

Carbon dioxide and methane exchange at a cool-temperate freshwater marsh

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Carbon dioxide and methane exchange at a cool-temperate freshwater marsh

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**Abstract**

Freshwater marshes have been shown to be strong sinks for carbon dioxide (CO₂) on an annual basis relative to other wetland types; however it is likely that these ecosystems are also strong emitters of methane (CH₄), reducing their carbon (C) sequestration potential. Multiyear C balances in these ecosystems are necessary therefore to determine their contribution to the global C cycle. Despite this, the number of multiyear studies in marshes is few, with, to the best of our knowledge, only one other Northern marsh C balance reported. This study presents five years of eddy covariance flux measurements of CO₂, and four years of warm-season chamber measurements of CH₄ at a cool-temperate *Typha angustifolia* marsh. Annual average cumulative net ecosystem exchange of CO₂ (NEE) at the marsh was $-224 \pm 54 \text{ g C m}^{-2} \text{ yr}^{-1}$ (\pm SD) over the five-year period, ranging from -126 to $-284 \text{ g C m}^{-2} \text{ yr}^{-1}$. Enhancement of the ecosystem respiration during warmer spring, autumn and winter periods appeared the strongest determinant of annual NEE totals. Warm season fluxes of CH₄ from the *Typha* vegetation (avg. $1.0 \pm 1.2 \text{ g C m}^{-2} \text{ d}^{-1}$) were significantly higher than fluxes from the water surface ($0.5 \pm 0.4 \text{ g C m}^{-2} \text{ d}^{-1}$) and unvegetated mats ($0.2 \pm 0.2 \text{ g C m}^{-2} \text{ d}^{-1}$). Air temperature was a primary driver of all CH₄ fluxes, while water table was not a significant correlate as water levels were always at or above the vegetative mat surfaces. Weighting by the surface cover proportion of water and vegetation yielded a net ecosystem CH₄ emission of $127 \pm 19 \text{ g C m}^{-2} \text{ yr}^{-1}$. Combining CO₂ and CH₄, the annual C sink at the Mer Bleue marsh was reduced to $-97 \pm 57 \text{ g C m}^{-2} \text{ yr}^{-1}$, illustrating the importance of accounting for CH₄ when generating marsh C budgets.

1. Introduction

Freshwater wetlands include a variety of waterlogged habitats, such as small lakes, floodplains, marshes and peatlands, and are found in large concentration in temperate-cold climates of the Northern hemisphere (Lehner and Dröll 2004, Limpens *et al* 2008). While wetlands cover only ~6% of global land area, they store ~30% of terrestrial soil carbon (C) (Turunen *et al* 2002, Mitra *et al* 2005, IPCC 2007) and play an important role in global C dynamics through high methane (CH₄) emissions, regionally redistributing dissolved organic matter, and having a large potential for carbon dioxide (CO₂) sequestration (e.g. Bridgman *et al* 2006, IPCC 2007, Limpens *et al* 2008). Because Northern peatlands likely contain >80% of the wetland C store (Gorham 1991, Mitra *et al* 2005),

research into trace gas exchange and C sequestration has concentrated on these ecosystems (e.g. Roulet *et al* 2007, Nilsson *et al* 2008). Ignoring other wetland types, however, has resulted in large uncertainties (>100%) on wetland C sequestration and CH₄ emissions, decreasing the accuracy of predictions of the role of wetlands as potentially positive or negative feedbacks to climate change (Bridgman *et al* 2006). Within the range of ecosystems falling under the 'wetland' umbrella, freshwater marshes have been identified as the largest unknown in the North American wetland budget (Bridgman *et al* 2006).

Freshwater marshes are a unique environment known for two defining features: anaerobic mineral soils and large emergent plant species, macrophytes (Richardson 2001, Van der Valk 2012). Macrophytes, such as *Phragmites* and *Typha* spp., are known to have

a large potential for C uptake. Temperate marsh studies report cumulative net ecosystem exchange of CO₂ (NEE) of -100 to -212 g C m⁻² (where negative values represent uptake by the ecosystem) over a growing season (Song *et al* 2011, Chu *et al* 2014), compared to -21 to -166 g C m⁻² in temperate and boreal bogs and fens (Glenn *et al* 2006, Roulet *et al* 2007, Nilsson *et al* 2008, Christensen *et al* 2012, Olson *et al* 2013, Peichl *et al* 2014, Helfter *et al* 2015). A significant portion of accumulated C in marshes can be lost through CH₄ emissions to the atmosphere however (Song *et al* 2011, Chu *et al* 2015), as macrophytes not only provide a source of C for CH₄ production, but also facilitate CH₄ release through a system of interconnected internal gas spaces (aerenchyma) that act as conduits between the root zone and atmosphere (Laanbroek *et al* 2010). As a result of CH₄ offset, freshwater marshes are estimated to sequester only ~ 18 Tg C yr⁻¹ in sedimentation compared with ~ 29 Tg C yr⁻¹ stored as peat in natural peatlands (Bridgman *et al* 2006).

The seasonality in CO₂ exchange in marsh ecosystems is strongly related to the growth and senescence of macrophytes, driven by light and temperature (Rocha and Goulden 2008, Zhou *et al* 2009). In a limited number of studies, inter-annual variability in net CO₂ exchange has been attributed to climatic influences such as the timing of snow melt and water table drawdown during drought conditions, which manifest in biophysical changes to the marsh vegetation (Zhou *et al* 2009, Rocha and Goulden 2010, Dušek *et al* 2012, Chu *et al* 2014, 2015). These structural changes in turn have implications for plant-mediated transport of CH₄ (Colmer 2003, Evans 2003). Plant-mediated gas transport can explain up to 90% of a wetland's CH₄ efflux (Holzapfel-Pschorn and Seiler 1986, Bergström *et al* 2007), indicating that macrophytes are key regulators of both CO₂ and CH₄ exchange in these ecosystems.

Given the potential importance of freshwater marshes in C sequestration, it is surprising that, with the exception of very recent studies (Chu *et al* 2014, 2015), the typical range and controls on multi-year CO₂ and CH₄ exchange from temperate freshwater marsh ecosystems remain poorly documented. Notably, the C balance measurements reported by Chu *et al* (2015) occurred over three years of abnormal climate conditions, which resulted in the marsh releasing on average 43 ± 23 g C m⁻² yr⁻¹. Two restored marshes in California report net C sequestration of 315 and 358 g C m⁻² yr⁻¹ (Knox *et al* 2015), yet applying restored marsh C budgets to natural marshes may not be the best solution; restoration generally occurs over organic soils (e.g. Herbst *et al* 2011, Knox *et al* 2015) and can include ongoing management activities (Herbst *et al* 2011). Furthermore, cold winters with snow present entirely different climate controls. Here, we report on a permanently flooded cool-temperate *Typha angustifolia* marsh using five years of near-

continuous eddy covariance measurements of CO₂, and four warm seasons of CH₄ exchange via the static chamber method. To the best of our knowledge, this study is only the second to provide multi-year annual estimates of CO₂ exchange for a marsh ecosystem within a cold winter environment. Our specific research objectives were: (1) to derive a long-term mean net annual C flux estimate; and, (2) to determine how CO₂ and CH₄ fluxes respond to seasonal and inter-annual variability in environmental conditions and vegetation feedbacks.

2. Methods

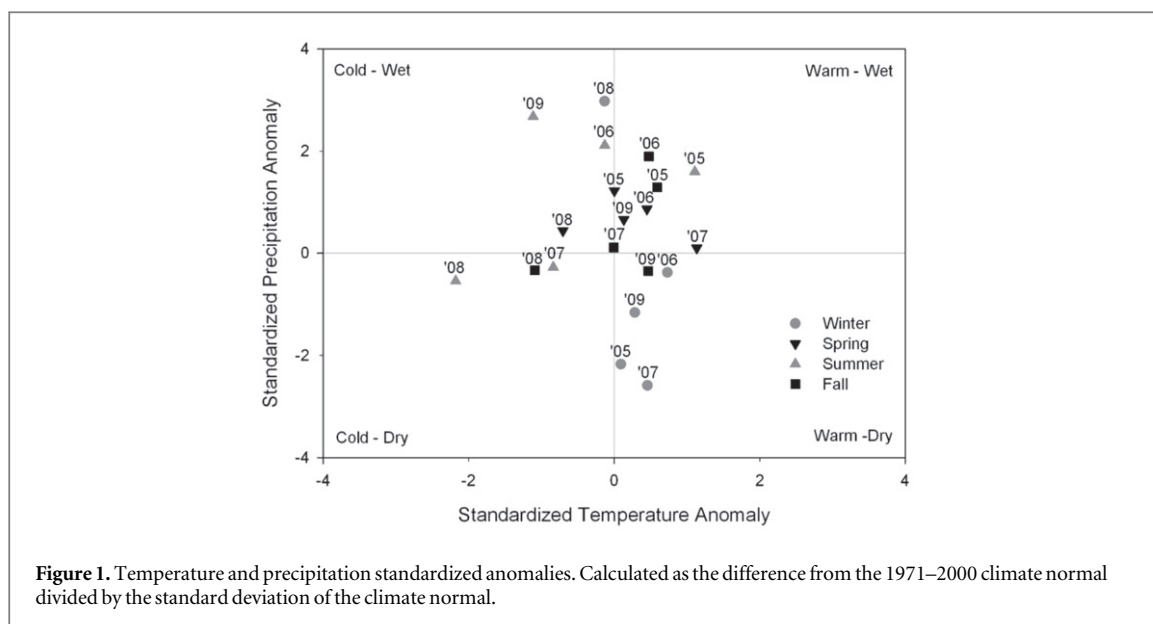
2.1. Site description

The freshwater marsh is located in the Southern portion of the Mer Bleue wetland complex (10 km East of Ottawa, Ontario; 45.4 °N, 75.5 °W). Narrow-leaved cattail (*Typha angustifolia*) covers 88% of the marsh area while the remaining 12% is classified as open water and ponds (Bonneville *et al* 2008). The study area is subject to a cool-temperate climate with 30 yr (1971–2000) annual average temperature and precipitation of 6 °C and 944 mm, respectively (Environment Canada 2012). Precipitation is proportionately spread over the year with maximum in July and minimum in February (Environment Canada 2012).

2.2. Instrumentation and flux calculations

The eddy covariance technique (Baldocchi 2003) was used to measure the surface-atmosphere exchanges of CO₂ flux density at a frequency of 10 Hz and averaged over 30 min periods from 8th May 2005 to 17th November 2009. A three-dimensional sonic anemometer (CSAT3, Campbell Scientific, Edmonton, Canada), an open-path infrared gas analyzer (IRGA: LI-7500, LI-COR, Lincoln, N) and a fire-wire thermocouple were mounted 4.6 m above the water/vegetated mat surface and 2.2 m above the fully grown vegetation on a scaffold tower. Half-hour NEE was computed following corrections for fluctuations in temperature and water vapour density (Webb *et al* 1980) and including the change in storage of CO₂ between the surface and instrument height. We used the friction velocity threshold ($u^* = 0.1$ m s⁻¹) determined by Bonneville *et al* (2008) for the same site to reject low turbulence periods. More details on the instrument set up, data processing and quality control are found in Bonneville *et al* (2008). In presenting fluxes, we follow the atmospheric convention of negative indicating a surface sink and positive a surface source.

Annual cumulative NEE was calculated based on a 'hydrological year' (1st November to 31st October (e.g. Roulet *et al* 2007)). The winter period ahead of the study (i.e. 1 November 2004 to 7 May 2005) was modeled using an average of the other years. The data set will henceforth be referred to using the year



containing the warm season for the purposes of simplification (i.e. Nov 2004–Oct 2005 = 2005).

2.3. Measurements of CH₄ and biophysical characteristics

2.3.1. Sampling open water, mats and *Typha*

The static chamber method was used to measure CH₄ fluxes over portions of the period May to August in 2005, 2006, 2008 and 2009. An 18 L opaque floating chamber was used to measure CH₄ fluxes from the water channel at the flux tower and at the marsh outflow culvert. The chamber had a Styrofoam floatation collar and was tethered during measurements to the tower platform, or canoe. Following air homogenization within the chamber using a syringe, gas samples were extracted every five minutes over a 20 min period. Each 60 mL sample was split into three replicate pre-evacuated vials and then kept in a cooler. Measurements from cattail and mats were conducted along two transects 150 m apart, accessed by boardwalks, with a three-section PVC chamber (26 cm diameter) which allowed sampling at different growth stages. The chamber had a total height of 2.17 m and sections were connected on site using clamps affixed to the sides. At each sampling location, depth of collar relative to the water surface and water and/or soil temperature at the surface and at 10 cm depth was measured. In the collars containing *Typha*, the number of plants and their respective heights were recorded. Methane samples were analyzed within one day of collection on a gas chromatograph (Shimadzu GC-8AIF with FID). Fluxes of CH₄ were calculated from the change in concentrations over the measurement period of 20 min, with adjustments for chamber volume and surface (or air) temperature. Fluxes with coefficients of determination (r^2) lower than 0.85 and sampling events showing large nonlinear increases in CH₄ concentration were rejected (18% of data). Mean

fluxes from vegetation and water were used to estimate the overall area-weighted ecosystem fluxes. Area-weighting was based on a classification of satellite imagery by Bonneville (2006) of vegetation and open water.

2.3.2. Determination of biophysical characteristics

Destructive sampling was done 4–6 times (11 times in 2005) over the period early May to late September each year to determine aboveground *Typha* biomass, height, density, and leaf area index (LAI). A bench area meter (Area Measurement System, Delta-T Devices Ltd, Cambridge, England) was used to obtain the area of harvested leaves in 2005 and 2006 following Bonneville *et al* (2008). Due to inconsistent instrument calibration in subsequent years, an allometric relationship between the 2005 and 2006 aboveground biomass and LAI was used to derive the LAI maxima.

3. Results

3.1. Climate

The average temperature for the 2005–2009 study period was 6.0 °C, equivalent to the 30 yr average. The average annual precipitation for the 2005–2009 study period was 1026, 82 mm above the 30 yr average. 2005 and 2006 were generally warmer and wetter than normal with winters which were warmer and drier (figure 1). 2007 experienced normal to drier conditions with the warmest spring of the study period. 2008 was overall cool, particularly during the summer and fall, and had the only wetter winter of the study period. 2009 was normal except the summer which was cool and wet.

3.2. Canopy biophysical properties

Each year, *Typha* broke dormancy and initiated shoot growth in May, rapidly grew until canopy completion

Table 1. *Typha* canopy biophysical properties during the study period.

	Biomass (g m^{-2})	Density (plants m^{-2})	Height (cm)	LAI _{max} $\text{m}^2 \text{m}^{-2}$
2005	1149 ± 96	46 ± 3	240 ± 3	3.6 ± 0.3
2006	1484 ± 85	51 ± 2	234 ± 3	3.9 ± 0.2
2007	1398 ± 130	51 ± 3	n/a	4.1 ± 0.4
2008	1073 ± 58	59 ± 3	207 ± 4	3.2 ± 0.2
2009	670 ± 81	41 ± 4	208 ± 7	2.2 ± 0.2

mid-summer, and were fully senesced by October. For the purposes of this study, the warm season has been defined as May to the end of September while the cold season includes October through April. While sampling likely missed peak biomass in 2007 (before) and 2008 (after), the general pattern for cattail growth was captured. Biomass ranged from (mean ± standard deviation) 670 ± 81 to 1484 ± 85 g m^{-2} , density at the time of peak biomass was between 41 ± 4 and 59 ± 3 plants m^{-2} , height ranged from 207 ± 4 to 240 ± 3 cm and maximum LAI (LAI_{max}) was between 2.2 ± 0.2 and 4.1 ± 0.4 $\text{m}^2 \text{m}^{-2}$ (table 1).

3.3. Intra- and inter-annual patterns of CO₂ exchange

Over the warm season, net CO₂ uptake followed the vegetative growth cycle of *Typha*, with uptake initiating in May, maximum uptake during mid-summer (DOY 214 ± 9) and decreasing uptake by September. The marsh was a net CO₂ sink during the warm season with mean daily fluxes averaging $-1.7 \pm 0.3 \text{ g C m}^{-2} \text{ d}^{-1}$; the marsh was a CO₂ source of $0.5 \pm 0.1 \text{ g C m}^{-2} \text{ d}^{-1}$ during the cold season (table 2). While the marsh remained a net annual CO₂ sink in each of the five years, a large range, from a minimum in 2009 to a maximum in 2008 was noted (figure 2). Approximately 42% of the annual NEE was lost through cold season ecosystem respiration (ER) in 2005, 2006 and 2007. 2008 and 2009, by contrast, had cold season losses of 28 and 61%, respectively. We used the simple monthly coefficient of variation (CV) to express variability in cumulative NEE. CVs were largest in Jan–March, June and October (data not shown). ER CVs were largest in March and October while those for GEP were largest in May and October.

3.4. CH₄-C flux by surface features

CH₄ fluxes from *Typha* were significantly higher than those from open water and mats (t-test; $p = 0.05$) (figure 3(a)). Plant-mediated fluxes ranged from 0.0 to $5.8 \text{ g C m}^{-2} \text{ d}^{-1}$ (mean ± SD = $0.97 \pm 1.19 \text{ g C m}^{-2} \text{ d}^{-1}$; $n = 49$). Prior to active vegetation, fluxes in May 2006 averaged $0.1 \text{ g C m}^{-2} \text{ d}^{-1}$, with collars containing dead shoots showing higher emissions ($0.2 \text{ g C m}^{-2} \text{ d}^{-1}$) than those without any shoots ($0.0 \text{ g C m}^{-2} \text{ d}^{-1}$). Fluxes from water were significantly higher than from mats

($p < 0.001$); fluxes from the channel ranged from 0.0 to $2.2 \text{ g C m}^{-2} \text{ d}^{-1}$ ($0.45 \pm 0.44 \text{ g C m}^{-2} \text{ d}^{-1}$; $n = 66$) compared to the mat fluxes, which ranged from 0.0 to $0.6 \text{ g C m}^{-2} \text{ d}^{-1}$ ($0.18 \pm 0.17 \text{ g C m}^{-2} \text{ d}^{-1}$; $n = 13$). Methane fluxes increased through the season and in response to temperature (figure 3(b)) and plant growth (not shown).

4. Discussion

4.1. Marsh is a net sink for CO₂

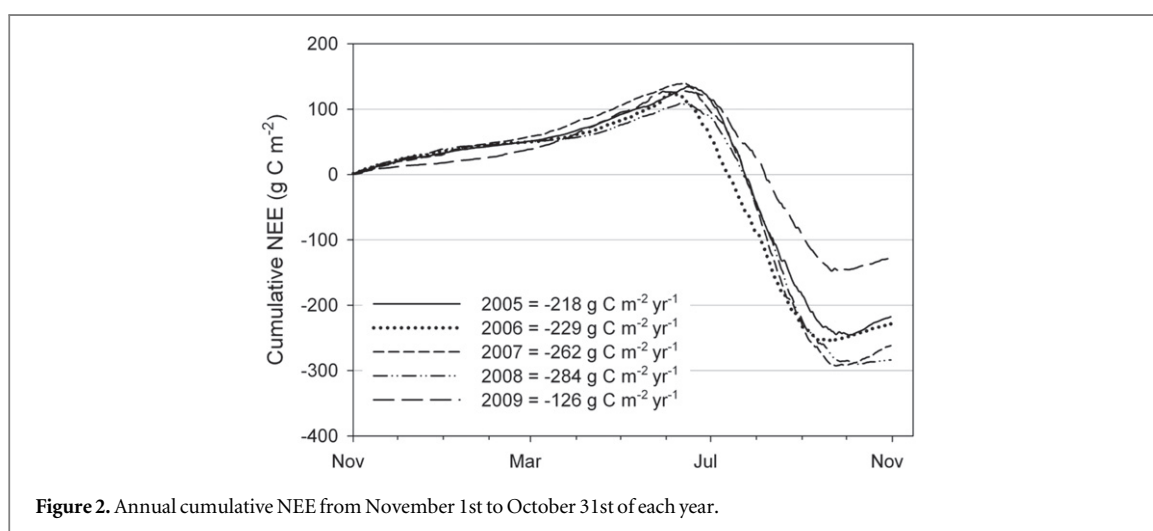
To the best of our knowledge, only one other long-term study exists (Chu *et al* 2015) presenting CO₂ exchange in a North American cool-temperate freshwater marsh. The authors indicate that their NEE results (net source of $14.6 \text{ g C m}^{-2} \text{ yr}^{-1}$) are inconsistent with the site's long-term sediment C accumulation rate ($97 \text{ g C m}^{-2} \text{ yr}^{-1}$); an effect that they attribute to anomalous weather conditions over their three year study period. In comparison, the Mer Bleue marsh was an annual sink for CO₂ in each of the five years of our study with an average of $-224 \pm 54 \text{ g C m}^{-2} \text{ yr}^{-1}$. Our mean NEE is also much larger than those reported for other wetland types including the ombrotrophic bog portion of the Mer Bleue complex ($-40 \pm 41 \text{ g C m}^{-2} \text{ yr}^{-1}$; Roulet *et al* 2007), an Atlantic blanket bog in Ireland ($-48 \pm 30 \text{ g C m}^{-2} \text{ yr}^{-1}$, Koehler *et al* 2011), boreal fens in Sweden ($-58 \pm 21 \text{ g C m}^{-2} \text{ yr}^{-1}$, Peichl *et al* 2014; $-66 \pm 29 \text{ g C m}^{-2} \text{ yr}^{-1}$, Christensen *et al* 2012) and Finland ($-22 \pm 20 \text{ g C m}^{-2} \text{ yr}^{-1}$, Aurela *et al* 2004) and a moderately-rich treed fen in Canada ($-189 \pm 47 \text{ g C m}^{-2} \text{ yr}^{-1}$, Flanagan and Syed 2011). For freshwater marshes globally, long-term published data are sparse. Zhou *et al* (2009) report an annual sum equivalent to $-65 \pm 14 \text{ g C m}^{-2} \text{ yr}^{-1}$ in Northeast China, while Song *et al* (2011) report -143 ± 10 and $-100 \pm 9 \text{ g C m}^{-2} \text{ yr}^{-1}$ for two years of continuous data at a sedge marsh, also in Northeast China. Rocha and Goulden (2008) report annual sums ranging from a net release ($515 \text{ g C m}^{-2} \text{ yr}^{-1}$) to a net uptake ($-251 \text{ g C m}^{-2} \text{ yr}^{-1}$) for five study years at a seasonally dry California marsh, while Knox *et al* (2015) report young and mature restored marshes in California sequestering 368 ± 46 and $397 \pm 20 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively.

4.2. Within- and between-year variation is driven by climate

Annual cumulative NEE (figure 2) was strongly determined by prevailing climatic conditions, which ultimately affected cold season emissions, the timing of the spring and fall transitions in CO₂ uptake and the magnitude of peak CO₂ uptake during the warm season. The CV on NEE was large around small mean values in the cold season, likely because the regional climate is subject to freeze-thaw cycles which can enable respiratory losses. In March, the transition to

Table 2. Daily averaged net CO₂ exchange (g C m⁻² d⁻¹) for the warm and cold seasons. Negative values indicate net CO₂ uptake and positive values indicate net release.

Warm season (May–September)	2005	2006	2007	2008	2009	2005–09
Maximum release	2.0	3.2	2.2	1.7	3.9	2.6 ± 0.8
Average	-1.7	-1.7	-2.0	-2.0	-1.2	-1.7 ± 0.3
Maximum uptake	-9.4	-7.2	-8.6	-8.3	-7.2	-8.2 ± 0.9
Cold season (October–April)	2004–05	2005–06	2006–07	2007–08	2008–09	2004–09
Average	0.5	0.5	0.6	0.4	0.5	0.5 ± 0.1
Maximum release	1.2	1.7	1.5	1.4	1.8	1.5 ± 0.2

**Figure 2.** Annual cumulative NEE from November 1st to October 31st of each year.**Table 3.** Rectangular hyperbola curve fit average and (standard error) parameters for the months of June, July, August and September of 2005–2009. α is the quantum yield, A_{\max} is the maximum gross productivity and ER_d is the dark respiration.

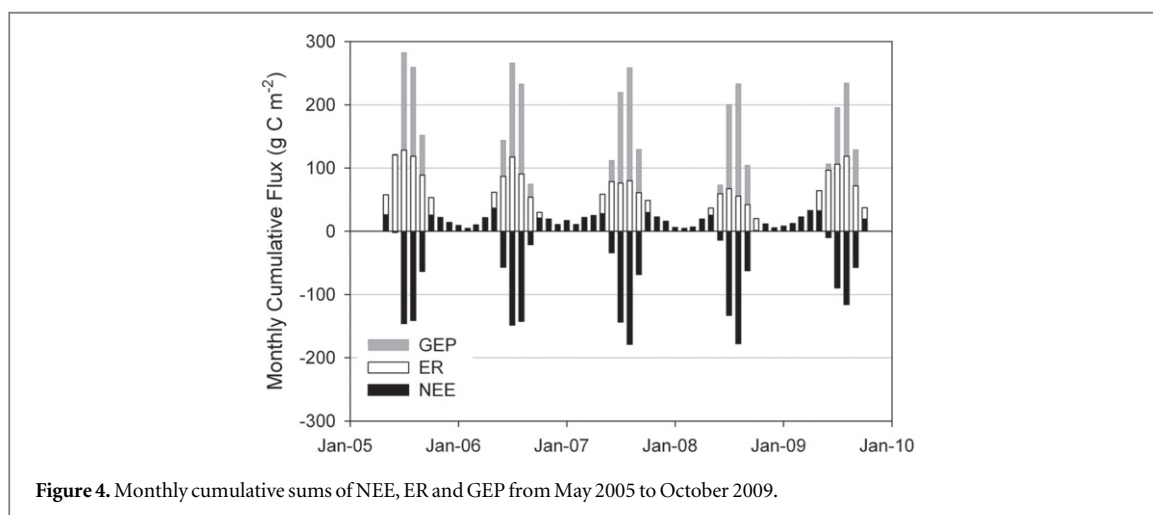
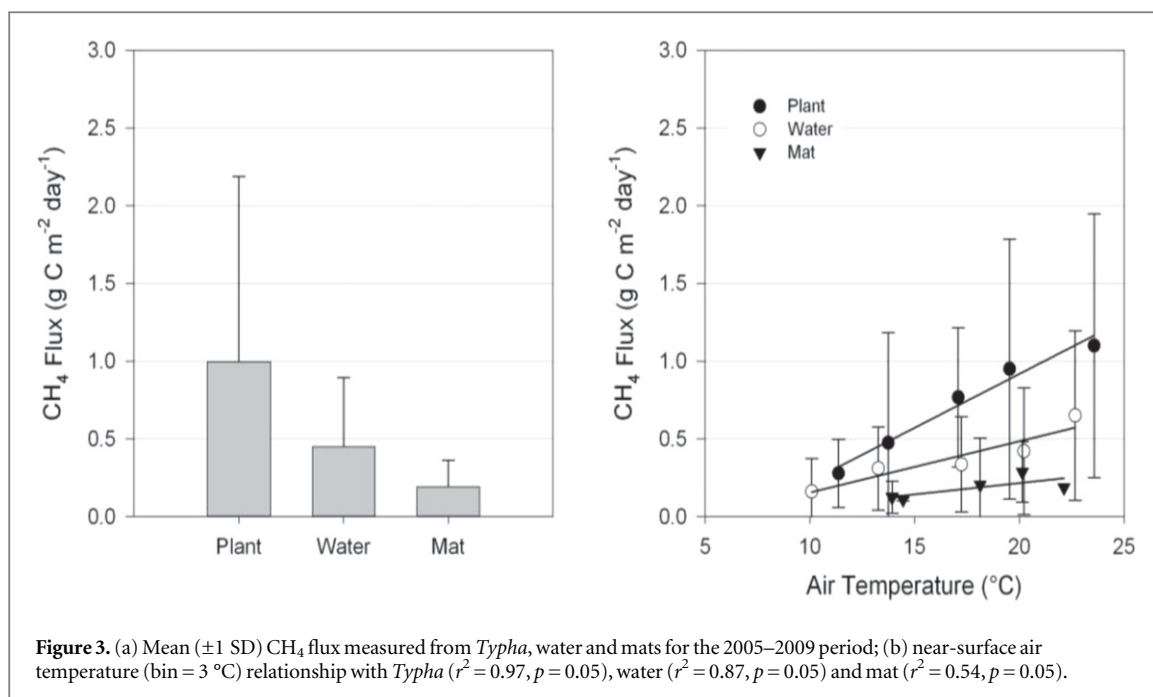
Year	Month	α	^a A_{\max}	^a ER_d	r^2
2005	June	-0.028 (0.004)	-6.9 (0.3)	2.8 (0.1)	0.31
	July	-0.047 (0.002)	-29.0 (0.7)	4.6 (0.2)	0.78
	August	-0.046 (0.002)	-34.3 (0.9)	4.7 (0.1)	0.87
	September	-0.028 (0.002)	-27.3 (1.5)	3.3 (0.1)	0.77
2006	June	-0.023 (0.002)	-16.2 (1.0)	3.0 (0.2)	0.46
	July	-0.041 (0.002)	-28.7 (0.9)	4.4 (0.2)	0.74
	August	-0.030 (0.002)	-20.5 (1.3)	2.6 (0.1)	0.78
	September	-0.019 (0.002)	-9.8 (0.7)	1.6 (0.1)	0.44
2007	June	-0.020 (0.003)	-9.0 (0.6)	1.9 (0.2)	0.27
	July	-0.035 (0.002)	-29.8 (1.2)	3.7 (0.2)	0.71
	August	-0.037 (0.002)	-41.9 (1.6)	3.6 (0.1)	0.90
	September	^b n/a	^b n/a	^b n/a	^b n/a
2008	June	^b n/a	^b n/a	^b n/a	^b n/a
	July	-0.026 (0.002)	-23.2 (1.0)	4.1 (0.2)	0.70
	August	^b n/a	^b n/a	^b n/a	^b n/a
2009	June	^b n/a	^b n/a	^b n/a	^b n/a
	July	-0.006 (0.002)	-6.6 (0.9)	1.7 (0.3)	0.60
	August	-0.034 (0.002)	-24.4 (1.0)	3.5 (0.2)	0.82
	September	-0.034 (0.002)	-31.0 (1.2)	3.8 (0.2)	0.89
	September	-0.027 (0.002)	-21.9 (1.1)	2.8 (0.5)	0.76

^a Values of A_{\max} and ER_d are in $\mu\text{mol m}^{-2} \text{s}^{-1}$.

^b Instrument problems resulted in too few data points for curve fit.

spring brings the passage of frontal systems and swings in temperatures which drive differences in ER; warmer temperatures in 2005, 2006 and 2009 resulted in larger

ER compared to the other years (figure 4). June is the period of leaf emergence and larger CVs indicate that the timing of this event and rate of growth vary with



the spring weather conditions. 2006 and 2007 had substantial net sequestration in June (-57 and -34 g C m^{-2}) due to high GEP relative to ER.

In the absence of drastically unfavorable summer conditions, once the cattails were fully developed there was very little limitation on GEP, hence the low CVs for July and especially August. The CV increased in September and October, showing the effect of weather on the onset of senescence. Significantly cooler temperatures in October 2008 resulted in neutral NEE for the month while 2007 had a net release of 30 g C m^{-2} due to abnormally warm conditions. The lower annual GEP CV suggests that inter-annual variability in NEE at the marsh was driven more by changes in ER; perhaps not surprising considering that ER is a 12 month process, but this highlights the importance of the winter and the early- and later warm season responses to variability in temperature.

4.2.1. Cold season

Daily cold season emissions are generally low, however, their cumulative values are important for annual sums (e.g. Oechel *et al* 1997, Aurela *et al* 2002, 2004). Cumulative emissions at the Mer Bleue marsh in the cold season accounted for 28–61% of the annual cumulative CO_2 uptake. In comparison, Zhou *et al* (2009) determined a cold season loss of 83% in their reed dominated ecosystem in 2005; their study was conducted within a warmer and dryer than normal winter (Zhou *et al* 2009, figure 1(b)). In our study, air temperature and snow cover appeared to be the primary drivers of differences in CO_2 losses during the cold season (data not shown). Warmer air temperature and less snow cover over the 2007 winter likely contributed to a thinner ice layer over the channels, promoting more cracks and thus more conduits for CO_2 release; 150 cm of snow fell compared with the

normal of 236 cm. Cumulative CO₂ release during the cold season of 2007 was the highest recorded at 163 g C m⁻² (143, 140, 102 and 146 g C m⁻² in 2005, 2006, 2008 and 2009, respectively). The lowest release, in 2008, coincided with the greatest snowfall (433 cm) and more consistently colder temperatures. It has been well documented that snow can decouple the surface from the environment by protecting soils from extreme air temperatures and creating favorable conditions for ongoing microbial activity and therefore respiration releases through diffusion (Goodrich 1982, Campbell *et al* 2005, Larsen *et al* 2007). At our marsh, in contrast, it is likely that cracks along the mat and channel edges allow CO₂ diffusing through the water channel beneath the ice to escape to the atmosphere more readily in the absence of a significant snow pack.

4.2.2. Warm season

The magnitude of peak CO₂ uptake during the warm season was strongly determined by the photosynthetic response of *Typha* to light availability. The relationship between NEE and PPFD using a rectangular hyperbola fit revealed a strong seasonal pattern and significant year-to-year variations in NEE (table 3). The least and best fit occurred in June and August of each year, respectively, as *Typha* emerged and grew to peak leaf area. We compared our results with other wetland ecosystems (both towers and chambers) and found that peak warm season (July–August) A_{\max} at our site (23.1–35.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$) was higher than that of temperate and boreal bogs (10.0–16.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Bubier *et al* 2003, Strilesky and Humphreys 2012) and fens (7.0–25.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Bubier *et al* 2003, Sonnentag *et al* 2010) and similar to the *Phragmites* marsh in Northeast China ($\sim 24.3 \mu\text{mol m}^{-2} \text{s}^{-1}$; Zhou *et al* 2009). In contrast to other wetlands where the water table position is a significant control on NEE patterns (e.g. Bubier *et al* 1998, Alm *et al* 1999, Aurela *et al* 2007, Pelletier *et al* 2011), in the marsh where the water is at or close to the surface, there was no significant relationship (data not shown).

4.3. Temperature controls CH₄ exchange

Daily average methane emissions from areas with *Typha* and areas of open water were found to increase with air temperature, when pooling the four years of data together (figure 3(b)). This is similar to the relationships found by Song *et al* (2011) (temperature at 5 cm depth), Kankaala *et al* (2004) (sediment temperature) and Chu *et al* (2014) (soil temperature 10 and 30 cm above the sediment surface). We were not able to use sediment or mat temperature across years because of gaps in these time series, however Song *et al* (2011) argue that since methanogenesis occurs across a range of soil depths, the best fit may simply represent the average temperature condition conducive to methanogenesis for that site. Our measurements were restricted to the active growing season.

If measurements continued through the fall when temperatures decrease, it is likely that *Typha* would continue to act as conduits for CH₄ release thus weakening this air temperature relationship. Note that the CH₄ response is unlike the components of NEE (GPP, autotrophic and heterotrophic respiration) which respond directly to temperature and/or light availability (Rocha and Goulden 2008, Zhou *et al* 2009, Song *et al* 2011).

In other wetlands types, depth to water table is a significant correlate of CH₄ flux (e.g. Moore and Roulet 1993, MacDonald *et al* 1998, Pelletier *et al* 2007, Moore *et al* 2011, Nadeau *et al* 2013). However, water depth in the marsh channel was not significantly correlated with any of the CH₄ sources (data not shown). Hargreaves *et al* (2001) and Song *et al* (2011) also found no significant effect of water depth when water levels were at or above the surface, as they are at our site. Although the water levels were slightly lower in mid-summer due to higher evapotranspiration, continued higher fluxes during that period further suggest a dominant effect of seasonality rather than water depth on emission rates (e.g. Moore *et al* 1990, Bubier *et al* 1993, Nykänen *et al* 1998) when water levels are near the vegetated surface.

There was no clear association between emission rates and the number of live or dead shoots present in the collar; higher *Typha* density would be expected to enhance CH₄ transport from sediments to the atmosphere, however, the lack of a relationship may simply mean that gas transport to the atmosphere was not limited by the availability of plant conduits (Hyvönen *et al* 1998). We did find a strong positive correlation between CH₄ emissions from mats and the number of dead broken shoots present in the sampling collars ($r^2 = 0.80, p < 0.001$). This suggests that broken shoots provide an alternate route for CH₄ to be emitted in the atmosphere that allows bypassing of the methane consumption zone (e.g. Kankaala *et al* 2004, Dingemans *et al* 2011).

4.4. Integrated marsh CH₄ emissions

Using the fractions of open water channels (12%) and vegetation (88%) and the monthly averaged daily rates of CH₄ emission multiplied by number of days per month, we calculated that the marsh releases an estimated $117 \pm 19 \text{ g C m}^{-2}$ over the course of an average warm season. This is comparable to emissions from a boreal reed marsh (20–123 g C m⁻², Kankaala *et al* 2004) and significantly higher than that of a boreal sedge marsh (41.7–42.9 g C m⁻², Song *et al* 2011) and the temperate Winous Point marsh (37.1–49.2 g C m⁻², Chu *et al* 2015).

CH₄ emissions can occur during the cold season if trapped CH₄ is released (e.g. Moore *et al* 1990), resulting in an increased annual flux. As chamber measurements were not taken during the winter, CH₄ loss was modeled based on an open water air temperature

relationship from the warm season. The resulting emissions of 10 g C m^{-2} for the cold period added to the warm season measurements yield an integrated yearly efflux of $127 \pm 19 \text{ g C m}^{-2}$. The cold season represents 8% of the annual total methane emissions which is less than that reported in temperate (Kim et al 1998; winter is 20% of growing season) and boreal (Kankaala et al 2004; <10%) *Phragmites*-dominated marshes. The cold season value corresponds to an average daily flux of about $0.05 \text{ g C m}^{-2} \text{ d}^{-1}$. Clearly this approach is deficient as CH_4 does not freely diffuse from the ice covered channel; rather it is released periodically through cracks along the edges. It may however, represent the system in the early part of the cold season prior to the hard frozen cover that persists from December/January through March.

Despite the small estimated cold season efflux, the annual marsh CH_4 estimate is on the high end of recent reports from other Northern marshes ($20\text{--}123 \text{ g C m}^{-2} \text{ yr}^{-1}$; Kankaala et al 2004, Altor and Mitsch 2006, 2008, Nahlik and Mitsch 2010, Sha et al 2011, Song et al 2011, Chu et al 2015) and peatlands ($4\text{--}20 \text{ g C m}^{-2} \text{ yr}^{-1}$; Rinne et al 2007, Roulet et al 2007, Koehler et al 2011, Christensen et al 2012, Olson et al 2013, Peichl et al 2014). Lower CH_4 emissions at peatlands relative to marshes are expected due to the general lack of plant-mediated transport and because of the presence of an aerobic layer which favors CH_4 oxidation and consumption. Lower pH and substrate quality may also limit methanogenesis and C mineralization in peatlands (Valentine et al 1994, Waddington and Roulet 1996, Best and Jacobs 1997). For comparison, Bubier et al (1993) found that beaver ponds and marshes contributed more CH_4 emissions than other wetland types found in Northern Ontario.

4.5. Estimation of marsh C flux budget

In the four years where CO_2 and CH_4 were routinely measured, the net C flux balance of the marsh ecosystem varied between a sink of $-152 \text{ g C m}^{-2} \text{ yr}^{-1}$ and a source of $8 \text{ g C m}^{-2} \text{ yr}^{-1}$ with an average net carbon uptake of $-97 \pm 57 \text{ g C m}^{-2} \text{ yr}^{-1}$. The relatively large net CO_2 uptake does not necessarily lead to a corresponding C storage within the marsh ecosystem. While *Typha* mats are likely thickening and an organic soil layer slowly accumulating (Bonneville et al 2008), more than half of the C fixed through *Typha* primary productivity is expected to return via plant-mediated pathway to the atmosphere as methane. NEE and ecosystem CH_4 exchange are strongly correlated on a seasonal basis as both flux terms are dependent on seasonal *Typha* growth ($r^2 = 0.96$, $p = 0.05$; data not shown). The fact that the CO_2 and CH_4 components are of the same order of magnitude emphasizes that methane must be included in any annual C balance. Furthermore, since CH_4 in this system was driven by temperature, and we found that dead shoots remain

conduits for CH_4 emission, it is possible that marsh CH_4 emissions could persist beyond the senescence of the *Typha* mediated by the aerenchymatous tissues, while also continuing from the open water sources. Therefore if the warm season lengthens, there may be increases in CH_4 and CO_2 respiration, which are not counterbalanced by photosynthetic uptake. The net ecosystem C balance may shift towards neutrality or even a net source.

For a more complete net ecosystem carbon budget, dissolved organic carbon (DOC) should be determined. This is more difficult in this marsh where the water flow input and output were diffuse in nature. We measured DOC concentration at the upstream and downstream ends of the marsh and found that in general, the marsh was a small net exporter of DOC throughout the main part of the warm season (data not shown). Peatland studies have determined a net dissolved C export term of $\sim 13\text{--}15 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Roulet et al 2007, Koehler et al 2011). In comparison, Chu et al (2014) determined an average net hydraulic C import of $\sim 23 \pm 13 \text{ g C m}^{-2} \text{ yr}^{-1}$ for Winous Point marsh, the difference of substantial fluxes at the inflow and outflow. Future work should explore the seasonal and longer-term role of macrophytes in driving DOC flux through root exudation.

5. Conclusions

This study reports a four-year mean annual net C flux for a natural *Typha angustifolia* marsh located in the cool-temperate zone of North America. Methane efflux and net CO_2 uptake were comparable in magnitude and opposite in sign throughout the warm season. Both C flux terms were linked to seasonal *Typha* growth: NEE through plant photosynthesis and autotrophic respiration, CH_4 through plant-mediated transport to the atmosphere. Combining CO_2 and CH_4 fluxes gave an annual small source to strong sink, dependent on *Typha* biophysical responses to weather conditions. Cold season ecosystem respiration, driven by temperature and snowfall was an important determinant of the annual budget. The effect of leakage along the ice margins on winter CO_2 and CH_4 emissions should be studied more closely in these ecosystems. The variability in NEE and CH_4 illustrates that both flux terms must be taken into account in order to have an accurate portrayal of the net C balance within an individual year. This suggests the need for more long-term measurements of these flux terms under a range of climatic conditions and over a range of marsh types to better quantify C exchange in wetlands, with particular emphasis on climate warming responses. Further investigation should include greater measurement frequency of the CH_4 especially during the transition between cold and warm seasons (e.g. spring melt and post senescence). Clearly

however, the substantial CH₄ emissions from marshes need to be considered in national and global estimates of wetland greenhouse gas contribution to the global carbon cycle.

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