Vegetation affects timing and location of wetland methane emissions

Sheel Bansal[1], Olivia Johnson[2], Jacob Meier[1], and Xiaoyan Zhu[3]

[1]U.S. Geological Survey
[2]US Geological Survey Northern Prairie Wildlife Research Center
[3]Jilin Jianzhu University

November 21, 2022

Abstract

Common assumptions about how vegetation affects wetland methane (CH) flux include acting as conduits for CH release, providing carbon substrates for growth and activity of methanogenic organisms, and supplying oxygen to support CH oxidation. However, these effects may change through time, especially in seasonal wetlands that experience drying and re-wetting, or change across space, dependent on proximity to vegetation. In a mesocosm study, we assessed the impacts of on CH flux using clear flux-chamber measurements directly over plants ('whole-plant'), adjacent to plants (where roots were present but no stems; 'plant-adjacent'), and plant-free soils ('control'). During the establishment phase of the study (first 30-days), the whole-plant treatment had ~5-times higher CH flux rates (51.78±8.16 mg-C md) than plant-adjacent or control treatments, which was primarily due to plant-mediated transport, with little contribution from diffusive-only flux. However, high fluxes from whole-plants depleted porewater CH concentrations both directly below whole-plant and in neighboring plant-adjacent treatments, while controls accumulated a highly concentrated reservoir of porewater CH. When the water table was drawn down to simulate seasonal drying, reserve porewater CH from control soil was released as a pulse, equaling the earlier higher CH emissions from whole-plants. Plant-adjacent treatments, which had neither plant-mediated CH transport nor a concentrated reservoir of porewater CH, had low CH flux throughout the study. Our findings indicate that in seasonal wetlands, vegetation affects the timing and location of CH emissions. These results have important mechanistic and methodological implications for understanding the role of vegetation on wetland CH flux.

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Sheel Bansal[1*†], Olivia F Johnson[1†], Jacob Meier[1†], Xiaoyan Zhu[2*]

[1]U.S. Geological Survey, Northern Prairie Wildlife Research Center, 8711 37th St. Southeast, Jamestown, North Dakota, 58401 USA

[2]Key Laboratory of Songliao Aquatic Environment, Ministry of Education, Jilin Jianzhu University, Xincheng St., Dist. 5088, Changchun, 130118 China

**Corresponding author: Sheel Bansal, sbansal@usgs.gov, tel: +1 701 253 5544, fax: +1 701 253 5553*

**Corresponding author: Xiaoyan Zhu, zhuxy0613@126.com, tel: +86 431 84566407, fax: +86 431 84566071*

†these authors contributed equally to the manuscript

Key Points:

- In a mesocosm study, methane (CH_4) flux rates directly over *Typha* were higher than from soils adjacent to *Typha* or from plant-free controls, but only at the beginning of the study during plant establishment.
- Toward the end of the study, a water-table drawdown caused a pulse of CH_4 release from plant-free control soils, which resulted in cumulative CH_4 emissions that were comparable to emissions from directly over *Typha* over the course of the study.

- Combined measurements of CH_4 flux and porewater CH_4 concentrations indicated there was lateral CH_4 transport via roots/rhizomes toward *Typha* from adjacent, non-vegetated locations, leading to relatively low CH_4 emissions from soils directly adjacent to *Typha* plants, which has important methodological implications for measuring CH_4 fluxes.

Abstract

Common assumptions about how vegetation affects wetland methane (CH_4) flux include acting as conduits for CH_4 release, providing carbon substrates for growth and activity of methanogenic organisms, and supplying oxygen to support CH_4 oxidation. However, these effects may change through time, especially in seasonal wetlands that experience drying and re-wetting, or change across space, dependent on proximity to vegetation. In a mesocosm study, we assessed the impacts of *Typha* on CH_4 flux using clear flux-chamber measurements directly over *Typha* plants ('whole-plant'), adjacent to *Typha* plants (where roots were present but no stems; 'plant-adjacent'), and plant-free soils ('control'). During the establishment phase of the study (first 30-days), the whole-plant treatment had ~5-times higher CH_4 flux rates (51.78±8.16 mg-C $m^{-2}d^{-1}$) than plant-adjacent or control treatments, which was primarily due to plant-mediated transport, with little contribution from diffusive-only flux. However, high fluxes from whole-plants depleted porewater CH_4 concentrations both directly below whole-plant and in neighboring plant-adjacent treatments, while controls accumulated a highly concentrated reservoir of porewater CH_4. When the water table was drawn down to simulate seasonal drying, reserve porewater CH_4 from control soil was released as a pulse, equaling the earlier higher CH_4 emissions from whole-plants. Plant-adjacent treatments, which had neither plant-mediated CH_4 transport nor a concentrated reservoir of porewater CH_4, had low CH_4 flux throughout the study. Our findings indicate that in seasonal wetlands, vegetation affects the timing and location of CH_4

emissions. These results have important mechanistic and methodological implications for understanding the role of vegetation on wetland CH_4 flux.

Key words: aerenchyma, carbon, conduit, flux, greenhouse gas, hydrology, invasive, mesocosm, porewater, seasonal, *Typha*

1 Introduction

Wetlands take up carbon dioxide (CO_2) via primary productivity and emit methane (CH_4) via anaerobic decomposition (Segers, 1998). Relative to other ecosystems, wetlands cover only 5–8% of the terrestrial landscape (Mitch & Gosselink, 2007), but play a significant role in climate regulation (Bastviken et al., 2011; Dean et al., 2018). Estimates of wetland greenhouse gas flux and understanding of carbon storage are limited by high uncertainty. This uncertainty is, in part, due to variation attributable to vegetation-effects on CH_4 production, consumption, and transport, which ultimately influence cumulative wetland CH_4 emissions (Carmichael et al., 2014).

1.1 The role of vegetation on CH_4

Production and transport of CH_4 from wetlands are controlled by a series of interacting biophysical mechanisms. Production of CH_4 is dependent on carbon availability, anoxic conditions, soil pH, redox potential, and temperature (Bridgham et al., 2013; Neubauer et al., 2005), while CH_4 emissions are controlled by diffusion, convection, ebullition, and ventilation (Bridgham et al., 2013; Kayranli et al., 2010; Yavitt & Knapp, 1998). Wetland vegetation influences many of these mechanisms. In terms of CH_4 production and consumption, vegetation provides carbon substrates to fuel microbial processes (Christensen et al., 2003). These carbon

substrates are derived from decomposition of dead plant materials or more directly through root exudates (Carmichael et al., 2014; Tittel et al., 2019). However, the lacunar air-ventilation system of many wetland species that supplies oxygen (O_2) to the rhizosphere can also re-oxidize alternative electron acceptors such as sulfate, which inhibits methane production due to microbial competition for carbon substrates (Dalcin Martins et al., 2017; Neubauer et al., 2005; Sutton-Grier & Megonigal, 2011). In addition, plant transport of O_2 stimulates aerobic oxidation of CH_4 by methanotrophic bacteria (Conrad, 2009; Faußer et al., 2012; Laanbroek, 2010). It has been reported that 30–90% of CH_4 produced in the anaerobic environment is oxidized before reaching the atmosphere (Holzapfel-Pschorn et al., 1986). In terms of CH_4 transport, the same air-ventilation system for O_2 also allows porewater CH_4 to diffuse directly from the rhizosphere to the atmosphere, bypassing the hydrologic diffusive barrier along the sediment-water-atmosphere continuum (Bendix et al., 1994; Colmer, 2003; Knoblauch et al., 2015; Laanbroek, 2010). Thus, a large portion of CH_4 released from wetlands has been attributed to plant-mediated transport (Bhullar, Edwards, et al., 2013; Carmichael et al., 2014; Shannon et al., 1996) at rates faster than diffusion through the water column. Clearly there are several interactions and tradeoffs among mechanisms that influence the ultimate role of vegetation in wetland CH_4 emissions. Given these mechanistic links between vegetation and CH_4, it is not surprising that wetland CH_4 flux has been linked to phytomass and net primary productivity (Bhullar, Iravani, et al., 2013; Cheng et al., 2007; Christensen et al., 2003; Turetsky et al., 2014).

1.2 Spatial and temporal considerations on the role of vegetation on CH_4

While many studies have examined individual plant-mediated mechanisms of CH_4 production, consumption, and transport, relatively few studies address how these mechanisms

interact through space and time to influence cumulative CH_4 emissions (Neubauer et al., 2005). For example, transport through macrophyte stems can occur after emergence, during peak growth, and following senescence, albeit the degree of transport is dependent on phenology (J Kim et al., 1999; Yavitt & Knapp, 1998). In contrast, non-vegetated areas of wetlands emit CH_4 through transport processes independent of plant phenology, such as diffusion and ebullition (Chanton et al., 1989), which may occur across different time frames during the growing and non-growing seasons. Plant-mediated transport can deplete porewater CH_4 directly below plants (Shannon et al., 1996), which may create a spatial porewater CH_4 gradient causing lateral CH_4 transport toward plants and away from non-vegetated locations adjacent to plants. This loss of porewater CH_4 adjacent to plants not only affects CH_4 emissions in non-vegetated locations, but also has important implications for the placement of chamber-based measurements of CH_4 flux. A chamber over plant stems captures the combined effects of plant-mediated transport and carbon substrate supply (Hu et al., 2016; Jeffrey et al., 2019; Kankaala et al., 2005; Martin & Moseman-Valtierra, 2015; Milberg et al., 2017), while a chamber adjacent to plants only captures the effects of carbon substrate supply (Lawrence et al., 2017; Picek et al., 2007).

Finally, hydrological dynamics interact with wetland vegetation and CH_4 production, consumption, and transport (Bansal et al., 2018; D Kim et al., 2012). The role of plant-mediated transport may diminish when the diffusion barrier is lost during drying events (Bhullar, Iravani, et al., 2013), which can occur daily in coastal wetlands, or seasonally in ephemerally ponded wetlands. Similarly, the presence of vegetation may enhance recovery of CH_4 following re-wetting through supply of carbon substrates or delay recovery through supply of O_2 (D Kim et al., 2012). Linking these spatiotemporal considerations has important implications for

interpreting and assessing the overall effects of vegetation on wetland CH_4 emissions and will strengthen our understanding and modeling of wetland carbon cycling.

The role of vegetation in CH_4 dynamics is increasingly relevant as wetland plant communities shift, often toward dominant invasive macrophytes such as *Typha* × *glauca*, *Phragmites australis*, and *Phalaris arundinacea* (Bansal et al., 2019; Lawrence et al., 2017; Rey-Sanchez et al., 2018; Zedler & Kercher, 2004), and as practitioners try to balance multiple ecosystems services during management (Badiou et al., 2011; Eviner et al., 2012). The objective of this study was to improve our mechanistic understanding of how emergent vegetation affects CH_4 flux over space, time, and variable hydrological conditions. Specifically, we sought to quantify how CH_4 flux rates change from directly over vegetation compared to adjacent or in plant-free soils, and explore temporal changes in CH_4 flux rates through stages of vegetation and hydrologic phenology in a simulated seasonal wetland mesocosm.

2 Materials and Methods

2.1 Study site and species

The Prairie Pothole Region (PPR) is the largest wetland ecosystem in North America covering over 820,000 km^2 and consists of millions of glacially formed, depressional wetlands (Dahl, 2014). Hydroperiods of PPR wetlands range from ephemeral (~2-weeks) to permanent (year-round) with a majority (87%) of these basins classified as seasonal, emergent wetlands (Dahl, 2014). The seasonality of PPR wetlands is not unique; many wetlands worldwide experience hydrologic drawdown during parts of the year (Galatowitsch, 2012; Kayranli et al., 2010; D Kim et al., 2012). The PPR region is particularly important for migratory bird and

waterfowl habitat, but PPR wetlands are also important to national, continental, and global carbon budgets (Euliss et al., 2006) and have been identified as CH_4 hotspots (Bansal et al., 2016; Tangen et al., 2015). *Typha* is a dominant genus in the region, with a recent expansion of non-native *T. angustifolia* and hybrid *T.* × *glauca* since the 1960s (Ralston et al., 2007; Stewart & Kantrud, 1971). *Typha* can influence soil organic carbon content via litter accumulation (Vaccaro et al., 2009) and can increase soil CH_4 emissions (Lawrence et al., 2017). We chose to use *Typha* in this study not only because of its prevalence in the PPR, but also its ubiquitous distribution in freshwater-wetlands worldwide (Bansal et al., 2019).

2.2 Mesocosms, treatments, and design

We used a mesocosm approach to isolate mechanisms of vegetation effects on CH_4 emissions and avoid confounded sources of variation that occur under field conditions, such as episodic weather events, soil-porosity heterogeneity, and seasonal temperature variability. Mesocosms were established in 40-liter glass aquaria (30 × 50 × 25 cm). Soils for the mesocosms were collected from a wetland at Northern Prairie Wildlife Research Center in Jamestown, North Dakota, USA (46°52'N, 98°38'W). The wetland has a dominant ring of emergent macrophytes (mostly *Typha*) around the edge and open water in the center. The mineral soils of PPR wetlands are classified within the Mollisol order, Aquoll suborder (Soil Survey Staff, 1999). Soils for this study consist of black and very dark grey, silty clay loam of the Parnell series (Soil Survey Staff, 2020). In autumn 2017, following *Typha* senescence, soils were collected from the top 20 cm of sediment where water depth was ~50 cm and stored in buckets under saturated, anoxic conditions. Saturated soils were passed through a 6-mm sieve to remove coarse vegetation and debris, and homogenized. The average soil organic matter was

3.9% and the average % C was 2.9%, which is typical of PPR wetlands (Tangen & Bansal, 2019b). We assumed any low-molecular-weight, labile-carbon substrates from previous plant exudates were consumed before soil was distributed in mesocosms, however non-labile C likely remained (Waldo et al., 2019). Each mesocosm was filled with uniform soil to a depth of 10 cm.

Our experiment consisted of three treatments: 'whole-plant', 'plant-adjacent' and 'control'. In total there were 18 replicates (n=6 per treatment). The 'whole-plant' and 'plant-adjacent' treatments were located within the same mesocosm separated by an acrylic barrier that extended 2 cm into the sediment but not completely to the mesocosm bottom. 'Control' treatments were located in separate mesocosms with no plants (Figure 1). Two control treatments were placed in a single mesocosm with a complete physical barrier between each side. Mesocosms were rearranged in the laboratory periodically to avoid confounding effects of environmental heterogeneity in the laboratory.

Mesocosms were kept in laboratory conditions, with an air temperature ~23° C, and under full spectrum LED lights (KingLED, Shenzhen, China; VYPRx PLUS LED, Fluence Bioengineering, TX, USA). Lights were kept on a 12- to 16-hour photoperiod. Water levels were maintained at approximately 4 cm above the sediment surface except during drawdown (see *Timeline*). An opaque PVC collection-chamber base (diameter = 20 cm) was permanently placed in the center of each treatment for gas flux measurements. Supports were used to keep each base raised above the bottom of the aquarium to allow lateral movement of water and root growth. PVC porewater sampling pipes of 2.5 cm diameter with 1-mm slits around the bottom 2 cm (Geoprobe, Salinas, KS, USA) were installed in all treatments for dissolved gas porewater measurements. Porewater sampling pipes were capped between sampling events. PVC pipes of

5-cm diameter with 1-mm slits around bottom 2 cm were inserted into a subset of two mesocosms per treatment for dissolved-oxygen (DO) probes.

The 'whole-plant' treatments were planted with *T. latifolia* (Roundstone Seeds, KY, USA) seedlings that were germinated in potting soil and reached an approximate plant height of 7 cm. As plants grew, their roots and rhizomes were free to grow into the 'plant-adjacent' treatment of the mesocosm. Shoots that emerged in 'plant-adjacent' treatment were clipped weekly to maintain a roots/rhizomes-only condition. The 'control' mesocosms were maintained plant-free by clipping any germinates from the remnant seed bank. Excessive surface algae were removed manually from all mesocosms when present.

2.3 Timeline

The experiment took place from autumn 2017 to spring 2019, for a total of 400 days. There were five phases related to phenology or hydrological conditions: ~1 month of establishment (days 1–28), ~8 months of growth (days 29–274), ~1 week of surface water drawdown (days 275–286), ~1 week of dry soil (days 287–295), and ~3 months after re-wetting (days 296–400). Each phase had periodic CH_4 flux measurements: establishment (3 rounds of flux measurements), growth (4 rounds), drawdown (2 rounds), dry soil (1 round), and re-wetting (3 rounds). Uptake of CO_2 rapidly increased during the establishment phase as plants grew in height; the growth phase was distinguished from the establishment phase as the point when CO_2 uptake by plants leveled off (Bansal et al., 2020). Dissolved CH_4 was measured in surface water during the establishment, growth, and re-wetting phases, and in porewater during the growth and re-wetting phases. Water levels were maintained at ~4-cm depth throughout the study except during drawdown and dry soil phases. During the drawdown phase, soils were allowed to dry

until the water table was below the sediment surface, with 40–50% volumetric water content (10-cm Hydrosense II, Campbell Scientific, Logan, Utah). We characterized the dry-soil phase by cracks in the soil surface and < 40% volumetric water content. Soils were re-wetted to ~4-cm standing water for the re-wetting phase.

At the conclusion of the experiment, soil samples (~10 g) were collected and analyzed for % organic matter; soils were sieved, dried at 105˚C for 72 hours then 500˚C for 5 hours. A set of sieved soil samples (~10g) were analyzed of % C (combustion method, North Dakota State University Soil Testing Lab). Belowground biomass was assessed in three of the mesocosms with plants to confirm lateral root and rhizome growth from the whole-plant into the plant-adjacent treatments. All soil was rinsed from plant structures, roots and rhizomes were separated, and all material was dried at 60°C for 72 hours. The whole-plant treatment had greater rhizome biomass than plant-adjacent treatment (866.2 g m^{-3} ±235.4 and 289.4 g m^{-3} ±158.8, respectively) and similar root biomass (232.9 g m^{-3} ±35.7 and 176.7 g m^{-3} ±81.7, respectively). While we did not measure root and rhizome growth throughout the study, the first clipping of shoots in the plant-adjacent treatment began within the first 30 days of the study, indicating roots and rhizomes had grown into the plant-adjacent treatment during the establishment phase.

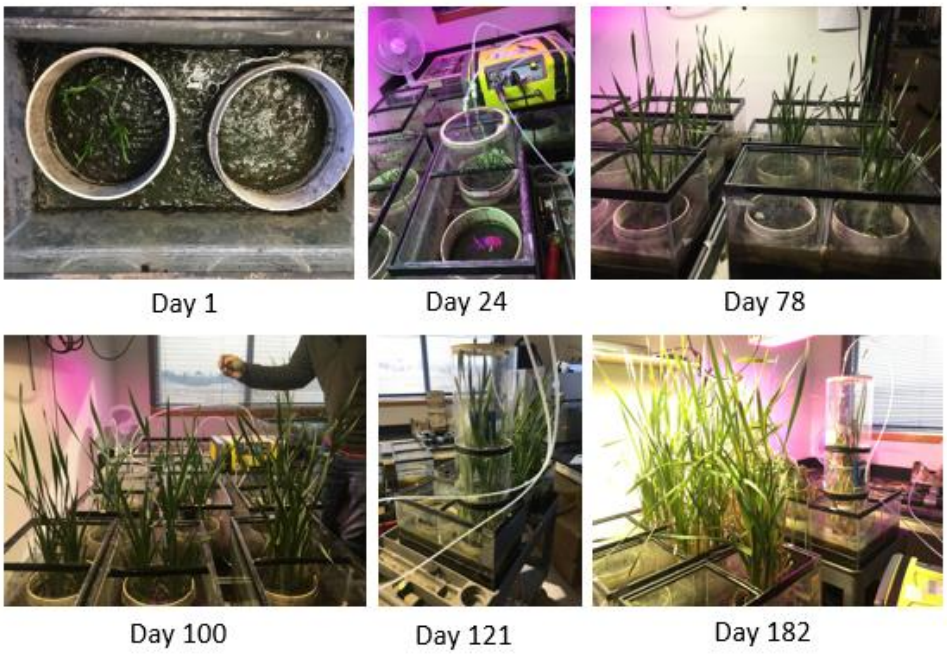

Figure 1. Experimental design and timeline. Day 1 (top left) image shows an example of the whole-plant treatment and plant-adjacent treatment immediately after transplanting *Typha* seedlings.

2.4 Methane-flux measurement, Surface and porewater methane concentrations

CH_4 gas flux measurements were conducted periodically throughout the experiment (see *Timeline*). Gas flux was measured using a closed, static-chamber system with a high-frequency, infrared, gas analyzer (Gasmet DX4040, Gasmet Technologies Oy, Helsinki, Finland). Measured gas flux thus integrates flux due to plant-mediated transport and flux due to diffusion through the water column. Care was taken to minimize disturbance to soil and plants to diminish artificially induced ebullition. Due to our mesocosm and chamber design, determining experimental from natural ebullition was not possible, and measurements indicating ebullition were re-measured. A clear acrylic chamber (diameter = 20 cm, height = 20 to 100 cm, varied with height of plant, Figure 1), with two internal fans to circulate air within the chamber, was placed onto the PVC

base for 10–30 minutes. Air and soil temperature (Fluke 54 II B thermometer, Fluke Co, WA, USA) were recorded during each flux sampling. Flux rates were calculated and checked for appropriate fit using the *HMR* package in R 3.5.1 (Pedersen et al., 2010), which accounts for chamber volume, air temperature, and changes in gas concentrations over time. Surface-water, CH_4 concentrations were used to calculate diffusive flux rates using a k_{600} value of 0.01 (Bansal et al., 2020).

Surface and porewater, dissolved-gas concentrations were measured using the headspace equilibration method (Hope et al., 1995; Jahangir et al., 2012). Duplicate surface-water samples were collected 2 cm below the surface, and duplicate porewater samples were collected from the bottom of the 2.5-cm diameter PVC sampling pipes after evacuation of standing water. Nitrogen gas was added to the sample water at a ratio of 7:5 followed by vigorous shaking for at least three minutes. Headspace gas was analyzed on a gas chromatograph (SRI Instruments, CA, USA), equipped with a flame ionization detector and electron capture detector. Optical sensors (PME minidot, Vista, California) measured continuous DO at 1-hour intervals. Surface-water electrical conductivity and pH (ExStick EC500, Extech Instruments, Nashua, NH, USA) were recorded in February 2018, 2019 and October 2018, with average values of and 2835 ±35 $\mu S\ m^{-1}$ and 8.7 ±0.07 respectively.

2.6 Statistical analyses

We used linear mixed effects analysis of variance (ANOVA) to test the effects of treatment, phase, and their interaction on CH_4 flux rates and dissolved CH_4 concentrations. Mean value of gas flux rates or dissolved gas concentrations across rounds within each phase for each replicate were used in the ANOVAs. In total, there were n=90 values for gas flux rates (18

replicates per phase × 5 phases), 54 values for surface dissolved gas concentrations (18 replicates per phase × 3 phases), and 36 values for porewater dissolved gas concentrations (18 replicates per phase × 2 phases). Replicate was considered a random effect to account for repeated measurements over the course of the study. Least Significant Difference tests were used to compare means among treatments within phases. Data were log-transformed to meet ANOVA assumptions of homoscedasticity of error variance and normality. Analyses were conducted using the *lmertest* package in R 3.5.1 (Kuznetsova et al., 2017), with Kenward-Roger estimates for degrees of freedom, and assessed significance at $\alpha = 0.05$. All mean values are reported as mean ±standard error throughout results.

To model CH_4 flux rates over time (to help separate signal from noise), data were fitted to a mixed general additive model (GAM), with day of experiment, treatment, and their interaction as fixed effects and replicate as a random effect, using the *mgcv* package in R 3.5.1 (Wood, 2017) using a Gaussian family object. The modeled CH_4 flux rates were used to calculate cumulative CH_4 emissions over time for each treatment. It is important to note that day of experiment indirectly accounts for our experimental manipulation of water level (intended to mimic seasonal draw down of temporary wetlands).

3 Results

3.1 Methane flux, Surface and porewater methane concentrations

There were significant effects of treatment, phase, and treatment × phase interaction on CH_4 flux rates (Table 1, Figure 2a). During the establishment phase of the study, the whole-plant treatment had CH_4 flux rates 4–6 times higher than plant-adjacent and control treatments

(Figures 2a). Measured CH_4 flux rates from the whole plant-treatment were 96% greater than calculated diffusive flux rates (calculated using surface CH_4 concentrations), indicating plant-mediated CH_4 transport as the dominant process contributing to measured flux during establishment (Figure 3). The average chamber-measured CH_4 flux rate for control treatment during the establishment phase was 13.18 ±9.35 mg-C m^{-2} d^{-1}, and the average calculated diffusive flux rate was 6.18 ±1.37 mg-C m^{-2} d^{-1}, thus chamber-based measurements had a higher magnitude, but also greater variability (Figure 3). The discrepancy is likely due to sampling differences; for measured emissions, the "foot print" of flux was the entire surface area of chamber area, giving a more integrated measurement that may have also included microbubbles of CH_4 in addition to diffusive flux, as opposed to the two single syringes of water collected from surface water for calculated diffusive flux. Likewise, there is a known time frame over which chamber flux was measured, while the calculated diffusive rate is based on an estimated piston velocity, which is related to tank size and assumed laboratory conditions. Control treatment chamber CH_4 flux rates increased almost three-fold from 13.18 ±9.35 mg-C m^{-2} d^{-1} in the establishment phase to 30.88 ±10.31 mg-C m^{-2} d^{-1} in the growth phase. During the growth phase, all three treatments had similar flux rates (Figure 2a). From the growth phase to the water table drawdown phase, whole-plant treatment CH_4 flux rates declined, plant-adjacent flux rates remained consistent, while control treatment CH_4 flux increased to a rate (432.50 ±9.35 mg-C m^{-2} d^{-1}) that was 14 times greater than during the growth phase (Figure 2a). During drawdown, control flux rates were significantly higher than whole-plant treatment. Finally, during the dry and re-wet phases, CH_4 flux rates were low and similar among treatments (Figure 2a).

The temporal patterns of CH_4 flux rates over the course of the study for whole-plant treatment were relatively high in the beginning and then steadily declined; for plant-adjacent

treatment, flux rates were consistently low; and for the control treatment, flux rates were low in the beginning, peaked in middle, and then low at the end (Figure 4a). This temporal pattern of CH_4 flux rates resulted in relatively high cumulative CH_4 emissions early in the study from the whole-plant treatment, but overall similar cumulative CH_4 emissions between whole-plant and control treatment by the end of the study (Figure 4b). There were much lower cumulative CH_4 emissions from plant-adjacent treatment over the course of the study compared to whole-plant or control treatments (Figure 4b).

Porewater dissolved CH_4 concentrations were significantly affected by treatment, phase and treatment × phase interaction (Table 1, Figure 2b). During the growth phase, porewater CH_4 concentration was lowest in whole-plant treatment, highest for control treatment, and intermediate for plant-adjacent treatment (Figure 2b). All treatments had low and similar porewater CH_4 concentrations during the re-wetting phase. There were no treatment differences in porewater DO concentrations ($F_{2,3}$= 6.02, $p = 0.08$), which were < 1% maximum saturation during the growth phase, increased to ~18% during the drawdown phase, up to 90% during dry phase, and then returned to < 1% after re-wetting.

Table 1. Analysis of variance results from linear mixed effects model testing the effects of treatment, phase, and their interaction on CH_4 flux rates, and surface and porewater dissolved CH_4 concentrations. 'n' represents number of values used each test

	Treatment		**Phase**		**Treatment × phase**		
	F	*p*	*F*	*p*	*F*	*p*	n
CH_4 flux rate	3.79	0.046	24.48	<0.001	6.68	<0.001	90
Surface water CH_4 concentration	3.01	0.080	8.73	0.001	1.81	0.152	54
Porewater CH_4 concentration	7.46	0.006	14.94	0.002	4.63	0.005	36

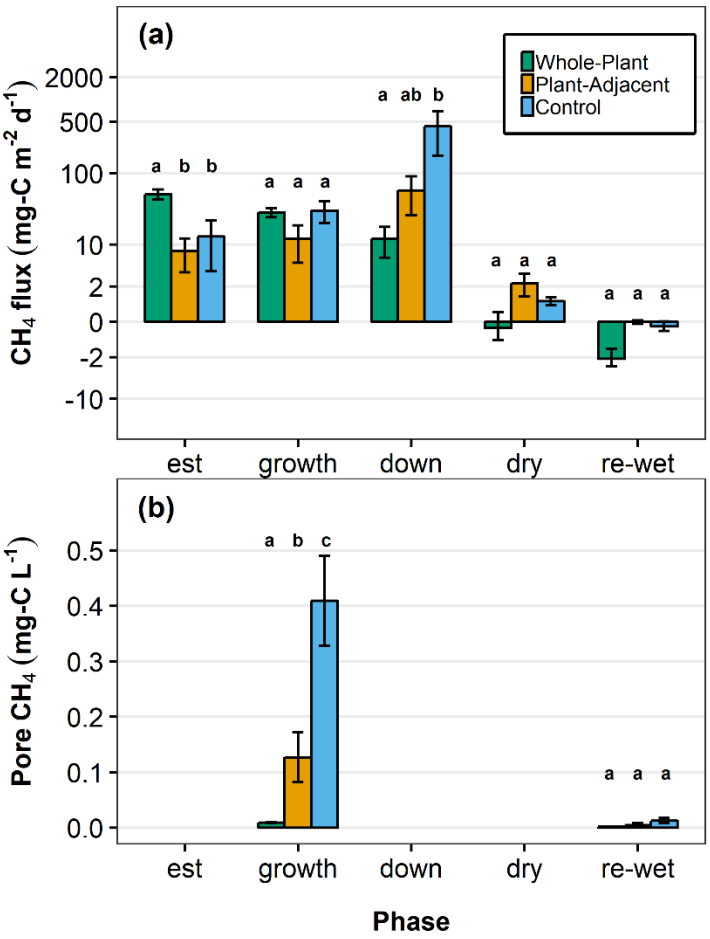

Figure 2. Whole-plant (green), plant-adjacent (orange), and control (blue) treatment means (±SE) of (a) CH_4 flux rates and (b) dissolved porewater CH_4 concentrations within each phase of the experiment. Within each phase, different letters indicate significant differences among treatments (ANOVA results in Table 1). Phases were establishment ('est'), growth, drawdown ('down'), dry, and re-wet. Note the log scale on the y-axis of CH_4 flux rates

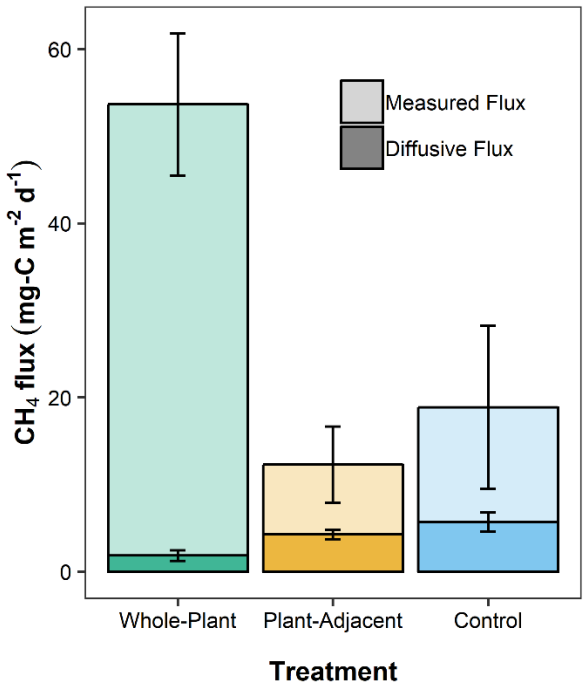

Figure 3. Whole-plant (green), plant-adjacent (orange), and control (blue) treatment means (±SE) of CH_4 flux during the establishment phase (first 30-days); shading indicates measured flux using chamber-based measurements (top lighter bar) and CH_4 diffusive flux calculated using surface water dissolved CH_4 concentrations (bottom darker bar)

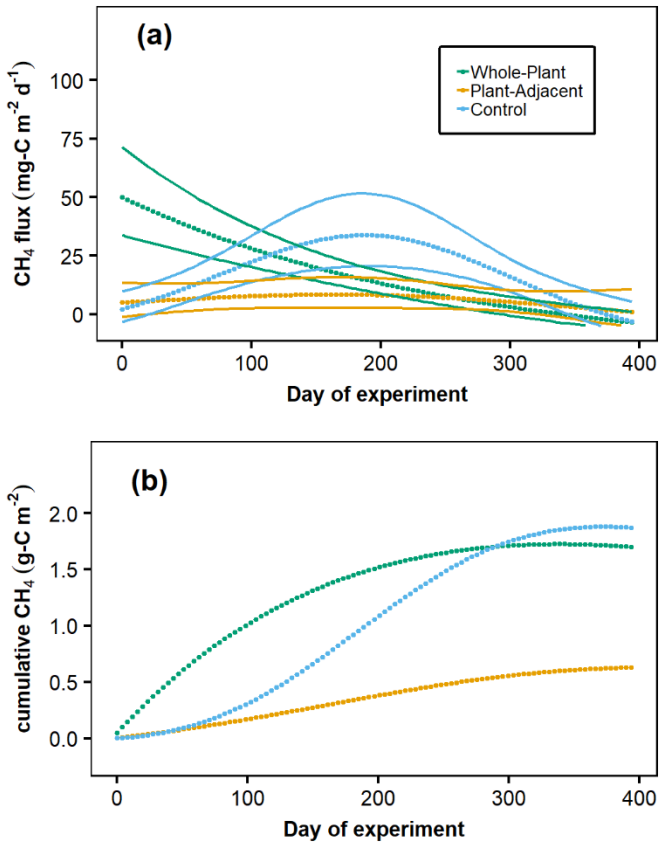

Figure 4. Time series of modeled (a) CH_4 flux rates (means = dots, SE = lines) and (b) cumulative CH_4 emissions across days of the experiment for whole-plant (green), plant-adjacent (orange), and control (blue) treatments. Flux rates were modeled from periodic measurements across the experiment using generalized additive modeling

4 Discussion

4.1 Temporal- and spatial-effects of vegetation on CH_4 flux

Our study demonstrates how CH_4 emissions are affected by the linkage between plant-mediated transport, porewater CH_4 concentrations, and the timing of water inundation. The elevated flux rates that we measured during *Typha* establishment align with the current consensus that vegetation acts as a conduit for CH_4 transport from the rhizosphere to the atmosphere at rates much higher than diffusive-only flux (Bendix et al., 1994; Colmer, 2003; Laanbroek, 2010). However, high rates of plant-mediated transport appeared to deplete the porewater CH_4 reservoir below and around vegetation, which likely led to lower flux rates from the whole-plant and plant-adjacent treatments later in the experiment. In contrast, non-vegetated controls had a highly concentrated CH_4 porewater reservoir that contributed to higher flux rates during simulated draw down of the water table that typically occurs later in the growing season in seasonal wetland. Ultimately, there were comparable total CH_4 emissions between whole-plant and control treatments. This finding challenges the common assumption that actively growing emergent vegetation increases CH_4 emissions from wetlands (Bhullar, Edwards, et al., 2013; Carmichael et al., 2014), as the generalization may not apply in seasonally inundated wetlands (Altor & Mitsch, 2006, 2008). However, it should be noted that the soils used in our mesocosms were collected from locations that historically had vegetation, thus there may have been residual, older plant-C inputs to fuel CH_4 production in our plant-free control treatment.

Through combined measurements of dissolved porewater CH_4 and CH_4 flux rates, our study revealed potentially significant mechanisms in plant-mediated CH_4 flux. Low porewater

CH_4 concentrations below plants was somewhat unexpected, as vegetation is known to supply fresh carbon substrates (i.e., root exudates) to fuel methanogenic CH_4 production (Christensen et al., 2003; King & Reeburgh, 2002; Knorr et al., 2008; Waldo et al., 2019). By observing high plant-mediated flux rates in combination with depleted porewater CH_4, we infer that CH_4 was being transported to the atmosphere relatively quickly after it was produced in the sediment below plants. Similar patterns of decreased sediment CH_4 in vegetated compared to non-vegetated sites have been observed in brackish tidal systems (Chanton et al., 1989; Gross et al., 1993) and in northern peatlands (Shannon et al., 1996).

Porewater CH_4 was moderately greater in the plant-adjacent treatment than in the whole-plant treatment. This finding suggests that higher CH_4 flux via plant-mediated transport is, in part, enhanced by a supply of CH_4 that is produced and laterally transported via roots from adjacent soils within wetlands. This effect may have been magnified in our experiment due to the shallow depth of our aquarium soils. Root growth was bound by mesocosm volume and soil depth, therefore the distance required for porewater CH_4 to diffuse via roots is likely shorter than in a natural wetland. To better assess the complete impact of vegetation on wetland CH_4 budgets, future studies should consider a 'zone of influence' surrounding aerenchymous wetland plants, which accounts for root and stem transport of porewater CH_4.

Typha not only affected the timing of CH_4 emissions, but also the residence time of the porewater CH_4 reservoir, which has implications for CH_4 oxidation potential. A common assumption is that wetland vegetation increases oxidation of porewater CH_4 due to a supply of O_2 to the rhizosphere (Conrad, 2009; Faußer et al., 2012; Laanbroek, 2010). However, plant-mediated transport allows CH_4 to quickly bypass the primary zone of oxidation that occurs near the water-table surface (Bendix et al., 1994; Colmer, 2003; Knoblauch et al., 2015; Laanbroek,

2010). The elevated CH_4 flux rates we observed in tandem with depleted porewater reservoir indicate a low residence time of CH_4 and provides evidence that the depleted porewater reservoir is due to plant-transport, not rhizosphere oxidation. Therefore, *Typha* reduces CH_4 oxidation spatially (by allowing CH_4 to avoid the zone of oxidation) and temporally (through short residence time of porewater CH_4).

4.2 Drying CH_4 pulse and re-wetting CH_4 recovery

The majority of depressional wetlands in the PPR are temporary or seasonal, as are many tropical and subtropical wetlands, vernal pools, and swamps. These systems are subject to regular drying and re-wetting events across entire wetlands, or at wetland-upland transition zones (Dahl, 2014; Jeffrey et al., 2019; Keeley & Zedler, 1998; Tangen & Bansal, 2019a). Drying and re-wetting also occur during episodic events such as droughts or floods (Altor & Mitsch, 2006, 2008; Beringer et al., 2013), during agricultural actions such as wetland drainage for agriculture, and mid-season drying of rice fields (Runkle et al., 2019; Tangen et al., 2015), or during wetland restoration (Audet et al., 2013; Tuittila et al., 2000). Thus, drying (or water-table drawdown) and re-wetting of wetlands can have notable impacts on a wide span of wetland CH_4 budgets (Badiou et al., 2011; Brown et al., 2014; Goodrich et al., 2015; Kroeger et al., 2017; Marcé et al., 2019).

During a drying event, the water table drops, hydrostatic pressure is lowered, and the hydrologic barrier to free gas flow is removed, thereby allowing a rapid, pulsed release of porewater CH_4 to the atmosphere (Roslev & King, 1996). The rapid release of CH_4 during drying is not only dependent on water table dynamics, but also requires a sufficiently large and concentrated porewater CH_4 reservoir to fuel the CH_4 pulse. Our study suggests that a drying-induced pulse of CH_4 may be considerably dampened in the presence of vegetation due to

depletion of porewater CH_4 from plant-mediated transport. In contrast, a drying-induced CH_4 pulse may be a dominant factor controlling annual CH_4 budgets for unvegetated wetlands (or unvegetated location within wetlands) if there is a sufficiently large reserve pool of porewater CH_4.

Water-logged soils facilitate anoxic conditions that promote CH_4 production. However, as exemplified in the present study and other recent research, the timing of inundation affects the magnitude of CH_4 emissions and how vegetation affects CH_4 flux. Altor & Mitsch (2006) found greater CH_4 emissions from permanently inundated areas than from intermittently flooded areas of experimental riparian marshes, and found no difference in CH_4 flux between vegetated and non-vegetated plots in intermittently flooded areas. In *Typha*-dominated constructed wetlands, plants enhanced CH_4 emissions in wetlands with 40–60% soil moisture content but had no effect in a wetland with <40% soil moisture (McInerney & Helton, 2016). Still, more field studies are needed from seasonal wetlands to further elucidate how plant-mediated fluxes change across variable hydrology in natural conditions (Beringer et al., 2013; D Kim et al., 2012).

Recovery of CH_4 production and emissions following re-wetting after drying is also potentially affected by the presence of wetland vegetation. During drying, there is consumption of labile carbon substrates by aerobic respiration, regeneration of alternate electron acceptors, reduction in size of methanogenic communities, and increased CH_4 oxidation, all of which delay recovery of CH_4 emissions by days to months following re-wetting (Boon et al., 1997; Conlin & Crowder, 1989; D Kim et al., 2012; Knorr et al., 2008; Sundh et al., 1994; Tian et al., 2012). Vegetation can speed up the rate of recovery by priming microbial activity via fresh carbon substrates (Ström et al., 2005; Waldo et al., 2019), but can also delay recovery by supplying O_2 for methanotrophic communities (Faußer et al., 2012), and by extending dry conditions through

transpiration. In our study, O_2 levels were minimal in all treatments following re-wetting and none of the treatments exhibited high CH_4 flux rates or accumulated a porewater CH_4 reserve after three months. Although not significant, we observed a slight trend of lower flux rates and lower porewater CH_4 in 'whole plant' treatments during the re-wetting phase. The lack of CH_4 recovery after re-wetting may be a result of limitations on carbon substrate from sources such as groundwater and decomposing plant material not being replenished in mesocosms as they would in a natural wetland, or because the fresh carbon inputs did not have enough time to accumulate for microbial consumption (Neubauer et al., 2005; Sutton-Grier & Megonigal, 2011; Updegraff et al., 1995).

4.3 Modeling and management implications

Budgets of CH_4 at local- to global-scales are often estimated using process-based models such as DNDC (Li, 2000), *Ecosys* (Grant & Roulet, 2002), and CLM4Me (Riley et al., 2011). These models couple biological and physical processes, and are highly sensitive to water table depth, vegetation, and various CH_4 transport pathways. A recent review on CH_4 models identified a need to increase understanding of individual CH_4 processes over vertical and horizontal space, as well as hot moments and hot spots, as crucial for improving model predictions (Xu et al., 2016). In this paper, we outline several relevant mechanisms to help improve the underlying assumptions that drive these models. In particular, we demonstrate how vegetation can influence the timing of CH_4 emissions and residence time of porewater CH_4, lateral transport of porewater CH_4, and effects of water table drawdown. Our findings also have implications for empirically derived, data-driven models that predict flux at annual time steps over entire wetland systems. We demonstrate the dynamic temporal and spatial interaction

between wetland vegetation and hydrology on seasonal CH_4 fluxes (Riley et al., 2011). Thus, process-based and empirical CH_4 models need to consider intra-annual hydrologic dynamics (e.g., drying and re-wetting events) and spatial wetland heterogeneity (e.g., vegetated and non-vegetative cover, aerenchymous and non-aerenchymous vegetation types) for accurate predictions of CH_4 budgets.

Wetland drainage and restoration also have important impacts on CH_4 budgets. While wetland drainage generally decreases CH_4 emissions (Tangen et al., 2015), we show how drainage can produce a temporary, large pulse of CH_4, offsetting the subsequent decrease in CH_4 flux. While the flooding that is required to restore wetlands may increase CH_4 emissions (Audet et al., 2013; Tuittila et al., 2000), our results suggest re-wetting wetlands later in the season could result in lower CH_4 emissions relative to early-season flooding. A better understanding of the mechanisms affecting CH_4 recovery could aid in reducing CH_4 emissions with wetland restoration (Jerman et al., 2009; Runkle et al., 2019). More research is needed, ideally using high frequency data such as from eddy covariance flux towers (e.g., FLUXNET-CH4 database, [Knox et al., 2019]) to understand short-term effects of drying and re-wetting on CH_4 flux.

Wetland management actions to control problematic invasive macrophytes include crushing, cutting above/below water, harvesting, and herbicide (Bansal et al., 2019; Carson et al., 2018; Hazelton et al., 2014; Keyport et al., 2019). These manipulations of emergent vegetation could affect plant-mediated CH_4 production, consumption, and transport (Zhu et al., 2007). In terms of ecosystem services, the role of vegetation on CH_4 flux and wetland carbon budgets (and consequently carbon storage potential) should be considered when deciding management actions (Eviner et al., 2012). Our study highlights how the timing of management may affect CH_4. For example, cutting and drowning *Typha* stems during their establishment may prevent the large

CH_4 flux rates we observed early on in our study, but this action may only be effective in permanently inundated wetlands. If a wetland dries later in the season, there may be a CH_4 release that eliminates any benefit from early season cutting. Including the effect of vegetation on the timing of CH_4 fluxes, drying-induced pulses of CH_4, and re-wetting recovery time frames will improve wetland CH_4 budgets and management decisions.

Acknowledgements

We thank B. Hanson for assistance measuring gas flux. Funding for this study was provided by the U.S. Geological Survey Climate and Land Use Change R&D Program. The data are in the ScienceBase repository and are available at Bansal et. al. (2020). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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