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Relationships between methane and carbon dioxide fluxes in a temperate cattail-dominated freshwater wetland

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Key points:

There are opposing relationships between CH_4 and CO_2 fluxes during the daytime and nighttime.

We found evidence that the relationship between CH_4 and CO_2 fluxes is the result of covariation of physical drivers.

Combining water levels and water temperature reveals patterns of “hot conditions” that enhance CH_4 and CO_2 flux.

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Abstract

Wetlands are the most important natural source of methane (CH_4) to the atmosphere, and there is still considerable uncertainty of CH_4 flux and net carbon budgets of wetlands. This uncertainty is due in part to the complex role of wetland vegetation in controlling methane production, oxidation and transport, which challenge the modeling and forecast of CH_4 fluxes. We combined CH_4 and carbon dioxide (CO_2) fluxes measured by the eddy covariance (EC) technique during two consecutive growing seasons with continuous measurements of water levels and water temperature in a *Typha angustifolia* L patch of a temperate wetland. We seek to evaluate the role of vegetation in CH_4 flux processes. To this end we determined the relationship between CH_4 and CO_2 fluxes, directly and indirectly linked to plant activity. Our results indicated significant but opposing relationships between CH_4 and CO_2 fluxes during the daytime and nighttime. Consequently, when analyzed on a diel time-scale, this relationship was not significant. Both CH_4 and CO_2 fluxes were highly dependent on environmental drivers, and thus the correlations observed at both the nighttime and daytime were likely the result of a shared response to environmental variables. Focusing on water temperature (the most commonly observed environmental variable in wetlands), and water level (the most commonly controlled one) as operational control variables for wetlands, we identified "hot" condition combinations when CH_4 flux and net ecosystem CO_2 uptake are maximized at half-hourly and diel scales.

Keywords: Methane fluxes, Net Ecosystem Exchange, Gross Primary Productivity, Respiration, Freshwater marsh, Hot moment

1. Introduction

Wetlands cover only about 8% of the land surface (Davidson et al., 2018), but have a disproportionately important role in the global carbon (C) cycle compared to other terrestrial ecosystems. They uptake and store vast amounts of organic C in their soils for long terms, accounting for up to 29 – 45 % of the terrestrial organic C pool (Lal, 2008; Mitsch & Gosselink, 2015). However, wetlands are responsible for about 40 – 50 % of methane (CH_4) emitted from natural sources, constituting the largest single natural source (Tian et al., 2016). This interlinked, dual functioning of wetland as both, sources and sinks of C greenhouse gases, places them as a critical component of global C budgets and as a key component in modeling efforts evaluating negative and positive feedbacks to climate change from the land surface (Frolking et al., 2006; Roulet et al., 2007; Charman et al., 2015; Zhang et al., 2017; Comyn-Platt et al., 2018).

CH_4 emissions from wetlands are the result of a dynamic balance between CH_4 production – methanogenesis, and consumption – methanotrophy (Segers, 1998). Ecosystem primary productivity has long been held as a critical variable controlling CH_4 emissions from wetlands (Whiting & Chanton, 1993). This controlling effect is attributed to the production of labile, easily-degradable organic substrates during photosynthesis that becomes available for methanogens' CH_4 production via root exudation (Chanton et al., 1995; Megonigal et al., 1999) or the decomposition of recently-deposited litter (Chanton et al., 2008; Dungait Jennifer et al., 2012). Productivity is also linked to CH_4 emissions indirectly through plant gas transport that can be proportional to leaf area, xylem flow, and/or stomatal conductance (Whiting & Chanton, 1992; Morrissey et al., 1993; Rusch & Rennenberg, 1998; Nisbet et al., 2009). Emergent macrophytes are rooted in oxygen-limited soils. To cope with that environment, they have developed a complex lacunar system with air spaces to supply the root system with oxygen from the atmosphere. Gas transport inside the leaf is induced by gradients of temperature and humidity or by molecular diffusion (Whiting & Chanton, 1996). When gas is transported to belowground organs, CH_4 is vented out. Methane can be also transported dissolved in the water taken up by plants and eventually released during transpiration through stomata, linking CH_4 emissions and stomatal carbon dioxide (CO_2) uptake during photosynthesis (Chanton et al., 1997; Garnet et al., 2005), and thus leading to an apparent relationship with daytime productivity. Alternatively, studies at the ecosystem-scale attribute the apparent relationship between CH_4 emissions and productivity to covariation of physical drivers affecting CH_4 production and transport, and productivity in a similar way. Specifically, air and water temperature, wind speed, and turbulent mixing of the water column and atmospheric boundary layer (Morin at al., 2014a; Rey-Sanchez et al., 2018).

Despite an increased knowledge of the underlying processes leading to CH_4 production, consumption, and transport in wetland environments and their links with ecosystems productivity, there are still significant discrepancies between estimates from large-scale top-down and small-scale, bottom-up observations, and correspondingly, between the results of top-down inversions and bottom-up mechanistic biochemical scaling approaches (Riley et al., 2011; Saunois et al., 2017). Many process-based models at the ecosystem scale include productivity and respiration as a state variable to estimate CH_4 emissions (e.g., Walter & Heimann, 2000; Zhang et al., 2002; Bohn et al., 2007; Oikawa et al., 2017; Riley et al., 2011). However, wetlands are highly spatially heterogeneous systems with dynamic land-surface covers where plant community distribution is continuously changing in response to seasonal and inter-annual hydrological conditions. Given this dynamic heterogeneity, a more exhaustive understanding of the relationships between CH_4 flux and productivity at the community level and their environmental drivers is needed to improve the parametrization of process-based models (Kirschke et al., 2013; Melton et al., 2013). Such improvements will advance our mechanistic understanding of the underlying processes involved and will lead to better scaling from plot to regional and global models (Bridgham et al., 2013; Li et al., 2016). A detailed knowledge on the relationship between CH_4 flux and productivity at the community level could also lead to informed management practices of current wetlands and design considerations in future restored sites that include reducing the negative feedbacks from CH_4 emissions and/or maximizing C uptake (Kayranli et al., 2010; Badiou et al.; 2011).

In this study, we used CH_4 and CO_2 fluxes measured by the eddy covariance (EC) technique during two consecutive growing seasons from a cattail-dominated patch in a freshwater temperate wetland. We used the data to determine the relationship between CH_4 and CO_2 fluxes at this cattail plant-community level at half- hourly and diel temporal scales. A previous study at this site by Rey-Sanchez et al., (2018) reported that at the ecosystem level, considering all patch types in the site, including open water, mud flats and multiple plant communities, CO_2 flux was an important predictor of CH_4 flux. However, that finding did not infer any particular mechanisms or causal relationship that were responsible for the observed empirical correlation between CH_4 and CO_2 fluxes.

In this study, we test whether the empirical relationship between CH_4 and CO_2 fluxes relationship within the emergent vegetation patch type is the result of a direct control of productivity on CH_4 production and transport, or if is driven by the co-dependence of CH_4 and CO_2 fluxes on environmental drivers. We focus of emergent cattail vegetation as this patch type holds the highest vegetation biomass and leaf area, and hypothetically, should be the patch type where direct mechanistic relationships between CH_4 and CO_2 are most strongly expected. We further used the data to identify the conditions that optimize the greenhouse gas budget of wetlands, particularly, minimize CH_4 flux and maximize net ecosystem CO_2 uptake at both half-hourly and diel scales. We focused on the effects of temperature (the most commonly observed environmental variable in wetlands), and water level (the most commonly controlled one) as operational control variables for carbon fluxes in wetlands. We sought to provide ecosystem managers in similar cattail-dominated systems with carbon-cycle considerations to maximize the climate regulating function of wetlands.

2. Materials and Methods

2.1 Study site

This study was conducted in northwestern Ohio at the Old Woman Creek (OWC) National Estuarine Research Reserve (NERR) (41°22.758' N, 82° 30.743', Figure 1). Meteorological data and water conditions for the site are available at the NEER website (NOAA, 2018). Flux, wind, and gas concentration data for the site is available through the AmeriFlux project, site ID US-OWC (Bohrer, 2018).

The OWC estuary is a drowned-river mouth wetland with a semi-permanent connection to the lake, controlled by the formation of a sand barrier that restricts flow at the mouth. This sand barrier typically forms in the estuary mouth with cycles of build-up and break-up about 1-3 times per year. On average, the barrier remains closed during 38 % of the year (calculated from NERR system data). When the sand barrier is closed, constant inflow from the creek drives higher water levels, reaching a steady-state condition where creek and runoff inflows are balanced by a slow subsurface outflow through the sand barrier. When the barrier opens, a rapid flush between the wetland and Lake Erie occurs, and after some time the water levels in the estuary equalizes with that of the Lake. The wetland water level is then tied to that of the Lake until the barrier forms again.

The OWC is a mineral-soil freshwater wetland. The primary source of mineral sediments is from watershed runoff (Matisoff et al., 2002). Elevated soil deposits set the conditions for the development of distinct patches of macrophyte vegetation. The dominant vegetation corresponds to two functional groups: emergent (mostly *Typha angustifolia* L, cattail, hereafter) and floating-leaved (*Nelumbo lutea* Willd. *and Nymphaea odorata* Aiton), with the former dominating the shallowest areas. The relative cover of these dominant patches varies in response to the hydrologic dynamic of the wetland (Klarer & Millie, 1992). In this study, we focused on a large cattail-dominated patch. During the study period (growing seasons of 2015 and 2016) cattail covered about 41 % of the 61 ha that comprises the estuarine wetland (Rey-Sanchez et al., 2018) (Figure 1). Cattail is a cosmopolitan macrophyte present in wetlands throughout the temperate zone, from the Arctic Circle to 30°S (Schulthorpe, 1967) and is usually recognized as an invasive species in Great Lakes coastal wetlands (Tulbure et al., 2007). The cattail patches present in OWC feature high-density monocultures with some associated submerged aquatic vegetation, mostly species from the *Potamogeton* genera.

2.2 Data collection

We measured carbon fluxes and meteorological conditions at the site with an eddy covariance tower from June to October of 2015 and from April to October 2016 (Rey-Sanchez et al., 2018). The tower was equipped with open-path infrared gas analyzers (IRGAs) for CO_2/H_2O and CH_4 (LI-7500 and LI-7700, respectively. LiCOR Bioscience, Lincoln, NE), and a 3D ultrasonic anemometer (CSAT3, Campbell Scientific Inc., Logan, UT). The tower included an air temperature and humidity sensor (HMP45, Vaisala Inc., Vantaa, Finland). IRGA sensors were installed at 2.7 m above the average water level of the wetland. Soil temperature at the cattail patch was measured with a 107 – L temperature sensor (Campbell Scientific Inc., Logan, UT) installed at approximately 13 m east of the tower at a depth of 10 cm below the soil surface. Sensors were connected to a datalogger (CR3000, Campbell Scientific Inc., Logan, UT) accessed wirelessly via FM radio (RF450, Campbell Scientific Inc., Logan, UT). Water levels at this location during the study period were calculated relative to the water level records of the estuary at a NOAA-operated aquatic monitoring station located 300 m north of the tower. Water temperature records were collected at this monitoring station as well. Carbon concentration and wind measurements were recorded at 10 Hz. Air temperature, humidity, and soil temperature were recorded every 1 min, while water levels and temperature were recorded every 15 min. The data were binned into half-hours averages before flux calculation and data analyses.

2.3 Flux calculation

The EC flux process we used to process the data is detailed in Morin et al., (2014b), including the quality control and despiking procedures to eliminate outliers in the fast-frequency data. Additional details for flux observations in this site are provided in Rey-Sanchez et al. (2018). In brief, we applied a 3-D rotation to wind observations to force the vertical and crosswind components to be zero (Finnigan et al., 2003). Temperature measurements from the sonic anemometer were corrected to account for changes in pressure and water vapor concentration (Kaimal & Gaynor, 1991). We corrected the time lag between the sonic anemometer and the IRGAs by the maximal covariance approach and applied the Webb-Pearman-Leuning correction on H_2O, CO_2 and, CH_4 molar densities that account for the effects of fluctuations in air density (Webb et al., 1980). We used a minimum frictional velocity (u^*) value of 0.2 m s^{-1} to filter and reject data with an insufficient level of turbulent mixing.

2.4 Data filtering – seasonality and footprint conditions

For this analysis we only used data during the growing seasons of 2015, and 2016. The OWC estuary is a very productive ecosystem, exhibiting negative NEE values even after macrophyte senescence and through the early winter due to remaining algal productivity. Therefore, our approach to determining the macrophyte growing season was based on first and last exceedance of threshold of *NEE* = -10 µmol m^{-2} s^{-1}. Consequently, the growing season in 2015 extended from the beginning of the study, June 1, through September 24. In 2016 the growing season extended from May 17 through October 5 (Figure 2).

We further limited the growing season using a 20 °C soil temperature threshold (first to last exceedance day). This was done to limit our data analysis to peak growing season and avoid confounding processes association with spring and fall transitions of vegetation growth and senescence, which co-occur with cooler temperatures. The threshold of 20 °C soil temperature defined the peak growing season in 2015 from June 4 through September 16 and in 2016 from May 18 through September 27 (Figure 2). Finally, to avoid higher than usual flux pulses caused by rapid water level withdrawal during barrier break-up episodes, we removed from the analysis periods starting when the barrier broke open, up to a day after its re-closure. The sand barrier opened 4 times during the study periods, all times occurring during 2015. The barrier remained open 2 days in each of the June and August events, and 10 days in September (Figure 2).

To determine the origin of each 30-min aggregate flux observation and the proportion of contribution from each point to the observed flux, we used the footprint model of Hsieh et al. (2000) with the 2-D expansion developed by Detto et al., (2006) allowing us to determine a footprint likelihood matrix for multiple patches (Morin et al., 2014b). The patches considered in this footprint model included the dominant land cover types in and around OWC: open water, cattail (dominated by *Typha angustifolia*), floating leaved vegetation (dominated by *N. lutea and N. odorata*), mudflats, and upland forest. Because the tail of the distribution used in footprint models is infinite, the full source area typically extends beyond the defined area of interest, and the sum of the likelihood of the flux originating from all patches within the wetland is < 100% (Forbrich et al., 2011). During the study period, we used only data when the flux-footprint likelihood from land cover types corresponding to the wetland (i.e.

excluding upland forest), was higher than70% (e.g. Morin et al., (2014b)). As this study is focused on the cattail patch type, we further limited out data for half hours when the footprint likelihood from cattail patches was greater than 65%, as we consider that likelihood to represent fluxes strongly dominated by the cattail community. The fluxes during these half hours typically corresponded with a large cattail patch located southeast of the tower (Figure 1). Fluxes during other half hours, which originated from other patch types, were treated as missing observations.

2.5 Gap filling and partitioning of CO_2 fluxes

We partitioned the CO_2 net ecosystem exchange (*NEE*) into gross primary productivity (*GPP*) and ecosystem respiration (R_e). We assumed that during nighttime $NEE = R_e$ and we used nighttime *NEE* data to train an artificial neural network (ANN) to predict R_e. The ANN model for R_e was used to fill gaps at nighttime R_e and *NEE*, and to model daytime R_e (Papale & Valentin, 2003; Moffat et al., 2007; Morin et al., 2014b; Rey-Sanchez et al., 2018). During daytime we used the ANN to model *NEE* and used the modeled data to gap-fill missing and filtered *NEE* observations. Finally, we modelled $GPP = \{NEE + \text{modeled } R_e \,|\text{daytime; } 0 \,|\, \text{nighttime}\}$. As drivers to the ANN models we used half-hourly wind speed (*U*), vapor pressure deficit (*VPD*), air temperature (*AT*), water level (*WL*), water temperature (*WT*), sensible heat (*H*), and latent heat (*LH*). Any gaps in the environmental drivers data were gap-filled before being used in the ANN model using observations from the near-by NOAA meteorological station, or using a bi-linear interpolation. *H* and *LH* were gap-filled using ANN models before being used as an input for the R_e and *NEE* models (Rey-Sanchez et al. 2018). For the daytime *NEE* model we also included photosynthetically available radiation (*PAR*) as a driver. These variables were selected as environmental drivers based on their pairwise ecosystem-level correlation with CO_2 and CH_4 fluxes in OWC (Rey-Sanchez et al., 2018).

We ran 1000 ANN models and selected the top 10%. The final ANN model was the ensemble average of these 100 best fitting models. Training was done using 50% of the data, validation was based on another 255 of the data and evaluation of model fit was done using the remaining 25% of the data. The ensemble standard deviation of the top 100 ANN models during the evaluation period was used as a conservative estimate for the upper limit of the flux observation uncertainty (Moffat et al., 2007; Richardson et al., 2008).

We use a similar ANN approach to gap fill methane. Before running the model, we determined the lag time for maximal covariation between observed CH_4 flux and *WT*, *WL* and *GPP*. We found that CH_4 flux was best correlated with *WL* with a lag of 56 hours and showed no lag-time with *WT* and *GPP*. Consequently, we used *WL* data lagged by 56 hours. Input for the ANN to model CH_4 included the same environmental drivers as the ANN CO_2 models with addition of the gap-filled *GPP* and R_e (we indicate this model as: $Env + GPP + R_e + LH$).

2.6 Codependence of CH_4 and CO_2 fluxes on environmental drivers

To explore the codependence of CH_4 and CO_2 fluxes on environmental drivers we ran three additional alternative CH_4 ANN models. They differed in the input variables as follows: (1) environmental drivers (*U, VPD, AT, WL, WT, H,* and *PAR*), including *LH* (*Env* + *LH*). (2) Environmental drivers excluding *LH* (*Env*). And (3) Environmental drivers excluding *LH* but including *GPP* and R_e (Env + *GPP* + Re). We assume that if the apparent correlation of CH_4 and CO_2 fluxes is purely a result of co-variation with environmental drivers, adding *GPP* and R_e to an ANN model that already includes all other common environmental drivers will not significantly improve the model. Alternatively, if carbon fluxes had a direct effect on CH_4, adding GPP and R_e as input to a CH_4 model will significantly improve the model. We single out LH in addition to GPP and R_e because LH is highly correlated with both with GPP (through stomatal conductance) and with any surface flux from the water (through common drivers that control the turbulent mixing of the upper water layer and the atmospheric surface layer). We expect that the improvement caused by adding LH as an input to the ENV CH_4 model will be higher than the improvement by adding GPP and R_e if CO_2 and methane fluxes are not directly related but vary similarly with turbulence mixing. We evaluated the change in the goodness of fit (estimated through the coefficient of determination, r^2) of the model created to gap filled CH_4 fluxes ($Env + GPP + R_e + LH$), relative to the r^2 of the Env and $Env + LH$ model.

2.7 Data analyses

Linear regressions were used to determine the significance of daytime and nighttime correlations between half-hourly and diel CH_4 and CO_2 fluxes (NEE, GPP, R_e). For the diel analysis we used the 24-hours averages of CH_4 fluxes and NEE. We did not include gap-filled data in these correlation tests, and therefore, to prevent biases due to larger number of missing observations during nighttime than during daytime, we only considered days were at least 12 nighttime and 12 daytime half-hourly observations (without gap-filling) were available for both CO_2 and CH_4 fluxes. In all half-hourly regressions, we used only data points when both CH_4 and CO_2 data were available from observations and not gap-filled. To estimate the robustness of the significance of the regressions to uncertainty in flux observations we used a Monte Carlo approach, adding to each flux a random error term drawn from a Laplace distribution with mean 0 and standard deviation representing the observation uncertainty estimate as determined by the ANN ensemble. We retested each regression 1000 times with independently drawn random errors. We reported the mean slopes of the regressions of the observed data ± the standard deviation of the 1000 regressions with random errors. All data processing and statistical analyses were performed using Matlab R2018a, except for the check of the normality of the data sets before running statistical tests and the linear regressions, which was performed using the Shapiro-Wilk test in JMP® pro 13.1.0.

We used an analysis of covariance (ANCOVA) to test for the difference between the slopes in the regressions between CH_4 and *NEE*, and CH_4 and *GPP*. For the difference between mean CH_4 flux during daytime and nighttime we used a two-sample t-test. To identify the conditions that enhance CH_4 and CO_2 fluxes, i.e., “hot conditions”, we created heat maps of the 24-hour averages of daytime, nighttime and diel CH_4 and CO_2 fluxes as a function of diel average water levels and water temperatures as site-diagnostic variables. To avoid biases introduced by uneven flux measurements, we filtered our data for the daytime and nighttime analyses to include only 24-hour periods with at least 8 half-hourly paired CH_4 and CO_2 daytime or nighttime observations, respectively. For the diel analysis we used gap-filled fluxes but only included days when both daytime and nighttime periods each had at least 6 half-hourly paired observations.

3. Results and discussion

3.1 Relationships between CH_4 and carbon fluxes

While direct regulation of CH_4 flux through productivity at the ecosystem level has been detected in other systems (e.g., Joabsson & Christensen, 2001; Chu et al., 2014; Knox et al., 2016), our results at the half-hourly scale provide some indication that in the plant community studied the effect of vegetation productivity, through substrate supply or transport regulation, is not directly responsible for sub-diel variations of CH_4 flux.

The regulation of CH_4 flux at diurnal and seasonal scales by primary productivity has been proposed by several studies as the cause of the apparent relationship between CH4 fluxes and productivity (Hatala et al., 2012; Rinne et al., 2018). Direct regulation of CH_4 flux through productivity results from the supply of recent photosynthates that act as substrates for methanogenesis. Studies conducted under laboratory and field conditions with labeled C, shows that recently assimilated carbon can be reduced microbially to CH_4 within hours (i.e., 3 – 24 h) (Minoda & Kimura, 1994; Wieder & Yavitt, 1994; Megonigal et al., 1999; King & Reeburgh, 2002). The lag between Gross Ecosystem Productivity (*GEP*) and CH_4 flux can be as short as 1 hour, highlighting the apparent role of photosynthesis in hourly and daily patterns of CH_4 flux (Hatala et al., 2012; Lai et al., 2014). However, we did not find any significant lag between *GPP* and CH_4 flux in our data that evidence the thesis of direct regulation by substrate supply. It was suggested that methanogens are more limited by temperature than by substrate in sites with high CH_4 emission rates such as OWC (Kankaala et al., 2005). Although it might be possible that the effect of substrate supply is being masked by corresponding variation in CH_4 oxidation. In addition, we disregard an alternative indirect control of productivity on CH_4 flux through stomata conductance, as stomatal aperture is known to have little control on CH_4 emissions from cattails (Whiting & Chanton, 1996).

Although our findings do not provide direct evidence of CH_4 flux regulation by productivity, we found significant correlations between CH_4 flux and both productivity and respiration. Observed half-hourly CH_4 flux during the daytime was negatively correlated with *NEE* and *GPP*. Slopes (-0.022 ± 0.0012 and -0.026 ± 0.0008) were not significantly different (ANCOVA, $F(1,2924) = 1.89$, $p = 0.17$), with *GPP* explaining more of the variation of CH_4 than *NEE* given the higher r^2 value. We attributed the weaker correlation between CH_4 and *NEE* to the additional variability introduced to *NEE* by R_e, which includes heterotrophic respiration as an additional source of noise (Valentini et al., 2000; Jungkunst & Fiedler, 2007).

During nighttime, observed CH_4 flux showed a significant positive correlation with R_e (slope = 0.082 ± 0.0052, Figure 3C), i.e., an opposite relationship than during the day. The magnitude of the slope of the correlation between half-hourly CH_4 and R_e was nearly twice as large as the slope of the CH_4-GPP correlation during the day, and r^2 of the correlation during nighttime was higher than during the day. The increase in slope and r^2 suggest a stronger association of CH_4 flux with respiration, than with photosynthesis. This finding may be explained by the covariation of environmental drivers controlling microbial processes leading to aerobic and anaerobic respiration and to turbulence transport mechanisms that drive surface fluxes. Temperature is a key variable determining the rates of anaerobic and aerobic respiration in wetland soils (Inglett et al., 2012) and controlling molecular diffusion and convective flow from the water surface (Koebsch et al., 2015). Convective surface flow from the water may account for up to 32% of CH_4 annual flux in cattail-dominated wetlands (Poindexter et al., 2016). Interestingly, CH_4 flux rates were similar during the daytime and nighttime (0.77 ± 0.47 and 0.72 ± 0.4 µmol CH_4 m^{-2} s^{-1}, respectively: t-test, $t(1847) = 1.43$, $p = 0.1542$). A similar finding at the ecosystem-scale was reported by Rey-Sanchez et al. (2018) that included all dominant land cover types in and around OWC and included the shoulder seasons, which suggest that CH_4 transport processes during nighttime in the cattail community, contribute in a similar proportion to diel CH_4 fluxes as daytime processes.

At the diel scale we found a weak correlation between CH_4 flux and NEE (Figure 4, linear regression, $r^2 = 0.18$, $p = 0.07$, n = 14). This correlation seems to support previous findings at the community level using daytime chamber measurements and nighttime respiration modeling (Whiting & Chanton, 1992; Whiting et al., 1991; Lai et al., 2014). It is worth noting though, that these studies report stronger correlations, which may be reflecting the reduction of external noise, which is intrinsic in the chamber method they used, whereas our diel estimation based on open path eddy-covariance measurements may have captured additional sources of variation (source footprint, bubbling) which cannot be captured by chamber measurements, thus leading to a reduced correlation. The fact that out of all the days we considered in our study during two growing seasons, only 14 had at least 12 nighttime and 12 daytime half-hourly valid observations (footprint 65% from cattail patch, high u*, high data quality) speaks of the difficulty of capturing an unbiased daily CH_4 flux and *NEE* relationships at the plant community scale using the EC technique. Nonetheless, the number of diel observations correspond to average values and is comparable with the number of hourly observations typically used for correlations the chamber studies (Whiting & Chanton, 1992; Whiting et al., 1991; Lai et al., 2014).

3.2 Codependence of CH_4 and CO_2 fluxes on environmental drivers

The observed correlations between CH_4 flux and *NEE* or *GPP* are likely the result of covariation with physical drivers, affecting CH_4 production and transport and photosynthesis in a similar way. The ANN models were able to capture very large portion of the variation in CH_4 flux and *NEE*, indicating that both of these fluxes are predictable as functions of environmental drivers (Table 1). During daytime CO_2 flux prediction was better (r^2 = 0.87) than during the nighttime (r^2 = 0.55). In comparison, the goodness of fit of predictions of CH_4 fluxes based on the same environmental drivers (*Env* + *LH*) did not show any substantial difference between day and nighttime (r^2 = 0.79 and 0.76, respectively). Including *GPP* and R_e in the ANN model did not improve CH_4 flux predictions (1 and 2 % change in r^2, respectively). If productivity had a direct effect on CH_4 flux, we would expect to find better predictions of CH_4 flux with the *Env* + *LH* + *GPP* + R_e model than with the *Env* + *LH* model. The lack of improvement is a clear indication that *GPP* is not directly driving CH_4

flux and supporting the hypothesis that covariation with physical drivers explains the correlation between CH_4 and CO_2 fluxes (*GPP* during the day and R_e during the night).

Moreover, excluding *LH* from the *Env* and *Env* + *GPP* + R_e models reduced CH_4 predictions goodness of fit especially during nighttime (% change in r^2 of -18 and -9.2, respectively). In wetlands, where water stress does not affect stomatal conductance *LH* is primarily controlled by turbulence mixing and thermal gradients that drives volatilization from the water surface (Verburg & Antenucci, 2010). The same physical drivers that control water volatilization drive fluxes of dissolved CH_4 and CO_2 from the water surface to the air (Godwin et al., 2013; Franz et al., 2016) and through plant tissue (Morrissey et al., 1993). Convective throughflow, the dominant gas transport mechanism in cattails is driven by temperature gradient inside the leaf and humidity gradients between the leaf and the surrounding air. Both gradients increase with air temperature and solar radiation, which closely correlate with water temperature and *PAR*, strongly affecting photosynthesis (Grosse et al., 1991; Brix et al., 1992; Bendix et al., 1994; Whiting & Chanton, 1996).

The previous study at the ecosystem scale (i.e., including all land cover types) by Rey-Sanchez et al. (2018) also noted the importance of air and water temperatures and wind speed in CH_4 flux as environmental drivers at OWC. Using hierarchical stepwise neural network models, that work showed strong correlations between half-hourly CH_4 flux and air and water temperatures, and wind speed, during both daytime and nighttime. Their analysis included shoulder seasons when plants were absent or senesced, emphasizing the relevance of the physical drivers in CH_4 fluxes from the site, even when plants are not present.

3.3 “Hot conditions” of CH_4 and CO_2 fluxes

Up to this point, our data provides evidence of the codependence of CH_4 and CO_2 fluxes on environmental drivers, which is of relevance to help model and gap-fill observations from cattail-dominated systems. However, the typical wetland or land management managers do not have the observations needed to conduct such models. Temperature and water levels are the most commonly measured variables in wetland ecosystems. Water level is also often controlled. In the next section we investigate the insight for co-optimization of CH_4 and CO_2 based solely on these two environmental drivers.

Observed CH_4 flux during daytime and nighttime was larger at high temperatures and high-water levels (Figures 5A and 5B). During daytime, high methane fluxes (> 1 g C-CH_4 m^{-2} d^{-1}) where observed at all water levels when the temperature was higher than 25.5 ^oC, and above 21.5 ^oC when the water level was higher than 0.8 m (Figure 5A). At nighttime, the range of hot conditions was more limited, and high CH_4 fluxes were observed at a combination of temperature between 21.5-23.5 ^oC and water level between 0.8-1 m, and when temperature was above 25 ^oC and water level above 0.7 m. At the diel scale CH_4 flux is larger at high temperatures and water levels above 0.5 m (Figure 6A).

As expected, observed *NEE* showed a contrasting behavior between daytime and nighttime, acting as net CO_2 sink in the daytime and source at night (Figures 5C and 5D). The strongest carbon uptake rates were observed at high temperatures (> 25 ^oC) or high-water levels (>7.5 m), while maximal CO_2 emissions occurred at intermediate water levels (0.5-0.8 m) at all temperatures. The diel *NEE* show that the plant community can act as a net sink of CO_2 at high temperatures and as a source of CO_2 at low temperature and high water levels (Figure 6B).

Studies of the relationship between CH_4 and CO_2 fluxes, water levels, and temperature in temperate freshwater marshes are limited. Studies conducted with the chamber method suggest that CH_4 flux (Ding et al., 2002) and R_e (Song et al., 2008) increase at higher water levels, while water level variation has no apparent effects on *GPP* (Altor & Mitsch, 2008). Through the same method, temperature has been identified as the driver of seasonal patterns in CH_4, *GPP* and R_e (Wilson et al., 1989; Song et al., 2009) with more flux during the growing season. More recent studies using the EC technique in other freshwater wetlands dominated by the same cattail species in our study partially support these findings. In a Lake Erie coastal marsh Chu et al. (2014) reported seasonal trends of CH_4, R_e, and GEP, associated with soil temperature. They reported half-hourly correlations between CH_4 and soil temperature and CH_4 and water levels. Similarly, in a freshwater marsh of the *Mer Bleue* wetland complex (Ottawa, CAN), Strachan et al. (2015) reported seasonal trends in CH_4, *NEE*, and R_e associated with air temperature. In addition, both studies did not find hourly or daily correlations between CO_2 fluxes and water levels, supporting studies conducted with chambers. However, studies with the EC technique did not report correlations between CH_4 flux and water levels, probably due to the constant presence of water above the soil surface in most wetland EC sites.

In comparison, our results show relatively higher CH_4 flux during daytime and nighttime periods at higher water levels during the growing season (Figures 5A and 5B). Unlike other site that may have no, or only seasonal changes to water levels, in OWC water levels are fluctuating over a relatively wide range, at relatively short timescales (days). As a result, water levels have been found important in determining half-hourly and daily CH_4 fluxes at this site (Rey-Sanchez et al., 2018).

The temporal and spatial distribution of hot conditions (i.e., hot moment and hot spot, respectively) is crucial in incorporating spatially and temporally explicit phenomena in models representing biochemical processing in wetlands (Groffman et al., 2009; Savage et al., 2014). In the case of CH_4 emissions, accounting for hot moments and hot spots is vital for designing management practices to mitigate the negative climate feedbacks (McClain et al., 2003; Wilson et al., 2009). Hot spots and moments can also account for the contrasting activity of methanogenic and methanotrophic consortia (e.g. Narrowe et al., 2017), which have important implications when connecting plant and microbial interactions modeling efforts (Bridgham et al., 2013).

Using water level and water temperature as site-diagnostic variables we were able to identify hot conditions enhancing CH_4 and CO_2 flux as a first step to understanding hot moments in a cattail community of a temperate freshwater marsh. Adding spatial and temporal (season/phenology) dimensions to these hot conditions is a research priority to advance proceed-based mechanistic prediction of CH_4 flux from cattail communities. In the meantime, our results offer a valuable tool to managers to mitigate CH_4 feedbacks in OWC and possibly similar wetlands along the coast of Lake Erie. Based on our results we propose that during the growing season and particularly during weeks with high temperatures, water levels should be maintained low (i.e., < 0.6 m) to reduce CH_4 emissions and increase CO_2 uptake (Figure 6A and 6B).

4. Conclusions

In this study, we used EC measurements of CH_4 and CO_2 fluxes from a cattail-dominated plant community patch in a mineral soil riverine wetland to assess the relationships between CH_4 flux and plant productivity during daytime and respiration during nighttime at half-hourly and diel scales. There are opposing relationships between CH_4 and CO_2 fluxes during daytime and nighttime, and a weaker correlation at the diel scale than at the half-hourly scale, and during the day than during the night. The relationships are attributable to the covariation of both CH_4 and CO_2 fluxes with physical drivers affecting both fluxes in a similar way. These findings support and expand previous findings at the ecosystem scale on the relevance of physical drivers at the site. Combining our CH_4 and CO_2 flux measurements with site diagnostic variables commonly recorded or controlled in wetlands offered a valuable tool for managing greenhouse gas emissions at the site and possible other cattail-dominated wetlands in temperate climates.

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Table 1. Goodness of fit, evaluated by the coefficient of determination (r^2) of observed and predicted CO_2 and CH_4 fluxes with the different Artificial Neural Network (ANN) models. CO_2 flux during daytime is *GPP* and during nighttime is R_e. Environmental variables (*Env*) included as drivers in the models were: wind speed (*U*), vapor pressure deficit (*VPD*), air temperature (*AT*), water level (*WL*), water temperature (*WT*), sensible heat (*H*), latent heat (*LH*), and photosynthetically available radiation (*PAR*) only for daytime models. % change represent the variation between the r^2 of the CH_4 *Env* model and the r^2 of each corresponding CH_4. * represents the model that was used to gap fill CH_4 fluxes.

Model	Daytime			Nighttime		
	r^2	Error	% change	r^2	Error	% change
CO_2 (*Env* + *LH*)	0.87	6.0	--	0.55	6.9	--
CH_4 (*Env* + *LH*)	0.79	0.046		0.76	0.039	
CH_4 (*Env*)	0.67	0.071	-15	0.62	0.061	-18
CH_4 (*Env* + *GPP* + *Re*)	0.73	0.060	-8	0.68	0.051	-10
CH_4 (*Env* + *LH* + *GPP* + *Re*)*	0.80	0.046	1	0.77	0.039	2

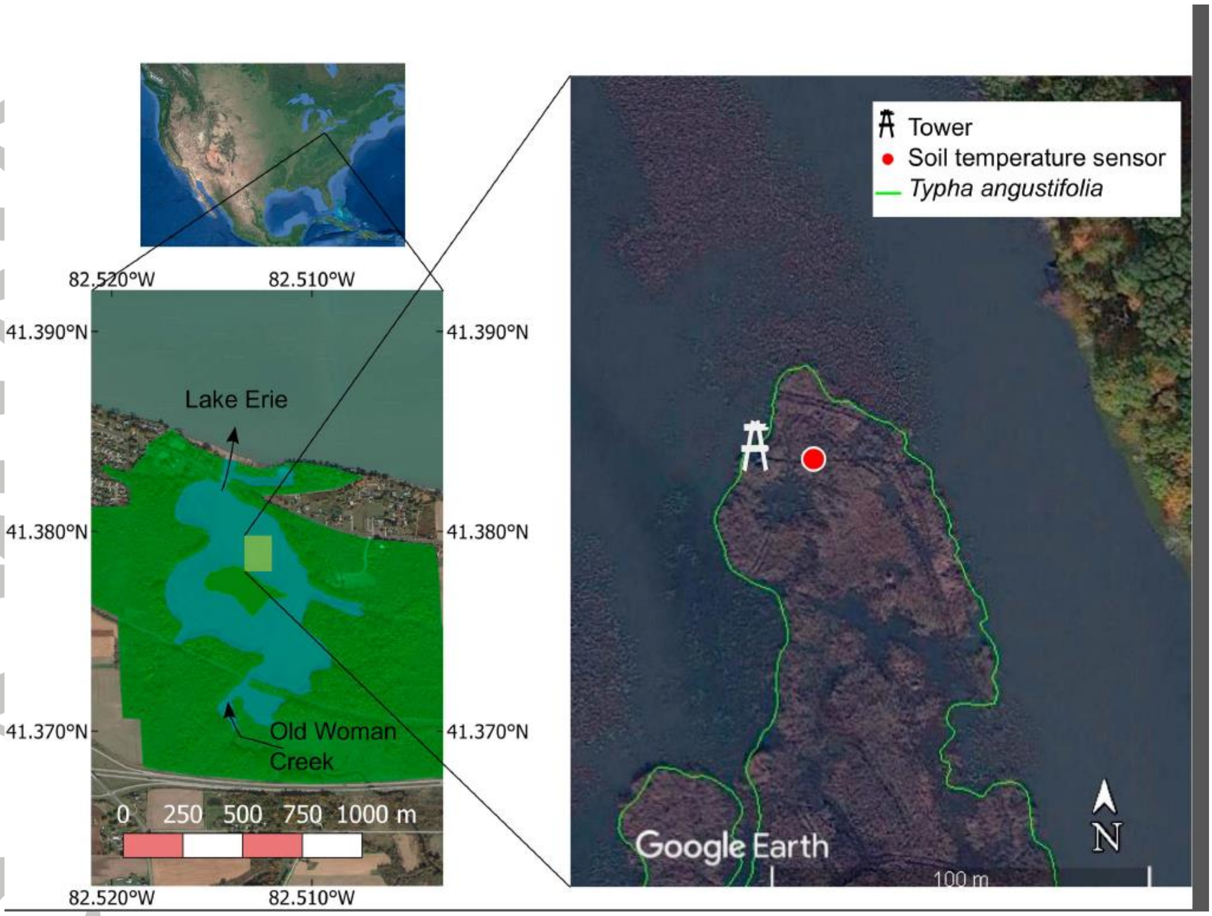

Figure 1. Location of the study site, Old Woman Creek (OWC) National Estuarine Research Reserve (NERR) in Lake Erie.

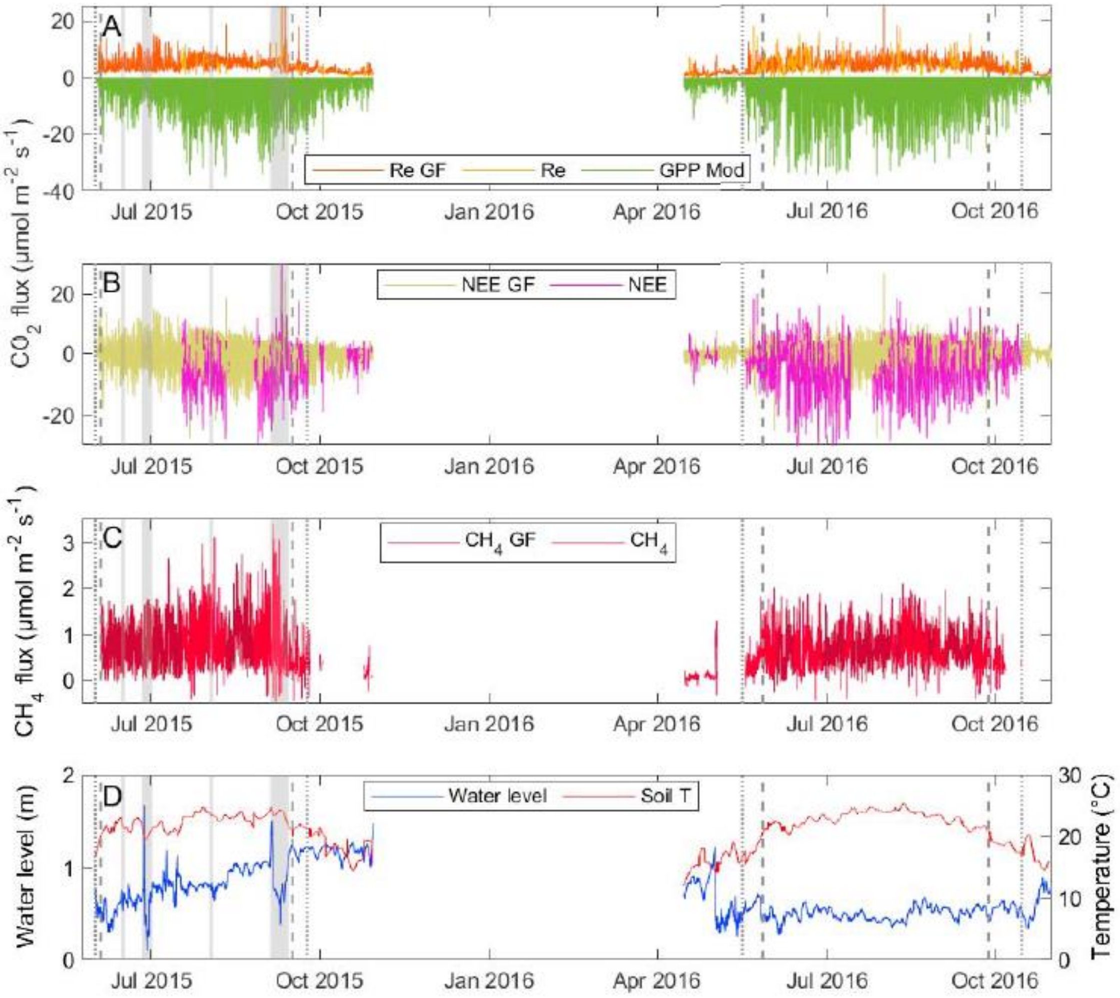

Figure 2. Fluxes (A – C) and environmental conditions (water level and water temperature) (D) during the study period. Dotted vertical lines in 2015 indicate the beginning of data collection and the end of the growing season. In 2016, dotted vertical lines indicate the beginning and end of the growing season. Dashed lines indicate the peak growing periods when soil temperature exceeded 20 °C. Gray bars indicate the periods in 2015 when the sand barrier was open. Abbreviations GF: gap filled, Mod: modelled, Re: Respiration, NEE: net ecosystem exchange, CH4: methane, Soil T: temperature at 10 cm below the soil surface.

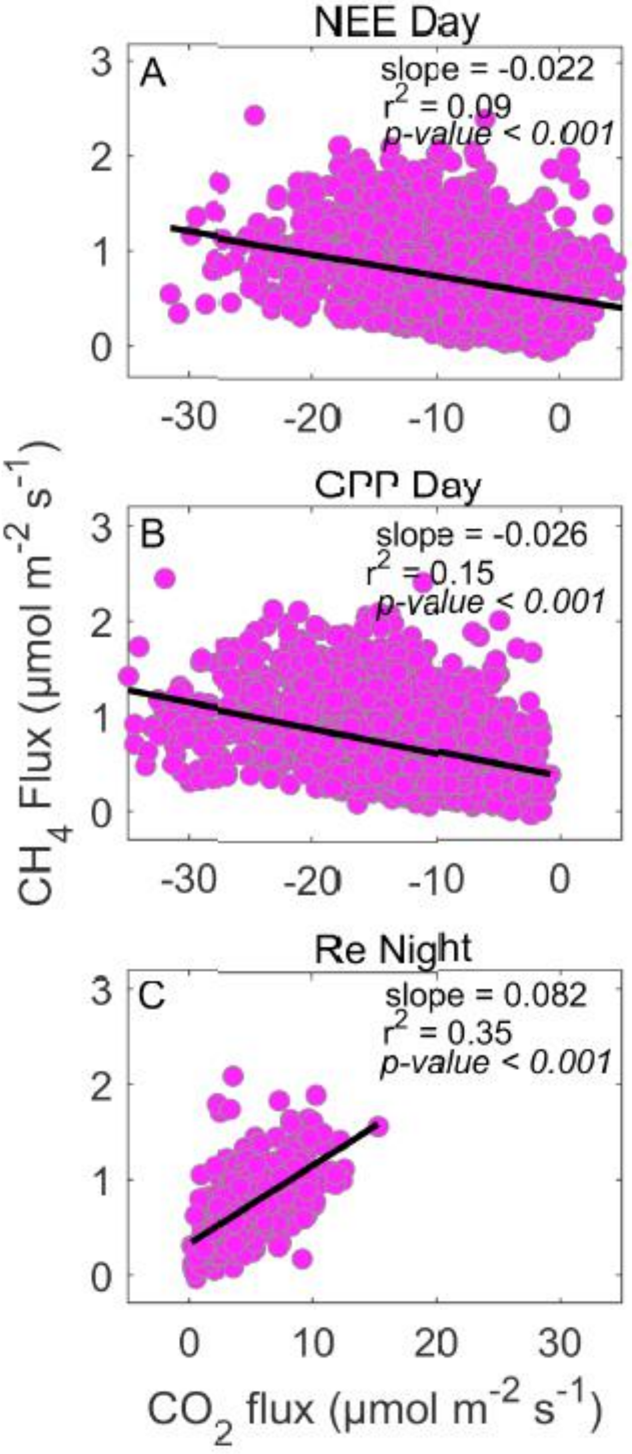

Figure 3. Half-hourly relationships between CH_4 flux and net ecosystem productivity (NEE) during the day (A), gross primary productivity ($GPP = NEE - R_e$) (B), and Respiration ($R_e = NEE$ during the night).

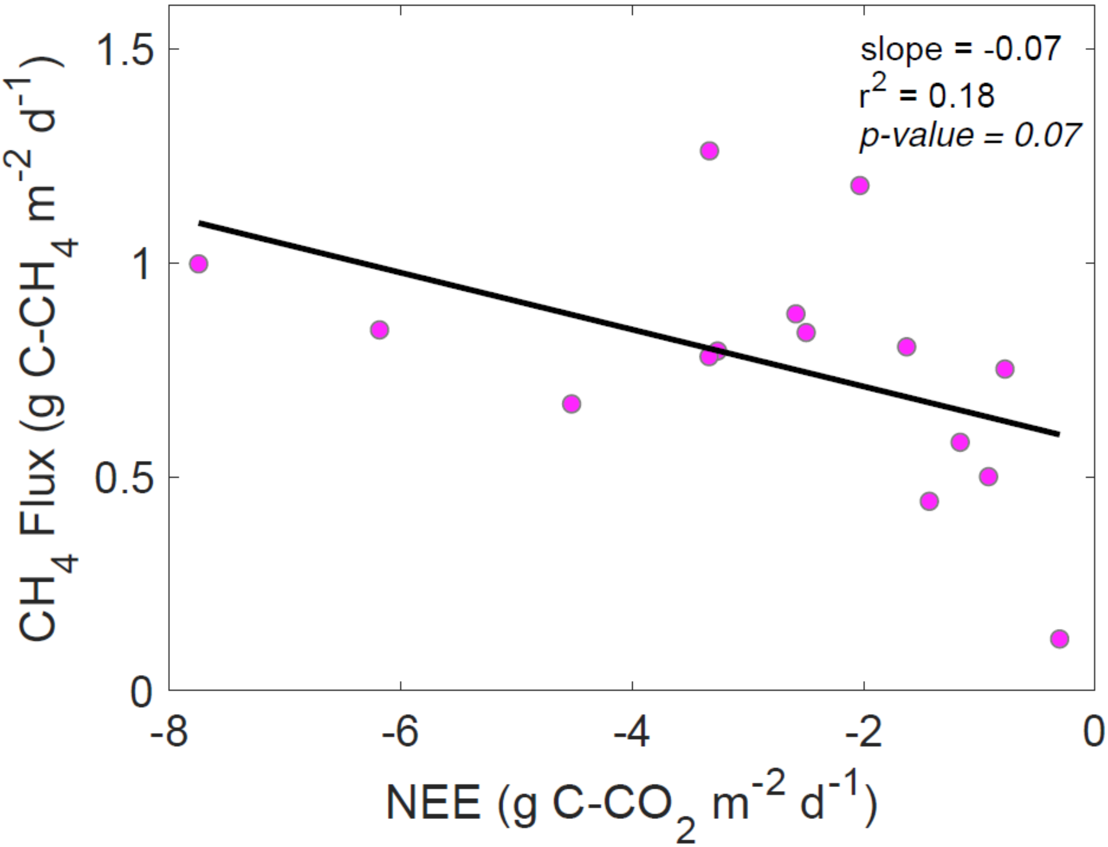

Figure 4. Scatterplot of diel CH_4 flux as a function of diel net ecosystem productivity (NEE). Data correspond to 24-hours averages of CH_4 fluxes and *NEE*, considered only day were at least 12 nighttime and 12 daytime half-hourly observations (without gap-filling) were available for both CH_4 and CO_2 fluxes.

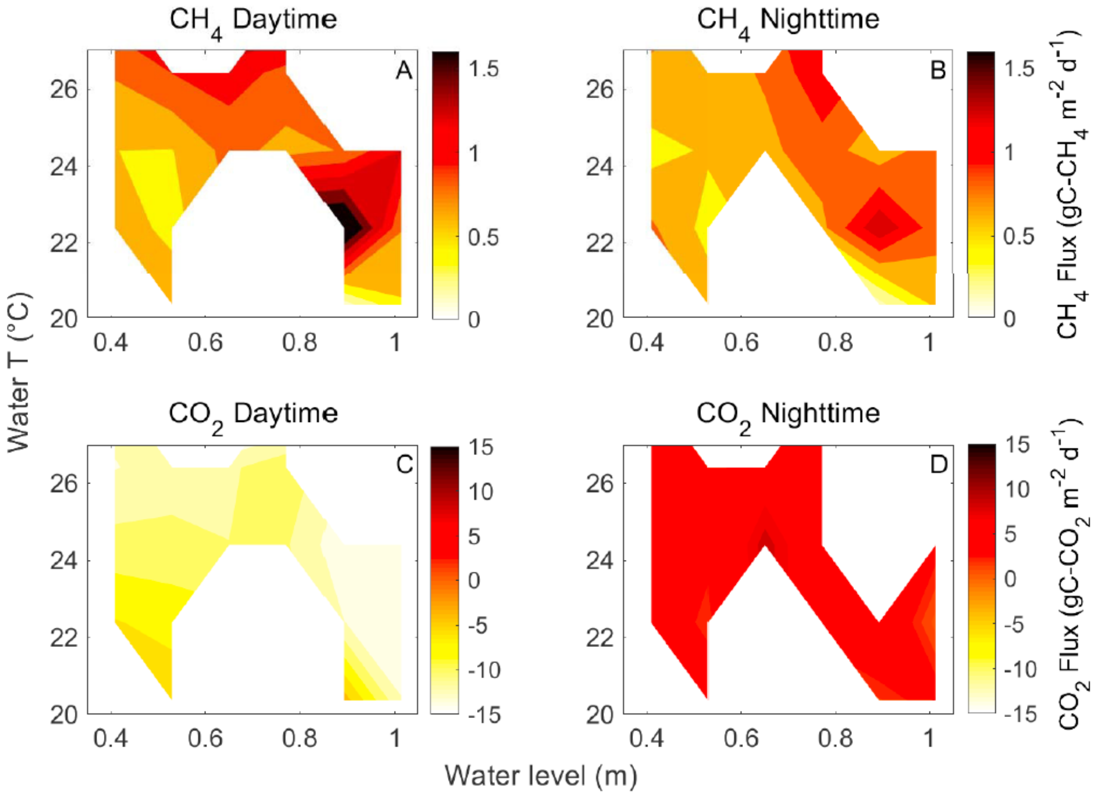

Figure 5. CH$_4$ (A and B) and CO$_2$ (C and D) as a function of water levels and water temperature during daytime and nighttime. Data correspond observations when daytime or nighttime periods had at least 8 half-hourly paired records of CH$_4$ and CO$_2$ fluxes.

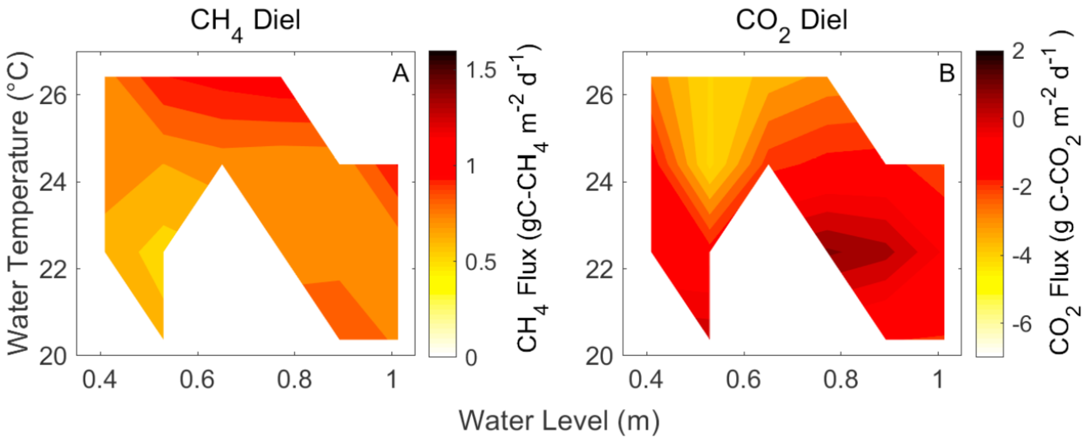

Figure 6. Diel CH_4 and CO_2 fluxes as a function of water levels and water temperature. Data correspond to averages of gap-filled fluxes but only include days that had at least 6 half-hourly paired observations during both daytime and nighttime period.