

Sensitivity of spectral indices to CO₂ fluxes for several plant communities in a *Sphagnum*-dominated peatland

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Abstract. Peatlands may play an important role in global carbon cycles, and thus developing better estimates of carbon exchange in those ecosystems has become a main concern. In this study, the relationship between spectral indices and CO₂ fluxes was tested for different communities in a *Sphagnum*-dominated peatland. Fluxes were measured with a portable climate-controlled chamber while reflectance was simultaneously recorded using a hand-held spectroradiometer. A laboratory experiment was also conducted to select the water-related index most correlated with *Sphagnum* water content to regulate the normalized difference vegetation index (NDVI) values obtained in the field. The laboratory experiment showed a strong correlation between *Sphagnum* water content and all spectral indices, namely the water index (WI), normalized difference water index (NDWI), and relative depth index (RDI) ($r = 0.753\text{--}0.993$). WI was the index selected for regulating NDVI values. Indices tested in the field for CO₂ flux estimations were (i) NDVI, (ii) NDVI/WI, (iii) NDVI \times sPRI (photochemical reflectance index), and (iv) the chlorophyll indices CI and CIm. NDVI alone was a poor predictor of net ecosystem exchange (NEE, $r^2 = 0.12$) and gross photosynthesis (P_G , $r^2 = 0.15$), and NDVI \times sPRI and NDVI/WI showed moderate adjustments to CO₂ fluxes (NEE, $r^2 = 0.26$ and 0.30 ; P_G , $r^2 = 0.38$ and 0.43 , respectively, for each index). The relationship between CO₂ fluxes and chlorophyll indices was reasonably well adjusted (CI and NEE, $r^2 = 0.37$; CI and P_G , $r^2 = 0.55$; CIm and NEE, $r^2 = 0.38$; CIm and P_G , $r^2 = 0.57$), and these indices may be the most promising for mapping the spatial distribution of CO₂ fluxes in the future.

Résumé. Un intérêt s'est développé récemment pour les techniques d'estimation des échanges de carbone dans les tourbières. Nous avons testé la relation directe entre les flux de CO₂ et plusieurs indices spectraux pour différentes communautés dans une tourbière à sphaignes. Les flux ont été mesurés avec une chambre de climat contrôlé alors que la réflectance spectrale a été enregistrée simultanément avec un spectroradiomètre portable. Une expérience de laboratoire a aussi été réalisée pour sélectionner un indice relié à la teneur en eau des sphaignes afin d'ajuster les valeurs de NDVI (« normalized difference vegetation index ») obtenues sur le terrain. Cette expérience a montré des corrélations très fortes entre la teneur en eau des sphaignes et tous les indices spectraux testés (WI, « water index »; NDWI, « normalized difference water index »; et RDI, « relative depth index »; $r = 0,753$ à $0,993$). WI fut l'indice sélectionné pour ajuster les valeurs de NDVI. Les indices testés sur le terrain étaient donc : (i) NDVI, (ii) NDVI/WI, (iii) NDVI \times sPRI (« photochemical reflectance index ») et (iv) CI et CIm (« chlorophyll indices »). Le NDVI seul s'est avéré être un mauvais indicateur de l'échange écosystémique net (NEE, $r^2 = 0,12$) et de l'absorption brute (P_G , $r^2 = 0,15$) alors que NDVI \times sPRI et NDVI/WI présentaient des ajustements modérés aux flux de CO₂ (NEE, $r^2 = 0,26$ et $0,30$; P_G , $r^2 = 0,38$ et $0,43$). La relation entre les flux de CO₂ et les indices CI et CIm était bonne (CI et NEE, $r^2 = 0,37$; CI et P_G , $r^2 = 0,55$; CIm et NEE, $r^2 = 0,38$; CIm et P_G , $r^2 = 0,57$) et ces indices pourraient être prometteurs pour cartographier les flux de CO₂ à grande échelle dans le futur.

Introduction

The postglacial carbon accumulation in boreal and subarctic peatlands represents approximately 30% (approx. 455 Pg; Gorham, 1991) of the global pool of soil carbon (Post et al., 1982), and yet the carbon balance of peatlands in the northern hemisphere varies through space and time (Roulet, 2000). In that respect, CO₂ fluxes, which are important carbon fluxes in peatlands, vary according to many factors, including photosynthetically active radiation (PAR), vegetation type and biomass, water table depth, and air and soil temperature

(Shurpali et al., 1995; Frokling et al., 1998; Bubier et al., 2003a; 2003b). In addition to the huge amount of the carbon pool stored in peat deposits, this great variability of CO₂ fluxes underlines the importance of developing better estimates of CO₂ exchange in peatlands.

Over the last few decades, remote sensing has been proposed as a tool to acquire information on carbon cycling in boreal ecosystems. Advances in land cover mapping (e.g., Zarco-Tejada and Miller, 1999; Fuentes et al., 2001) offer the possibility to assign measured CO₂ fluxes to large areas for which vegetation has been mapped. On the other hand, gross

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CO₂ flux mapping can be done by directly linking fluxes to spectral indices (e.g., Rahman et al., 2001). This recently developed method may facilitate the upscaling of carbon flux estimations in the future. Our study focuses on this last method, that is, the direct relationship between CO₂ fluxes and spectral indices in peatlands, at a single site for different communities.

Numerous spectral indices have been developed based on their association with vegetation parameters and could be of interest for tracking CO₂ fluxes. The normalized difference vegetation index (NDVI), developed by Rouse et al. (1974), and other indices related to the ratio of near-infrared (NIR) reflectance to red reflectance are the most widely used indices in vegetation studies. NDVI has been associated with both structural (biomass) and physiological (chlorophyll content, water stress) properties of vegetation (Tucker, 1979; Peñuelas et al., 1993a) and to the photosynthetically active radiation absorbed (APAR) by green vegetation (Sellers, 1985; Bartlett et al., 1990). Since APAR is linked to vegetation photosynthetic capacity, NDVI has been considered promising for CO₂ flux inferences (Tucker et al., 1986; Bartlett et al., 1990). In natural ecosystems dominated by vegetation that is structurally similar to peatland vegetation, ground-based NDVI has been directly linked to CO₂ fluxes measured with chamber techniques. For instance, Bartlett et al. (1990) showed that NDVI was near-linearly related to the net ecosystem exchange (NEE) of a homogeneous canopy of *Spartina alterniflora*, a wetland grass. As well, NDVI has been shown to be a good predictor of NEE, gross photosynthesis, and total respiration of tundra ecosystems (Whiting et al., 1992; McMichael et al., 1999; Boelman et al., 2003).

However, results from Whiting (1994) showed broadband NDVI to be an inadequate predictor of NEE when measured along a minerotrophic–ombrotrophic gradient in a peatland complex: one plot with high *Sphagnum* cover had particularly high NDVI values compared with other plots characterized by vascular plants and even brown mosses. *Sphagnum* is a dominant moss in ombrotrophic peatlands (bogs) and is a key plant responsible for peat accumulation processes. It may also be abundant in minerotrophic peatlands (fens). As the study of Whiting did not focus on *Sphagnum* mosses, we need to further investigate the link between CO₂ fluxes and spectral indices in the presence of *Sphagnum* mosses.

In the present study, we focussed on a remote sensing approach that attempts to directly link spectral indices to CO₂ fluxes. Such studies could highlight the potential of remote sensing for mapping the spatial distribution of CO₂ fluxes. With a hand-held spectroradiometer, we assessed the possibility of using spectral indices to estimate CO₂ fluxes in *Sphagnum*-dominated peatlands (bogs). We tested different spectral indices and combinations of indices for different communities in a boreal peatland. One of the combinations included an index related to water content, as we hypothesized that it would improve the relationship with CO₂ fluxes when *Sphagnum* mosses are present. The spectral reflectance of *Sphagnum* mosses is strongly influenced by their water content (Vogelmann and Moss, 1993; Bubier et al., 1997). It has been

shown that spectral indices developed to track leaf water content are strongly correlated with both near-surface *Sphagnum* water content in *Sphagnum* cores analysed in the laboratory (Bryant and Baird, 2003; Harris et al., 2005) and near-surface hydrological conditions of *Sphagnum* patches in the field (Harris et al., 2006). Due to the high water holding capacity of *Sphagnum* mosses (Vitt, 2000), we hypothesized that normalizing NDVI by an index related to water content would correct the high NDVI values revealed by Whiting (1994). To find the best water-related index, we therefore conducted a laboratory experiment on the correlation between *Sphagnum* water content and several spectral indices known to respond to water content. The specific objectives were (i) to conduct a laboratory experiment for selecting the water-related index most correlated with *Sphagnum* water content for the particular species found at the study site, and (ii) to conduct a field survey to test the relationship between CO₂ fluxes (net ecosystem exchange, gross photosynthesis) and different spectral indices and combinations of these indices extracted from ground-based reflectance in diverse bog communities.

Methods

Laboratory experiment

The aim of this laboratory experiment was to select a spectral index strongly correlated with *Sphagnum* water content for *Sphagnum* species in boreal peatlands. This index was required for field applications to test if it could improve the relationship between CO₂ fluxes and NDVI by normalizing NDVI with an index related to *Sphagnum* water content.

Pure *Sphagnum* samples were collected at the Pointe-Label peatland (see the Field survey section for a description of the site). Four species (*Sphagnum rubellum* Wils., *Sphagnum fuscum* (Schimp.) Klinggr., *Sphagnum magellanicum* Brid., and *Sphagnum fallax* (Klinggr.) Klinggr.) were studied using four replicates for a total of 16 samples. Samples were collected in circular metal cores 10 cm in diameter and 3.7 cm in height that were painted matte black (Vogelmann and Moss, 1993; Bubier et al., 1997). The water holding capacity of *Sphagnum* varies with depth, even in the first centimetres (Hayward and Clymo, 1982; Yoshikawa et al., 2004). Thus a low core height was chosen to reduce the humidity gradient between the top and bottom of the *Sphagnum* cores. For *S. rubellum* and *S. fuscum*, samples were collected by inserting the core in the *Sphagnum* carpet. For *S. magellanicum* and *S. fallax*, the carpets were looser, and *Sphagnum* stems were collected and reorganized individually in the cores in slightly denser communities than in natural carpets. In all cores, *Sphagnum* stems were orientated vertically with capitula on top (Vogelmann and Moss, 1993; Bubier et al., 1997). The top and bottom of the stems were levelled with the core to avoid microtopography problems with reflectance measurements in the laboratory. Samples were kept moist during transport to the laboratory. Prior to the experiment, *Sphagnum* cores were immersed in deionized water for 60–90 min to reach maximum water content. During

the experiment, *Sphagnum* cores were left to dry for 180 h in a growth cabinet (19–20 °C and 57%–60% relative humidity) under constant neon lighting. Every 12 h, spectral reflectance and wet weight were taken for all *Sphagnum* cores. At the end of the experiment, the *Sphagnum* samples were oven dried (60 °C) to a constant weight. Wet and dry weights were used to calculate the gravimetric water content at each stage of the drying process. The gravimetric water contents were then converted to volumetric water contents (VWC). The following equation was used to obtain VWC values:

$$\text{VWC} = \frac{[(\text{wet weight} - \text{dry weight}) / (\text{total } Sphagnum \text{ core volume})] / \rho_{\text{water}}}{1} \quad (1)$$

where ρ_{water} is the density of water (assumed equal to 1 g·cm⁻³).

Spectral measurements were made with the same instrument used for field measurements (see the Field survey section), namely an Analytical Spectral Devices, Inc. (Boulder, Colo.) FieldSpec Pro Spectroradiometer, which records data in the 350–2500 nm spectral region. The instrument has a spectral resolution of approximately 3 nm around 700 nm and 10–12 nm between 900 and 2500 nm. Measurements were done in a darkroom where the only light was provided by a halogen lamp (600 W) orientated at a 45° angle to the core surface at a distance of 40 cm. The head of the optic fibre was held by a fixed stand 15 cm from the core surface, forming a circular target of 6.7 cm in diameter. For each sampling run (every 12 h), four spectra were taken per sample by rotating the core by 90° between each spectrum (Bubier et al., 1997; Bryant and Baird, 2003; Harris et al., 2005). Data were recorded in reflectance mode. The white reference (Spectralon, LabSphere, Inc., North Sutton, N.H.) was taken before each series of four spectra. Results presented here are postprocessed averages of the four spectra taken for each core every 12 h. Averages were directly calculated in View Spec Pro software version 4.02 (Analytical Spectral Devices, Inc.) after first checking for consistency between replicates. Consistency was checked visually by superposing the replicates. No spectrum was eliminated. Reflectance spectra were automatically interpolated to 1 nm intervals by the software. No further data corrections were made. Several reflectance indices were then calculated from the reflectance data as follows:

$$\text{RDI} = \frac{(R_{1116} - R_{\min(1120-1250)}) / R_{1116}}{1} \quad (2)$$

(Rollin and Milton, 1998)

$$\text{NDWI} = \frac{(R_{860} - R_{1240}) / (R_{860} + R_{1240})}{1} \quad (3)$$

(Gao, 1996)

$$\text{WI} = \frac{(R_{900} / R_{970})}{1} \quad (4)$$

(Peñuelas et al., 1993b)

The absorption features in the region 700–2500 nm are largely related to water content for vegetation (Ustin et al., 2004). Many spectral indices have therefore been developed from these wavelengths to assess vegetation water content. Like other mosses, *Sphagnum* has a strong absorption feature at

1200 nm (Bubier et al., 1997). The RDI is based on that particular water absorption feature and was built by using the reflectance value near the maximum of the leading shoulder (1116 nm) and the minimal reflectance value between 1120 and 1250 nm (Rollin and Milton, 1998). The NDWI is related to the same water absorption feature, as it uses 860 and 1240 nm wavelengths in a normalized formula similar to that of NDVI (Gao, 1996). The WI refers to another water absorption feature: 950–970 nm. Calculated as R_{900}/R_{970} , it is associated with plant water content (Peñuelas et al., 1997) as opposed to the original formula that was reversed and thus indicative of plant water stress (Peñuelas et al., 1993b).

Field survey

Site description

The study was conducted in an open raised bog named Pointe-Lebel, which is located on the north shore of the St. Lawrence River, Canada (49°07'N, 68°15'W), in the bioclimatic domain of fir and white birch of the boreal vegetation zone (MRNF, 2007). The Pointe-Lebel peatland covers 2600 ha with an average peat depth of 4.8 m (Buteau, 1989). Mean annual air temperature and precipitation are 1.5 °C and 1014 mm, respectively (30-year normal; Environment Canada, 2006). In 2005, during the sampling months of July, August, and September, air temperatures were warmer than normal by 1.2 °C, 0.9 °C, and 2.4 °C, respectively (Figure 1). July and September were also drier than normal, with 18% and 37% less precipitation than normal. In contrast, August was wetter than normal, with more than two times the normal amount of rainfall. However, since nearly half of the rainfall occurred in a single event (31 August 2005), August can be otherwise considered normal.

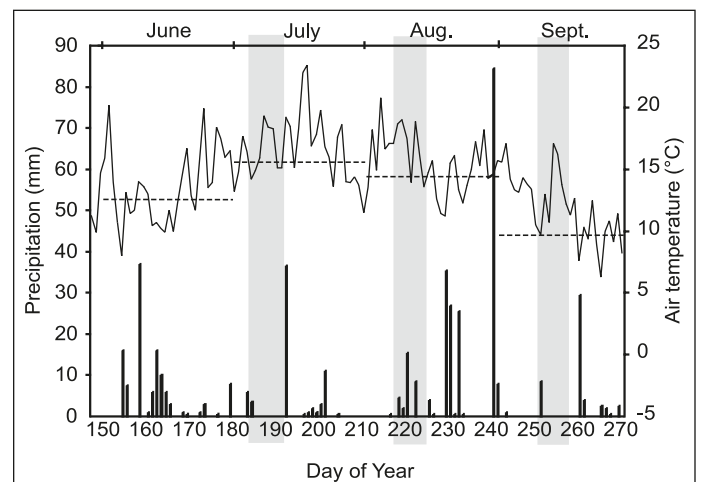


Figure 1. Daily mean air temperature (solid line) and total daily precipitation (water equivalent in mm; vertical bars) from June to September as recorded by Environment Canada (2006) at Baie Comeau (49°08'N, 68°12'W). Horizontal broken lines indicate monthly means for air temperature (30-year normal). Sampling periods are indicated with vertical grey bands (6–11 July, 9–15 August, and 11–16 September).

The Pointe-Label peatland is dominated by ericaceous shrubs (*Chamaedaphne calyculata* (L.) Moench, *Kalmia angustifolia* L.) and *Sphagnum* (mainly *S. fuscum* and *S. rubellum*), interspaced with pools. Spruce thickets (*Picea mariana* (P. Mill.) B.S.P.) are also present at many locations on the site. Graminoids such as *Trichophorum caespitosum* (L.) Hartman and *Eriophorum vaginatum* var. *spissum* (Fern.) Boivin are sparse. *Rubus chamaemorus* L. is the only herbaceous species that becomes abundant by the middle of the growing season.

A total of 14 plots were established following a randomized design stratified to represent a continuous gradient of both total vascular plant and bryophyte covers. The stratification was based on vascular plant cover. Areas with lichens were discarded to limit ground reflectance to mosses. The 14 plot locations were chosen along three transects for which stratification was applied to randomly select two to three plots for each of the six vascular cover classes predetermined as present along the transects. The exact plant cover was measured and varied from 2% to 88% for vascular plants and from 32% to 100% for mosses and liverworts (**Table 1**). Ericaceous species were the main vascular plants, and mosses were dominated by *S. rubellum* and *S. fuscum*. *Sphagnum* was present in all plots, but we hereafter refer to *Sphagnum*-dominated plots when *Sphagnum* cover was high and vascular cover was low. To quantify the gradual increase in vascular plant cover among plots, the leaf area index (LAI) was measured in each plot in mid-September using a SunScan Canopy Analysis System (SS1-UM-1.05; Delta-T Devices Ltd., Cambridge, UK). LAIs ranged from 0.0 in *Sphagnum* lawns to 1.2 in spruce thickets (**Table 1**). Water table depth followed the vegetation gradient (**Table 1**). Water table depth averaged over all sampling periods ranged from 15 cm in *Sphagnum*-dominated plots to nearly 40 cm in plots characterized by spruce thickets and hummocks.

CO₂ flux measurements

Sample plots were surrounded with aluminium collars (58 cm × 58 cm) that were installed in late April in the frozen peat. Data were collected during three sampling periods: 6–11 July, 9–15 August, and 11–16 September (**Figure 1**). Each collar was sampled for 10 or 11 days within a total of 14 sampling days throughout the growing season (5 days in July, 4 in August, and 5 in September). All measurements were made during daylight hours and only on sunny days.

CO₂ exchange measurements were taken with a ventilated and climate-controlled transparent plastic chamber (0.110 m³), similar to those used by Tuittila and Komulainen (1995) and Alm et al. (1997; 1999), and the chamber was used in a closed system. The chamber was placed in a groove around the rim of the collar, which was filled with water before sampling to ensure an air-tight seal. Chamber CO₂ concentrations were measured with a portable infrared gas analyser (IRGA; model EGM-2; PP Systems, Hitchin, UK). Net ecosystem exchange (NEE) was measured under stable prevailing light conditions generally within 135–150 s. Measurements of total respiration (R_{TOT}) were made after the NEE measurements by covering the

chamber with an opaque plastic lid. Between NEE and R_{TOT} measurements, the chamber was removed for a few minutes to permit the equilibration of gas concentration in the plot. During flux sampling, CO₂ concentrations were recorded every 15 s along with temperature inside and outside the chamber, soil temperature, and PAR for NEE measurements (PAR-1; PP Systems). Gross photosynthesis (P_G) was calculated a posteriori: NEE is the instantaneous difference between P_G and R_{TOT} . The sign convention adopted here is that CO₂ uptake is positive (+) and CO₂ release to the atmosphere is negative (–).

CO₂ fluxes were calculated from linear regressions of CO₂ concentration changes as a function of time, base area, chamber volume, and molar volume of CO₂ at chamber air temperature. Regression coefficients (r^2) ranged from 0.85 to 1.00, with a mean value of 0.99. On some occasions, CO₂ flux calculations were performed for a shorter period than 150 s, although never for less than 60 s (or five readings). We examined fluxes in detail and discarded four sampling runs out of 150 runs due to irregular behavior of fluxes. The following rationale was employed to discard runs. In the first case, the PAR (<500 μmol·m⁻²·s⁻¹) was much lower than for other sampling runs; this sampling run should simply not have taken place. In the second case, we observed CO₂ release during the NEE sampling, whereas this situation never occurred during the previous or subsequent days for the same collar. In the last two cases, the progression of gas concentration was truly unstable, r^2 was lower than 0.85, and the flux values were dissimilar to those from the previous or subsequent days.

Canopy reflectance

Ground-based reflectance was measured concurrently with CO₂ fluxes over the 14 permanent collars, similar to the method used by Whiting et al. (1992). The reflectance measurements were made within 15 min of CO₂ flux measurements to sample both parameters under the same light conditions. Sampling was done between 9:00 AM and 4:30 PM under clear sky. Reflectance was measured with the same instrument used for laboratory measurements (see the previous section titled Laboratory experiment; Analytical Spectral Device FieldSpec Pro Spectroradiometer). The head of the optic fibre was hand-held 1 m above the ground surface (even in the presence of a dense canopy), at the centre of the collar, in a nadir position (Bartlett et al., 1990; Peñuelas et al., 1993a; McMichael et al., 1999). The instrument had a field of view of 25°. Consequently, the target surface at the ground level within the collar was a circle approximately 45 cm in diameter.

Three series of three spectra were collected for each target, on each sampling run, for a total of nine spectra per collar per day. Data were recorded in reflectance mode. The white reference was acquired using a 99%-reflective white reference panel (Spectralon, Labsphere, Inc.) a few seconds prior to each series. Results presented here are postprocessed averages of the nine spectra for each collar per day, which was calculated in View Spec Pro software version 4.02 after first checking for consistency between replicates. Consistency was checked visually by superposing the replicates. In total, only four

Table 1. General description of sampled plots.

Collar	Species														% cover		Habitat [†]	LAI	WT			
	Vasculars													Mosses + liverworts	Vasc.	Moss						
	<i>Picea mariana</i> (P. Mill.) B.S.P.	<i>Chamaedaphne calyculata</i> (L.) Moench	<i>Kalmia angustifolia</i> L.	<i>Ledum groenlandicum</i> Oeder	<i>Kalmia polifolia</i> Wangenh.	<i>Andromeda polifolia</i> var. <i>glaucoophylla</i> (Link) DC.	<i>Empetrum nigrum</i> L.	<i>Vaccinium oxycoccos</i> L.	<i>Vaccinium angustifolium</i> Ait.	<i>Rubus chamaemorus</i> L.	<i>Sarracenia purpurea</i> L.	<i>Trichophorum caespitosum</i> (L.) Hartman	<i>Eriophorum vaginatum</i> var. <i>spissum</i> (Fern.) Boivin	<i>Sphagnum fuscum</i> (Schimp.) Klinggr.	<i>Sphagnum rubellum</i> *	<i>Dicranum</i> Hedw. spp.	Liverworts					
1														●				2	100	<i>Sphagnum</i> lawn	0	15.2 ± 1.1
2														●				6	100	<i>Sphagnum</i> lawn	0	17.8 ± 1.5
9														●				7	98	<i>Sphagnum</i> lawn	0	20.6 ± 1.4
4														●	●			11	97	eric. and sph. flat hummock	0.1	22.9 ± 1.3
11														●		●		70	43	spruce shrub hollow	0.9	27.1 ± 1.6
6														●	●			47	85	eric. and sph. flat hummock	0.4	27.6 ± 1.4
3														●	●			20	93	eric., herb. and sph. flat hummock	0.2	29.7 ± 1.3
14														●	●			33	95	eric. and sph. flat hummock	0.6	30.3 ± 2.4
7														●	●			23	93	eric. and sph. flat hummock	0.2	30.9 ± 2.2
5														●	●			30	98	eric. and sph. flat hummock	0.3	31.1 ± 1.5
12														●	●			37	91	eric. and sph. peak hummock	0.2	33.9 ± 3.5
10														●	●			70	60	ericaceous peak hummock	0.8	34.7 ± 1.6
13														●	●			78	72	ericaceous peak hummock	0.6	35.2 ± 2.1
8														●	●			88	32	spruce shrub peak hummock	1.2	38.1 ± 2.7

Note: Vegetation cover corresponds to percent cover averaged over all three sampling periods (July, August, and September). Dark grey squares and circles correspond to dominant species, and light grey squares to codominant species for both vasculars and mosses (in July and August). Leaf area index (LAI) was measured in mid-September. Water table depth (WT) was recorded for each collar on every CO₂ sampling run; it was measured manually in nylon-covered PVC slotted wells located next to each collar within a maximum distance of 1.4 m and in similar vegetation and microtopography. WT values are averaged (±1 SE) from all combined CO₂-reflectance measurements. Plots are ordered from shallow to deep WT relative to the surface.

* Collars 1, 2 and 9 = *Sphagnum rubellum* Wils. For other collars, distinction between *Sphagnum rubellum* Wils. and *Sphagnum capillifolium* (Ehr.) Hedw. was impossible as picking plants would disturb carbon flux measurements. Nevertheless, we are confident that most individuals were *S. rubellum* Wils.

† eric. = ericaceous; herb. = herbaceous; sph. = *Sphagnum*.

spectra were deleted due to the presence of important noise. Reflectance spectra were automatically interpolated to 1 nm intervals by the software. No further data corrections were made. Several reflectance indices were then calculated from the reflectance data as follows:

$$NDVI = (R_{800} - R_{660}) / (R_{800} + R_{660})$$

(modified from Rouse et al., 1974) (5)

$$PRI = (R_{531} - R_{570}) / (R_{531} + R_{570})$$

(Gamon et al., 1992) (6)

$$CI = (R_{750} - R_{705}) / (R_{750} + R_{705})$$

(Gitelson and Merzlyak, 1994) (7)

$$CI_m = (R_{750} - R_{705}) / (R_{750} + R_{705} - 2R_{445})$$

(Sims and Gamon, 2002) (8)

We based our choices for indices on the following rationale. All indices are narrow-band and use normalized formulae similar to that for NDVI. At first, we tested the relationship between a narrow-band NDVI and CO₂ fluxes. NDVI is related to canopy greenness and uses the maximum absorption feature in the red

region (660 nm) and the reflectance in the near-infrared region (800 nm) as a reference. This particular narrow-band formula with 660 and 800 nm has already been used for vegetation types similar to peatland vegetation (Rahman et al., 2001; Boelman et al., 2003). We also tried to normalize NDVI by one of the indices related to water content tested with the laboratory experiment. This ratio, reversed, has already been applied by Peñuelas et al. (1997), who used the ratio between the WI and the NDVI to better estimate vegetation water content.

We also combined the NDVI with the PRI. The wavelength 531 nm is related to xanthophyll pigments (Gamon et al., 1990) and has been integrated in a normalized formula using 550 nm, and later 570 nm, as a reference to give the PRI (Gamon et al., 1992; Peñuelas et al., 1995). The PRI is based on the correlation between the epoxidation state of the xanthophyll pigment cycle and the associated changes in the green reflectance (Gamon et al., 1990; 1992). It is an indicator of the photosynthetic radiation-use efficiency (Peñuelas et al., 1995; Gamon et al., 1997), as xanthophyll pigments are involved in the dissipation of the extra energy absorbed by chlorophyll for photosynthetic uses (Demmig-Adams and Adams, 1996). Unlike NDVI, which is related to “stable” green canopy structure and biomass, PRI has been proposed to detect fine temporal changes in photosynthetic activity occurring under fluctuating light conditions (Gamon et al., 1990; 1992). Kumar and Monteith (1981) have worked on a model of net primary productivity explained by the fraction of PAR absorbed by green vegetation multiplied by an efficiency factor. Based on this work and on the demonstration of the relationship between the reflectance at 531 nm and photosynthetic light-use efficiency, Rahman et al. (2001) proposed to modify the model and use NDVI to represent the fraction of APAR and a rescaled PRI (hence sPRI) to express light-use efficiency (LUE); this last combination was well correlated with uptake and net fluxes of CO₂ for fen and boreal forest stands. Also, close correspondence was demonstrated in a bog between springtime productivity estimates from tower measures and those from the Moderate Resolution Imaging Spectroradiometer (MODIS) which are calculated with LUE, the fraction of absorbed PAR, and a global network station (Moore et al., 2006). The sPRI is calculated from PRI as $(PRI + 1)/2$ to obtain a measure of radiation-use efficiency between 0 and 1.

Lastly, we tested the CI, which was essentially developed for chlorophyll content assessments (Gitelson and Merzlyak, 1994). This index is calculated from the reflectance at the edge of the chlorophyll absorption feature (705 nm), with the reflectance at 750 nm as a reference (Gitelson and Merzlyak, 1994; Stylinski et al., 2002). Stylinski et al. (2002) showed that CI was weakly related to CO₂ uptake for chaparral systems. Nevertheless, as CI has already been shown to be a good estimator of chlorophyll content at both the leaf and canopy levels and for a wide range of species, including bog vascular plants and mosses (Gamon and Surfus, 1999; Sims and Gamon, 2002; Kuusk et al., 2004), we believe that CI may be worth testing as a surrogate for CO₂ fluxes in bog vegetation. We also tested a slightly modified version of the chlorophyll index

(CI_m), which has been developed to compensate for high reflectance associated with certain leaf types (Sims and Gamon, 2002).

Data analyses

For the laboratory experiment, the association between spectral indices (RDI, WI, NDWI) and *Sphagnum* volumetric water content (VWC) was first tested using Pearson correlations for each individual species (4 replicates × 16 measurements, giving $n = 64$) and for all species together (4 species × 4 replicates × 16 measurements, giving $n = 256$). The significance of the Pearson coefficient should be tested against the hypothesis of multinormality for raw data. Although all Pearson correlations did not meet this hypothesis, they were used after confirming that the results were similar to those resulting from nonparametric Spearman correlations (same P values). Lastly, the index most strongly correlated with water content was identified with a test of equality between correlation coefficients based on the Williams statistic (Neill and Dunn, 1975). The statistical test compares the coefficients obtained from two indices. If the coefficients for the two indices are significantly different, the highest coefficient indicates which index is most strongly correlated with VWC.

For the field data, the relationship between paired spectral measurements (spectral indices) and CO₂ fluxes (NEE, P_G) was studied using simple linear regressions. Considering that these variables were measured on the same collars on repeated occasions, non-independence of error terms was presumed and tested with the likelihood ratio chi-square (χ^2) test. Non-independence of error terms was confirmed at $p < 0.01$ for eight regressions out of 10 (χ^2 ranging from 2.4 to 62.3; p ranging from <0.0001 to 0.1213; degrees of freedom $df = 1$). Subsequently, all regressions were analysed under the PROC MIXED procedure of SAS version 8.0 (SAS Institute Inc., Cary, N.C.) following a repeated-measure analysis of variance (ANOVA) with first-order autoregressive error structure. Residuals were homogeneously and normally distributed for all regressions. Sampling took place in three different periods (July, August, and September) to maximize the variation of both reflectance and CO₂ fluxes during the growing season. By adding an interaction term to each model, we tested whether the period (July, August, and September) had to be considered in the relationship between spectral indices and CO₂ fluxes. As this term was not significant for any regressions, data from all three sampling periods were pooled together for analyses ($n = 146$). The regression adjustments were evaluated with the regression coefficient r^2 . As r^2 cannot be calculated with the PROC MIXED procedure, we estimated the coefficients by averaging the coefficients resulting from two formulae proposed by Xu (2003) for linear mixed effect models. It should be noted that our work did not focus on producing daily or seasonal estimates of NEE. Thus models for NEE were not investigated, and measured fluxes were directly used to test the relationships with spectral indices.

Table 2. Pearson coefficients of correlation (r) and equality test of correlation (based on the Williams statistic) between volumetric water content (VWC) of *Sphagnum* cores and spectral indices WI, NDWI, and RDI (see Methods for formulae) measured in the laboratory.

(A) Pearson coefficients of correlation (r)											
Spectral index	<i>S. fallax</i>		<i>S. fuscum</i>		<i>S. magellanicum</i>		<i>S. rubellum</i>		All species		
WI	0.990		0.950		0.993		0.958		0.753		
NDWI	0.982		0.941		0.980		0.947		0.773		
RDI	0.975		0.927		0.970		0.924		0.855		

(B) Equality test of correlation											
	<i>S. fallax</i>		<i>S. fuscum</i>		<i>S. magellanicum</i>		<i>S. rubellum</i>		All species		
	Williams		Williams		Williams		Williams		Williams		
	statistic	p	statistic	p	statistic	p	statistic	p	statistic	p	
WI vs. NDWI	2.583	0.0122	0.651	0.5173	3.982	0.0002	0.921	0.3607	0.956	0.3401	
WI vs. RDI	4.521	<0.0001	1.740	0.0869	7.418	<0.0001	2.876	0.0055	4.721	<0.0001	
NDWI vs. RDI	1.933	0.0579	1.088	0.2810	3.414	0.0011	1.952	0.0555	3.756	0.0002	

Note: All coefficients of correlation are significant at $p < 0.0001$; $n = 64$ for each individual species (4 replicates \times 16 measurements), and $n = 256$ for all species pooled together (4 species \times 4 replicates \times 16 measurements).

Results and discussion

Laboratory experiment: selection of an index correlated with *Sphagnum* volumetric water content

There were strong correlations between spectral indices and *Sphagnum* volumetric water content (VWC) for all four species and all three indices tested (Table 2). Correlations were stronger for individual species than for all species pooled together (Table 2). The following conclusions can be drawn from the tests of equality between coefficients of correlation. RDI was more strongly correlated with volumetric water content than were WI and NDWI when all species were pooled. However, when considering individual species, VWC was more strongly correlated with WI for both *S. fallax* and *S. magellanicum*. For *S. rubellum*, WI and NDWI were not significantly different, but WI was more strongly correlated with VWC than RDI. Lastly, all three indices gave similar results for *S. fuscum*. No index appeared to be significantly better correlated with both *S. fuscum* and *S. rubellum*, the two species that accounted for almost all *Sphagnum* cover in the collars at the Point-Lebel study site.

As the three indices behaved similarly, we chose to present detailed curves for WI only. Figure 2 shows relations between the WI and VWC for the four *Sphagnum* species. Differences among species occurred in the initial water content and drying rates. Cores of *S. fuscum* and *S. rubellum* began the experiment with higher volumetric water content and dried more slowly than those of *S. fallax* and *S. magellanicum*. These differences can be explained by species morphology and community structure. In a *Sphagnum* carpet, water is retained in the external capillary space between individuals; species of the taxonomic *Acutifolia* section, such as *S. fuscum* and *S. rubellum*, are small and grow in dense mats that optimize their capillarity capacity and thus compensate for their small hyalines cells (Hayward and Clymo, 1982). For *S. fuscum*, the spectral index WI stabilized at a constant value as the VWC fell below approximately 0.2, likely due to the presence

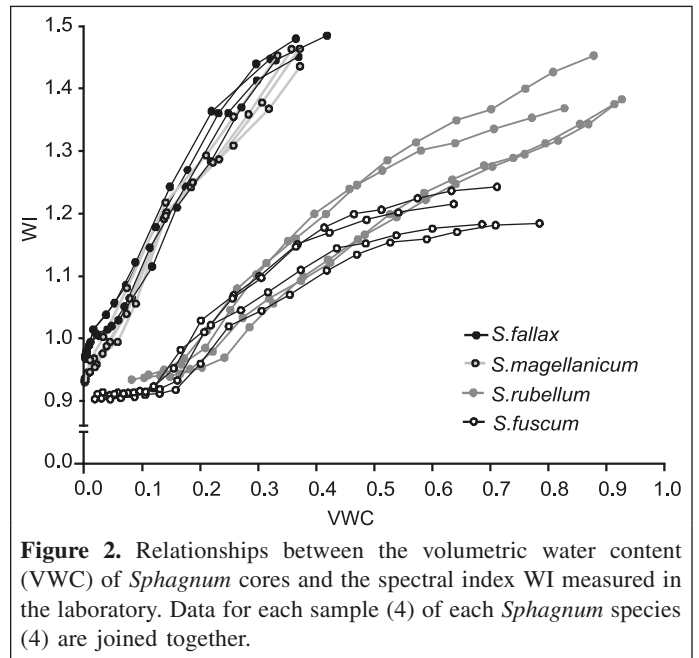


Figure 2. Relationships between the volumetric water content (VWC) of *Sphagnum* cores and the spectral index WI measured in the laboratory. Data for each sample (4) of each *Sphagnum* species (4) are joined together.

of a gradient of water content in the cores. Indeed, capitula dried faster than the bottom of the samples because their capacity to retain water is lower than that farther down the stem (Hayward and Clymo, 1982). In fact, the water content at a depth of 4 cm in a *Sphagnum* hummock colony, comparable to the height of our sample cores, has been shown to be greater than that at the surface by one order of magnitude during dry periods (Murray et al., 1989). Thus, the characteristics of different *Sphagnum* species and their community structure appear to affect not only the ability of the species to retain water but also the relationship between water content and WI.

It follows that the relationship between *Sphagnum* volumetric water content and WI was similar between *S. fuscum* and *S. rubellum* and between *S. fallax* and

S. magellanicum (Figure 2). The same association between species was also observed with NDWI, but less markedly with RDI (data not shown). The discrepancies between species are in accordance with previous studies. Initially, Vogelmann and Moss (1993) showed a strong relationship between TM5:TM4 (1550–1750 nm:760–900 nm) and *Sphagnum* water content and, afterward, detailed studies concluded on species-specific relationships between spectral indices and *Sphagnum* water content (Bryant and Baird, 2003; Harris et al., 2005). A unique relationship between spectral indices and volumetric water content for all *Sphagnum* species would facilitate field applications. Still, species grouping in the response of spectral indices to volumetric water content can facilitate water content assessment in the field compared to when the relationship is strictly species-specific. Since WI was the most effective index when considering *S. fallax* and *S. magellanicum* and was better than RDI for *S. rubellum*, we chose WI for normalizing NDVI values recorded during the field survey. The literature also suggests that WI should be appropriate to estimate the water content of a whole canopy with ground-level measurements (Peñuelas et al., 1993b; Peñuelas and Filella, 1998). Even if near-infrared reflectance only samples the surface water content, using wavelengths such as 970 nm that penetrate deeper into the vegetation than middle-infrared radiation (Bull, 1991; Peñuelas et al., 1993b) would be advantageous for *Sphagnum*, which usually shows a vertical moisture gradient (Hayward and Clymo, 1982; Harris et al., 2006).

Field survey: CO₂ fluxes and relationships with ground-based reflectance

CO₂ exchange

During the 2005 field season, when 14 collars were measured 10 or 11 times during July, August, and September, NEE ranged from 53 to 858 mg CO₂ m⁻²·h⁻¹ at the study site on a per collar per day basis (positive values indicate net uptake), and P_G ranged from 375 to 1339 mg CO₂ m⁻²·h⁻¹, which was approximately twice as high as R_{TOT}. All collars acted as CO₂ sinks on each sampling day in July, August, and September.

All measurements of CO₂ fluxes were obtained under full sunshine (PAR average ± SD = 1435 ± 241 μmol·m⁻²·s⁻¹). When compared with values from the literature, the Pointe-Lebel NEE values were similar to or higher than the maximum NEE uptake or NEE at high PAR (1500; 1800 μmol·m⁻²·s⁻¹) reported for bog vegetation, ranging from approximately 250 to 585 mg CO₂ m⁻²·h⁻¹ (Neumann et al., 1994; Frokling et al., 1998; Alm et al., 1999; Moore et al., 2002; Lafleur et al., 2003). P_G values at the Pointe-Lebel site are in accordance with those from other studies in bogs where the highest gross photosynthesis (or gross photosynthesis reached at maximum PAR values) ranges from nearly 850 to more than 1600 mg CO₂ m⁻²·h⁻¹ (Shurpali et al., 1995; Bellisario et al., 1998; Bubier et al., 2003a). While the light conditions were optimal, we could think that the dry and hot sampling conditions should have reduced CO₂ uptake. However, our sampling did not cover conditions diverse enough to discuss the possible effects of

temperature or other climatic conditions on the obtained values of CO₂ uptake.

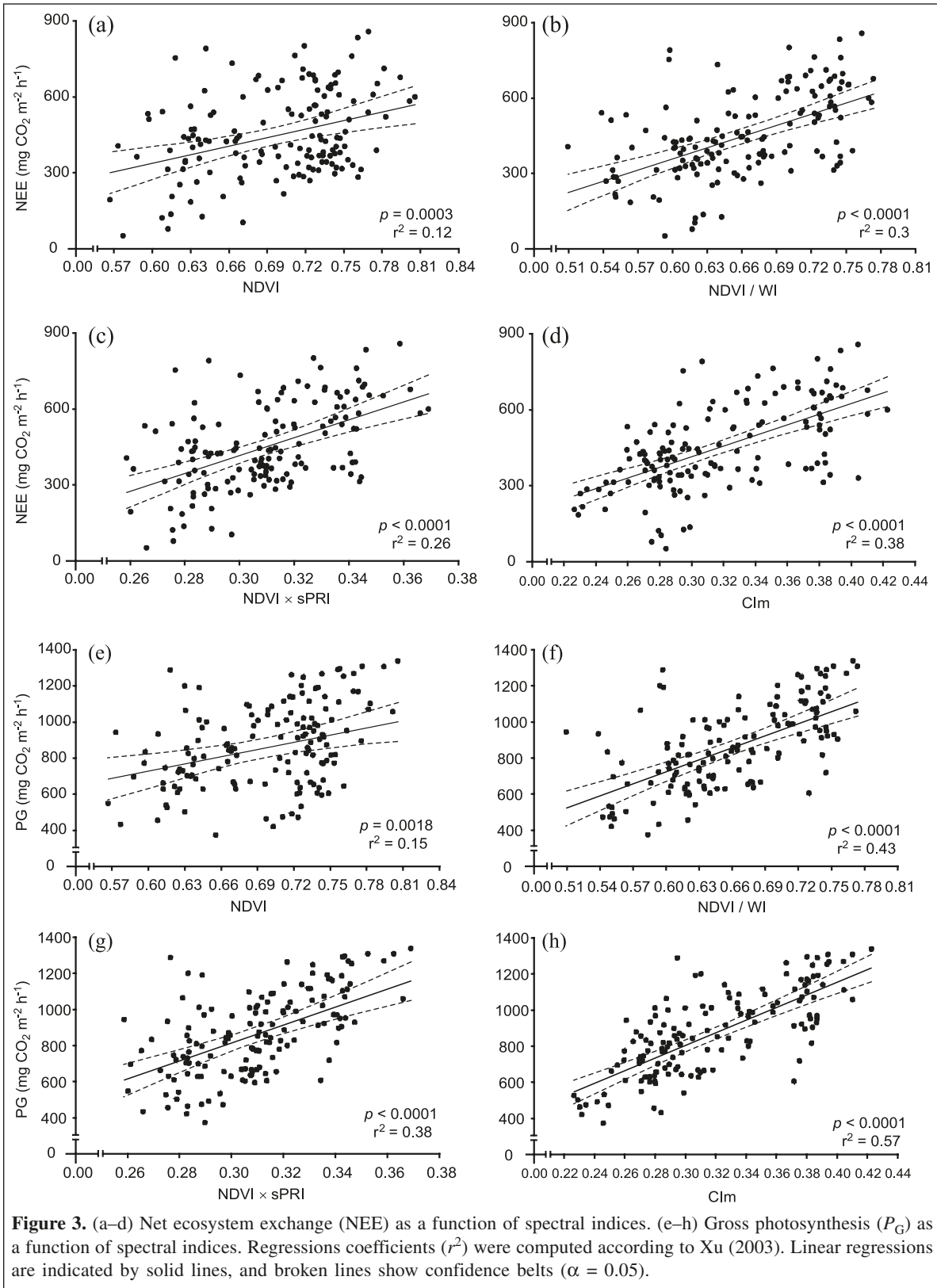
Spectral indices as predictors of CO₂ fluxes

Reflectance was measured concurrently with CO₂ fluxes on a total of 146 occasions (14 collars measured 10 or 11 times). Regressions of both P_G and NEE with spectral indices were all significant, but adjustments varied from weak to moderate across indices (Figure 3). Regression adjustments with P_G were stronger than those with NEE in all cases. Many authors proposed normalizing NEE by PAR in relation to spectral indices to account for different lighting conditions (Bartlett et al., 1990; Whiting et al., 1992; McMichael et al., 1999). We did not consider it worthwhile in this study because NEE was always measured at near-saturated PAR conditions (average ± SD = 1435 ± 241 μmol·m⁻²·s⁻¹) (Frokling et al., 1998).

NDVI values measured at the Pointe-Lebel site ranged from 0.57 to 0.81. The relationship between NDVI and CO₂ fluxes was quite weak (Figure 3; NEE, r² = 0.12 and p = 0.0003; P_G, r² = 0.15 and p = 0.0018), which corresponds to the findings of Whiting (1994). Whiting used a broadband NDVI, but the narrow-band NDVI used here was highly correlated with broadband NDVI (630–690 nm for red and 760–900 nm for NIR; r = 0.99670 and p < 0.0001; data not shown). Therefore using narrow-band NDVI rather than broadband NDVI without further modifications does not improve relationships with CO₂ fluxes. Yet, clear outliers associated with *Sphagnum* plots as in Whiting did not occur here, likely because nearly all collars in our study had a high *Sphagnum* cover, which was discernible through the continuous gradient of vascular plant cover. In contrast, Whiting's study site encompassed a single plot with a high *Sphagnum* cover.

The ratio NDVI/WI was moderately adjusted to CO₂ fluxes (Figure 3; NEE, r² = 0.3 and p < 0.0001; P_G, r² = 0.43 and p < 0.0001). Nevertheless, this combined index was more strongly correlated with CO₂ fluxes than was NDVI alone. Field-derived WI for all collars ranged from 0.96 to 1.33, with most values around 1.00 (median = 1.04; data not shown). The highest WI values at the site, ranging from 1.04 to 1.33, were obtained in *Sphagnum*-dominated collars, since *Sphagnum* can reach higher water content than vascular plants. Therefore, a stronger relationship between CO₂ fluxes and spectral indices can be partly obtained using the normalizing effect of WI to lower the NDVI of *Sphagnum*. Moreover, the combination of these two indices may improve the regressions for all communities, since greenness and moisture are strongly related (Peñuelas et al., 1997; Rollin and Milton, 1998).

Using sPRI in combination with NDVI also led to better relationships for NEE and P_G than using NDVI alone, although the adjustments were moderate (NEE, r² = 0.26 and p < 0.0001; P_G, r² = 0.38 and p < 0.0001). Nevertheless, the improvement in the adjustments indicates that using the complementary nature of NDVI and sPRI is beneficial. NDVI is related to absorbed photosynthetically active radiation (APAR), whereas sPRI is associated with photosynthetic light-use efficiency (LUE). Furthermore, NDVI responds to seasonal changes in the



vegetation spectral properties, whereas PRI may better respond to daily changes (Gamon et al., 1992).

NDVI is a canopy greenness index related to vegetation structure. In peatlands, the multilayer vegetation structure of

standing vascular plants and underlying mosses can display different spectral properties. Indeed, the spectral reflectance measured in the present study varied considerably along the gradient of moss and vascular plant covers. The particular

spectral characteristics of *Sphagnum* described in the literature were apparent in the spectral reflectance curves throughout this gradient and among the different species of *Sphagnum* (Figure 4). In fact, according to the literature, the genus *Sphagnum* has spectral properties distinct from those of green vascular plants. *Sphagnum* reflectance is lower than vascular reflectance in the NIR (Bubier et al., 1997) and shortwave infrared and shows pronounced water absorption features at approximately 1000 and 1200 nm (Vogelmann and Moss, 1993; Bubier et al., 1997). Also, *Sphagnum* reflectance in the visible part of the spectrum can be characterized by a peak in the green, red, or brown according to the dominant colour of the species. For instance, a broad peak centred between 570 and 640 nm has been observed for brown *S. fuscum* (Bubier et al., 1997), and red individuals of *Sphagnum capillifolium* or *S. magellanicum* showed a red peak centred at 630 nm and no green peak (Vogelmann and Moss, 1993; Bubier et al., 1997). The red colour of *Sphagnum*, and likely the reflectance peak in the red region, results partly from sphagnorubin (Rudolph and Jöhnk, 1982), a cell wall pigment associated with anthocyanins (Vowinkel, 1975). In our study, those spectral characteristics of the genus *Sphagnum* were noticeable except for the lower reflectance in the NIR for *Sphagnum* than for vascular plants (Figure 4). However, the reflectance values reached in the NIR for collars dominated by *S. rubellum* were similar to those obtained by Harris et al. (2006) for field patches of *S. pulchrum* in their driest sampling period. As well, the reflectance of *P. mariana* in the NIR has been shown in the literature to be lower (Fuentes et al., 2001) than that for other vascular species involved in the studies mentioned previously.

Along the gradient of moss and vascular plant cover in the present study, the NDVI extracted from the spectra did not follow the same pattern as CO₂ fluxes, leading to poor adjustments between these parameters across the different bog communities. Additionally, PRI (and hence sPRI) may also have been affected by the spectral properties of *Sphagnum*. Indeed, the PRI formula (531, 570 nm) is centred on the green peak, which simply did not appear for many of the collars in the present study, as the *Sphagnum* mosses were often red. The absence of a typical green peak in the green does not necessarily mean that xanthophyll pigment activity is not represented by change at or near 531 nm, but exploratory analysis indicates that more in depth analysis would be necessary, and of interest, to characterize the relationship between LUE and PRI for *Sphagnum* mosses.

This study showed that the use of an index centred on the red edge (680–750 nm) (Horler et al., 1983), like CI, corresponded well to CO₂ fluxes and therefore seems potentially appropriate to assess CO₂ fluxes along a gradient of *Sphagnum* and vascular plant cover in peatlands. The relationships between CO₂ fluxes and the chlorophyll indices CI (NEE, $r^2 = 0.37$ and $p < 0.0001$; P_G , $r^2 = 0.55$ and $p < 0.0001$) and CI_m (NEE, $r^2 = 0.38$ and $p < 0.0001$; P_G , $r^2 = 0.57$ and $p < 0.0001$) were indeed rather well adjusted. Only the results for CI_m are illustrated in Figure 3 because they are similar to those for CI. These two indices were the only indices tested that did not include the reflectance at 660

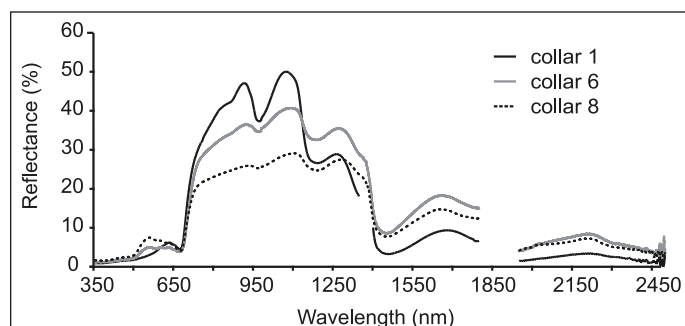


Figure 4. Field spectral reflectance (average of three series of three spectra) for a collar largely dominated by *S. rubellum* (collar 1), a collar characterized by a medium cover of vascular plants and mainly *S. fuscum* (collar 6), and a collar essentially dominated by *P. mariana* (collar 8). All measurements were taken on 9 July 2005, a dry and hot day.

and 800 nm used in NDVI. The better performance of CI over NDVI may be surprising because both indices are closely related. The chlorophyll index CI (750, 705 nm) can be considered as a modified version of the NDVI: CI is the result of investigations to find new wavelengths for the NDVI formula to avoid saturation in chlorophyll determination at high pigment concentrations (Gitelson and Merzlyak, 1994). Moreover, in the present study, CI and NDVI were strongly correlated ($r = 0.75$ and $p < 0.0001$; data not shown). Nevertheless, the relationships between CI (or CI_m) and CO₂ fluxes at the Pointe-Lebel site were stronger than those for NDVI.

Conclusion

Our results show that a narrow-band index like the chlorophyll index (CI) could be used as an indicator of CO₂ fluxes (i.e., both gross photosynthesis and net ecosystem exchange) across several communities of bogs, whereas the relationships between CO₂ fluxes and both NDVI/WI and NDVI × sPRI are moderate. Other studies should be undertaken before mapping of CO₂ fluxes can be considered. Indeed, the assumption that the best index at the stand level is also the best index at the landscape level for mapping the different components of CO₂ fluxes across bog vegetation types needs to be examined. Also, the application of CI on a larger range of peatland communities needs to be tested, particularly on fens and bogs, as both peatland types are frequently mixed over large areas.

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References

- Alm, J., Talanov, A., Saarnio, S., Silvola, J., Ikkonen, E., Aaltonen, H., Nykänen, H., and Martikainen, P.J. 1997. Reconstruction of the carbon balance for microsites in a boreal oligotrophic fen, Finland. *Oecologia*, Vol. 110, pp. 423–431.
- Alm, J., Schulman, L., Walden, J., Nykänen, H., Martikainen, P.J., and Silvola, J. 1999. Carbon balance of a boreal bog during a year with an exceptionally dry summer. *Ecology*, Vol. 80, pp. 161–174.
- Bartlett, D.S., Whiting, G.J., and Hartman, J.M. 1990. Use of vegetation indices to estimate intercepted solar radiation and net carbon dioxide exchange of a grass canopy. *Remote Sensing of Environment*, Vol. 30, pp. 115–128.
- Bellisario, L.M., Moore, T.R., and Bubier, J.L. 1998. Net ecosystem CO₂ exchange in a boreal peatland, northern Manitoba. *Écoscience*, Vol. 5, pp. 534–541.
- Boelman, N.T., Stieglitz, M., Rueth, H.M., Sommerkorn, M., Griffin, K.L., Shaver, G.R., and Gamon, J.A. 2003. Response of NDVI, biomass, and ecosystem gas exchange to long-term warming and fertilization in wet sedge tundra. *Oecologia*, Vol. 135, pp. 414–421.
- Bryant, R.G., and Baird, A.J. 2003. The spectral behaviour of *Sphagnum* canopies under varying hydrological conditions. *Geophysical Research Letters*, Vol. 30, pp. 1134–1137.
- Bubier, J.L., Rock, B.N., and Crill, P.M. 1997. Spectral reflectance measurements of boreal wetland and forest mosses. *Journal of Geophysical Research*, Vol. 102, pp. 29 483 – 29 494.
- Bubier, J.L., Bhatia, G., Moore, T.R., Roulet, N.T., and Lafleur, P.M. 2003a. Spatial and temporal variability in growing-season net ecosystem carbon dioxide exchange at a large peatland in Ontario, Canada. *Ecosystems*, Vol. 6, pp. 353–367.
- Bubier, J., Crill, P., Mosedale, A., Frohling, S., and Linder, E. 2003b. Peatland responses to varying interannual moisture conditions as measured by automatic CO₂ chambers. *Global Biogeochemical Cycles*, Vol. 17, No. 2, pp. 1–15.
- Bull, C.R. 1991. Wavelength selection of near-infrared reflectance moisture meters. *Journal of Agricultural Engineering Research*, Vol. 49, pp. 113–125.
- Buteau, P. 1989. *Atlas des tourbières du Québec méridional*. Direction générale de l'exploration géologique et minérale, Ministère de l'Énergie et des Ressources (Mines) du Québec, DV 89-02. 304 pp.
- Demmig-Adams, B., and Adams, W.W., III. 1996. The role of xanthophyll cycle carotenoids in the protection of photosynthesis. *Trends in Plant Science*, Vol. 1, pp. 21–26.
- Environment Canada. 2006. *Canadian climate normals or averages 1971–2000*. Environment Canada, Toronto, Ont. Available from www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html [cited 6 March 2006].
- Frohling, S.E., Bubier, J.L., Moore, T.R., Ball, T., Bellisario, L.M., Bhardwaj, A., Carroll, P., Crill, P.M., Lafleur, P.M., McCaughey, J.H., Roulet, N.T., Suyker, A.E., Verma, S.B., Waddington, J.M., and Whiting, G.J. 1998. Relationship between ecosystem productivity and photosynthetically active radiation for northern peatlands. *Global Biogeochemical Cycles*, Vol. 12, pp. 115–126.
- Fuentes, D., Gamon, J.A., Qiu, H.-L., Sims, D.A., and Roberts, D.A. 2001. Mapping Canadian boreal forest vegetation using pigment and water absorption features derived from the AVIRIS sensor. *Journal of Geophysical Research*, Vol. 106, pp. 33 565 – 33 577.
- Gamon, J.A., and Surfus, J.S. 1999. Assessing leaf pigment content and activity with a reflectometer. *New Phytologist*, Vol. 143, pp. 105–117.
- Gamon, J.A., Field, C.B., Bilger, W., Bjorkman, O., Fredeen, A.L., and Peñuelas, J. 1990. Remote sensing of the xanthophyll cycle and chlorophyll fluorescence in sunflower leaves and canopies. *Oecologia*, Vol. 85, pp. 1–7.
- Gamon, J.A., Peñuelas, J., and Field, C.B. 1992. A narrow-waveband spectral index that tracks diurnal changes in photosynthetic efficiency. *Remote Sensing of Environment*, Vol. 41, pp. 35–44.
- Gamon, J.A., Serrano, L., and Surfus, J.S. 1997. The photochemical reflectance index: an optical indicator of photosynthetic radiation use efficiency across species, functional types, and nutrient levels. *Oecologia*, Vol. 112, pp. 492–501.
- Gao, B.-C. 1996. NDWI: A normalized difference water index for remote sensing of vegetation liquid water from space. *Remote Sensing of Environment*, Vol. 58, pp. 257–266.
- Gitelson, A., and Merzlyak, M.N. 1994. Spectral reflectance changes associated with autumn senescence of *Aesculus hippocastanum* L. and *Acer platanoides* L. leaves: spectral features and relation to chlorophyll estimation. *Journal of Plant Physiology*, Vol. 143, pp. 286–292.
- Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological Applications*, Vol. 1, pp. 182–195.
- Harris, A., Bryant, R.G., and Baird, A.J. 2005. Detecting near-surface moisture stress in *Sphagnum* spp. *Remote Sensing of Environment*, Vol. 97, pp. 371–381.
- Harris, A., Bryant, R.G., and Baird, A.J. 2006. Mapping the effects of water stress on *Sphagnum*: preliminary observations using airborne remote sensing. *Remote Sensing of Environment*, Vol. 100, pp. 363–378.
- Hayward, P.M., and Clymo, R.S. 1982. Profiles of water content and pore size in *Sphagnum* and peat, and their relation to peat bog ecology. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, Vol. 215, pp. 299–325.
- Horler, D.N.H., Dockray, M., and Barber, J. 1983. The red edge of plant leaf reflectance. *International Journal of Remote Sensing*, Vol. 4, pp. 273–288.
- Kumar, M., and Monteith, J.L. 1981. Remote sensing of crop growth. In *Plants and the daylight spectrum*. Edited by H. Smith. Academic Press, London, UK. pp. 133–144.
- Kuusik, A., Lang, M., and Nilson, T. 2004. Simulation of the reflectance of ground vegetation in sub-boreal forests. *Agricultural and Forest Meteorology*, Vol. 126, pp. 33–46.
- Lafleur, P.M., Roulet, N.T., Bubier, J.L., Frohling, S., and Moore, T.R. 2003. Interannual variability in the peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog. *Global Biogeochemical Cycles*, Vol. 17, pp. 1036–1049.

- McMichael, C.E., Hope, A.S., Stow, D.A., Fleming, J.B., Vourlitis, G., and Oechel, W. 1999. Estimating CO₂ exchange at two sites in Arctic tundra ecosystems during the growing season using vegetation index. *International Journal of Remote Sensing*, Vol. 20, pp. 683–698.
- Moore, T.R., Bubier, J.L., Frolking, S.E., Lafleur, P.M., and Roulet, N.T. 2002. Plant biomass and production and CO₂ exchange in an ombrotrophic bog. *Journal of Ecology*, Vol. 90, pp. 25–36.
- Moore, T.R., Lafleur, P.M., Poon, D.M.I., Heumann, B.W., Seaquist, J.W., and Roulet, N.T. 2006. Spring photosynthesis in a cool temperate bog. *Global Change Biology*, Vol. 12, pp. 1–13.
- MRNF. 2007. *Zones de végétation et domaines bioclimatiques du Québec*. Ministère des Ressources naturelles et de la Faune du Québec (MRNF), Québec City, Que. Available from www.mrnf.gouv.qc.ca/forets/connaissances/connaissances-inventaire-zones-carte.jsp [cited 21 February 2007].
- Murray, K.J., Harley, P.C., Beyers, J., Walz, H., and Tenhunen, J.D. 1989. Water content effects on photosynthetic response of *Sphagnum* mosses from the foothills of the Philip Smith Mountains, Alaska. *Oecologia*, Vol. 79, pp. 244–250.
- Neill, J.J., and Dunn, O.J. 1975. Equality of dependent correlations coefficients. *Biometrics*, Vol. 31, pp. 531–543.
- Neumann, H.H., Hartog, G.D., King, K.M., and Chipanshi, A.C. 1994. Carbon dioxide fluxes over a raised open bog at the Kinosheo Lake tower site during the Northern Wetlands Study (NOWES). *Journal of Geophysical Research*, Vol. 99, pp. 1529–1538.
- Peñuelas, J., and Filella, I. 1998. Visible and near-infrared reflectance techniques for diagnosing plant physiological status. *Trends in Plant Science*, Vol. 3, pp. 151–156.
- Peñuelas, J., Gamin, J.A., Griffin, K.L., and Field, C.B. 1993a. Assessing community type, plant biomass, pigment composition, and photosynthetic efficiency of aquatic vegetation from spectral reflectance. *Remote Sensing of Environment*, Vol. 46, pp. 110–118.
- Peñuelas, J., Filella, I., Biel, C., Serrano, L., and Savé, R. 1993b. The reflectance at the 950–970 nm region as an indicator of plant water status. *International Journal of Remote Sensing*, Vol. 14, pp. 1887–1905.
- Peñuelas, J., Filella, I., and Gamon, J.A. 1995. Assessment of photosynthetic radiation-use efficiency with spectral reflectance. *New Phytologist*, Vol. 131, pp. 291–296.
- Peñuelas, J., Pinol, J., Ogaya, R., and Filella, I. 1997. Estimation of plant water concentration by the reflectance Water Index WI (R900/R970). *International Journal of Remote Sensing*, Vol. 18, pp. 2869–2875.
- Post, W.M., Emanuel, W.R., Zinke, P.J., and Stangenberger, A.G. 1982. Soil carbon pool and world life zones. *Nature (London)*, Vol. 298, pp. 156–159.
- Rahman, A.F., Gamon, J.A., Fuentes, D.A., Roberts, D.A., and Prentiss, D. 2001. Modeling spatially distributed ecosystem flux of boreal forest using hyperspectral indices from AVIRIS imagery. *Journal of Geophysical Research*, Vol. 106, pp. 33 579 – 33 591.
- Rollin, E.M., and Milton, E.J. 1998. Processing of high spectral resolution reflectance data for the retrieval of canopy water content information. *Remote Sensing of Environment*, Vol. 65, pp. 86–92.
- Roulet, N.T. 2000. Peatlands, carbon storage, greenhouse gases, and the Kyoto protocol: prospects and significance for Canada. *Wetlands*, Vol. 20, pp. 605–615.
- Rouse, J.W., Jr., Haas, R.H., Schell, J.A., and Deering, D.W. 1974. Monitoring vegetation systems in the Great Plains with ERTS. In *Proceedings of the 3rd Symposium on the Earth Resources Technology Satellite-1*, 10–14 December 1973, Washington, D.C. Edited by S.C. Freden, E.P. Mercanti, and M.A. Becker. National Aeronautics and Space Administration (NASA), Goddard Space Flight Center, Greenbelt, Md. Vol. 1, Sect. A, pp. 309–317.
- Rudolph, H., and Jöhnk, A. 1982. Physiological aspects of phenolic compounds in the cell walls of *SPHAGNA*. *The Journal of the Hattori Botanical Laboratory*, Vol. 53, pp. 195–203.
- Sellers, P.J. 1985. Canopy reflectance, photosynthesis and transpiration. *International Journal of Remote Sensing*, Vol. 6, pp. 1335–1372.
- Shurpali, N.J., Verma, S.B., Kim, J., and Arkebauer, T.J. 1995. Carbon dioxide exchange in a peatland ecosystem. *Journal of Geophysical Research*, Vol. 100, pp. 14 319 – 14 326.
- Sims, D.A., and Gamon, J.A. 2002. Relationship between leaf pigment content and spectral reflectance across a wide range of species, leaf structures and developmental stages. *Remote Sensing of Environment*, Vol. 81, pp. 337–354.
- Stylinski, C.D., Gamon, J.A., and Oechel, W.C. 2002. Seasonal patterns of reflectance indices, carotenoid pigments and photosynthesis of evergreen chaparral species. *Oecologia*, Vol. 131, pp. 366–374.
- Tucker, C.J. 1979. Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sensing of Environment*, Vol. 8, pp. 127–150.
- Tucker, C.J., Fung, I.Y., Keeling, C.D., and Gammon, R.H. 1986. Relationship between atmospheric CO₂ variations and a satellite-derived vegetation index. *Nature (London)*, Vol. 319, pp. 195–199.
- Tuittila, E.-S., and Komulainen, V.-M. 1995. Vegetation and CO₂ balance in an abandoned harvested peatland in Aitoneva, southern Finland. *Suo*, Vol. 46, pp. 69–80.
- Ustin, S.L., Roberts, D.A., Gamon, J.A., Asner, G.P., and Green, R.O. 2004. Using imaging spectroscopy to study ecosystem processes and properties. *BioScience*, Vol. 54, pp. 523–534.
- Vitt, D.H. 2000. Peatlands: ecosystems dominated by bryophytes. In *Bryophyte biology*. Edited by A.J. Shaw and B. Goffinet. Cambridge University Press, Cambridge, UK. pp. 312–343.
- Vogelmann, J.E., and Moss, D.M. 1993. Spectral reflectance measurements in the genus *Sphagnum*. *Remote Sensing of Environment*, Vol. 45, pp. 273–279.
- Vowinkel, E. 1975. Cell wall pigments of peat mosses, 2: the structure of sphagnorubin. *Chemische Berichte*, Vol. 108, pp. 1166–1181.
- Whiting, G.J. 1994. CO₂ exchange in the Hudson Bay lowlands: community characteristics and multispectral reflectance properties. *Journal of Geophysical Research*, Vol. 99, pp. 1519–1528.
- Whiting, G.J., Bartlett, D.S., Fan, S., Bakwin, P.S., and Wofsy, S.C. 1992. Biosphere/atmosphere CO₂ exchange in tundra ecosystems: community characteristics and relationships with multispectral surface reflectance. *Journal of Geophysical Research*, Vol. 97, pp. 16 671 – 16 680.
- Xu, R. 2003. Measuring explained variation in linear mixed effects models. *Statistics in Medicine*, Vol. 22, pp. 3527–3541.
- Yoshikawa, K., Overduin, P.P., and Harden, J.W. 2004. Moisture content measurements of moss (*Sphagnum* spp.) using commercial sensors. *Permafrost and Periglacial Processes*, Vol. 15, pp. 309–318.
- Zarco-Tejada, P.J., and Miller, J. 1999. Land cover mapping at BOREAS using red-edge spectral parameters from CASI imagery. *Journal of Geophysical Research*, Vol. 104, pp. 27 291 – 27 933.