

Partitioning Water and Vegetation CO₂ and CH₄ Fluxes from Eddy Covariance in a Restored California Wetland

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ABSTRACT

Wetland restoration can potentially reduce carbon emissions in California and worldwide. Carbon fluxes vary spatially in wetlands, so developing a mechanistic spatially dependent understanding of emissions can help model, manage, and scale up local measurements. To better understand the role of vegetation vs. open water in controlling wetland carbon fluxes, we measured CH₄ and CO₂ fluxes using the eddy covariance method at multiple locations within a restored wetland located in the Sacramento San-Joaquin delta. Using a flux footprint model and aircraft imagery, we modeled the variability in fluxes according to the vegetated fraction and other variables. For the CO₂ model we found percent vegetation and air temperature are important ($R^2=0.28$). For the CH₄ model we found percent vegetation, soil temperature, latent heat flux, and conductivity are important ($R^2=0.69$). We extrapolated the percent vegetation factor to zero to model fluxes from the water alone. The average modeled water CH₄ flux was 53 ± 1.0 nmol m²s⁻¹ and the average CO₂ flux was 0.13 ± 0.11 μmol m²s⁻¹, accounting for approximately 33% of CH₄ and 7% of average nighttime CO₂ fluxes between July 23, 2014 and September 30, 2014. Our findings suggest that vegetated areas account for a majority of carbon fluxes within a restored wetland. CO₂ fluxes from the water were near zero and CH₄ fluxes from the water were relatively small but not negligible for the wetland's carbon budget. We also conclude that wind-speed based water carbon flux estimates should be used with caution in wetland systems due to flux dependence on many other environmental factors.

KEYWORDS

Sacramento San-Joaquin Delta, Carbon Flux, Carbon Modeling, Open Water, Wetland Management

INTRODUCTION

Wetlands have shown strong potential for carbon sequestration (Kayranli et al. 2010). Some agricultural land in the Sacramento-San Joaquin Delta (the Delta) was recently converted into a restored wetland to test its ability to offset California's greenhouse gas emissions. In order to quantify the potential impacts of restored wetlands, measurements of carbon fluxes have been made over a portion of the wetland (Knox et al. 2014). However, understanding the spatial and temporal variation of carbon fluxes in wetlands is important in order to understand the fluxes from the whole system (Matthes et al. 2014).

Geographic location, meteorological conditions, and many other factors can affect the magnitude of carbon fluxes in and out of an ecosystem (Pielke 2005). Specifically, wind speed, dissolved gas concentration, and temperature are often used to calculate gas exchange between open water and the atmosphere (Wanninkhof 2014). Water-atmosphere exchange is of particular interest to wetland ecosystems because up to 50% of global methane fluxes come from wetlands (Whitling and Chanton 1993) due to decomposition in the soil under the flooded, anaerobic conditions. Methane emissions are especially relevant to climate change because methane has a warming potential about 25 times higher than that of CO₂ on a 100-year timescale (IPCC 2014). Despite these substantial carbon sources, restored wetlands appear to be beneficial for carbon sequestration in comparison to drained peatland agriculture (Knox et al. 2014). However, the contributions of open water and vegetation to these fluxes are not fully understood. Further understanding of the spatial variability of the fluxes could provide valuable insight to best management practices and future restorations to maximize carbon uptake.

In order to understand the magnitude and mechanisms of carbon exchange, we took continuous eddy covariance (EC) measurements at the Mayberry wetland in the Delta. At the Mayberry site, there is one permanent and one temporary eddy covariance tower that measure gas fluxes over a portion of the wetland. EC relates 3D wind speeds and concentration measurements to measure CO₂ and CH₄ fluxes (Baldocchi 2003). Measurements are scaled by multiplying the total area of the wetland by the rate of emission and/or uptake of gas per meter squared. To improve this estimate, it would be beneficial to understand spatial variability caused by the irregular distribution of vegetation. The site consists of regions of aquatic vegetation and patches of open water that have high concentrations of carbon relative to the atmosphere. This concentration

gradient may mean that the open water is a significant source of carbon (Wanninkhof 2014). Measurements have been made over open water areas elsewhere in the world such as at a boreal lake in Finland (Vesala 2006), and models have been constructed to estimate variability specifically in the Mayberry wetland (Matthes 2014). However, no attempts have been made to use EC to calculate wetland water fluxes. Separating the fluxes from water and the fluxes from the vegetated areas would help clarify of the sources of methane and carbon dioxide and therefore help in scaling and management of the wetland.

The basic question of the research was: How does open water influence the spatial variability of CO₂ and CH₄ fluxes in a Delta wetland? To help answer this question, the following subquestions are addressed: a) What is the theoretical flux of CO₂ and CH₄ from open water? b) How well can wetland fluxes be modeled from half hourly carbon flux data? c) Using the modeled data, how does the theoretical flux match the predicted flux from water? Using EC data from three different locations in the Mayberry wetland, we try to capture some of the spatial variability by sampling areas of close to 0% to nearly 100% vegetation cover. From percent vegetation and other site variables, we model carbon fluxes and use the model to estimate open water carbon fluxes. We then calculate theoretical fluxes from a widely used empirical model (Wanninkhof 2014, Cole 2010) to compare our own estimates to an accepted method.

METHODS

Study Site

The Mayberry wetland is the study site for this research. It is a restored wetland located on Twitchell Island at the west end of the Sacramento-San Joaquin Delta in Northern California and is managed by the California Department of Water Resources (DWR). Until 2010 when the land was flooded as part of a restoration project, the site was a peatland pasture that was largely dominated by *Lepidium latifolium* L. (pepperweed). Mayberry is approximately 3 meters below sea level but the water has very low salinity. The site consists of open water and highly irregular regions of aquatic vegetation (Figure 1). The vegetation at the site is almost entirely *Schoenoplectus acutus* (tule) and *Typha latifolia* (cattail). The study period is July 27 – September

30, 2014 because this corresponds to growing season for the vegetation at the wetland and is after an invasion of caterpillars destroyed much of the vegetation at and around all three tower locations.

Caterpillars ate much of the vegetation at the low vegetation site in mid-July, which may have caused uncommon fluxes at that site. Fluxes decreased over the course of a few days due to lower vegetation activity. To limit the impact of the caterpillars on the study, we only used data after the change occurred. Some sources of data were limited before this period, so the later period was used.



Figure 1. Mayberry Wetland Map. A Google Earth image of the Mayberry wetland and the San Joaquin River taken in June 2014 with the three tower locations and an arrow indicating the average wind direction. The Medium Vegetation location is the permanent tower. The other tower is moved approximately every two weeks between the High Vegetation and Low Vegetation locations.

Fluxes and Environmental Measurements

To measure CO_2 and CH_4 fluxes we used eddy covariance at three locations with two towers. Eddy covariance is a technique that uses the covariance between vertical wind speed and

trace gas concentrations measured at high frequencies to calculate gas fluxes from an upwind region (Baldocchi 2003). One tower was moved between two locations within the site approximately every two weeks and the other tower was fixed in place. The location of the permanent tower was chosen to have a representative sample area of the wetland. The two portable tower locations were chosen to sample areas of high and low vegetation cover. The locations of the towers are shown in Figure 1 and will be referred to as “Low Veg,” “Medium Veg,” and “High Veg” although there are only two towers for the three locations. Both towers are equipped with a sonic anemometer, Gill WindMaster WM-1590; Gill Instruments Ltd, Lymington, (Hampshire, England) to measure 3D wind speeds and an open path infrared gas analyzer, LI-7500A; LI-COR Biogeosciences, (Lincoln NE, USA) to measure CO₂ molar concentrations. Each tower also has a LI-7700; LI-COR Biogeosciences, (Lincoln NE, USA) to measure CH₄. The sonic anemometer uses short sound pulses and a known path length between the emitter and detector of the sound to calculate the wind speed at 20 Hz. The gas analyzers detect the absorbance of infrared light at certain wavelengths that increases with the concentration of CO₂ and CH₄ respectively. This allows CO₂ and CH₄ concentration measurements to also be made at 20 Hz. We collected data at the sites using a digital data logger system (LI-7550A; LI-COR Biogeosciences, Lincoln NE, USA) and retrieved the data about every two weeks. We subsequently calculated half hour average fluxes using in-house MATLAB processing code.

Water Carbon Concentrations

To determine water CO₂ and CH₄ concentrations we used a continuous Forerunner CO₂ probe and intermittent grab samples. The forerunner probe measures half hour average air-equivalent CO₂ concentrations in the open water near the permanent tower. We took water samples in the open water in the sample area (footprint) of the low, permanent, and high vegetation towers. We analyzed the CO₂ and CH₄ concentrations of the samples in the lab using a Los Gatos Research (LGR) gas analyzer. We mixed nitrogen gas and the water until the CO₂ and CH₄ concentrations in the water equilibrated with the nitrogen gas. That gas mixture was then run through the LGR analyzer and the peaks were integrated using in-house MATLAB processing code to measure CO₂ and CH₄ concentrations in the gas. Then, using Henry’s law, we calculated the initial carbon concentration in the water.

We only used the probe data for CO₂ concentrations at the Medium Veg location. All other CO₂ and all CH₄ water concentrations are from the grab samples. If more than one sample was taken at a location at one time, the average of those samples was used.

Imagery

To determine vegetation cover for different tower footprints, we used images taken during a contracted fly-over of the Delta on August 15th, 2014. The imagery has 15cm spatial resolution for three bands in the visible range and one in the infrared (IR). Classified maps that indicated vegetated pixels were generated by Dr. Iryna Dronova using object-oriented rule-based classification in eCognition software (Trimble Inc.). Pixels were first classified by using a normalized difference vegetation index (NDVI) threshold and were then manually corrected. Errors in classification are small due to the high resolution of the image and the clear difference between water and vegetation in the four available spectral bands. We then reduced the image resolution to 30cm to decrease processing times by averaging four pixels into one. A comparison of pre- and post-reduction showed very low differences in percent vegetation calculations.

Footprint Model

We calculated the footprint for each half hour measurement from eddy covariance data using a two dimensional footprint model (Hsieh 2000, Detto et al. 2006). The inputs to the footprint model are the friction velocity (u^*), the Monin-Obakov stability length scale (L), the average wind speed (u), tower height (z), zero plane displacement (d_0), wind direction, and the standard deviation of the crosswind velocity. The model assigns a fractional source weight to each pixel in the aerial image during a given half-hour interval. The footprint was truncated at the edges of the image since the footprint gets very large as the flux contribution approaches 100%. The output of calculated probabilities was then overlaid onto the imagery to calculate a percent vegetation cover for each half-hour time period (Figure 2).

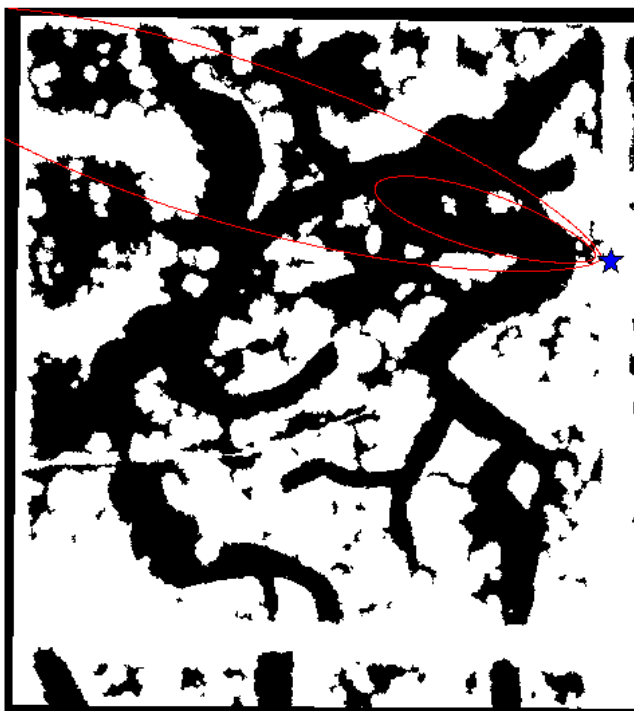


Figure 2. Aerial image of low veg location with footprint contour. An aerial image of the low vegetation location in the Mayberry wetland. Black is open water and white is vegetation. Sample 50% and 80% footprint contours from August 15th, 2014 show that a large fraction of the footprint falls in open water.

Data Filtering

We imposed several constraints on the data that we used for the analysis to ensure that only relevant points were used. Analyzed data was constrained to periods of carbon loss; thus CH₄ flux data was analyzed during all times of day but CO₂ flux data was limited to nighttime periods (zenith angle > 90°). We used average half-hour wind directions between 190 and 330 degrees from North because the towers' locations were chosen based on prevailing winds, which are largely dominated by these directions. For the medium vegetation tower, we used 235 degrees as the minimum instead of 190 because a berm in the footprint at lower wind directions is neither vegetation nor open water. Any footprints with less than 70% source footprint within the image were excluded from the study. For the CH₄ points, any negative fluxes were excluded due to the log transform performed in the model. However, this is a very small number of points (11 of 4239). Lastly, we only used points that met the condition: $-0.1 < z/L < 0.1$, where z is the height of the

sonic anemometer and L is the Monin-Obukov length. A z/L value near zero indicates a neutral boundary layer, which is an assumption of the footprint model.

Analysis

We performed a log transform to model methane data because without the transform we observed heteroschedasity between modeled and observed values. Methane emissions from wetlands are known to often have a lognormal distribution (Whalen 2005).

In order to account for multiple environmental factors that affect carbon fluxes we constructed multivariate models for CH_4 and CO_2 fluxes. We tested multiplicative and additive models:

$$F = \prod_{i=1}^n \beta_i^{X_i} \quad (1)$$

$$F = \beta_1 + \sum_{i=2}^n \beta_i \cdot X_i \quad (2)$$

where F is the carbon flux, β are empirical coefficients, and X are environmental variables.

Many variables were included initially and only statistically significant terms that improved the R^2 by at least 0.03 were retained in the final models. The tested environmental variables were: wind speed, air temperature, conductivity, soil temperature, latent heat flux, sensible heat flux, percent vegetation, percent of footprint in the imagery, atmospheric pressure, relative humidity, photosynthetically active radiation (PAR), normalized difference vegetation index (NDVI), and footprint-weighted NDVI.

To validate the models and calculate statistics, we randomly selected half of the Low and High Veg points and 500 of the medium veg points to create a best-fit model. We used a set number of points from the medium vegetation location to avoid oversampling because many more points were available from this location during the study period. We then calculated modeled fluxes from the points not used in the creation of the model. This was repeated 100 times for each model. Reported R^2 values and their standard deviations are the average and standard deviation of these 100 repetitions.

We found that the multiplicative model with soil temperature (Soil T), percent vegetation (%Veg), latent heat flux (LE), and conductivity (Cond) best represented CH_4 fluxes and the

additive model with air temperature (Air T) and percent vegetation (% Veg) best represented CO₂ fluxes. Lastly, because we found that the influence from vegetation saturated in the CH₄ model, we included a hyperbolic function for the percent vegetation. This saturation relationship cannot be achieved with the same multiplicative formulation because relationships are constrained to be convex. The additive β_2 term in the numerator of the hyperbolic relationship was included so that fluxes would not be zero when percent vegetation is set to zero to model water fluxes. The final models used were:

$$\log F_{CH_4} = \frac{\beta_1 \cdot \beta_2 \cdot \%Veg + \beta_1}{\beta_1 \cdot \%Veg + \beta_2} \cdot \beta_3^{SoilT} \cdot \beta_4^{LE} \cdot \beta_5^{Cond} \quad (3)$$

$$F_{CO_2} = \beta_1 + \beta_2 \cdot AirT + \beta_3 \cdot \%Veg \quad (4)$$

The β values for (3) are: $\beta_1 = 9.1504$, $\beta_2 = 3.6769$, $\beta_3 = 1.0244$, $\beta_4 = 1.0005$, $\beta_5 = 0.9815$

The β values for (4) are: $\beta_1 = -3.8072$, $\beta_2 = 0.2005$, $\beta_3 = 3.1132$

In order to model water fluxes, we excluded latent heat flux from the model, found the empirical coefficients using the same method as above, and then set percent vegetation to zero. Latent heat flux was excluded due to its dependence on vegetation so when setting vegetation to zero, it is no longer physically relevant to include latent heat flux. Therefore, instead of equation (3), we use:

$$\ln F_{CH_4} = \frac{\beta_1 \cdot \beta_2 \cdot \%Veg + \beta_1}{\beta_1 \cdot \%Veg + \beta_2} \cdot \beta_3^{SoilT} \cdot \beta_4^{Cond} \quad (5)$$

The β values for (5) are: $\beta_1 = 6.6567$, $\beta_2 = 3.2130$, $\beta_3 = 1.0342$, $\beta_4 = 0.984$

We compared our modeled water fluxes derived from eddy covariance to a theoretical formula for gas exchange over open water using the measured water concentrations (Cole et al. 2010, Cole and Caraco 1998). The formula is:

$$F = 2.07 + 0.215 \cdot U_{10}^{0.17} \Delta pC \quad (6)$$

Where U_{10} is the wind speed at a height of 10 meters, Sc is the Schmidt number of the gas at the current temperature, and ΔpC is the gradient of partial pressures of CO₂ or CH₄ between the air

and the water (in ppm air equivalent). The sonic anemometers on the towers are at heights substantially lower than 10 meters, so U_{10} was calculated from the theoretical log-wind profile:

$$U_{10} = \bar{u} \cdot \frac{\log\left(\frac{10}{z_0}\right)}{\log\left(\frac{z}{z_0}\right)} \quad (7)$$

where \bar{u} (ms^{-1}) is the mean wind speed, z (m) is the height of the sonic anemometer above the ground, and z_0 (m) is the roughness length. Atmospheric conditions for this extrapolation were approximately neutral.

RESULTS

Site Characterization

Both the in-situ probe and the grab samples indicated that CO_2 and CH_4 concentrations were consistently higher than atmospheric concentrations at all locations. The CO_2 concentrations measured from the grab samples were consistently within the range of the probe CO_2 measurements (Figure 3).

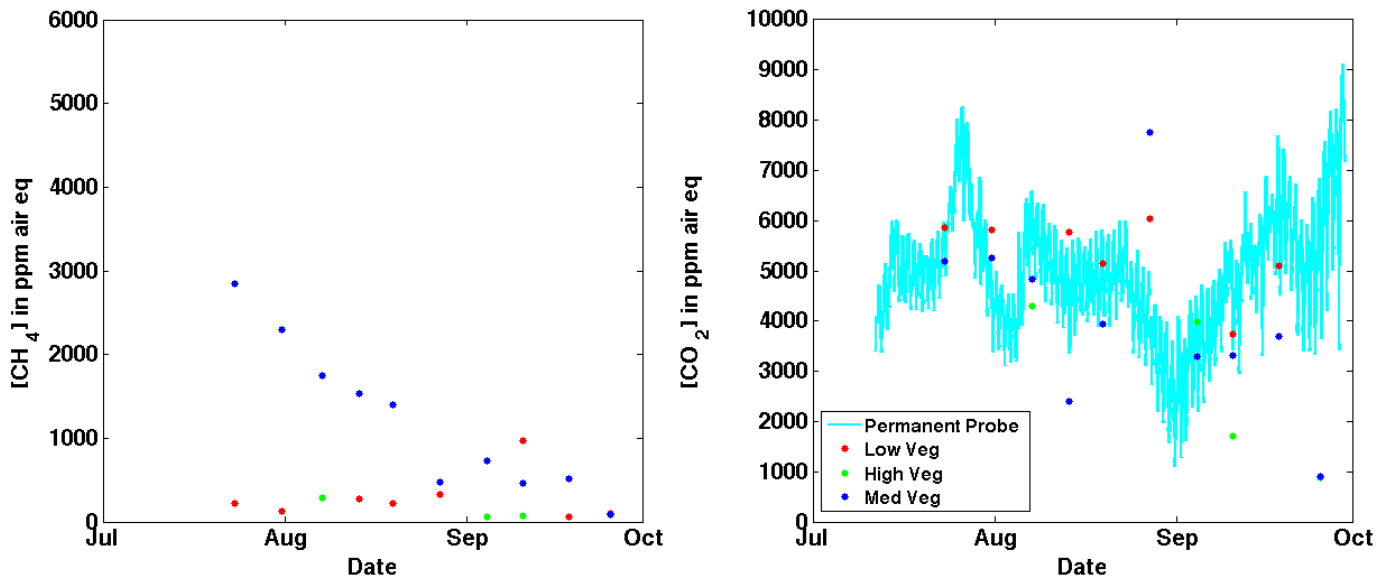


Figure 3. Water carbon time series. Forerunner in-situ probe and grab sample CO_2 concentrations in ppm air equivalents in 2014. The green and red points indicate grab sample data from the medium veg and low veg sites respectively. The CO_2 points fall generally in the range of the probe.

Over the course of the study period, aqueous CH₄ concentrations ranged from 126 to 4820 ppm in air equivalent and varied substantially between sites. The Low Veg and High Veg locations both generally had lower CH₄ concentrations than the Medium Veg location, especially during the earlier period of the study. The aqueous CO₂ concentrations ranged from 2704 to 5904 ppm in air equivalents and were consistent between locations. The largest source of temporal variability was the diurnal cycle, which caused fluctuations of about 1000-2000 ppm (Figure 3).

CO₂ fluxes measured from eddy covariance showed diurnal variation with uptake during the day and emission at night. This pattern corresponds to daytime photosynthesis and plant growth and nighttime respiration (Figure 4). In late July, there was an abrupt drop in uptake that corresponds to a large number of caterpillars eating the vegetation. The low vegetation location showed little uptake relative to other sites because less vegetation implies less photosynthesis. The High Veg location had very similar uptake to the Medium Veg location despite having a higher percentage of vegetation cover. This was probably due to the older vegetation at the High Veg location. Since the study period was at the end of the growing season (late July – late September), CO₂ flux generally decreased during this time.

CH₄ fluxes measured from eddy covariance show emissions of CH₄ during all times of day with very few exceptions (Figure 4). Like CO₂, CH₄ fluxes decrease during the study period. However, the temporal variations are smaller than for CO₂.

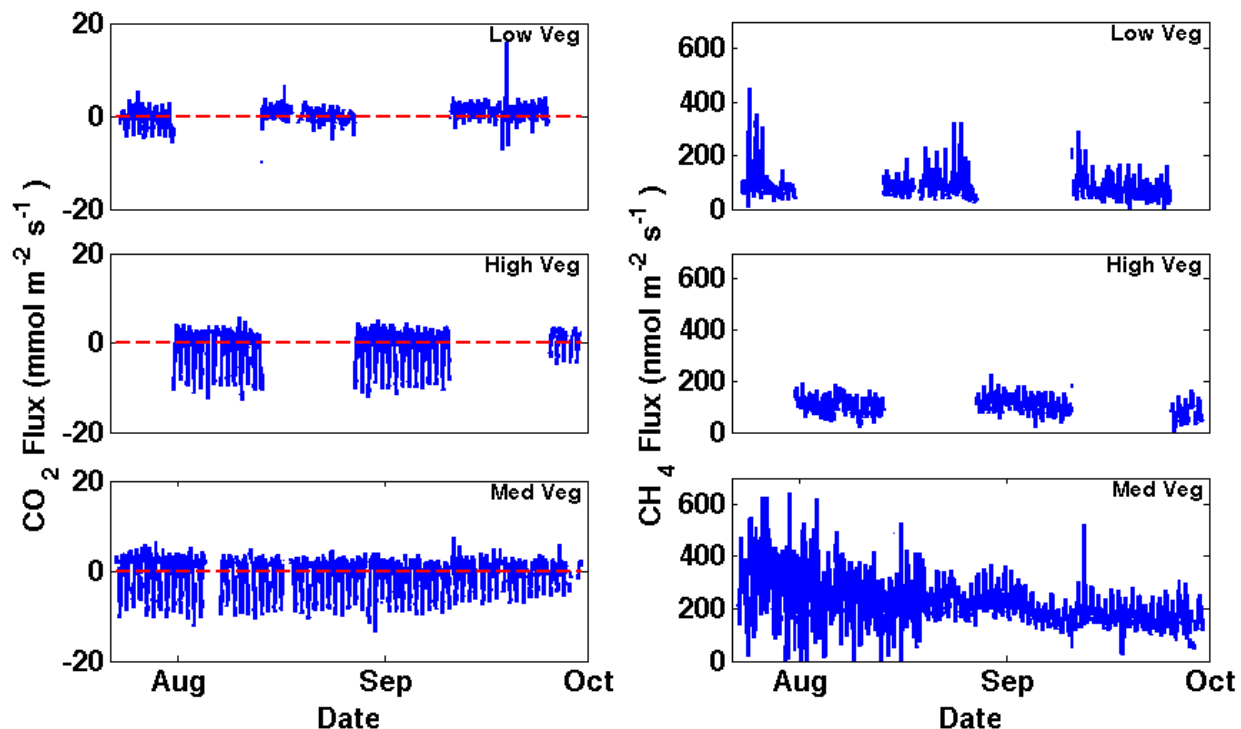


Figure 4. Timeseries of eddy covariance measurements at each location in the wetland. The CO_2 and CH_4 for each location are shown. The gaps in the low and high veg locations are a result of the tower movement. The dotted red lines are zero CO_2 fluxes. Negative fluxes indicate uptake by the ecosystem.

CH₄ model

The variables used for the CH_4 flux multiplicative model are: conductivity (mili-Siemens), soil temperature ($^{\circ}\text{C}$), latent heat flux ($\text{J m}^{-2}\text{s}^{-1}$), and percent vegetation in the footprint. After 100 simulations, the CH_4 flux model yields an average R^2 of 0.69 ± 0.01 when compared to observations (Figure 5). Soil temperature is the largest explanatory variable in the model although percent vegetation individually explains the largest portion of the variance (Figure 6). The response of conductivity, soil temperature, and latent heat of evaporation are all positive and the response of conductivity is negative (Figure 7). The model predicts the highest fluxes at the medium vegetation location because although it has less vegetation than the high vegetation location, it also had a higher soil temperature. High soil temperatures also account for the few particularly high fluxes at the low vegetation location. No large changes in the trends occur when latent heat is excluded from the model but the R^2 decreases to 0.61 ± 0.01 .

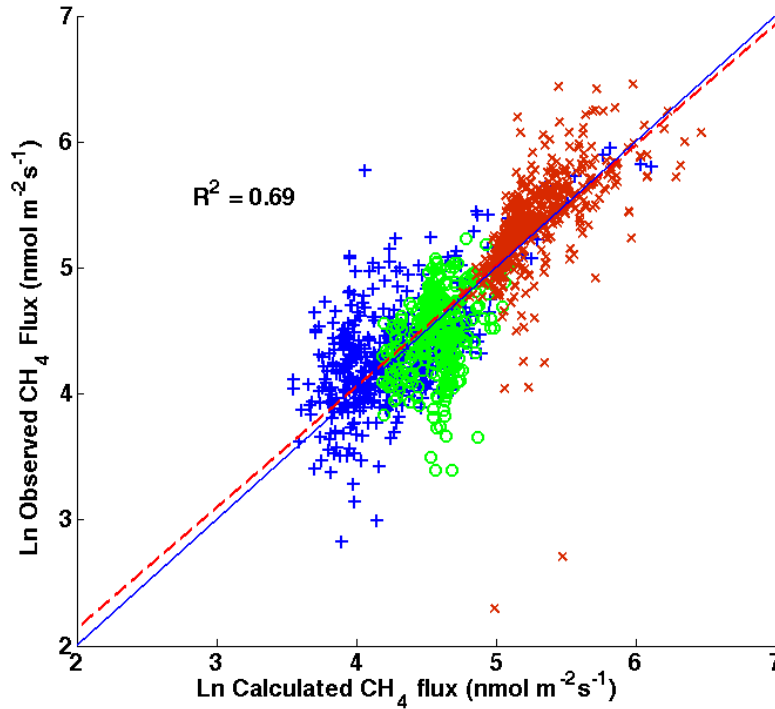


Figure 5. Natural log modeled vs. natural log observed CH₄ fluxes. A model output plotted against observed half-hour CH₄ fluxes with a 1:1 line for reference. The dotted line is the best-fit line. Points from all three locations fall on the 1:1 line ($R^2 = 0.69$).

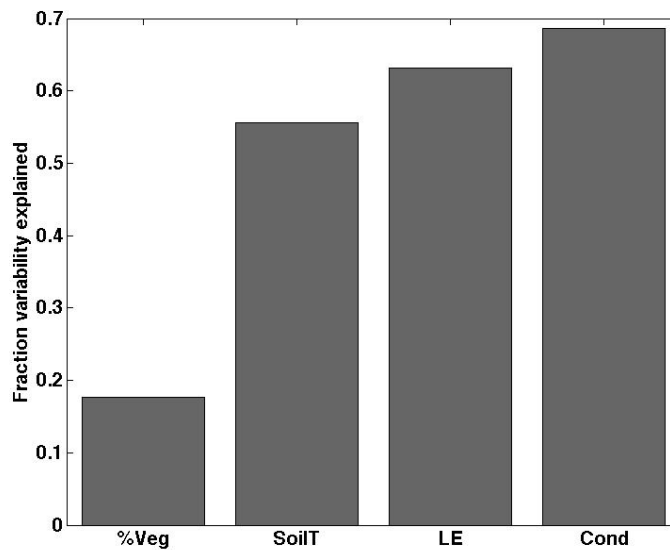


Figure 6. Cumulative response of multiplicative model for CH₄ fluxes. Cond is the conductivity (mili-Siemens), Soil T is the soil temperature (°C), LE is the latent heat flux (J m⁻²s⁻¹), and %Veg is the percent of vegetation in the footprint. Soil temperature has the largest effect when added to the model, but percent vegetation has the largest individual effect.

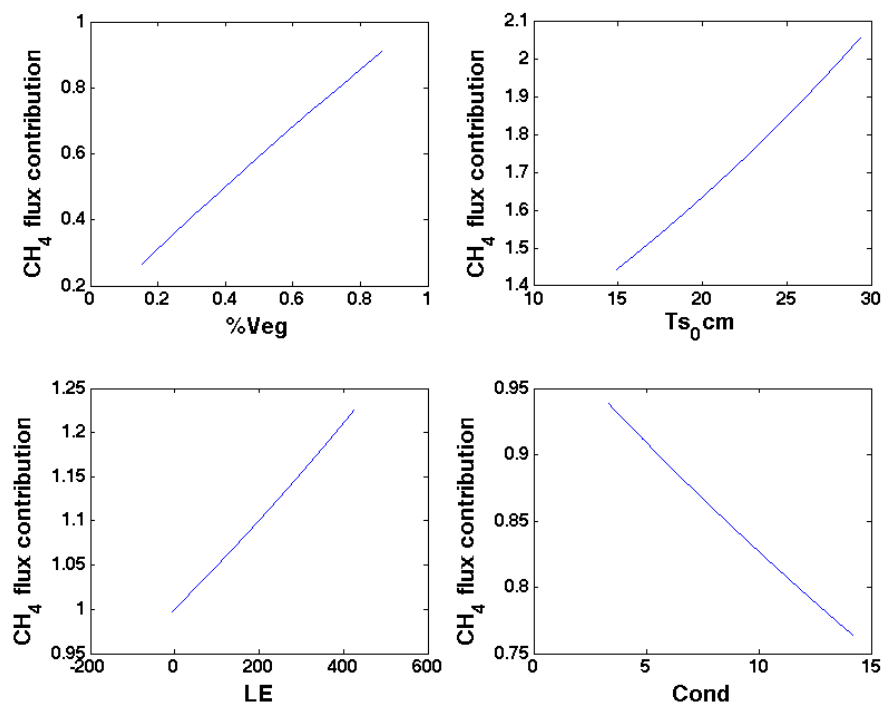


Figure 7. The individual multiplicative response of each variable in the CH₄ model. All responses are positive except conductivity, which has a negative dependence.

CO₂ Model

The variables used for the CO₂ flux additive linear model are percent vegetation in the footprint and air temperature (°C). After 100 simulations, the CO₂ flux model yields an average R² of 0.28±0.02 when compared to observations (Figure 8). Percent vegetation is the largest individual predictor in the model (Figure 9). Unlike we predicted, wind speed did not explain a significant portion of the variance. Much of the variance of nighttime CO₂ fluxes was not explained. This is in part due to negative fluxes observed several times throughout the study period, which cannot easily be explained by any of the environmental variables being considered or concentration gradients at the water-atmosphere interface.

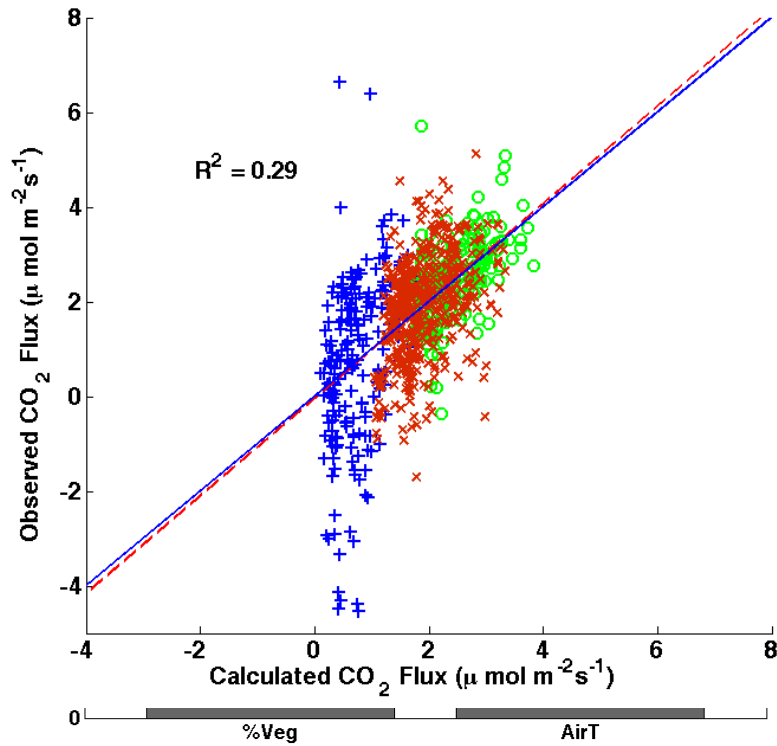


Figure 8. Modeled vs. observed CO₂ fluxes. A model output plotted against observed half-hour CO₂ fluxes with a 1:1 line for reference. The dotted line is the best-fit line. Points from all three locations fall on the 1:1 line ($R^2=0.28$).

Figure 9. Cumulative response of the multiplicative model for CO₂ fluxes. %Veg is the percent of vegetation in the footprint, and AirT is air temperature (°C). Percent vegetation accounts for the most variability.

Water carbon fluxes

After setting %Veg in the CH₄ and CO₂ models to zero, the average modeled water CH₄ flux was $53 \pm 1.0 \text{ nmol m}^2 \text{ s}^{-1}$ and the average modeled water CO₂ flux was $0.13 \pm 0.11 \text{ } \mu\text{mol m}^2 \text{ s}^{-1}$. Fluxes calculated from the theoretical wind-speed model (hereafter labeled “theoretical”) were lower for CH₄ flux but similar for CO₂ flux. From the grab samples, mean theoretical water CH₄ flux was $22 \pm 26 \text{ nmol m}^2 \text{ s}^{-1}$ and the mean theoretical water CO₂ flux was $0.14 \pm 0.08 \text{ } \mu\text{mol m}^2 \text{ s}^{-1}$. The mean theoretical water CO₂ flux from the forerunner CO₂ probe was $0.11 \pm 0.05 \text{ } \mu\text{mol m}^2 \text{ s}^{-1}$. Figure 10 compares average total EC fluxes and modeled water fluxes for each location. Figure 11 shows a time series of the modeled water fluxes (from equations 4 and 5) and the theoretical water fluxes (from equation 6). Diurnal variations from the diurnal temperature pattern can be observed in the time series.

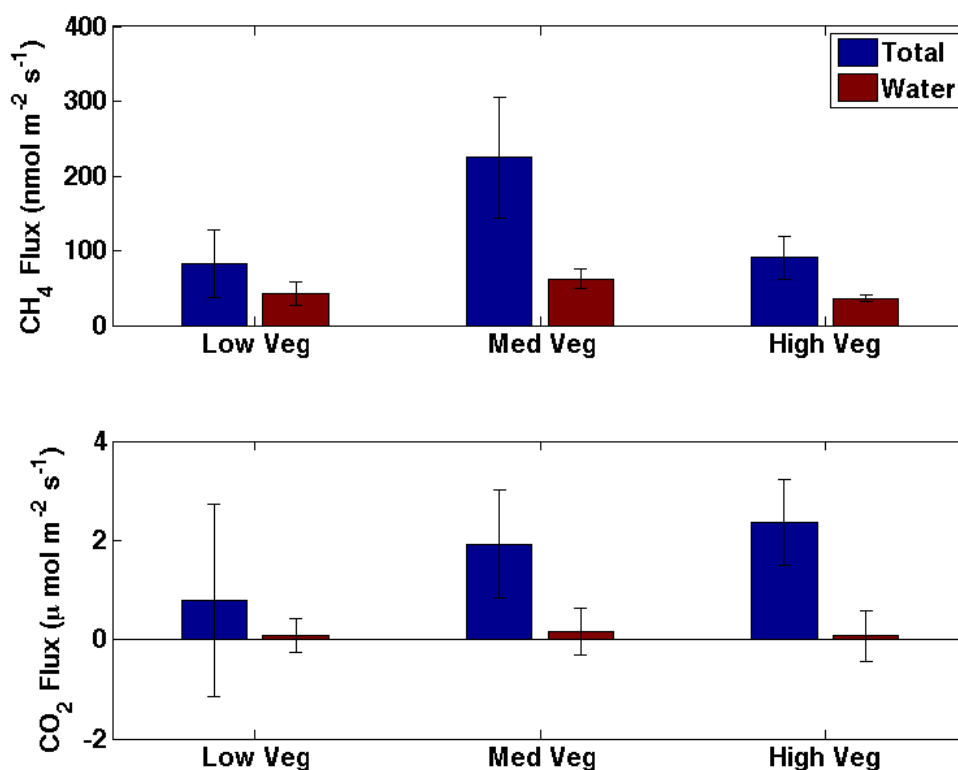


Figure 10. Average total and modeled water fluxes from EC measurements. CH₄ water fluxes are a significant portion of the total fluxes. CO₂ water fluxes are near zero.

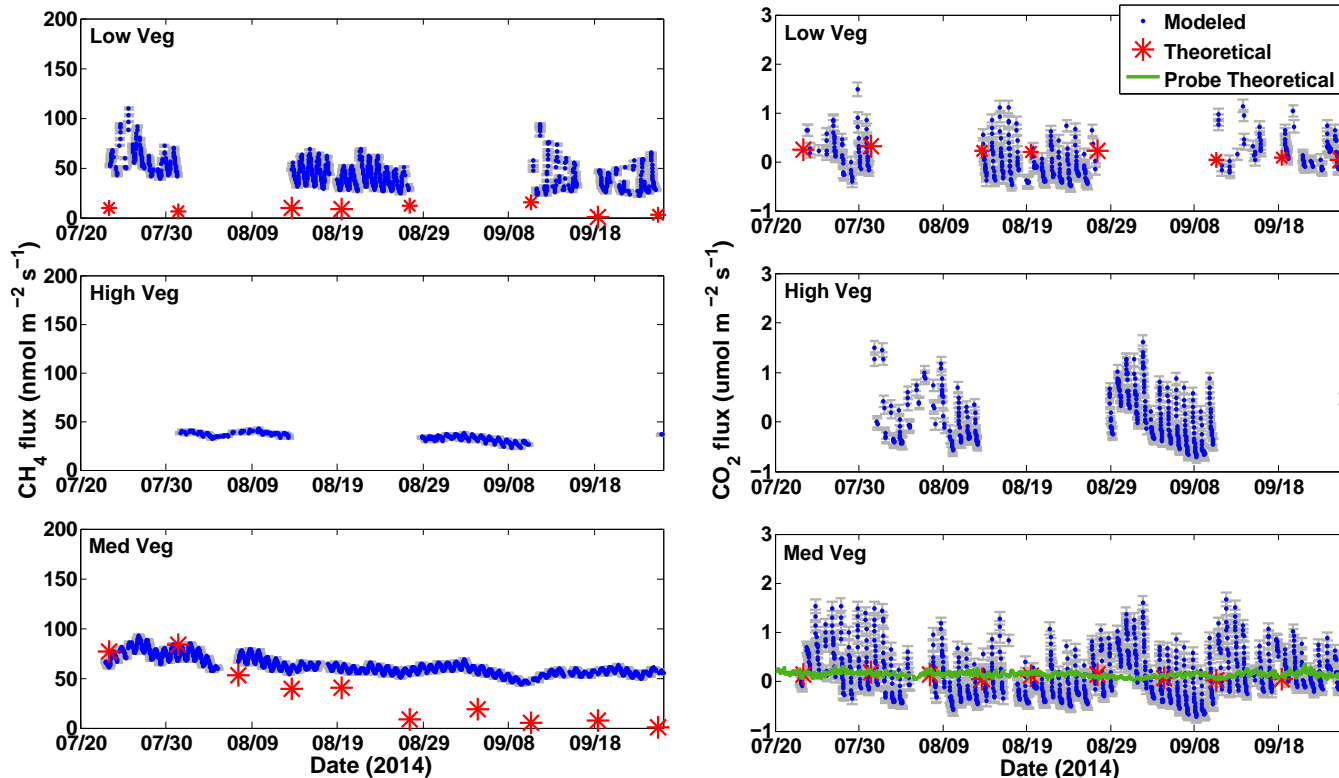


Figure 11. Timeseries of modeled and theoretical CH_4 and CO_2 fluxes. The CH_4 modeled and theoretical fluxes match well while the CO_2 modeled fluxes exhibit large variability around the theoretical fluxes. This is consistent with the large scatter left unexplained in the CO_2 flux model. The light gray errorbars indicate one standard deviation for each point from the 100 model runs. All modeled water carbon fluxes are lower than the total fluxes at the sites.

DISCUSSION

The multiplicative model used for CH_4 fluxes accounts for much of the variance despite many factors that may influence fluxes. The modeled CH_4 water fluxes somewhat match with theoretical calculations, but the modeled CO_2 fluxes are very variable around the theoretical fluxes. CO_2 fluxes are harder to predict but percent vegetation in the EC footprint proves to be a significant parameter. The methane fluxes can be explained well by known factors of plant-mediated transport while the carbon dioxide fluxes are less well understood.

CH₄ Model Parameters

The model parameters determined to be significant for the CH₄ (soil temperature, percent vegetation, latent heat flux, conductivity) have physical significance and compare well to other studies (Matthes et al. 2014). Soil temperature is the most important parameter in the CH₄ model, which agrees with previous studies that have found strong exponential relationships with soil temperature (Christensen et al. 2003; Sachs et al. 2008). This nonlinearity comes from exponential increases in microbe activity with temperature (Dunfield 1993). Although the water at the site has very low salinity, there is a clear negative relationship with CH₄ fluxes and conductivity. This relationship has also been observed in other wetlands and is likely due to inhibited microbe activity (Poffenbarger et al. 2011).

The importance of latent heat in the model suggests that methane is partially controlled by stomata. This is because latent heat exchange increases with more open stomata. Due to this dependence, modeled water fluxes did not include the latent heat term. To further support this hypothesis, we calculated the linear correlation between methane flux and latent heat flux. For daytime data, $R^2 = 0.34$, whereas for nighttime data $R^2 = 0.03$. Similarly, aquatic vegetation mediated control of methane primarily through aerenchyma likely explains the dependence of fluxes on percent vegetation. The roots and stems allow molecular diffusion and bulk flow through the vegetation, which results in CH₄ transport to the atmosphere without oxidation in the water column (Joabsson et al. 1999). However, it is important to note that more vegetation does not necessarily imply more methane flux because canopy shading decreases soil temperature, which suppresses the production of methane.

CO₂ Model Parameters

The significant model parameters for CO₂ fluxes also include positive air temperature and percent vegetation dependencies. The dependence on temperature may be related to decreased solubility at higher temperatures, but correlations are slightly higher for air temperature than water temperature. The importance of air temperature could arise from the presence of aerobic decomposition of the standing dead material. Percent vegetation is a relevant variable because the decomposing vegetation is located in the same area as the live vegetation. Autotrophic respiration

also plays a role because the vegetation sustains itself at night though respiring CO₂. The relationship with percent vegetation is still relatively weak, but this could be due in part to differential effects of caterpillars on different vegetation patches.

Notably, neither wind speed nor aqueous CO₂ concentration are included in the model. Neither was determined to have a significant impact on the fluxes. However, wind speed is a dominant factor in the theoretical calculations that are often used for gas exchange calculation (Wanninkhof 2014; Cole et al. 2010). At the low veg site, which consists of a high percentage of open water, there is a significant negative linear relationship with U₁₀ ($R^2 = 0.22$). However, when combined with temperature and percent vegetation, its contribution becomes very small. Theoretical models used suggest high wind speed leads to high exchange from turbulence and follow a power law relationship with wind speed (Cole and Caraco, 1998). Despite supersaturated water, we found that there were several periods of time with nighttime CO₂ uptake, especially at the low veg site during periods of high wind speed. This negative relationship with U₁₀ and CO₂ fluxes is unlikely to be physically significant and may be due technological errors under specific conditions. Advection could be one of these errors. This is when the stable atmosphere of the surrounding area transports CO₂ into the wetland and is then mixed downward due to the unstable wetland boundary layer. Since the surrounding area produces CO₂ emissions but not significant methane emissions, this theory would also explain why CH₄ levels do not seem to drop during the same time periods. However, the conditions under which the uptake occurs could not be quantified and requires further research.

Modeled vs. Theoretical

It is important to note that neither of the models presented here include wind speed although wind speed has been established as a proxy for increased turbulence and therefore also for increased gas exchange between the water and the atmosphere (Wanninkhof 2014). This theory was originally developed for oceans, not for lakes or wetlands. Our study uses eddy covariance to show that the simple wind speed and concentration gradient models are not sufficient for wetland water carbon fluxes. Important variables, especially temperature, are required to model the true carbon flux from the water in these wetland systems. The high levels of decomposition as well as the addition of vegetative transport differentiate the wetland ecosystem from the ocean enough to

cause substantial differences between the theoretical and modeled carbon fluxes. These differences are more pronounced in the CH₄ fluxes because the water CO₂ fluxes in our system are quite small compared to total fluxes.

Limitations

The caterpillars decreased daytime photosynthesis, but they also may have decreased plant-mediated CH₄ transport. They probably account for some variability, but there are several other limitations that likely contribute to the scatter in the models. The use of a single image for percent vegetation calculations limits our ability to capture temporal variability. However, from regular site visits, we do not think that this is a large source of error. In addition, the study period is fairly short and the image was taken in the middle of the period. Another source of scatter may be the extent of the footprint in the image. Any footprint that was not at least 70% on the image was excluded from the study because the footprint gets very large as the percentage nears 100%. Therefore, some cutoff lower than 100% must be used. The combination of the size of the field site and the micrometeorological conditions lead us to conclude that 70% is a reasonable cutoff because it allows us to keep much of our data while still keeping much of the footprint in the image. The area surrounding the image is not a wetland, so a large footprint can result in errors. When included in the models, however, percent of the footprint in the image was not a significant factor.

Broader Implications and Future Work

Our study provides important knowledge regarding the role of vegetation and open water in controlling spatial variability of wetland carbon fluxes. The proportion of vegetation coverage was the most important factor to consider in modeling CO₂ and CH₄ fluxes, meaning that it is critical for scaling measured fluxes to the entire wetland. In order to manage wetlands for carbon sequestration, there may be an optimal vegetation coverage that maximizes carbon uptake and minimizes CH₄ loss. The largest CH₄ emissions were observed from the Medium Veg location because direct solar heating of the water allowed by the open canopy created higher soil temperatures. Thus, larger patches of closed canopy vegetation that shade the surface may

minimize the CH₄ emissions for the amount of carbon gained. Our analysis also supports previous findings that wetland carbon fluxes are strongly dependent on temperature. Therefore, fluxes are expected to increase as average temperatures increase due to global change.

Future work should expand on the presented models in order to find the optimal proportion of vegetation for carbon uptake by including analysis of daytime CO₂ fluxes. The distribution of vegetation should also be considered because patches of vegetation likely have different effects than large groups of vegetation. A more comprehensive model of both vegetation and water fluxes could be used to scale fluxes to the entire wetland and quantify the effects of expanding restorations to a larger portion of the Delta. The effect of projected temperature increases on wetland CO₂ and CH₄ emissions should also be considered when planning to convert more land to wetlands.

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