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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 \(-224 \pm 54 \, \text{g C m}^{-2} \, \text{yr}^{-1}\) (±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 ± 1.2 g C m\(^{-2}\) d\(^{-1}\)) were significantly higher than fluxes from the water surface (0.5 ± 0.4 g C m\(^{-2}\) d\(^{-1}\)) and unvegetated mats (0.2 ± 0.2 g C m\(^{-2}\) 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 ± 19 g C m\(^{-2}\) yr\(^{-1}\). Combining CO2 and CH4, the annual C sink at the Mer Bleue marsh was reduced to \(-97\) ± 57 g C m\(^{-2}\) 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. Bridgham 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 (Bridgham 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 (Bridgham 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 (Bridgham 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 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 flotation 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.

Figure 1. Temperature and precipitation standardized anomalies. Calculated as the difference from the 1971–2000 climate normal divided by the standard deviation of the climate normal.
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$_{\text{max}}$) was between 2.2 ± 0.2 and 4.1 ± 0.4 m$^{2}$ m$^{-2}$ (table 1).

3.3. Intra- and inter-annual patterns of CO$_2$ exchange

Over the warm season, net CO$_2$ 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 CO$_2$ sink during the warm season with mean daily fluxes averaging $-1.7 ± 0.3$ g C m$^{-2}$ d$^{-1}$; the marsh was a CO$_2$ source of $0.5 ± 0.1$ g C m$^{-2}$ d$^{-1}$ during the cold season (table 2). While the marsh remained a net annual CO$_2$ 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 January–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. CH$_4$-C flux by surface features

CH$_4$ 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 g C m$^{-2}$ d$^{-1}$ (mean ± SD = 0.97 ± 1.19 g C m$^{-2}$ d$^{-1}$; $n = 49$). Prior to active vegetation, fluxes in May 2006 averaged 0.1 g C m$^{-2}$ d$^{-1}$, with collars containing dead shoots showing higher emissions (0.2 g C m$^{-2}$ d$^{-1}$) than those without any shoots (0.0 g C m$^{-2}$ 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 g C m$^{-2}$ d$^{-1}$ (0.45 ± 0.44 g C m$^{-2}$ d$^{-1}$; $n = 66$) compared to the mat fluxes, which ranged from 0.0 to 0.6 g C m$^{-2}$ d$^{-1}$ (0.18 ± 0.17 g C m$^{-2}$ 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 CO$_2$

To the best of our knowledge, only one other long-term study exists (Chu et al 2015) presenting CO$_2$ exchange in a North American cool-temperate freshwater marsh. The authors indicate that their NEE results (net source of 14.6 g C m$^{-2}$ yr$^{-1}$) are inconsistent with the site’s long-term sediment C accumulation rate (97 g C m$^{-2}$ 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 CO$_2$ in each of the five years of our study with an average of $-224 ± 54$ g C m$^{-2}$ 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 ($-40 ± 41$ g C m$^{-2}$ yr$^{-1}$; Roulet et al 2007), an Atlantic blanket bog in Ireland ($-48 ± 30$ g C m$^{-2}$ yr$^{-1}$, Koehler et al 2011), boreal fens in Sweden ($-58 ± 21$ g C m$^{-2}$ yr$^{-1}$, Peichl et al 2014; $-66 ± 29$ g C m$^{-2}$ yr$^{-1}$, Christensen et al 2012) and Finland ($-22 ± 20$ g C m$^{-2}$ yr$^{-1}$, Aurela et al 2004) and a moderately-rich treed fen in Canada ($-189 ± 47$ g C m$^{-2}$ 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 $-65 ± 14$ g C m$^{-2}$ yr$^{-1}$ in Northeast China, while Song et al (2011) report $-143 ± 10$ and $-100 ± 9$ g C m$^{-2}$ 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 ($515$ g C m$^{-2}$ yr$^{-1}$) to a net uptake ($-251$ g C m$^{-2}$ 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 $397 ± 20$ g C m$^{-2}$ 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 CO$_2$ uptake and the magnitude of peak CO$_2$ 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
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 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.

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

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       | $A_{max}$ | ER$_d$ | r$^2$ |
|------|-------|---------|-----------|--------|-------|
| 2005 | June  | −0.028 (0.004) | −6.9 (0.5) | 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 | n/a | n/a | n/a | n/a |
| 2008 | June  | n/a | n/a | n/a | n/a |
|      | July  | −0.026 (0.002) | −23.2 (1.0) | 4.1 (0.2) | 0.70 |
|      | August | n/a | n/a | n/a | n/a |
|      | September | n/a | n/a | n/a | n/a |
| 2009 | June  | −0.006 (0.002) | −6.6 (0.9) | 1.7 (0.3) | 0.60 |
|      | July  | −0.034 (0.002) | −24.4 (1.0) | 3.5 (0.2) | 0.82 |
|      | August | −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 μmol m$^{-2}$ s$^{-1}$.

$^b$ Instrument problems resulted in too few data points for curve fit.
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; 130 cm of snow fell compared with the
normal of 236 cm. Cumulative CO$_2$ 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 CO$_2$ 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 CO$_2$ 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 $\mu$mol m$^{-2}$ s$^{-1}$) was higher than that of temperate and boreal bogs (10.0–16.6 $\mu$mol m$^{-2}$ s$^{-1}$; Bubier et al 2003, Strilesky and Humphreys 2012) and fens (7.0–25.5 $\mu$mol m$^{-2}$ s$^{-1}$; Bubier et al 2003, Sonnentag et al 2010) and similar to the Phragmites marsh in Northeast China (~24.3 $\mu$mol m$^{-2}$ 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 CH$_4$ 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 CH$_4$ release thus weakening this air temperature relationship. Note that the CH$_4$ 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 CH$_4$ 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 CH$_4$ 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 CH$_4$ 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 CH$_4$ 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 CH$_4$ 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 CH$_4$ emissions

Using the fractions of open water channels (12%) and vegetation (88%) and the monthly averaged daily rates of CH$_4$ emission multiplied by number of days per month, we calculated that the marsh releases an estimated 117 ± 19 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).

CH$_4$ emissions can occur during the cold season if trapped CH$_4$ is released (e.g. Moore et al 1990), resulting in an increased annual flux. As chamber measurements were not taken during the winter, CH$_4$ 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 ± 19 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 g C m⁻² d⁻¹. Clearly this approach is deficient as CH₄ 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 CH₄ estimate is on the high end of recent reports from other Northern marshes (20–123 g C m⁻² 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 2013) and peatlands (4–20 g C m⁻² 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 CH₄ 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 CH₄ 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 CH₄ emissions than other wetland types found in Northern Ontario.

4.5. Estimation of marsh C flux budget

In the four years where CO₂ and CH₄ were routinely measured, the net C flux balance of the marsh ecosystem varied between a sink of −152 g C m⁻² yr⁻¹ and a source of 8 g C m⁻² yr⁻¹ with an average net carbon uptake of −97 ± 57 g C m⁻² yr⁻¹. The relatively large net CO₂ 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 CH₄ 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 CO₂ and CH₄ components are of the same order of magnitude emphasizes that methane must be included in any annual C balance. Furthermore, since CH₄ in this system was driven by temperature, and we found that dead shoots remain conduits for CH₄ emission, it is possible that marsh CH₄ 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 CH₄ and CO₂ 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 ~13–15 g C m⁻² yr⁻¹ (Roulet et al 2007, Koehler et al 2011). In comparison, Chu et al (2014) determined an average net hydraulic C import of ~23 ± 13 g C m⁻² 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 CO₂ 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, CH₄ through plant-mediated transport to the atmosphere. Combining CO₂ and CH₄ 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 CO₂ and CH₄ emissions should be studied more closely in these ecosystems. The variability in NEE and CH₄ 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 CH₄ 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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