

The role of cotton-grass (*Eriophorum vaginatum*) in the exchange of CO₂ and CH₄ at two restored peatlands, eastern Canada¹

Michèle MARINIER, Department of Geography and Centre for Climate & Global Change Research, McGill University, 805 Sherbrooke St. W., Montréal, Québec H3A 2K6, Canada.

Stephan GLATZEL, Department of Geography and Centre for Climate & Global Change Research, McGill University, 805 Sherbrooke St. W., Montréal, Québec H3A 2K6, Canada, and Landscape Ecology Unit, Department of Geography, Georg-August-University, 37077 Goettingen, Germany.

Tim R. MOORE², Department of Geography and Centre for Climate & Global Change Research, McGill University, 805 Sherbrooke St. W., Montréal, Québec H3A 2K6, Canada, e-mail: tim.moore@mcgill.ca

Abstract: We measured methane (CH₄) and carbon dioxide (CO₂) exchanges from bare peat and *Eriophorum vaginatum* ssp. *spissum* tussocks at recently restored harvested peatlands near Shippagan, New Brunswick and Rivière-du-Loup, Québec over three growing seasons (May to October). Average seasonal CH₄ emission rates ranged from -1 to 65 mg·m⁻²·d⁻¹, with a generally weak relationship with water table position. A stronger relationship was seen between CH₄ emissions and above-ground plant biomass. CH₄ fluxes from *E. vaginatum* tussocks were larger than those from bare peat surfaces and increased with increasing above-ground biomass and photosynthetic rate. Clipping fresh leaves from tussocks reduced the CH₄ emission rates by 79%. Photosynthesis rates were large in tussocks, ranging from 0.9 to 3.4 g CO₂-C·m⁻²·h⁻¹ at high light levels, and respiration rates (autotrophic + heterotrophic) ranged from -0.1 to -1.3 g CO₂-C·m⁻²·h⁻¹. Some tussocks exhibited net CO₂ loss to the atmosphere, even under high light levels. Although the rapid colonization of restored peat surfaces by *E. vaginatum* aids the development of other vascular plants and mosses, it increases the flux of CH₄ to the atmosphere and provides little or no net C accumulation on the peat surface.

Keywords: CH₄, CO₂, cotton-grass, *Eriophorum vaginatum*, peatland, restoration.

Résumé : Nous avons mesuré les échanges de méthane (CH₄) et de dioxyde de carbone (CO₂) à partir de tourbe nue et de touradons de linaigrette (*Eriophorum vaginatum* ssp. *spissum*) dans des tourbières exploitées qui ont été récemment restaurées près de Shippagan (Nouveau-Brunswick) et de Rivière-du-Loup (Québec). L'étude s'est échelonnée sur trois saisons de croissance (mai à octobre). Les taux d'émission saisonniers moyens de CH₄ varient de -1 à 65 mg·m⁻²·d⁻¹ et sont faiblement reliés au niveau de la nappe phréatique. Une plus forte relation est observée entre les émissions de CH₄ et la biomasse aérienne des plantes. Les flux de CH₄ provenant des touradons de linaigrette sont plus élevés que ceux issus des surfaces de tourbe nue. Ils augmentent avec l'accroissement de la biomasse aérienne et du taux de photosynthèse. La coupe de nouvelles feuilles chez les touradons réduit de 79 % les taux d'émission de CH₄. Les taux de photosynthèse des touradons sont élevés, variant de 0,9 à 3,4 g CO₂-C·m⁻²·h⁻¹ à des hauts niveaux de luminosité, et les taux de respiration (autotrophe et hétérotrophe) varient de -0,1 à -1,3 g CO₂-C·m⁻²·h⁻¹. Certains touradons affichent une perte nette de CO₂ vers l'atmosphère, même en présence d'une luminosité élevée. Bien qu'une colonisation rapide des surfaces restaurées de tourbe par la linaigrette favorise le développement des autres plantes vasculaires et des mousses, elle accroît les flux de CH₄ vers l'atmosphère et n'apporte que peu ou pas d'accumulation nette de carbone à la surface de la tourbe.

Mots-clés : CH₄, CO₂, *Eriophorum vaginatum*, linaigrette dense, restauration, tourbière.

Nomenclature: Gleason & Cronquist, 1991.

Introduction

Northern peatlands store between one-fifth and one-third of the total terrestrial pool of soil carbon and are long-term sinks of carbon dioxide (CO₂) and sources of methane (CH₄) (Gorham, 1991). Peat moss is a valuable natural resource, and in 2000 approximately 12.5 km² were under active extraction in Canada, primarily from bogs (J. Cleary, pers. comm.). After harvesting, it is difficult for vegetation to successfully re-establish on the abandoned surface because of changes in hydrology,

microclimate, and peat properties (Waddington, Rottenberg & Warren, 2001).

In Canada, peatland restoration involves blocking the drainage ditches to raise the water table, stabilizing the surface against freeze-thaw cycles and wind erosion through the application of straw mulch, spreading *Sphagnum* diaspores on the peat surface to make up for the lack of a viable natural seed bank, and fertilizing with phosphorus to help increase the availability of nutrients (Ferland & Rochefort, 1997). Many studies have examined the progress of vegetation regrowth after restoration, and it has been observed that the cotton-grass sedge *Eriophorum vaginatum* ssp. *spissum* abundantly colonizes

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²Author for correspondence.

restored peat surfaces (Lavoie & Rochefort, 1996). This plant is of particular interest, as it is believed to act as a companion species for the regrowth of key peatland-forming vegetation, in particular *Sphagnum* and other mosses (Tuittila *et al.*, 2000a). In the past, it appears that *E. vaginatum* was important in the transition from fens to bogs in Britain (Hughes & Dumayne-Peaty, 2002).

The effects of *E. vaginatum* on the CO₂ and CH₄ dynamics of restored peatlands have been addressed only in Finland, where the restoration methods differ from those used in eastern Canada. In Finland, the water table is raised to the surface and pre-drainage inflow is re-established on minerotrophic sites, an approach that focuses on regaining the hydrological function without manually aiding in vegetation regrowth through adding seeds or fertilizing (Tuittila *et al.*, 1999).

The objectives of this study were to determine the role of *E. vaginatum* on the exchange of CH₄ and CO₂ (net ecosystem exchange or NEE) between the atmosphere and the surface of restored peatlands in eastern Canada. We compared fluxes between *E. vaginatum* tussocks and bare peat and conducted a clipping experiment to assess the role of fresh carbon on the fluxes.

Methods

SITE DESCRIPTION

The 1999 and 2000 study sites were located in Rivière-du-Loup, Québec (47° 51' N, 69° 32' W). The two sites, RR95 and RR97, were restored in 1995 and 1997, respectively, by the Groupe de recherche en écologie des tourbières (GRET) at Université Laval. Restoration at both sites involved blocking drainage ditches, adding straw mulch, and fertilizing with phosphorus. Both sites were vacuum harvested until the year before restoration and were located adjacent to areas that continue to be actively harvested. The RR95 and RR97 sites were revegetated with *E. vaginatum* tussocks and moss patches, but the largest coverage was still bare peat. The tussocks were larger and more vital at RR97 than at RR95. From May to October of 1999 and 2000, precipitation totalled 496 and 402 mm and average daily air temperature was 14.9 and 13.2 °C (Table I). Compared with the 30-y average, 1999 had a wet spring and early summer, whereas 2000 was generally drier than average for the whole season.

The 2001 study site, SR97, was located near Shippagan, northeastern New Brunswick (47° 40' N, 64° 43' W) and

comprised 750 m² of a 3-ha area that was restored by GRET in 1997. The restoration method used was the same at this site as at RR95 and RR97, except that the site was also terraced to prevent excessive runoff from the gently sloping surface (1 to 2%). SR97 was vacuum harvested until 1986, then abandoned before restoration began in 1997. Before restoration, the surface was free of vegetation (S. Boudreau, pers. comm.), while at the start of this experiment it was dominated by bare peat and *E. vaginatum*. From May to October 2001, precipitation was 600 mm and the average seasonal air temperature was 15.7 °C; this was warmer than average, with July and August being drier than average (Table I).

EXPERIMENTAL DESIGN

In 1999 and 2000, at RR95 three *E. vaginatum* tussocks and two bare areas and at RR97 two tussocks and one bare area were selected for analysis. Grooved PVC collars covering an area of 0.053 m² were placed around each tussock and in the bare area. Boards were placed around the collars to avoid excessive damage and allow ease of access for data collection.

At SR97, there were three treatments. Ten similarly sized *E. vaginatum* tussocks were selected, of which five were randomly assigned to be undisturbed (full vegetation treatment). The remaining five were clipped approximately once every 10 d (clipped treatment). The first clipping involved removing as much green plant tissue as possible, and subsequent clippings removed newly formed green plant tissue. Five additional bare areas were chosen as the bare peat treatment. Grooved PVC collars were placed around each tussock and the bare area, and boards were placed around the collars.

CH₄ AND CO₂ FLUX MEASUREMENTS

Methane flux was measured with an 18-L plastic chamber covered in tinfoil and fitted with a rubber serum stopper placed on the collar, with the grooved edge filled with water to ensure an airtight seal. After pumping with a 60-mL syringe to mix the air inside the chamber, 10 mL of air was withdrawn into a syringe once every 5 min over 20 min. CH₄ concentration was analyzed on a Shimadzu gas chromatograph (GC) within 72 h of sampling. We estimate that the detection limit of the GC was equivalent to 1 mg CH₄·m⁻²·d⁻¹. Flux was calculated from the change in headspace CH₄ concentration. Measurements were rejected if it was thought that a disturbance had occurred (resulting in very high outliers). If

TABLE I. Precipitation (P) and air temperature (T) at Rivière-du-Loup and Shippagan from May to October 1999-2001 and the 30-y averages.

Month	Rivière-du-Loup						Shippagan			
	30-y P (mm)	1999 P (mm)	2000 P (mm)	30-y T (°C)	1999 T (°C)	2000 T (°C)	30-y P (mm)	2001 P (mm)	30-y T (°C)	2001 T (°C)
May	82	24	93	9.8	14.1	9.5	85	124	9.7	12.1
June	79	127	27	15.8	18.1	14.5	85	115	15.8	17.6
July	84	110	32	18.8	19.0	17.5	98	82	19.1	18.8
August	93	43	76	17.4	17.7	18.1	96	78	18.0	20.4
September	90	87	74	12.5	15.4	12.7	87	97	12.7	15.7
October	71	106	100	6.8	5.2	6.8	93	105	6.8	9.4
Seasonal	499	496	402	13.5	14.9	13.2	544	601	13.7	15.7

the headspace concentrations were close to ambient CH₄ levels (1.8–2.0 ppm), with no real pattern of increase or decrease, the flux was taken to be zero. Approximately 10 to 20% of the measured values were rejected.

Carbon dioxide measurements at SR97 were made approximately once every 10 d using a portable infrared gas analyzer (EGM-1 or EGM-3, PP Systems, Hitchin, UK) attached to a closed Plexiglas chamber allowing 87% of incoming solar radiation and fitted with a fan, a cooling tube, and a thermistor. The cooling tube was attached to an external pump in a bucket of ice water to prevent condensation from forming on the walls of the chamber. The thermistor measured air temperature inside the chamber at the beginning and end of each measurement run. The chamber was placed on the collar, and the CO₂ flux over 3 min was calculated based on changes in CO₂ concentration measured once every 10 s for the first minute and every 30 s thereafter. The measurements were repeated first with a shroud allowing half of the incident photosynthetically active radiation (PAR) and then with a shroud allowing three-quarters of the incident PAR. A final 3-min measurement was made with a full shroud, simulating dark respiration conditions. Measurements at RR95 and RR97 were made in a similar fashion, except that only a half shroud and a full shroud were used and the measurement period was 5 min, with CO₂ concentrations measured once every minute. The time period over which the measurements were made was shortened in 2001 to better capture the initial change in CO₂ concentration. In most cases, the change in concentration over time followed a linear trend.

ANCILLARY DATA

Water table position was measured manually each week throughout the study. A meteorological station was used to measure PAR, air temperature, and water table level on an hourly basis.

In 2000, four of the five tussocks measured at RR95 and RR97 were collected at the end of the field season, dried at 70 °C for 48 h, and weighed for above-ground biomass. In 2001, all 10 experimental tussocks were collected from SR97 at the end of the field season and above-ground biomass was similarly determined.

DATA ANALYSIS

To test for differences between treatments over time, the CH₄ and CO₂ dark respiration data were separated into seasonal groups and analyzed using repeated-measures ANOVA. The early season represented May and June, the mid season July and August, and the late season September and October. All ANOVAs were done using SYSTAT (SPSS, 2000).

To estimate CO₂ exchange, the NEE data were separated by season, similar to above, and NEE was related to PAR using a rectangular hyperbola curve:

$$NEE = GP_{\max} \times \alpha \times PAR / ([\alpha \times PAR] + GP_{\max}) + R, \quad [1]$$

where GP_{max} is the asymptotic maximum for NEE, α is the initial slope of the curve, and R is the y-axis intercept (dark respiration). The fit was established using Table

Curve (Jandel, 1994) with sign convention positive for CO₂ uptake and negative for CO₂ release by the peat surface. Since the dark shroud flux measurements were taken within minutes of the light measurements, gross photosynthesis was calculated by subtracting the full shroud values from NEE at each shroud level. Maximum photosynthesis was taken to be that at light levels above PAR of 1,000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. This light level cutoff was chosen because photosynthesis in most plants, including *E. vaginatum*, saturates at approximately this level (Limbach, Oechel & Lowell, 1982; Robertson & Woolhouse, 1984).

Respiration relationships with temperature and water table position were assessed using linear regression with SYSTAT (SPSS, 2000). Water table at RR95 in 2000 remained below the depth of the well; therefore, only measurements from RR97 were used in 2000.

Results

CH₄ FLUX

The seasonal average CH₄ flux at SR97 ranged from 8 (clipped treatment) to 12 (bare peat) and 39 (full vegetation treatment) $\text{mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Table II), and emissions peaked at the full vegetation and clipped treatments at the end of the growing season, coinciding with a rise in the water table (Figure 1). At RR97 in 1999 and 2000, CH₄ fluxes ranged from -1 to 65 $\text{mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, with full vegetation > bare peat (Table II, Figure 1). The relationship between CH₄ emission and water table position for each of the sites and treatments was not significant, except for that from full vegetation at SR97 ($\log_{10}\text{CH}_4 = -0.017\text{WatertableLevel} + 0.66$; $r^2 = 0.54$, $P < 0.05$).

A positive relationship between the overall mean CH₄ emissions and end of season above-ground biomass was found at both SR97 ($P < 0.05$, $r^2 = 0.62$) and the two sites at Rivière-du-Loup using combined flux data from 1999 and 2000; however, due to the outliers in the dataset from the Rivière-du-Loup sites, a significant relationship was found only at SR97 ($r^2 = 0.62$, $P < 0.01$, Figure 2). Mean seasonal CH₄ fluxes were compared with mean seasonal maximum photosynthesis (at PAR > 1,000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), to test for the influence of plant production. CH₄ and CO₂ measurements were not made concurrently but occurred within a few of days of one another. A significant positive correlation was found with SR97 ($r^2 = 0.64$, $P < 0.01$), but not with the combined data from the Rivière-du-Loup sites (Figure 3).

TABLE II. Overall CH₄ fluxes ($\text{mg}\text{CH}_4\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) from full vegetation (FV), clipped (CL), and bare peat (BP) treatments at Shippagan and Rivière-du-Loup. In parentheses, SE.

Shippagan	Overall mean 2001	Rivière-du-Loup	Overall mean 1999	Overall mean 2000
Full vegetation	38.9 (6.5)	R95 Full vegetation	17.8 (3.8)	10.6 (1.7)
Clipped	8.2 (2.2)	R95 Bare peat	0.7 (0.1)	4.3 (2.9)
Bare peat	11.5 (4.6)	R97 Full vegetation	64.6 (28.1)	7.0 (1.9)
		R97 Bare peat	-0.7 (0.5)	7.7 (4.3)

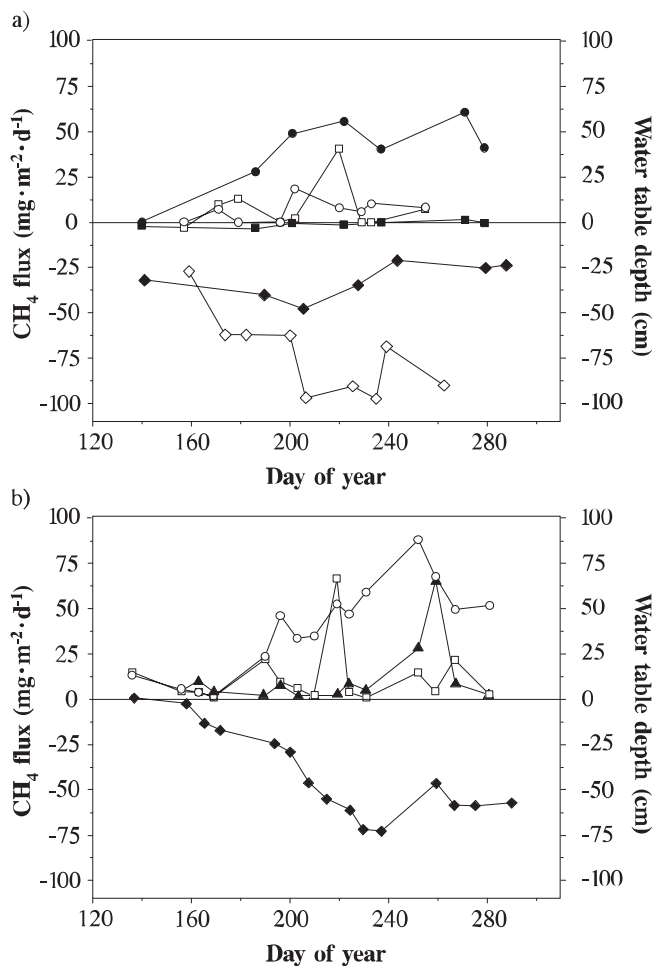


FIGURE 1. CH₄ emissions (mg·m⁻²·d⁻¹) and concurrent water table position (cm) at a) RR97 in 1999 and 2000 and at b) SR97 in 2001. Symbols are a) black diamonds = water table level in 1999, white diamonds = water table level in 2000; black circles = CH₄ from full vegetation treatment in 1999, white circles = CH₄ from full vegetation treatment in 2000; black squares = CH₄ from bare peat in 1999, white squares = CH₄ from bare peat in 2000, b) black diamonds = water table level in 2001; white circles = CH₄ from full vegetation treatment in 2001; white squares = CH₄ from bare peat in 2001; black triangles = CH₄ from clipped treatment in 2001.

At SR97, the early-season mean CH₄ emissions from the treatments were not significantly different ($P > 0.05$, Figure 4). The mid-season mean CH₄ emissions at SR97 show that full vegetation was significantly greater than clipped ($P < 0.05$), whereas full vegetation and bare peat were not significantly different ($P > 0.05$), nor were clipped and bare peat ($P > 0.05$). The mean late-season fluxes from full vegetation at SR97 were significantly greater than those from both bare peat and clipped ($P < 0.05$), whereas fluxes from bare peat and clipped were not significantly different from one another ($P > 0.05$). High variability at RR97 and RR95 prevented significant differences between emissions from full vegetation and bare peat.

CO₂ FLUX

The relationship between seasonal net ecosystem exchange of CO₂ (NEE) and photosynthetically active radiation (PAR) showed considerable variations among groups and with time (Figure 5 and Table III). GP_{max} val-

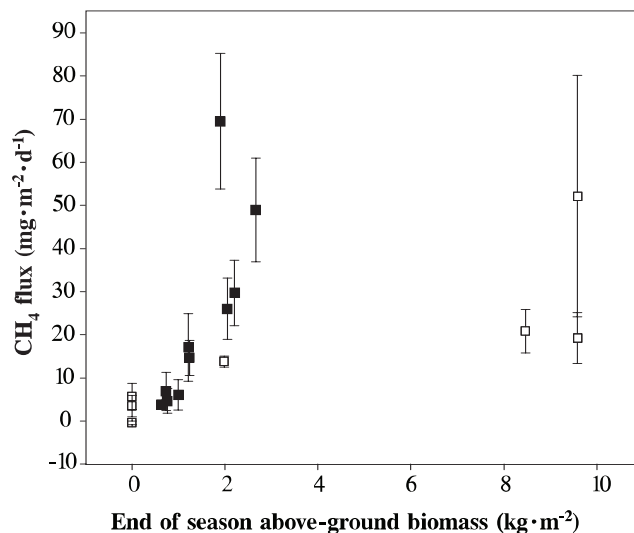


FIGURE 2. CH₄ flux (\pm SE) versus end-of-season above-ground biomass of *E. vaginatum* at Shippagan (black squares) and the two sites (RR95 and RR97) combined at Rivière-du-Loup (white squares). For the SR97 values, the regression equation is $y = 0.024x - 11.8$, $r^2 = 0.62$, $P < 0.01$.

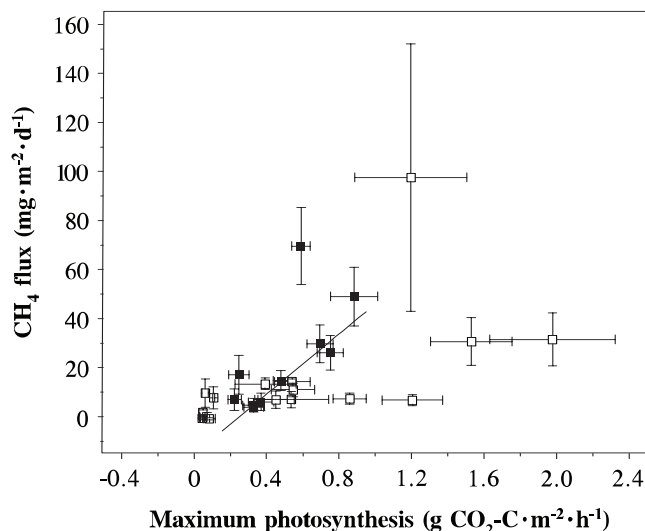


FIGURE 3. The relationship between CH₄ flux (\pm SE) and maximum photosynthesis (\pm SE) (at PAR $> 1,000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) at Shippagan (black squares) and the two sites (RR95 and RR97) combined at Rivière-du-Loup (white squares). Only the relationship at Shippagan was significant. $y = 61.5x - 15.5$, $r^2 = 0.64$, $P < 0.01$.

ues ranged from 0.4 to 3.4 g CO₂-C·m⁻²·h⁻¹ and were generally larger at the RR95 and RR97 tussocks than those at SR97. Values of the initial slope of the rectangular hyperbola regression (α) ranged from 0.001 to 0.006 g CO₂-C·m⁻²·h⁻¹/μmol·m⁻²·s⁻¹, and dark respiration ranged from -0.1 to -0.3 g CO₂-C·m⁻²·h⁻¹. The compensation point (the light level at which NEE = 0) ranged from 145 to $> 1,000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and there were several cases in which NEE was < 0 g CO₂-C·m⁻²·h⁻¹ (*i.e.*, a source of CO₂) at high light levels (Figure 5).

Among the sites, respiration was generally more strongly related to air temperature than water table position in the full vegetation treatment, whereas the reverse was the pattern for the bare peat treatment (Table IV).

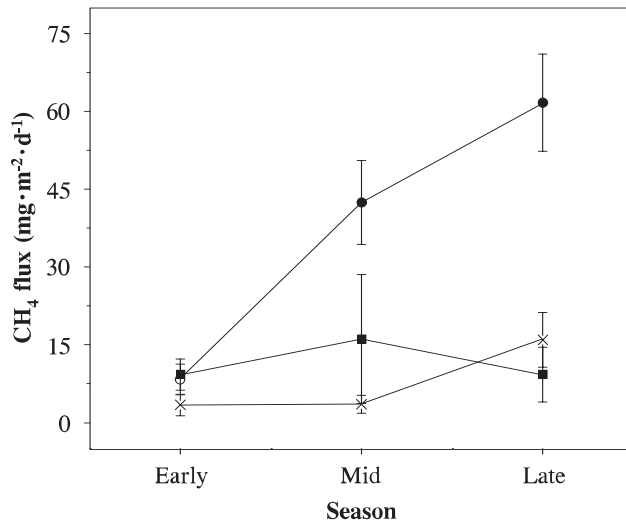


FIGURE 4. Mean CH₄ fluxes (± SE) for the full vegetation (black circles), clipped (x), and bare peat (black squares) treatments at Shippagan (SR97) for each season.

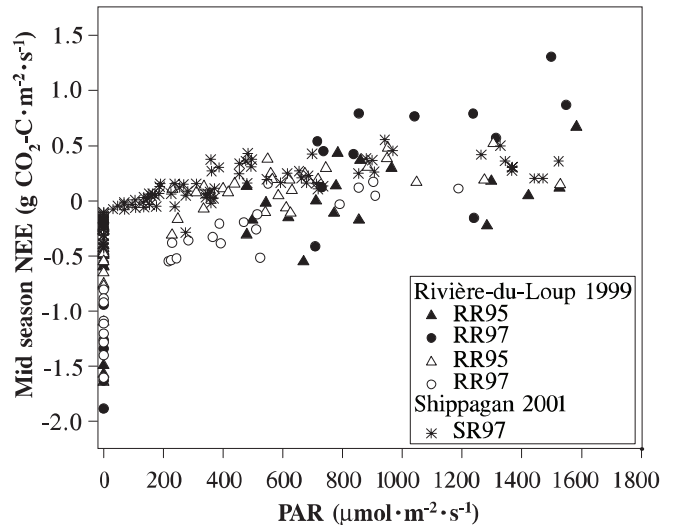


FIGURE 5. NEE-PAR relationships of *E. vaginatum* tussocks at the Rivière-du-Loup (RR95 and RR97) and Shippagan (SR97) sites in the mid (July-August) season.

TABLE III. Seasonal parameter estimates (SE) of the relationship between NEE and PAR at Rivière-du-Loup (RR95 and RR97) and Shippagan (SR97) using a rectangular hyperbola regression. GP_{max} refers to the asymptotic maximum for NEE, α is the initial slope of the curve, R is the y-axis intercept (dark respiration), and CP is the compensation point (the light level at which NEE = 0).

Season	Site	GP _{max} (g CO ₂ -C·m ⁻² ·h ⁻¹)	α (g CO ₂ -C·m ⁻² ·h ⁻¹) (µmol·m ⁻² ·s ⁻¹)	R (g CO ₂ -C·m ⁻² ·h ⁻¹)	CP (µmol·m ⁻² ·s ⁻¹)	r ²	n
Early	SR97	0.91 (0.11)	0.0023 (0.0006)	-0.31 (0.04)	235 (105)	0.63	100
	RR97-1999	0.81 (0.21)	0.0064 (0.0078)	-0.42 (0.11)	145 (29)	0.64	18
	RR95-1999	1.33 (0.42)	0.0023 (0.0015)	-0.51 (0.08)	414 (66)	0.76	26
	RR97-2000	0.74 (0.27)	0.0055 (0.0100)	-0.71 (0.12)	> 1,000	0.51	20
	RR95-2000	0.63 (0.19)	0.0022 (0.0020)	-0.39 (0.06)	512 (44)	0.61	27
Mid	SR97	0.69 (0.05)	0.0025 (0.0005)	-0.23 (0.02)	173 (67)	0.79	99
	RR97-1999	3.40 (1.58)	0.0037 (0.0022)	-1.27 (0.18)	507 (92)	0.82	18
	RR95-1999	1.44 (0.64)	0.0028 (0.0022)	-0.84 (0.13)	672 (74)	0.58	27
	RR97-2000	1.74 (0.29)	0.0044 (0.0012)	-1.14 (0.06)	826 (63)	0.88	27
	RR95-2000	1.00 (0.21)	0.0028 (0.0011)	-0.47 (0.05)	295 (60)	0.73	44
Late	SR97	0.71 (0.07)	0.0011 (0.0002)	-0.14 (0.01)	174 (80)	0.84	99
	RR97-1999	2.50 (1.05)	0.0066 (0.0032)	-0.96 (0.12)	260 (42)	0.83	15
	RR95-1999	0.61 (0.22)	0.0155 (0.0417)	-0.62 (0.11)	> 1,000	0.40	25
	RR97-2000	2.37 (1.41)	0.0021 (0.0011)	-0.78 (0.12)	580 (119)	0.71	21
	RR95-2000	0.38 (0.11)	0.0036 (0.0045)	-0.31 (0.05)	421 (20)	0.37	44

When combined in a multiple regression, the fit improved considerably when comparing the combined equation with that containing water table alone for full vegetation and when comparing the combined equation with that containing air temperature alone for bare peat (Table IV).

From the pattern of respiration (autotrophic + heterotrophic) observed at SR97, it is apparent that respiration from full vegetation was greater than clipped at the beginning of the season, but the two became very similar by mid season (Figure 6). To confirm this, mean respiration from full vegetation and clipped were compared using repeated-measures ANOVA, resulting in greater respiration from full vegetation than clipped in the early season (full vegetation: -0.30 ± 0.04 ; clipped: -0.20 ± 0.02 , $P < 0.05$), but no significant difference between the means in the mid (full vegetation: -0.20 ± 0.02 ; clipped: 0.18 ± 0.02 , $P > 0.05$) and late (full vegetation: 0.15 ± 0.01 ; clipped: 0.12 ± 0.01 , $P > 0.05$) seasons. Respiration from full vegetation and clipped were always greater than respiration from bare peat (Figure 6).

At both the Shippagan and the Rivière-du-Loup sites, the relationship between maximum photosynthesis and above-ground biomass was strongly positive, but due to the clumped distribution of the Rivière-du-Loup data, only the relationship at SR97 is presented ($r^2 = 0.95$, $P < 0.05$, Figure 7). The tussocks at the Rivière-du-Loup sites were larger than those at SR97, but those from SR97 photosynthesized more per unit of biomass than those from the Rivière-du-Loup sites (linear regression slopes of 0.32 and 0.12, respectively).

Discussion

CH₄ FLUX

CH₄ emissions from peatlands occur as a result of complex interactions between the environment and the rates of CH₄ production, consumption, and transport. Through its influence on anaerobism, water table position has often been associated with CH₄ fluxes, particularly when using seasonal averages from undisturbed peatlands

TABLE IV. Relationships between dark respiration (R, g CO₂-C·m⁻²·h⁻¹) and water table position (WT, cm), and air temperature (T, °C) from *E. vaginatum* and bare peat at Rivière-du-Loup and Shippagan.

Year	<i>E. vaginatum</i>	r ²	P
1999, 2000	R = -0.60 + 0.0058WT	0.17	0.03
	R = -0.054 - 0.031T	0.42	< 0.01
	R = -0.053 + 0.0016WT - 0.028T	0.43	< 0.01
2001	R = -0.34 - 0.002WT	0.23	0.03
	R = 0.12 - 0.01T	0.47	< 0.01
	R = 0.0087 - 0.0023WT - 0.014T	0.66	< 0.01
Year	Bare peat	r ²	P
1999, 2000	R = -0.094 + 0.0011WT	0.14	0.07
	R = -0.046 - 0.0038T	0.09	0.15
	R = -0.028 + 0.00094WT - 0.0028T	0.19	< 0.01
2001	R = -0.02 + 0.00080WT	0.33	0.02
	R = -0.02 - 0.0012T	0.08	0.25
	R = 0.023 + 0.00090WT - 0.0018T	0.50	< 0.01

in a wide range of conditions (Bubier, 1995). Although CH₄ emissions may not result from water table fluctuations alone (*e.g.*, peat temperature and plant phenology also influence emissions), in natural peatlands, the water table level has been shown to have an important influence (Moore & Roulet, 1993; Bubier, 1995). Water table-CH₄ flux relationships were weak in our study, and in the case where there was a significant relationship (*e.g.*, SR97), a higher water table produced smaller CH₄ fluxes. In a northern peatland where the water table level was close to the surface, Bellisario *et al.* (1999) also found a negative relationship between water table level and CH₄ flux at sites where the water table was close to the surface, and Shannon and White (1994) found no relation between water table depth and CH₄ emissions at a site with a low water table. It is thought that due to the disturbed nature of the studied sites, and the generally low water table depth, the influence of water table level on CH₄ emissions is not as great as that previously seen in undisturbed peatlands. The influence of *E. vaginatum* on CH₄ emissions, through stimulation of CH₄ production, facilitated gas transport through the plant, or a combination of both processes may be far more important than the influence of water table level.

Methane emissions can be affected by vascular plants in three ways: enhancement through the provision of substrate for methanogenesis, enhancement due to aerenchymous tissue that provides a pathway for gas release (vegetative transport), and suppression due to the transport of oxygen through the plant, causing CH₄ oxidation. At SR97, CH₄ emissions from the clipped treatment were 21% of those from the undisturbed *E. vaginatum*. This is larger than values of 11% and 6% reported by Waddington, Roulet, and Swanson (1996) and Whiting and Chanton (1992), respectively, who clipped plants beneath the water table. Over two 4-d periods, Greenup *et al.* (2000) showed that CH₄ emissions from *E. vaginatum* clipped above the water table were not significantly different from those from intact vegetation, suggesting that the plant is a strong conduit. *Eriophorum vaginatum* is known to be a deep rooted species (Wein, 1973), and large CH₄ emissions may occur even when the water table is deep.

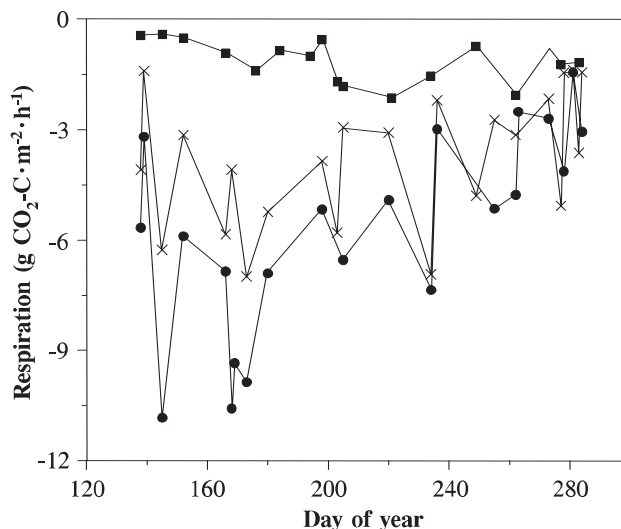


FIGURE 6. Respiration (autotrophic + heterotrophic) at Shippagan (SR97) over the growing season from the full vegetation (black circles), clipped (x), and bare peat (black squares) treatments.

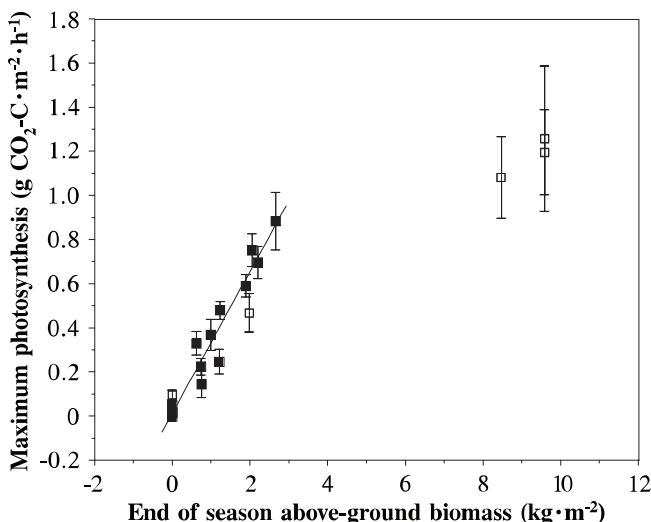


FIGURE 7. Relationship between maximum photosynthesis (\pm SE) and end-of-season above-ground biomass of *E. vaginatum* at Rivière-du-Loup (white squares) and Shippagan (black squares). For the Shippagan values, the regression equation is $y = 0.32x + 0.013$, $r^2 = 0.95$, $P < 0.01$.

In our study, the early-season CH₄ fluxes were small and the treatments were not significantly different, perhaps because plant growth was just beginning and the peat was cold. The opposite trend is seen with the respiration data from SR97, where emissions from full vegetation and clipped were significantly different only at the beginning of the growing season (Figure 6). It would be expected that since the peat was cold in the spring, respiration would also be limited. However, root and shoot growth were likely greatest in the spring, thereby leading to increased respiration (Robertson & Woolhouse, 1984). At SR97, mid-season CH₄ fluxes from the full vegetation treatment were significantly greater than those from the clipped treatment. Joabsson and Christensen (2001) compared CH₄ and CO₂ emissions from intact plants and plants that were shaded and showed that decreased CO₂

uptake led to decreased CH₄ emissions. A decrease in photosynthetic potential with clipping may have decreased CH₄ production by limiting labile carbon release in the rhizosphere, or reduction of the above- and below-ground biomass caused by clipping may have decreased the CH₄ transport ability of the plant.

Methane flux from the full vegetation treatment at SR97 peaked at the beginning of September, coinciding with a rise in the water table, despite the overall trend of increased CH₄ emissions with a decreasing water table level (Figure 1). Several researchers have shown peak CH₄ fluxes earlier in the season, and decreasing at the end of the season, a trend that is usually closely related to water table level (Waddington, Roulet & Swanson, 1996; King, Reeburgh & Regli, 1998; Joabsson & Christensen, 2001). The larger late-season CH₄ fluxes at SR97 may also be related to an influx of dead plant material to the system with the onset of senescence (Tuittila *et al.*, 2000b). In the case of restored peatlands, the influx of dead plant material may be particularly important because the surrounding peat is recalcitrant and new carbon additions have been shown to increase CH₄ production (Hogg, Lieffers & Wein, 1992). The CH₄ emissions from the clipped and bare peat treatments at SR97 were not significantly different, suggesting that it is the presence of new plant tissues that controls the fluxes of CH₄ from the full vegetation treatment, either through the provision of methanogenic substrate or through vegetative transport.

It has been suggested that increases in plant biomass lead to increases in root and stem cross-sectional area, thereby increasing the potential for gas transport through the aerenchyma to the atmosphere (Arenovski & Howes, 1992; Greenup *et al.*, 2000). The positive relationship between mean CH₄ emissions and end of season above-ground biomass at both SR97 and the Rivière-du-Loup sites is similar to that reported in other studies (Bellisario *et al.*, 1999; Joabsson & Christensen, 2001). The CH₄ emissions from small tussocks at the Rivière-du-Loup sites were comparable to emissions from similarly sized plants at SR97, while emissions from large tussocks at the Rivière-du-Loup sites were similar to those from tussocks with less than one third of their biomass at SR97 (Figure 2), suggesting that CH₄ emission enhancement is most effective in young *E. vaginatum*.

We found a significant, positive correlation between CH₄ emissions and maximum photosynthesis at SR97. Although SR97 remained quite dry over much of the growing season, the water table was at or near the surface during the spring, never falling below 20 cm (Figure 1). Whiting and Chanton (1993) showed that for a wide range of wetlands where the water table is close to the surface, CH₄ emissions are correlated with net primary production, with an average of 3% of net ecosystem production (NEP) emitted as CH₄. More recent studies have confirmed this phenomenon (Chanton *et al.*, 1995; Waddington, Roulet & Swanson, 1996; Bellisario *et al.*, 1999; Greenup *et al.*, 2000; Tuittila *et al.*, 2000b; Joabsson & Christensen, 2001), suggesting that, under wet conditions, methanogenesis may be stimulated by C input from the plant in the form of litter and exudates.

CO₂ EXCHANGE

The CO₂ exchange parameters GP_{max} and R from the *E. vaginatum* sites can be compared to those collated for other peatlands by Frohling *et al.* (1998). The mid-season GP_{max} values of 0.7 and 1.0 to 3.4 g CO₂-C·m⁻²·h⁻¹ for *E. vaginatum* tussocks at SR97 and the Rivière-du-Loup sites, respectively, are similar to those observed in fens and grasslands. The R (autotrophic + heterotrophic) values in mid-season ranged from -0.2 at SR97 to -0.5 to -1.3 g CO₂-C·m⁻²·h⁻¹ at RR95 and RR97, the former being close to those observed in grasslands, whereas the latter are comparable to most wetland ecosystems. The large R values at RR95 and RR97 resulted in small NEE values and the occurrence of negative NEE values even at high light levels (> 500 μmol·m⁻²·s⁻¹), especially during mid-season. In contrast, the NEE results from Shippagan were less variable, with a compensation point of 173 μmol·m⁻²·s⁻¹ and rare occurrences of negative NEE values at high light levels. Fens, poor fens, and bogs have similar mid-summer compensation points in the range 130 to 190 μmol·m⁻²·s⁻¹ (Frohling *et al.*, 1998).

The differences in NEE values between the *E. vaginatum* tussocks at Rivière-du-Loup and Shippagan may be related to differences in the size and age of the plants and temperature and water table position. In 2000, the small tussock at RR95 produced up to 85% fewer negative NEE values at high light levels and up to 75% fewer negative values at low light levels than the large tussocks, suggesting that as the plants grow and age, their photosynthesis per unit of biomass decreases. This is shown graphically in Figure 7, where large tussocks at the Rivière-du-Loup sites photosynthesize at similar rates to smaller tussocks at SR97. The differences also relate to differences in the peat surface: at SR97, the site was abandoned for 11 y before restoration began, whereas restoration at the Rivière-du-Loup sites began immediately after harvesting ceased. Tuittila *et al.* (1999) reports respiration values that were similar to those at SR97, and their site was also abandoned for 19 y before restoration began. The long abandonment may have changed the surface peat chemistry and microbial communities due to exposure to oxidation and decomposition without repeated disruption from harvesting machinery.

In 2000 at RR97 and RR95 and 2001 at SR97, respiration from bare peat had a stronger relationship to water table level than to air temperature, whereas the opposite pattern was found from vegetated collars (Table IV). In a microcosm experiment, Johnson *et al.* (1996) found that respiration rates from tussocks were more affected by temperature, whereas inter-tussock areas were more affected by water table level. In 1999, respiration from bare peat and full vegetation were not significantly related to either air temperature or water table level and may have been related to faster rates of plant production (*i.e.*, root and shoot growth). Higher rates of respiration may have been related to both increases in respiration from plant tissue (above and below ground), as well as possibly increased peat respiration. Silvola *et al.* (1996) attributed 35-45% of total soil respiration to roots in organic soils with abundant vegetation growth, suggesting that indeed root growth contributes a significant portion of autotrophic

+ heterotrophic respiration. As well, many previous studies have shown that high levels of photosynthesis lead to greater exudation of labile carbon around plant roots (Lambers, 1987; Bowen & Rovira, 1991; Jones, 1998; Joabsson, 2001). This easily decomposed labile carbon may increase microbial activities, leading to increased peat respiration (Bottner, Sallih & Billes, 1988; Cheng & Coleman, 1990; Kuzyakov, Friedel & Stahr, 2000). In a related study, Glatzel *et al.* (2003) found increased dissolved organic carbon concentrations at RR95 in Rivière-du-Loup; they suspect that this could be due to recently fixed carbon from root exudates, suggesting that plant-peat interactions are taking place.

At SR97, respiration (autotrophic + heterotrophic) from vegetated collars was significantly greater than that from clipped collars only in the early season. Archer and Tieszen (1983) conducted a clipping experiment on *E. vaginatum* and found that as the carbohydrate reserves were depleted, root initiation, root elongation, and leaf production decreased. At Shippagan, leaf regrowth occurred quickly after the first defoliation, probably because the reserves were full, but after repeated clippings leaf regrowth slowed, possibly because reserves began to deplete. Root initiation may have begun to decline soon after the initial clipping, as more energy went into producing new leaves to replace those that were clipped, resulting in the difference in respiration between full vegetation and clipped. Fewer live leaves, the decomposing roots under the clipped treatment, and a decreased input of labile carbon into the peat may have also contributed to the difference.

Respiration (autotrophic + heterotrophic) from vegetated and clipped collars at SR97 was not significantly different during the mid- and late seasons. Chapin and Slack (1979) found that respiration from *E. vaginatum* clipped at regular intervals was similar to respiration from non-defoliated tussocks and suggested that in nutrient-poor conditions, root respiration must continue if the plant is to receive nutrients necessary for new leaf growth. As leaf regrowth slowed over the season, there may have been a transfer of reserves from growth to maintenance, resulting in the sustained respiration from clipped tussocks in the mid- and late seasons. *Eriophorum vaginatum* can adapt to persistent defoliation: Archer and Tieszen (1983) found that even after two seasons of clipping, the reserves were still 34% above the minimum required for sustaining the growth and maintenance of the plant. It would be expected that since respiration and photosynthesis are tightly coupled, reducing photosynthesis would lead to a reduction in respiration. This was not found at SR97, although if the clipping experiment had continued over several growing seasons, the reserves might have been depleted and differences in respiration might have been more apparent.

Respiration (autotrophic + heterotrophic) from both vegetated and clipped tussocks was substantially larger than that from the bare peat surface, particularly in the early and mid-seasons at SR97, suggesting that most of the respiration may come from recently fixed carbon, including above-ground plant growth and below-ground root growth. In restored peatlands, the substrate on which

the plants grow is old and recalcitrant (Tuittila *et al.*, 1999), and new carbon added to the system may be very important, whether it is in the form of above-ground tissue, below-ground tissue, or below-ground plant-peat interactions.

Although *E. vaginatum* establishes rapidly in the early period after restoration and its presence improves the habitat for the initiation and growth of other vascular plants and mosses, it does affect the C budget of the restored peatland. The presence of the sedge increases CH₄ emission rates, probably through a combination of stimulation of methanogenesis and providing a conduit from the peat to the atmosphere. CO₂ emission rates (autotrophic + heterotrophic respiration) are also larger from *E. vaginatum* tussocks than peat, and our results suggest that the presence of new carbon (above-ground tissue, below-ground roots, and plant-peat interaction) on such degraded substrate may play an important role in restoration success.

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