctor *et al.*, 1992). (3) Methane consumption – Raghoebarsing *et al.* (2005) found that some submerged *Sphagnum* species consume CH_4 through symbiosis with methanotrophic bacteria that live on stem leaves and in hyaline cells. Methane is very depleted in the heavier isotope and might account for as much as 5–20% of the total carbon uptake of mosses, thus affecting their isotopic signatures.

Although it is clear with the current dataset that peat surface moisture significantly influences *Sphagnum* δ^{13}C values, the mechanisms presented above can complicate the interpretation of carbon isotopic signatures of hollow species. A better comprehension of these processes is inherent in the use

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Table 1 *Sphagnum* $\delta^{13}C$ values and relative position in the hummock–hollow gradient

Lac Le Caron Bog					Mosaik Bog				
Sample	Species	Microform	$\delta^{13}C$ vs. V-PDB (‰)	WTD (cm)	Sample	Species	Microform	$\delta^{13}C$ vs. V-PDB (‰)	WTD (cm)
LMA B1 SF2	*S. fuscum*	Hummock	−29.0	−21	MMA B1 SF1	*S. fuscum*	Hummock	−30.4	−37
LMA B1 SF3	*S. fuscum*	Hummock	−28.6	−21	MMA B1 SF2	*S. fuscum*	Hummock	−28.5	−37
LMA B1 SC2	*S. capillifolium*	Hummock	−29.4	−21	MMA B1 SC2	*S. capillifolium*	Hummock	−28.8	−37
LMA P1 SF1	*S. fuscum*	Lawn	−26.9	−7	MMA B1 SC3	*S. capillifolium*	Hummock	−29.2	−37
LMA P1 SF2	*S. fuscum*	Lawn	−26.7	−7	MMA P1 SF1	*S. fuscum*	Lawn	−27.6	−10
LMA P1 SM2	*S. magellanicum*	Lawn	−26.4	−7	MMA P1 SF2	*S. fuscum*	Lawn	−26.4	−10
LMA P1 SM3	*S. magellanicum*	Lawn	−26.3	−7	MMA P1 SM1	*S. magellanicum*	Lawn	−28.3	−10
LMA D1 SM2	*S. magellanicum*	Hollow	−26.3	0	MMA P1 SM7	*S. magellanicum*	Lawn	−27.7	−10
LMA D1 SM3	*S. magellanicum*	Hollow	−25.5	0	MMA D1 SM1	*S. magellanicum*	Hollow	−26.8	0
LMA D1 SP2	*S. pulchrum*	Hollow	−26.0	0	MMA D1 SM3	*S. magellanicum*	Hollow	−26.7	0
LMA D1 SP3	*S. pulchrum*	Hollow	−26.3	0	MMA D1 SP1	*S. pulchrum*	Hollow	−27.7	0
LMA B2 SF1	*S. fuscum*	Hummock	−29.6	−25	MMA D1 SP2	*S. pulchrum*	Hollow	−27.8	0
LMA B2 SF5	*S. fuscum*	Hummock	−29.7	−25	MMA D1 SP3	*S. pulchrum*	Hollow	−28.4	0
LMA B2 SC2	*S. capillifolium*	Hummock	−28.6	−25	MMA B2 SF1	*S. fuscum*	Hummock	−28.8	−40
LMA B2 SC3	*S. capillifolium*	Hummock	−30.2	−25	MMA B2 SF2	*S. fuscum*	Hummock	−29.2	−40
LMA P2 SF1	*S. fuscum*	Lawn	−27.6	−4	MMA B2 SC1	*S. capillifolium*	Hummock	−28.7	−40
LMA P2 SF4	*S. fuscum*	Lawn	−26.6	−4	MMA B2 SC2	*S. capillifolium*	Hummock	−28.7	−40
LMA P2 SM2	*S. magellanicum*	Lawn	−27.1	−4	MMA P2 SF2	*S. fuscum*	Lawn	−27.2	−5
LMA P2 SM3	*S. magellanicum*	Lawn	−26.5	−4	MMA P2 SF3	*S. fuscum*	Lawn	−26.7	−5
LMA D2 SM1	*S. magellanicum*	Hollow	−29.5	0	MMA P2 SM2	*S. magellanicum*	Lawn	−27.5	−5
LMA D2 SM2	*S. magellanicum*	Hollow	−29.2	0	MMA P2 SM6	*S. magellanicum*	Lawn	−26.3	−5
LMA D2 SP1	*S. pulchrum*	Hollow	−26.7	0	MMA D2 SM1	*S. magellanicum*	Hollow	−25.8	0
LMA D2 SP2	*S. pulchrum*	Hollow	−27.8	0	MMA D2 SM3	*S. magellanicum*	Hollow	−24.1	0
LMA D2 SP3	*S. pulchrum*	Hollow	−27.8	0	MMA D2 SP1	*S. pulchrum*	Hollow	−23.3	0
LRI B1 SF1	*S. fuscum*	Hummock	−27.2	−35	MMA D2 SP3	*S. pulchrum*	Hollow	−24.0	0
LRI B1 SF3	*S. fuscum*	Hummock	−27.1	−35	MRI B1 SF2	*S. fuscum*	Hummock	−28.4	−35
LRI B1 SC1	*S. capillifolium*	Hummock	−27.4	−35	MRI B1 SF3	*S. fuscum*	Hummock	−28.2	−35
LRI B1 SC2	*S. capillifolium*	Hummock	−27.4	−35	MRI B1 SC1	*S. capillifolium*	Hummock	−27.9	−35
LRI P1 SF1	*S. fuscum*	Lawn	−26.4	−8	MRI B1 SC4	*S. capillifolium*	Hummock	−27.5	−35
LRI P1 SF2	*S. fuscum*	Lawn	−26.0	−8	MRI P1 SF2	*S. fuscum*	Lawn	−26.4	−16
LRI P1 SM1	*S. magellanicum*	Lawn	−26.2	−8	MRI P1 SF3	*S. fuscum*	Lawn	−27.0	−16
LRI P1 SM3	*S. magellanicum*	Lawn	−26.9	−8	MRI P1 SM1	*S. magellanicum*	Lawn	−26.7	−12
LRI D1 SM2	*S. magellanicum*	Hollow	−26.3	0	MRI P1 SM3	*S. magellanicum*	Lawn	−27.1	−12
LRI D1 SM3	*S. magellanicum*	Hollow	−25.2	0	MRI D1 SM1	*S. magellanicum*	Hollow	−26.2	0
LRI D1 SP1	*S. pulchrum*	Hollow	−25.8	0	MRI D1 SM2	*S. magellanicum*	Hollow	−25.9	0
LRI D1 SP2	*S. pulchrum*	Hollow	−26.1	0	MRI D1 SM3	*S. magellanicum*	Hollow	−25.5	0
LRI B2 SF1	*S. fuscum*	Hummock	−28.3	−40	MRI D1 SP2	*S. pulchrum*	Hollow	−28.8	0
LRI B2 SF3	*S. fuscum*	Hummock	−28.0	−40	MRI D1 SP4	*S. pulchrum*	Hollow	−26.6	0
LRI B2 SC1	*S. capillifolium*	Hummock	−27.8	−36	MRI B2 SF1	*S. fuscum*	Hummock	−27.2	−36
LRI B2 SC2	*S. capillifolium*	Hummock	−28.5	−36	MRI B2 SF2	*S. fuscum*	Hummock	−27.6	−36
LRI P2 SF1	*S. fuscum*	Lawn	−26.2	−6	MRI B2 SC1	*S. capillifolium*	Hummock	−28.9	−36
LRI P2 SF3	*S. fuscum*	Lawn	−27.2	−6	MRI B2 SC2	*S. capillifolium*	Hummock	−29.2	−36
LRI P2 SM2	*S. magellanicum*	Lawn	−26.8	−3	MRI P2 SF1	*S. fuscum*	Lawn	−25.3	−12
LRI P2 SM3	*S. magellanicum*	Lawn	−27.2	−3	MRI P2 SF2	*S. fuscum*	Lawn	−25.1	−12
LRI D2 SM1	*S. magellanicum*	Hollow	−25.9	0	MRI P2 SM1	*S. magellanicum*	Lawn	−27.2	−12
LRI D2 SM2	*S. magellanicum*	Hollow	−25.3	0	MRI D2 SM1	*S. magellanicum*	Hollow	−26.6	0
LRI D2 SP1	*S. pulchrum*	Hollow	−26.6	0	MRI D2 SM3	*S. magellanicum*	Hollow	−26.7	0
LRI D2 SP6	*S. pulchrum*	Hollow	−28.5	0	MRI D2 SP1	*S. pulchrum*	Hollow	−29.4	0
					MRI D2 SP3	*S. pulchrum*	Hollow	−27.4	0

of *Sphagnum* $\delta^{13}C$ values as palaeohydrological proxy indicators.

Variations found within species

Results obtained for *Sphagnum fuscum* clearly indicate that isotopic signatures recorded within each species are more related to the water resistance to CO_2 diffusion than to species-specific leaf anatomy (Table 1). Significantly lighter isotopic signatures were measured for hummock samples (average: −28.5‰; data ranged from −30.4‰ to −27.1‰), and heavier values were obtained for lawn specimens (average: −26.7‰; data ranged from −27.6‰ to −25.1‰). *Sphagnum magellanicum* samples also showed interesting patterns along the moisture gradient (Table 1). While averaged isotopic signatures found within lawn (−27.0‰) and hollow (−26.3‰) samples were not statistically different, lawn specimens presented constrained values (from −28.3‰ to −26.2‰) and hollow specimens scattered values (from −29.5‰ to −24.1 ‰).

Overall, variations found within *Sphagnum fuscum* and *S. magellanicum* are in accordance with the results found within the microtopographic gradient. These results also demonstrate that *Sphagnum* $\delta^{13}C$ values can be better explained by the microtopographic position within the hummock–hollow gradient than by species-specific features ($r^2 = 0.39$ and 0.23, respectively).

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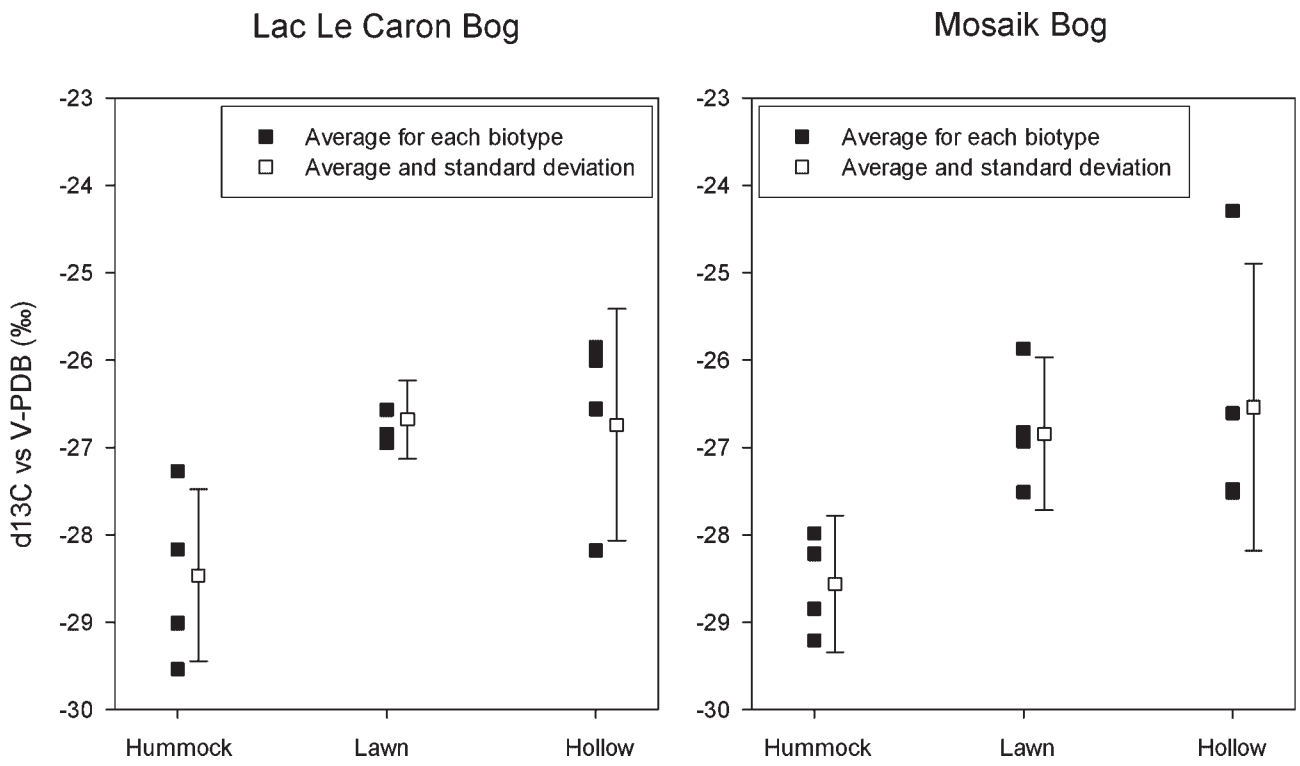

Figure 3 *Sphagnum* δ^{13}C values and relative position in the hummock–hollow gradient

Table 2 Sphagnum δ^{13}C values: averages and standard deviations

Peatland	Set	Microform	Average δ^{13}C (‰ vs. V-PDB)	SD	Number of samples
Lac Le Caron Bog	LMa B1	Hummock	−29.0	0.4	3
	LMa P1	Lawn	−26.6	0.3	4
	LMa D1	Hollow	−26.0	0.4	4
	LMa B2	Hummock	−29.5	0.7	4
	LMa P2	Lawn	−27.0	0.5	4
	LMa D2	Hollow	−28.2	1.2	5
	LRi B1	Hummock	−27.3	0.1	4
	LRi P1	Lawn	−26.9	0.4	4
	LRi D1	Hollow	−25.9	0.5	4
	LRi B2	Hummock	−28.2	0.3	4
	LRi P2	Lawn	−26.9	0.5	4
	LRi D2	Hollow	−26.6	1.4	4
Mosaik Bog	MMa B1	Hummock	−29.2	0.8	4
	MMa P1	Lawn	−27.5	0.8	4
	MMa D1	Hollow	−27.5	0.7	5
	MMa B2	Hummock	−28.8	0.3	4
	MMa P2	Lawn	−26.9	0.5	4
	MMa D2	Hollow	−24.3	1.1	4
	MRi B1	Hummock	−28.0	0.4	4
	MRi P1	Lawn	−26.8	0.3	4
	MRi D1	Hollow	−26.6	1.3	5
	MRi B2	Hummock	−28.2	1.0	4
	MRi P2	Lawn	−25.9	1.2	3
	MRi D2	Hollow	−27.5	1.3	4

Conclusion

As seen in previous studies (e.g. Rundel *et al.*, 1979; Price *et al.*, 1997), *Sphagnum* species that were analysed showed a wide range of δ^{13}C values (~6‰). Hummock species presented a larger discrimination against the heavier isotope than lawn and hollow species, which is consistent with a lower water content on hummocks and hence an 'easier' CO_2 diffusion through photosynthetic cells.

The greatest range of isotopic values was found in hollow species. The heaviest isotopic values from this microform are associated with the thick water film, which increases resistance to CO_2 diffusion, while the lighter values might be explained by a carbon source depleted in ^{13}C (DIC or CH_4, for example). A few studies also pinpointed that desiccation, which is more likely to occur in hollows, leads to an increased discrimination against the heavier isotope (Williams and Flanagan, 1996; Ménot and Burns, 2001), implying that the depleted values recorded by mosses growing in hollows can be due to a

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fluctuating water table and to an indirect effect of moisture and temperature on their metabolic activity. Overall, our surface results demonstrate potential for application in palaeohydrological reconstructions based on stable carbon isotope analysis of *Sphagnum* preserved in peat, since drier and wetter samples showed different and consistent isotopic signatures. In such reconstructions, one should assume, however, that (i) diagenesis did not alter *Sphagnum* $\delta^{13}C$ values through time, and (ii) no important shifts in surface microforms have occurred on the site during *Sphagnum* growth and peat accumulation. For example, if a peat core is to be collected from a lawn, plant macrofossil analysis on this core should be conducted both to determine whether the actual lawn has always been one and to allow comparison of the isotopic results. *Sphagnum* $\delta^{13}C$ values are expected to provide complementary information to plant macrofossil reconstructions since, as shown in this paper, the isotopic signature of mosses seems more responsive to hydrological parameters than to species-specific features. Further analyses are needed, however, to better understand mechanisms underlying fractionation processes within moss tissues during plant growth as well as during decay, although Jedrysek and Skrypek (2005) and Aucour and Hillaire-Marcel (1994) suggested that $\delta^{13}C$ records in peat are not (or only slightly) modified by diagenetic processes.

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References

Aucour A-M, Hillaire-Marcel C. 1994. Late Quaternary biomass changes from ^{13}C measurements in a highland peatbog from Equatorial Africa (Burundi). *Quaternary Research* **41**: 225–233.

Aucour A-M, Bonnefille R, Hillaire-Marcel C. 1999. Sources and accumulation rates of organic carbon in an equatorial peat bog (Burundi, East Africa) during the Holocene: carbon isotope constraints. *Palaeogeography, Palaeoclimatology, Palaeoecology* **150**: 179–189.

Barber K, Chambers FM, Maddy D, Stoneman R, Brew JS. 1994. A sensitive high-resolution record of late Holocene climatic change from a raised bog in northern England. *The Holocene* **4**: 198–205.

Barber K, Dumayne-Peaty L, Hughes P, Mauquoy D, Scaife R. 1998. Replicability and variability of the recent macrofossil and proxy-climate record from raised bogs: field stratigraphy and macrofossil data from Bolton Fell Moss and Walton Moss, Cumbria, England. *Journal of Quaternary Sciences* **13**: 515–528.

Bastien DL, Garneau M. 1997. *Guide d'identification macroscopique des principales espèces de sphaignes rencontrées dans l'est du Canada*. Report 61, Geological Survey of Canada, Natural Resources Canada, Canada.

Blodau C. 2002. Carbon cycling in peatlands: a review of processes and controls. *Environmental Reviews* **10**: 111–134.

Coplen T. 1995. The discontinuance of SMOW and PDB. *Nature* **375**: 285.

Dever L, Laithier M, Hillaire-Marcel C. 1982. Caractéristiques isotopiques (^{18}O, $^{13}CO_2$, ^{3}H) des écoulements dans une tourbière sur pergélisol au Nouveau-Québec. *Canadian Journal of Earth Sciences* **19**: 1255–1263.

Environment Canada. 2007. Canadian climate normals or averages 1971–2000. www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html [23 September 2007].

Farquhar GD, Ehleringer JR, Hubick KT. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* **40**: 503–537.

Gauthier R. 2001. Les sphaignes. In *Écologie des tourbières du Québec-Labrador*, Payette S, Rochefort L (eds). Les Presses de l'Université Laval: Lavel, Québec; 91–128.

Gignac LD. 1994. Peatland species preferences: an overview of our current knowledge base. *Wetlands* **14**: 216–222.

Jedrysek M-O, Skrypek G. 2005. Hydrogen, carbon and sulphur isotope ratios in peat: the role of diagenesis and water regimes in reconstruction of past climates. *Environmental Chemistry Letters* **2Q**: 179–183.

Lavoie M, Richard PJH. 2000. The role of climate on the developmental history of Frontenac Peatland, southern Quebec. *Canadian Journal of Botany* **78**: 668–684.

Ménot G, Burns SJ. 2001. Carbon isotopes in ombrogenic peat bog plants as climatic indicators: calibration from an altitudinal transect in Switzerland. *Organic Geochemistry* **32**: 233–245.

Price GD, McKenzie JE, Pilcher JR, Hoper ST. 1997. Carbon-isotope variation in *Sphagnum* from hummock-hollow complexes: implications for Holocene climate reconstruction. *The Holocene* **7**: 229–233.

Proctor MCF, Raven JA, Rice SK. 1992. Stable carbon isotope discrimination measurements in *Sphagnum* and other bryophytes: physiological and ecological implications. *Journal of Bryology* **17**: 193–202.

Raghoebarsing AA, Smolders AJP, Schmid MC, Rijpstra WIC, Wolters-Arts M, Derksen J, Jetten MSM, Schouten S, Damste JSS, Lamers LPM, Roelofs JGM, op den Camp H, Strous M. 2005. Methanotrophic symbionts provide carbon for photosynthesis in peat bogs. *Nature* **436**: 1153–1156.

Rice SK. 2000. Variation in carbon isotope discrimination within and among *Sphagnum* species in a temperate wetland. *Oecologia* **123**: 1–8.

Rice SK, Giles L. 1994. Climate in the Pleistocene. *Nature* **371**: 111.

Rice SK, Giles L. 1996. The influence of water content and leaf anatomy on carbon isotope discrimination and photosynthesis in *Sphagnum*. *Plant, Cell and Environment* **19**: 118–124.

Rochefort L, Vitt DH, Bayley SE. 1990. Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. *Ecology* **7**: 1986–2000.

Rundel PW, Rundel JA, Ziegler H, Stichler W. 1979. Carbon isotope ratios of Central Mexican Crassulaceae in natural and greenhouse environments. *Oecologia* **38**: 45–50.

Rydin H, Jeglum J. 2006. *The Biology of Peatlands*. Oxford University Press: New York.

Titus JE, Wagner DJ. 1984. Carbon balance for two *Sphagnum* mosses: water balance resolves a physiological paradox. *Ecology* **65**: 1765–1774.

White JWC, Ciais P, Figge RA, Kenny R, Markgraf V. 1994. A high-resolution record of atmospheric CO_2 content from carbon isotopes in peat. *Nature* **367**: 153–156.

Williams TG, Flanagan LB. 1996. Effect of changes in water content on photosynthesis, transpiration and discrimination against $^{13}CO_2$ and $C^{18}O^{16}O$ in *Pleurozium* and *Sphagnum*. *Oecologia* **108**: 38–46.