Moisture controls on *Sphagnum* growth and CO_2 exchange on a cutover bog

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Summary

1. Abandoned cutover peatlands are persistent sources of atmospheric CO_2. Net ecosystem CO_2 exchange and *Sphagnum* net primary production of an abandoned block-cut bog were measured in the field and in the laboratory using gas exchange techniques to determine the processes controlling CO_2 exchange in these ecosystems.

2. *Sphagnum* net primary production was offset by peat respiration, resulting in the peatland becoming a net source of CO_2 during the summer months.

3. *Sphagnum* photosynthesis was greatest at wet sites. In addition, sites with vascular plant cover photosynthesized at approximately twice the rate of sites where vascular plants were removed.

4. Laboratory results indicate that drying and wetting cycles negatively affect *Sphagnum* net primary production and net ecosystem CO_2 exchange. *Sphagnum* and peat respiration increased 4–14-fold upon rewetting, whereas *Sphagnum* photosynthesis did not recover until 20 days of saturation.

5. *Synthesis and applications.* This research emphasizes the importance of stable moisture availability for the growth of *Sphagnum* and the eventual development of a new acrotelm on the cutover bog surface. Restoration techniques must therefore include companion species and a constant moisture supply above the minimum threshold for *Sphagnum* mosses.

Key-words: carbon dioxide, eco-hydrology, peatland, peat mining, restoration, *Sphagnum*

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Introduction

Peatlands store approximately one-third of the world's carbon supply (Gorham 1991) through long-term accumulation at an average rate of 12–23 g C m^{-2} $year^{-1}$ (Gorham 1991; Clymo, Turunen & Tolonen 1998; Turunen *et al*. 2001). However, human exploitation has disrupted the carbon balance of peatland ecosystems, so much so that global carbon stores are disappearing approximately 10 times faster than they have accumulated (Armentano & Menges 1986; Joosten 1998, 2000). Peat mining, through the combination of drainage, peat removal and subsequent abandonment, alters the environment so severely that *Sphagnum* spp. are unable to recolonize (Johnson, Maly & Malterer 2000).

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Sphagnum is the principal plant involved in peat accumulation (Rydin & McDonald 1985a; Gerdol *et al*. 1996) in stable bog ecosystems. However, little is known about the eco-hydrological controls on *Sphagnum* growth in cutover bogs. While studies have shown that species selection and mitigative measures increasing water availability are important methods of improving *Sphagnum* production in cutover peatlands, the relationship between *Sphagnum* growth, CO_2 exchange and water availability in these peatlands remains poorly understood (Grosvernier, Matthey & Buttler 1997; Chirino & Rochefort 2000; Johnson, Maly & Malterer 2000). The goal of this work therefore was to study the eco-hydrological controls on growth rates of *Sphagnum* and CO_2 exchange in an abandoned cutover bog.

Due to their limited ability to control water loss (Titus & Wagner 1984), *Sphagnum* plants are highly dependent on water availability. The tolerance of *Sphagnum* species to desiccation has been demonstrated through laboratory studies (Wagner & Titus 1984), and other studies have documented the ability of these mosses to recover from desiccation (Gerdol *et al*.

1996; Schipperges & Rydin 1998). Changes in gross ecosystem production (GEP) with desiccation and rewetting have been the focus of these studies rather than changes in respiration. Yet, decomposition, however minimal, is crucial in determining the limits to *Sphagnum* growth (Clymo 1984). *Sphagnum* growth in natural peatlands increases with higher water levels (Hayward & Clymo 1983; Rydin & McDonald 1985a) and the photosynthetic rate of *Sphagnum* mosses increases with the water content of the plant, with maximum rates occurring with gravimetric water contents of 400% to 2500% (Rydin & McDonald 1985b; Gerdol *et al*. 1996; Schipperges & Rydin 1998).

A cutover peatland is prone to summer water stress due to the removal of the surface peat layers. Without this regulating surface layer, the specific yield decreases, thereby increasing water table fluctuations (Price & Whitehead 2001; Van Seters & Price 2001), with abnormally large water table drawdowns during drought. As both photosynthesis and respiration show a strong dependence on water availability (Silvola 1990; Alm *et al*. 1999; Komulainen *et al*. 1999), these drawdowns can drastically alter the peatland carbon balance. Several studies have shown that the lack of photosynthesizing moss shifts the carbon balance to a large persistent net source of CO_2 into the atmosphere (Waddington, Warner & Kennedy 2002; Waddington & Price 2000). Consequently, the carbon storage function of the peatland can be restored through revegetation of the mined surface (Waddington & Warner 2001).

Improving moisture supply to *Sphagnum* is a crucial step in restoring growth on post-cutover peatlands. Studies have shown that *Sphagnum* regeneration increases with high water levels (Campeau & Rochefort 1996; Grosvernier, Matthey & Buttler 1997) and decreased soil tension (Price, Rochefort & Quinty 1998). However, *Sphagnum* is sometimes absent at sites where soil water tension is usually less than −100 cm (Price & Whitehead 2001) and Whitehead (1999) suggests that short periods of high tension may be sufficient to prevent *Sphagnum* growth. Recently, Smolders *et al*. (2002) suggested that hydrochemistry and peat quality have a large control on *Sphagnum* development in inundated bog remnants.

Little research has focused on the processes controlling *Sphagnum* growth and CO_2 exchange on cutover peatlands. Many Fennoscandian studies examining these processes (Silvola *et al*. 1996; Komulainen *et al*. 1999) are concerned with drained but uncut peatlands with an intact acrotelm. Moreover, gas exchange studies (Tuittila, Vasander & Laine 2000; Sundh *et al*. 2000; Waddington & Warner 2001) have not isolated *Sphagnum* photosynthesis and respiration from vascular plant and soil gas exchange processes. While several studies have investigated *Sphagnum* growth using seasonal measurements (e.g. the crank wire method) (Campeau & Rochefort 1996; Waddington, Rochefort & Campeau 2003), the hydrological processes fluctuate

on a much finer time scale (weekly, daily, hourly). The objective of this research therefore was to study *Sphagnum* growth rates using gas exchange approaches in cutover peatlands on a finer time scale in order to determine the moisture controls that limit and enhance *Sphagnum* growth rates during the productive season.

Materials and methods

STUDY AREA

The peatland studied, Cacouna Bog (Fig. 1), is situated in the Bas-Saint-Laurent region of Québec (47°53′N, 69°27′W), Canada. The Cacouna peatland is a domed bog, which is underlain by Champlain clay with peat depths of up to 4 m (Van Seters & Price 2001). The bog lies 83 m above sea level and occupies a total surface area of 172 ha (Girard 2000). The peatland originally covered 210 ha but was reduced through conversion to roads and agricultural land (Girard 2000). A railway constructed in the mid-1800s divides the peatland into north and south sections along a natural groundwater divide. The two sections of the bog are now hydrologically distinct (Van Seters & Price 2001). Peat extraction for horticultural use began in 1942 using the block-cut method before being abandoned in 1976 (Girard 2000). Drainage ditches, created to facilitate peat extraction, were blocked manually or naturally by peat slumping after the peatland was abandoned (Girard 2000).

The Cacouna peatland has been colonized by ericaceous shrubs such as *Ledum groenlandicum* Oeder., *Chamaedaphne calyculata* (L.) Moench, *Kalmia angustifolia* L. and *Vaccinium angustifolium* Ait. *Sphagnum capillifolium* (Ehrh.) Hedw. is the dominant *Sphagnum* species in the trenches of the Cacouna peatland (Girard 2000) and is the most common *Sphagnum* species to recolonize abandoned peatlands in Québec (L. Rochefort, personal communication).

This study was conducted in the south-east section of the peatland (Fig. 1) in seven trenches that were abandoned between 1967 and 1968 (Girard 2000). The dominant species in this section of the peatland included *S. capillifolium* and *Picea mariana* (Mill.) BSP as well as *L. groenlandicum*, *V. angustifolium*, *K. angustifolia* and *C. calyculata* (Girard 2000). Tree cover was greater than 25% in this section but *Sphagnum* cover ranged from less than 10% to more than 50% of the surface area of the trenches (Girard 2000).

FIELD METHODS

Data collection occurred from 23 May 2000 to 23 August 2000 with additional measurements taken in mid-October 2000. Thirty *S. capillifolium* (*sensu* lato) cushions were instrumented with crank wires and litter bags to determine seasonal growth and decay. Crank wires are 30-cm tall, 1·5-mm thick steel wires with a 2-cm bend in the middle. The wires are inserted into the
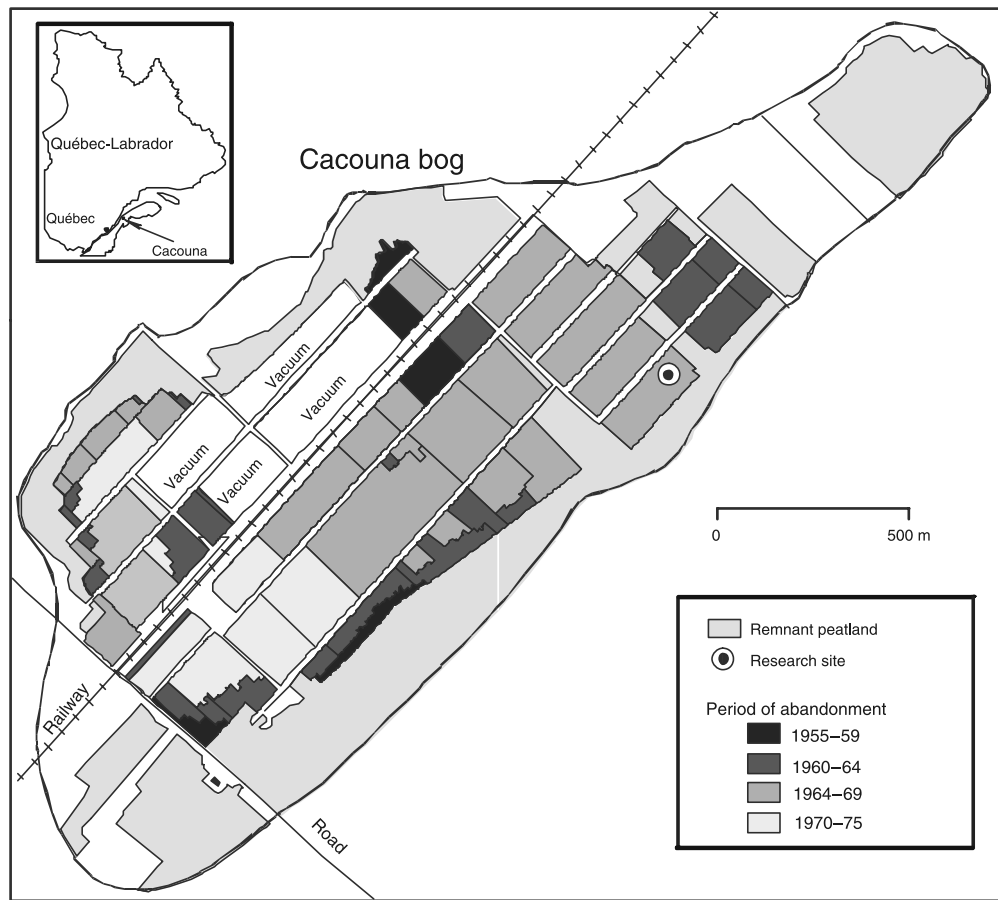
Fig. 1. Location of the Cacouna peatland research site (closed circle). The map shows the period in which peat extraction was abandoned. Vacuum refers to sections that were prepared for vacuum mining following block-cutting. Inset shows the study location within the province of Québec, Canada. Reprinted with permission from Marc Girard.

moss and the protruding end is measured initially and then every few weeks. The decrease in the distance from the top of the wire to the *Sphagnum* surface is used to determine growth in length (Clymo 1970). Both topographically high and low sections of the trenches, hereafter referred to as 'dry' and 'wet' locations, respectively (Whitehead 1999), were selected for net ecosystem CO_2 exchange (NEE) measurements. Three plots of bare peat and two pairs of *Sphagnum* cushions at the wet and dry sites (dry: A and B; wet: C and D) were measured to compare NEE of revegetated and non-revegetated sections of the cutover bog.

Nomenclature follows Scoggan (1978–79) for vascular plants and Anderson (1990) for *Sphagnum* species.

NET ECOSYSTEM CO₂ EXCHANGE

NEE was measured several times a week at each site using a clear plexiglass climate-controlled chamber (surface area = 0·03 m², volume = 0·008 m³) and an infrared gas analyser (IRGA) (Model EGM-2; PP Systems, Hitchin, UK) assembly placed and sealed over 0·03-m² polyvinyl chloride (PVC) collars. Fans inside the chambers ensured well-mixed air during the sampling period. The chamber contained a manual

pump that circulated cold water through a copper piping radiator inside the chamber to maintain the air temperature in the chamber within 1 °C of the ambient air temperature (Waddington & Roulet 1996, 2000). The CO_2 concentration within the chamber was recorded at 1-min intervals for a duration of 5 min. The chamber was removed and ventilated between measurement runs. The slope of the CO_2 concentrations over time represents the emission or uptake rate. Sample runs with r^2 values lower than 0·8 were discarded, resulting in the loss of 7% of the data.

A series of neutral density shrouds was used to measure gross ecosystem production (GEP) under low light conditions in order to develop a non-rectangular hyperbola relationship between photosynthetically active radiation (PAR or Q) and GEP:

$$A = \frac{\varphi Q + A_{max} - \sqrt{(\varphi Q + A_{max})^2 - 4\varphi Q k A_{max}}}{2k} \quad \text{eqn 1}$$

where Q is the measured PAR, A_{max} is the maximum gross photosynthetic exchange of CO_2, k is the convexity value, and the apparent quantum efficiency (φ) is the initial slope (Griffis, Rouse & Waddington 2001).

Total respiration (R_{TOT}) and soil respiration were measured using an opaque PVC chamber. Seasonal R_{TOT} was modelled using a multilinear regression relationship with water table position (WT) and −10 cm or −5 cm peat temperature (T_{PEAT}), as follows:

$$R_{TOT} = b_0 + b_1 \times WT + b_2 \times T_{PEAT} \qquad \text{eqn 2}$$

where b_0 represents the intercept, and b_1 and b_2 the coefficients for water table position and peat temperature, respectively.

Photosynthesis was obtained by removing all other plants, such as ericaceous shrubs, from within the collars. Soil respiration was measured by pairing each *Sphagnum* collar with an adjacent collar, where *Sphagnum* was removed and the chamber could be placed over the underlying peat. *Sphagnum* respiration was calculated as the difference between total respiration (R_{TOT}) and soil respiration.

The effect of the removal of vascular plant cover was assessed in mid-August. *Sphagnum* cushions adjacent to the clipped cushions were selected for comparison. The vascular plant cover was removed from these cushions and GEP was measured immediately after clipping. These sites are referred to as 'recently clipped' in Table 2. The original six clipped cushions were monitored on the same day and both sets of cushions were analysed again the following day.

ENVIRONMENTAL VARIABLES

Continuous measurements of environmental variables were made at a meteorological station located at the north-east end of the study area. PAR was recorded using a LI-COR (Lincoln, NE) quantum light sensor at a height of 1·5 m above the peat surface. Precipitation was measured with a manual rain gauge and a tipping bucket rain gauge, both set 0·5 m above the peat surface. Water table position was monitored using a modified 10-turn potentiometer water level recorder. Peat temperatures were measured at depths of 1, 5 and 10 cm below the surface and air temperature was measured using a shielded thermister located 1 m above the surface. All environmental variables were recorded continuously every minute and averaged hourly using a datalogger (Model CR10X; Campbell Scientific, Logan, UT).

Additional environmental variable measurements were made manually concurrently with the NEE measurements. PAR was recorded simultaneously with CO_2 using a PP Systems PAR sensor connected directly to the IRGA. Air temperature and peat temperatures (2, 5 and 10 cm depths) were measured using a Comark (Medfield, MA) thermoprobe. At each collar site, holes 1·5 m deep were hand-augered into the peat. Nylon-covered PVC slotted wells (diameter of 2·0 cm) were set in the holes and a manual water level recorder was used to monitor the water level fluctuations. Every 2 weeks, average volumetric moisture content was measured using a time domain reflectometry (TDR) probe.

SEASONAL GROWTH AND DECOMPOSITION

Thirty *Sphagnum* cushions in their natural state were installed with a total of 450 crank wires and 120 litter bags. Growth in length was measured once a month using 6–16 crank wires in each of the 30 *Sphagnum* cushions. In order to quantify lateral growth, four crank wires were inserted into the peat at the edges of each cushion. A core was taken from each *Sphagnum* cushion using a 100-cm³ cylinder at the end of the study period. A 3-cm layer (not including the capitula) was cut from each core, dried at 105 °C, and weighed to determine density in order to convert crank wire length measurements into growth per unit area.

Sphagnum was removed from the base of the cushion at three locations along the edge, as well as from the centre of the cushion. The samples were placed in fine 2-mm mesh litter bags, air-dried and weighed using an analytical balance (±0·0001 g). Random subsamples were also placed in litter bags, air-dried, weighed and then oven-dried at 105 °C for 24 h and reweighed. A relationship was determined between the subsample air-dried and oven-dried weights and all weights were then converted to oven-dried weights (Johnson & Damman 1991). The samples were returned to their initial locations and buried at the base of the cushions for the season. At the end of the season, all litter bags were removed from the cushions, rinsed with distilled water, oven-dried at 105 °C for 24 h and weighed. The difference between initial and final weights determined the mass lost over the study period. Comparison of data between sites (e.g. wet and dry) and locations were made using standard factorial analysis of variance techniques.

LABORATORY METHODS

In October 2000, three *Sphagnum* cushions (*c.* 20 cm high) with underlying peat (*c.* 15 cm deep) were placed in separate 30 × 45-cm plastic containers at natural density and transported to McMaster University, Ontario, Canada, for analysis. The plants were moist and partially frozen during removal, which prevented damage during sampling and transport.

Twenty-one samples were extracted from the cushions and placed in 204-cm³ PVC rings: seven samples were taken randomly from each of the actively photosynthesizing *Sphagnum* (top 5 cm), the middle depths of the cushion (*c.* 10 cm from the surface) and the underlying peat. Samples were placed in a growth chamber (Model E7; Conviron, Winnipeg, Manitoba, Canada) for the duration of the experiment.

At the beginning of the experiment, each surface *Sphagnum* ring was saturated with distilled water up to the capitula. No further water was supplied during the drying period of the experiment (7 days), after which time the water level was once again raised up to the capitula and maintained at that level (Gerdol *et al.* 1996). Monitoring of the *Sphagnum* samples continued until

photosynthesis rates approached initial (pre-drying) values (3 weeks).

The underlying *Sphagnum* and peat samples were saturated with distilled water and allowed to dry to determine the change in respiration rate with drying at 12 °C. Once dry, the samples were rewetted and gas exchange was also measured, while saturated at 20 °C, to determine Q_{10} values.

After each sampling set, the sample rings were weighed using an analytical balance. At the completion of the experiment, the peat and sphagna were placed in a drying oven at 105 °C for 24 h and reweighed to determine water content as a percentage of dry weight. Volumetric moisture content was determined using the volume of the PVC rings after adjusting for shrinkage in the peat samples.

At periodic intervals during a 3-week period, each of the surface *Sphagnum* rings was placed inside a 2650-cm^3 clear plexiglass chamber. PAR was maintained at a constant *c.* 350 µmol m^{-2} s^{-1}. NEE was measured by withdrawing 3 ml of CO_2 from the chamber using syringes at 2-min intervals over a 10-min incubation period. The chamber was then covered with an opaque shroud and respiration was measured using the same volume and sampling interval as NEE. This procedure was repeated for all seven *Sphagnum* samples. CO_2 concentration in the syringes was determined using a Varian 3800 (Palo Alto, CA) gas chromatograph (GC) equipped with a thermal conductivity detector and a Porapak Q packed column. The GC was standardized using a CO_2 standard gas (500 p.p.m.) after every five samples. Ambient CO_2 in the Conviron growth chamber was approximately 600 p.p.m., which is similar to levels recorded in the field at the moss layer (J. Laine, personal communication).

Photosynthesis and respiration rates were calculated from CO_2 concentrations over time and adjusted for temperature, pressure and volume. Measurement runs with r^2 values lower than 0·8 were discarded, resulting in the loss of 4% of the data.

The underlying *Sphagnum* and peat samples were placed in the growth chamber with no light and a temperature of 12 °C. Gas exchange measurements were taken from the shrouded chamber over a 2-week drying period using a 10-min incubation time with a 2-min interval. Gas samples were analysed with the GC.

Results

ENVIRONMENTAL VARIABLES

Precipitation events were relatively evenly distributed over the study period with the exception of 11- and 8-day rain-free periods in June and July, respectively (Fig. 2a). Rainfall events were small (< 5 mm) for the most part, with two *c.* 30 mm rainstorms in late July and early August. Total precipitation for the study period (23 May to 23 August) was 191 mm, which was 66 mm below the 30-year mean (Environment

Canada 1993). The drier than normal study period was concentrated during the early summer, as only 27 mm of rain fell in June (55 mm below average) and July precipitation was 11 mm below the 30-year mean.

The water table position followed the pattern of precipitation events, with the highest water table level occurring in late May (−0·9 cm) and reaching maximum depths on 21 July (−35·8 cm) and again on 5 August (−31·4 cm) (Fig. 2c). The mean water table position at the meteorological station during the study period was −19·7 cm. Water table position varied considerably between sites (Table 1), ranging from 0·2 cm to −30·7 cm at site wet C, while water table levels at site dry B ranged from −13·2 cm to −46·0 cm. Similarly, mean volumetric moisture content (VMC) of the sphagna at dry sites A and B were only 1·7% and 2·4% whereas the wet sites C and D had moisture contents of 5·6 and 8·2%, respectively. Minimum volumetric moisture contents at sites A, B and C were 0·6% and 2·4% at site D, while maximum values were 3·6% and 6·0% at sites A and B, and 16·8% and 19·8% at wet sites C and D. Based on water table and VMC data our expectation that the topographically high sites (dry A and dry B) would be drier than the topographically low sites (wet C and wet D) was valid.

The mean continuous air temperature of 14·4 °C was equal to the 30-year mean (Environment Canada 1993). The coolest average daily air temperature (6·7 °C) occurred at the beginning of the study period in late May and the warmest day occurred in mid-June (23·2 °C) (Fig. 2b). Peat temperatures 10 cm below the surface varied between 11·8 °C and 13·7 °C at the meteorological station. Differences in peat temperatures were observed between the bare peat surface and the *Sphagnum*-covered surface at the six study sites (Table 1).

SPHAGNUM GROWTH AND DECOMPOSITION

The *Sphagnum* cushions instrumented with crank wires and litter bags had a mean area of 0·45 ± 0·29 m^2 and a mean volume of 0·04 ± 0·03 m^3. Vertical and lateral growths were not significantly different, with mean values of 19 ± 7 and 18 ± 6 mm, respectively. This corresponded to vertical and lateral growth of 282 ± 95 and 281 ± 100 g organic matter m^{-2} $year^{-1}$, respectively. Vertical growth ranged from 6·0 to 34·0 mm for the season while lateral growth ranged from 8·5 to 30·6 mm. Mean daily growth was greatest during mid-June to mid-July (vertical = 2·6 g m^{-2} day^{-1}, lateral = 3·2 g m^{-2} day^{-1}); however, variability was large throughout the study period (Fig. 3). No significant relations were found between *Sphagnum* growth and proximity to ditches or within trench location. The mean growth on the edge of the cushion (22·7 ± 14·3 mm) was slightly greater than the growth in the centre of the cushion (19·7 ± 13·8 mm) but there was no significant difference ($P = 0.25$). Mean seasonal decomposition was 9·1 ± 6·2% and ranged from 0% to 30%. Variability was
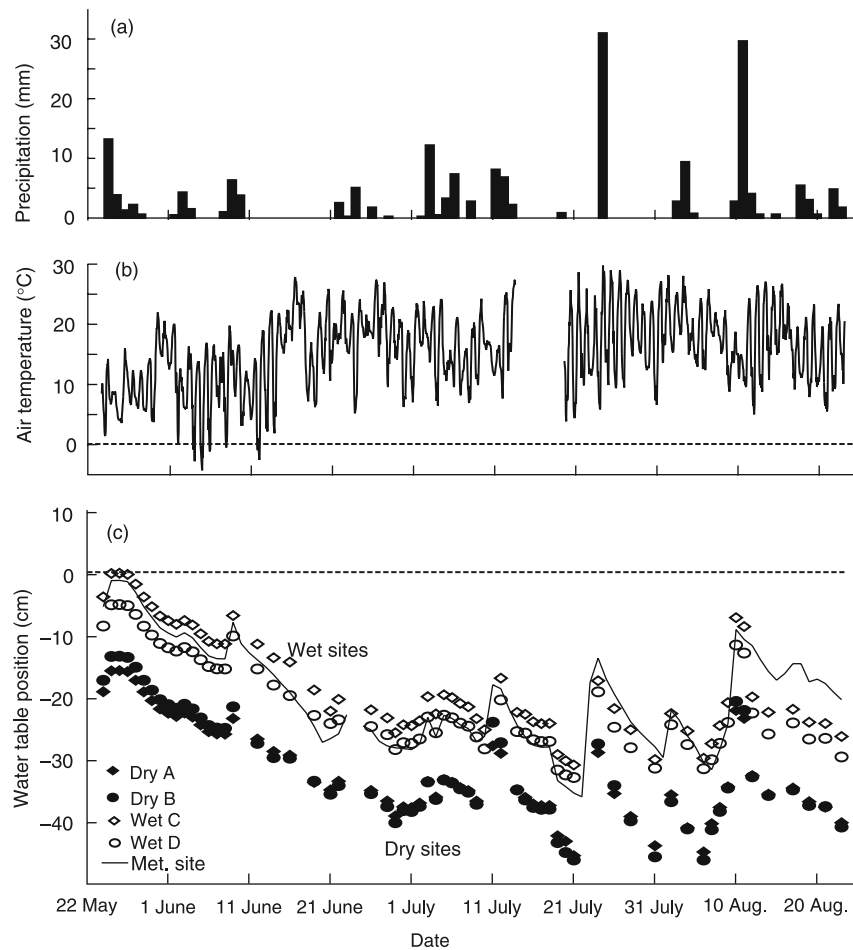
Fig. 2. (a) Daily precipitation, (b) hourly air temperature and (c) water table position at the wet (open symbols), dry (closed symbols) and meteorological station (solid line) sites.
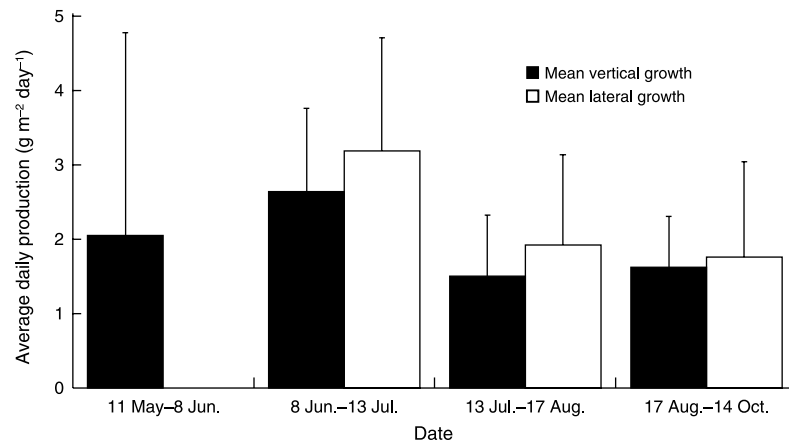
Fig. 3. Average daily production (vertical = solid and lateral = open) for four time periods using the crank wire methodology.

Table 1. Mean seasonal environmental conditions at the dry and wet sites between 23 May 2000 and 23 August 2000. Numbers in parentheses indicate standard deviation

	Dry sites		Wet sites	
	A	B	C	D
Water table (cm)	−31·5 (7·9)	−31·3 (8·9)	−17·7 (8·6)	−21·0 (7·8)
Peat temperature (−5 cm) (°C)	14·8 (3·0)	14·4 (2·9)	13·2 (3·5)	14·5 (3·6)
Peat temperature (−10 cm) (°C)	13·7 (3·0)	13·3 (3·1)	12·5 (2·8)	13·5 (3·3)
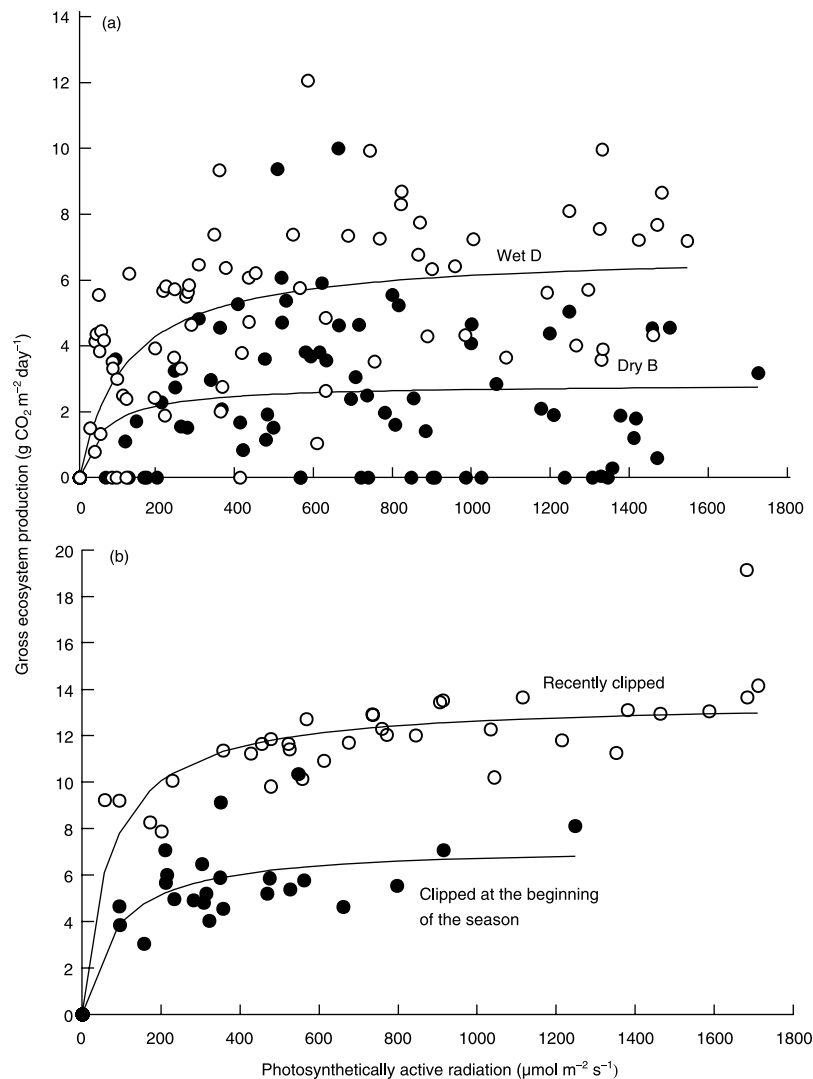
Fig. 4. (a) Seasonal gross ecosystem production light response curve at a dry site (dry B = closed circles) and a wet site (wet D = open circles), and (b) light response curves for *Sphagnum* cushions that were clipped at the beginning (closed circles) and end (open circles) of the season.

large, however, and *Sphagnum* decomposition was not significantly related to cushion size, growth or location within the cushion.
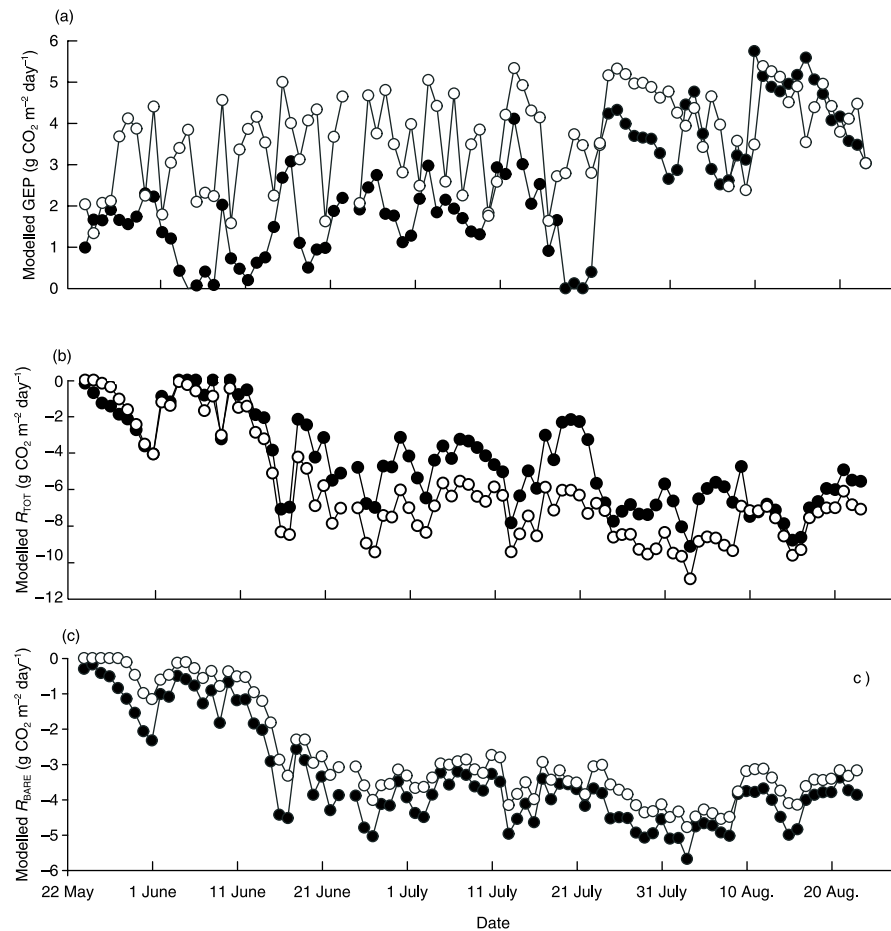
MODELLED CO_2 EXCHANGE

Ecophysiological parameters based on GEP–PAR light response curves, modelled respiration for the wet and dry sites (Fig. 4a) and vascular plant clipping experiment (Fig. 4b) parameters are presented in Table 2. Both the apparent quantum efficiency (φ) and the maximum GEP (A_{max}) of the recently clipped cushions were approximately double those of the clipped cushions. R_{TOT} was positively correlated to peat temperature, which concurs with other studies (Chapman & Thurlow 1996; Silvola *et al.* 1996).

Daily GEP was greater at the wet sites (C = $3\cdot4 \pm 0\cdot8$ g CO_2 m^{-2} day^{-1}, D = $3\cdot7 \pm 1\cdot1$ g CO_2 m^{-2} day^{-1}) than the dry sites (A = $1\cdot9 \pm 1\cdot5$ g CO_2 m^{-2} day^{-1}, B = $2\cdot4 \pm 1\cdot4$ g CO_2 m^{-2} day^{-1}). Maximum GEP of $6\cdot9$ g

CO_2 m^{-2} day^{-1} at site wet D was *c.* $2\cdot5$ times greater than the maximum GEP of $2\cdot8$ g CO_2 m^{-2} day^{-1} at site dry B (Fig. 4a). The dry sites reached a maximum GEP between 500 and 900 μmol m^{-2} s^{-1} and demonstrated a reduction in production at greater light levels. The wet sites also had a maximum value at approximately 600 μmol m^{-2} s^{-1} but, unlike the dry sites, production did not drop off with increased PAR. GEP was greatest in the month of August (Fig. 5a) when the water table level rose and precipitation was more frequent. Site wet D maximum GEP values for June, July and August were $4\cdot6$, $4\cdot9$ and $6\cdot2$ g CO_2 m^{-2} day^{-1}. Positive NEE values (i.e. a net carbon sink) were only recorded in late May, late August and October. Statistical regressions ranged from $0\cdot20$ to $0\cdot45$ for the entire season, but for the month of August the correlation improved to $0\cdot43$–$0\cdot78$.

Daily modelled R_{TOT} was also highly variable (Fig. 5b). Respiration responded strongly to precipitation by decreasing during the dry periods in June and

Fig. 5. Modelled CO_2 exchange of (a) gross ecosystem production, (b) total respiration and (c) bare peat respiration at a dry (dry B = closed circles) and a wet (wet D = open circles) site.

Table 2. CO_2 exchange modelling parameters with standard error in parentheses. Respiration is assigned a negative sign convention as a loss from the plant. The clipped and recently clipped GEP parameters from cushions adjacent to the wet and dry sites are from the 2-day measurement period in mid-August only

Site	Gross ecosystem production parameters					Total respiration parameters				
	n	φ	A_{MAX}	k	r^2	n	b_0	b_1	b_2	r^2
Dry site	109	0·05 (0·00)	2·83 (0·00)	5·57E-07	0·31	37	4·7	−0·14	−1·0	0·62
Wet site	110	0·06 (0·02)	6·85 (0·55)	5·69E-07	0·67	37	7·3	0·04	−0·9	0·64
Clipped	40	0·09 (0·04)	7·27 (0·84)	6·30E-03	0·85	NA	NA	NA	NA	NA
Recently clipped	36	0·20 (0·06)	13·50 (0·55)	1·91E-04	0·90	NA	NA	NA	NA	NA

φ, g CO_2 m⁻² day⁻¹ μmol ⁻¹ PAR.
A_{MAX}, g CO_2 m⁻² day⁻¹.
k, dimensionless.

July and reaching maximum R_{TOT} directly following precipitation events. Fluctuations in R_{TOT} were limited at the beginning and end of the study period when the water table was relatively constant and closer to the peat surface. On a seasonal basis, R_{TOT} at the wet sites (C = −5·0 ± 1·0 g CO_2 m⁻² day⁻¹, D = −6·0 ± 2·9 g CO_2 m⁻² day⁻¹) was 10–25% greater than at the dry sites (A = −4·3 ± 2·5 g CO_2 m⁻² day⁻¹, B = −4·5 ± 2·4 g CO_2 m⁻² day⁻¹). R_{TOT} was dominated by soil respiration rather than *Sphagnum* respiration. Soil respiration represented

81%, 67%, 46% and 95% of R_{TOT} for sites A, B, C and D, respectively. Interestingly, among the wet sites, R_{TOT} fluctuated little at site wet C (range: 3–7 g CO_2 m⁻² day⁻¹) whereas site wet D varied between 0 and 11 g CO_2 m⁻² day⁻¹ (Fig. 5b).

Daily modelled bare peat respiration (R_{BARE}) reflected the same peaks as R_{TOT} in response to drying and wetting events (Fig. 5c). All sites experienced respiration bursts immediately after precipitation events, and diminished respiration during dry periods. Bare peat
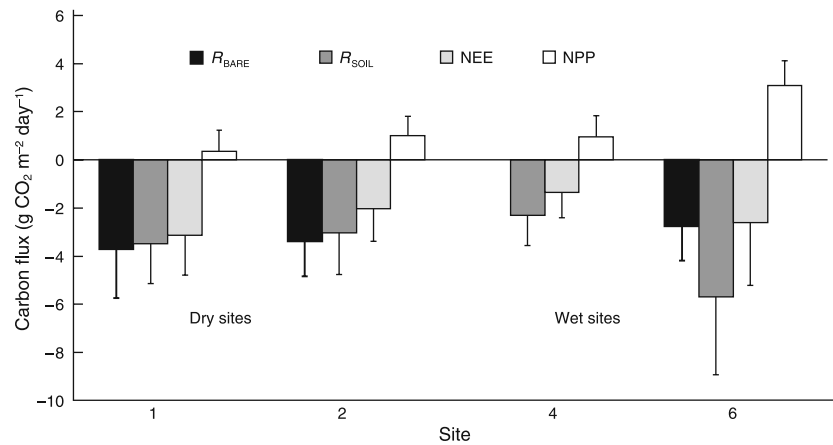
Fig. 6. Seasonal carbon fluxes (g CO_2 m^{-2} day^{-1}) at dry and wet sites. R_{BARE}, R_{SOIL}, NEE and NPP refer to bare peat respiration, soil respiration, net ecosystem CO_2 exchange and net primary productivity, respectively.
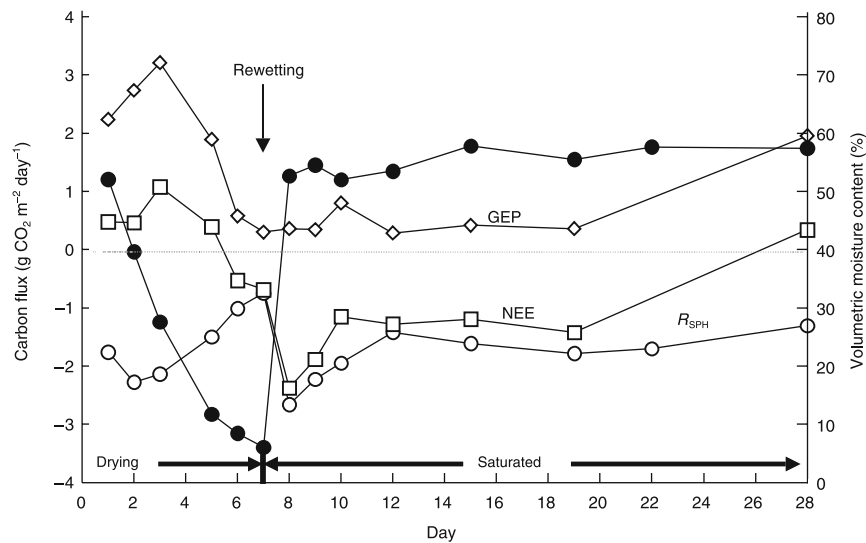
Fig. 7. Carbon flux response of *Sphagnum* to a drying and rewetting cycle with volumetric moisture content (closed circles), gross ecosystem production (open diamonds), *Sphagnum* respiration (R_{SPH}) (open circles) and net ecosystem CO_2 exchange (open squares).

respiration was quite similar between sites, with fewer fluctuations at the wet sites. Again respiration was at its minimum in late May when the water table was highest. Bare peat respiration was 16–24% greater at the dry sites than at the wet sites (Fig. 6). Combining GEP and R_{TOT}, NEE followed the trend: wet C (1.3 ± 1.1 g CO_2 m^{-2} day^{-1}) > dry B (-2.0 ± 1.4 g CO_2 m^{-2} day^{-1}) > wet D (-2.6 ± 2.6 g CO_2 m^{-2} day^{-1}) > dry A (-3.1 ± 1.6 g CO_2 m^{-2} day^{-1}). Averaging these sites and converting to a seasonal basis resulted in a net loss of 211 g CO_2 m^{-2} for the Cacouna study site. Although 254 g CO_2 m^{-2} were fixed through GEP, total respiration was −465 g CO_2 m^{-2}. Despite this, all sites exhibited a net growth of *Sphagnum* (positive net primary productivity, NPP) during the season (wet D = 3.1 ± 1.0 g CO_2 day^{-1} > wet C = 1.0 ± 0.9 g CO_2 m^{-2} day^{-1} = dry B = 1.0 ± 0.8 g CO_2 m^{-2} day^{-1} > dry A = 0.4 ± 0.9 g CO_2 m^{-2} day^{-1}).

Gas exchange estimates of NPP were converted to grams of organic matter in order to compare with crank wire results. Mean seasonal crank wire growth rates were 2.2 g m^{-2} day^{-1}, almost three times greater than the 0.8 g m^{-2} day^{-1} calculated using the gas exchange method. Rates varied from 0.6 to 3.2 g m^{-2} day^{-1} for crank wire measurements and between 0.2 and 2.0 g m^{-2} day^{-1} for gas exchange data. Because crank wire measurements extended beyond the period of gas exchange monitoring, data adjusted for the period from late May to late August indicated that gas exchange NPP (75 g m^{-2}) was less than crank wire NPP (207 g m^{-2}).

LABORATORY CO$_2$ EXCHANGE

During the first 7 days of the drying experiment, *Sphagnum* VMC decreased from 52% to 6% (hereafter referred to as the drying period), and upon rewetting *Sphagnum* VMC varied from 52% to 58% (hereafter referred to as the saturation period; Fig. 7). Mean *Sphagnum* VMC during the laboratory experiment was 42%. Mean CO_2 exchange values for the laboratory
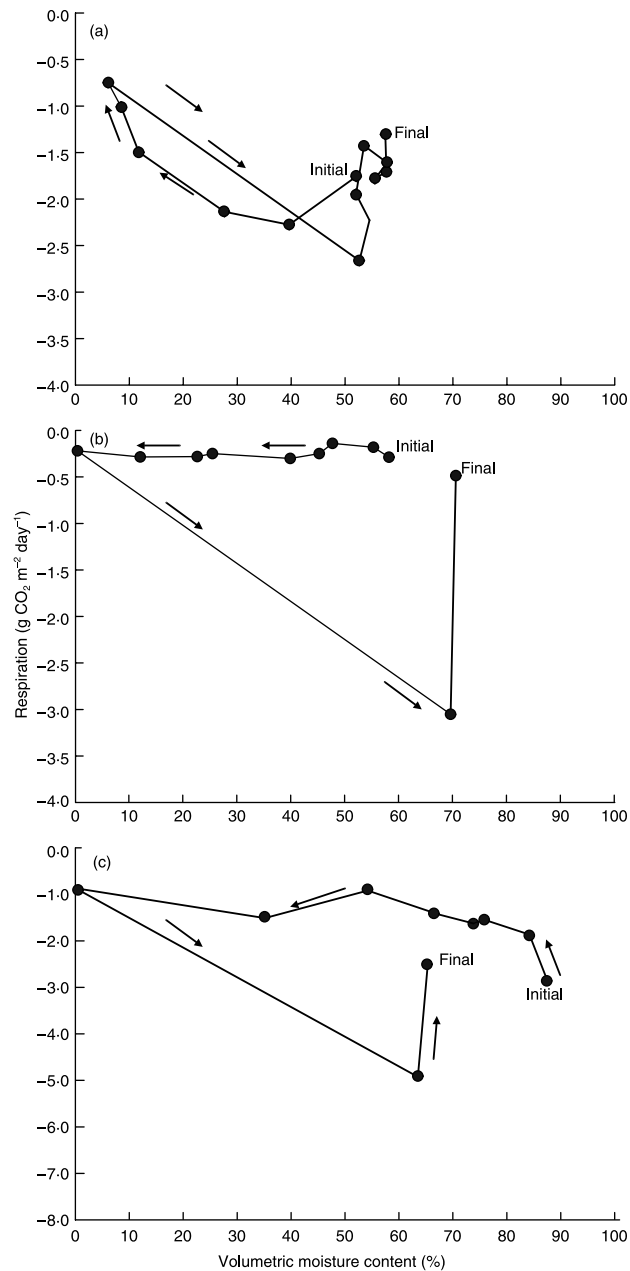
Fig. 8. Respiration response of (a) upper *Sphagnum*, (b) lower *Sphagnum* and (c) peat to a drying and rewetting cycle (from initial to final).

experiment on the top layer of *Sphagnum* were -0.7 g CO$_2$ m^{-2} day^{-1} for NEE, -1.7 g CO$_2$ m^{-2} day^{-1} for R_{TOT} and a GEP of 1.1 g CO$_2$ m^{-2} day^{-1}. During the drying period, GEP increased from 2.2 g CO$_2$ m^{-2} day^{-1} to a peak of 3.2 g CO$_2$ m^{-2} day^{-1} at a corresponding VMC of 28%. GEP then decreased abruptly to 0.3 g CO$_2$ m^{-2} day^{-1} at a VMC of 6% (Fig. 7). Upon rewetting (VMC $= 53\%$), GEP showed no significant change from pre-wetting values (0.3 g CO$_2$ m^{-2} day^{-1}). Only after 20 days of the saturation period at a VMC of *c*. 55% did GEP recover to 2.0 g CO$_2$ m^{-2} day^{-1} (similar to pre-drying levels).

R_{TOT} for the surface layer of *Sphagnum* increased to -1.7 g CO$_2$ m^{-2} day^{-1} at a VMC of 40% before falling to -0.8 g CO$_2$ m^{-2} day^{-1} at a VMC of 6% (Fig. 7). Re-saturation immediately produced a burst of respiration

to -2.7 g CO$_2$ m^{-2} day^{-1} at 53% VMC before stabilizing around -1.3 g CO$_2$ m^{-2} day^{-1}, 5 days into the saturation period (Figs 7 and 8a).

NEE peaked at 1.1 g CO$_2$ m^{-2} day^{-1} at a VMC of 28% and decreased to -2.4 g CO$_2$ m^{-2} day^{-1} following the rewetting. *Sphagnum* samples switched from a net sink to a net source of CO$_2$ at a VMC of 8.5% during the drying period.

The underlying *Sphagnum* produced a similar respiration pattern to the upper layer of *Sphagnum* in the previous experiment (Fig. 8), starting from -0.58 g CO$_2$ m^{-2} day^{-1} at an initial VMC of 58%, slightly increasing to -0.60 g CO$_2$ m^{-2} day^{-1} at 40% VMC, before dropping to reach -0.44 g CO$_2$ m^{-2} day^{-1} at 0% VMC (Fig. 8b). Resaturation to 70% produced a respiration

burst of $-6\cdot1$ g CO_2 m^{-2} day^{-1} for the underlying *Sphagnum*. Similarly, the respiration of the underlying peat dropped from $-1\cdot42$ g CO_2 m^{-2} day^{-1} to $-0\cdot43$ g CO_2 m^{-2} day^{-1} as the VMC decreased from 88% to 0% (Fig. 8c). Resaturation to 64% resulted in a respiration burst of $-2\cdot46$ g CO_2 m^{-2} day^{-1} before decreasing to near initial values.

Q_{10} values of $2\cdot1$ and $1\cdot8$ for *Sphagnum* and peat, respectively, were determined for an increase in temperature from 12 °C to 20 °C.

Discussion

CUTOVER BOG CO_2 BALANCE

NEE estimates for the study site revealed a loss of $-57\cdot5$ g C m^{-2} for the study period, while total respiration for the season was -127 g C m^{-2}. CO_2 losses from the bare peat in this study were -84 g C m^{-2}, which was $1\cdot5$ times greater than the seasonal loss from the revegetated *Sphagnum* sites. Tuittila (2000) also found that while respiration is greater at *Sphagnum*-covered surfaces than bare surfaces, overall bare sites lose more carbon than revegetated sites. *Sphagnum* re-establishment is therefore critical for limiting CO_2 loss and regaining carbon sink function over time.

NEE and the components thereof (R_{TOT}, GEP and NPP) all fall within the range of values for natural peatlands (Hayward & Clymo 1982; Moore 1989; Gerdol 1995; Gerdol *et al*. 1996; Griffis 2000). *Sphagnum capillifolium* cushions in a block-cut peatland are therefore capable of 'natural' growth but the variation in production is two to three times that of natural peatlands (Waddington & Roulet 1996; Waddington, Rochefort & Campeau 2002a). Therein lies the major difference between cutover and natural peatlands. Cutover peatlands are subject to environmental extremes (Lavoie & Rochefort 1996), such as drought, due to the lack of acrotelm and the corresponding changes in hydrological and physical peat properties (Van Seters & Price 2001).

LIMITS TO *SPHAGNUM* GROWTH IN CUTOVER BOGS

This study demonstrates that *Sphagnum* mosses are capable of growth in cutover peatlands; in fact, all sites exhibited positive NPP. Indeed, peat respiration is the major source of CO_2 loss, not *Sphagnum* respiration. The laboratory results clarify the processes that limit and enhance growth rates. The experiments show that the history of moisture availability is the dominant factor in these cutover systems. Without the self-regulating acrotelm, these mosses are prone to desiccation. Drying and subsequent rewetting created an immediate burst of respiration yet also shut down photosynthesis for a 20-day period. Gerdol *et al*. (1996) found similar results for *Sphagnum* photosynthesis and attributed the delay to damage of the cellular structure of the

plants. The effects of drying and wetting cycles have been well documented in other bryophytes and hepatics (Armstrong 1976; Brown, MacFarlane & Kershaw 1983; Oliver, Mishler & Quisenberry 1993; Bewley 1995). The timeframe for carbon exchange to return to initial rates depends upon the desiccation tolerance of the plant, i.e. its ability to repair cellular damage and fix carbon with the influx of water (Oliver, Mishler & Quisenberry 1993).

While a short period of rewetting will permit the moss to live, it is insufficient to allow growth (Dilks & Proctor 1976). Alm *et al*. (1999) cautioned that in order for carbon accumulation to occur at a long-term average rate of 25 g C m^{-2} year^{-1}, a ratio of five 'moist' summers for every 'dry' summer is necessary. The effects of a cessation in photosynthesis can quickly counterbalance any carbon accumulation.

While the *S. capillifolium* samples were able to return to their initial GEP in the laboratory setting, the same was not true of the field situation. The dry summer began in mid-June with 55 mm less precipitation than the long-term average (33% of the 30-year mean). Once dry, there were no extended periods of saturation until August. Indeed the only observed positive NEE (net carbon sink) occurred in late May, late August and October. On the other hand, while photosynthesis was suppressed for the majority of the summer, each rewetting event produced respiration bursts, further disrupting the carbon balance of the sphagna. Summer NEE was therefore characterized by negligible photosynthesis accompanied by periodic peaks of high respiration.

Several studies have linked changes in GEP with *Sphagnum* moisture contents (Titus, Wagner & Stephens 1983; Wagner & Titus 1984; Rydin & McDonald 1985b; Murray *et al*. 1989a; Gerdol *et al*. 1996). Maximum GEP for *Sphagnum* corresponds with 6–10 g water g dry weight^{-1} (g g^{-1}) and the compensation point when GEP ceases occurs at 1–2 g g^{-1} (Murray *et al*. 1989a; Titus, Wagner & Stephens 1983; Rydin & McDonald 1985b). Laboratory results show that maximum GEP occurred at a point between $11\cdot3$ and $26\cdot7$ g g^{-1}, which is higher than other reported values; however, the precise optimum was not determined in this experiment. In the field study, mean VMC at the dry sites were $1\cdot7$% and $2\cdot4$%, which are at or close to the compensation point for *S. capillifolium* (Titus, Wagner & Stephens 1983).

All *Sphagnum* species exhibit maximum GEP at light levels less than full intensity (Clymo & Hayward 1982; Harley *et al*. 1989; Murray, Tenhunen & Kummerow 1989b; Murray, Tenhunen & Nowak 1993). For example, *S. capillifolium* becomes light saturated at 500 µmol m^{-2} s^{-1} (Titus & Wagner 1984). Indeed, GEP decreased with light levels above 700 µmol m^{-2} s^{-1} at the dry sites. While Murray, Tenhunen & Nowak (1993) concluded that photo-inhibition can occur at high PAR, the dry sites were visibly desiccated during the study period. Therefore, the coincidence of high PAR and low GEP could also be the result of high PAR occurring on clear days that are generally warmer with higher evaporation,

thereby creating water stress (Murray, Tenhunen & Kummerow 1989b). The fact that GEP at site wet D, which was not as water-limited, did not decrease at high PAR suggests that water stress was the cause of the decline at high PAR rather than photo-inhibition.

ROLE OF COMPANION SPECIES

The use of companion species has often been considered in peatland restoration (Sagot & Rochefort 1996; Ferland & Rochefort 1997; Buttler, Grosvernier & Matthey 1998). As the goal of this research was to study the carbon dynamics of *Sphagnum*, vascular plant removal became a methodological necessity. However, the benefit of companion species was evident when the clipped cushions became pale and brittle over the summer. The cushions regained colour and elasticity with precipitation events, only to return to a state of desiccation with further drying. Natural cushions surrounding the clipped cushions remained intact in terms of structure and colour throughout the summer drying period. Both crank wire and gas flux measurements on natural cushions indicate that the growth of natural cushions with vascular plant cover was approximately double the rate of growth of clipped cushions. On a clear day with full light of 1602 µmol m^{-2} s^{-1}, PAR under the ericaceous shrubs was measured at 690 µmol m^{-2} s^{-1}, indicating that companion species allow sufficient light for maximum GEP to occur. The processes of water retention and transport within *Sphagnum* cushions have yet to be determined, but as it is the top 5 cm of *Sphagnum* that actively photosynthesizes (Titus, Wagner & Stephens 1983) the humidity at the surface is crucial. In fact, even with a high water table position *Sphagnum* re-establishment in cutover peatlands improves with a protective cover (Ferland & Rochefort 1997).

IMPLICATIONS FOR RESTORATION

The study of a naturally revegetated cutover peatland can provide management suggestions for peatland restoration. Restoration techniques aim to improve moisture availability (Price, Rochefort & Quinty 1998); however, a constant moisture supply is necessary to enhance photosynthesis and simultaneously suppress respiration. Proper ditch blocking would be an inexpensive yet effective aid to enhance restoration (Girard 2000). While blocking ditches will raise the water table level, the physical characteristics of deep peat (i.e. catotelm) will impede constant water table levels (Price & Whitehead 2001). It may be that fluctuations will remain problematic until a sufficiently deep acrotelm has been regenerated. However, it is not yet known what thickness of *Sphagnum* layer is needed to stabilize the water table.

Companion species must be considered for restoration practices. Currently, straw mulch is used to maintain humidity and shading; however, most of this protective cover decomposes within 3 years (J.M. Waddington & M.J. Greenwood, unpublished data). Companion species would maintain humidity and shade far beyond a few seasons (Boudreau & Rochefort 2000; Le Quéré & Samson 2000). If water stress does indeed persist until the creation of a self-regulating surface layer of peat (i.e. acrotelm) then certainly more than 3 years of protection is required. This research demonstrates that the surface layer of *Sphagnum* holds the key to reducing CO$_2$ emissions and recreating a peat-accumulating ecosystem. Increasing surface humidity and limiting evaporation are therefore crucial restoration techniques. Stimulating *Sphagnum* growth on floating mats in inundated bog remnants through increased methane production may also prove to be an important restoration technique (Smolders *et al.* 2002).

This study combined ecological and climatological methods to allow comparison with other studies. However, the model used for seasonal NEE estimation does not take into account the dynamic processes presented in the laboratory experiment but assumes an 'on/off' switch for plant growth and respiration that is common in many models (Griffis 2000). Instead we suggest that field measurements of *Sphagnum* moisture content be made to improve CO$_2$ exchange modelling efforts.

Sphagnum growth in cutover peatlands is limited not only by water availability but specifically by drying and wetting cycles. These moisture cycles suppress photosynthesis and enhance respiration losses. All *Sphagnum* cushions exhibited a positive NPP over the summer; however, all sites lost CO$_2$ to the atmosphere due to high peat respiration. *Sphagnum* cushions with vascular plant cover photosynthesized at twice the rate of exposed cushions. This research demonstrates that restoration of cutover peatlands must include companion species and a constant moisture supply above the minimum threshold for *Sphagnum* mosses.

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