



Greenhouse Gas Fluxes Vary Between *Phragmites Australis* and Native Vegetation Zones in Coastal Wetlands Along a Salinity Gradient

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Abstract The replacement of native species by invasive *Phragmites australis* in coastal wetlands may impact ecosystem processes including fluxes of the greenhouse gases (GHGs) carbon dioxide (CO₂) and methane (CH₄). To investigate differences in daytime CH₄ and CO₂ fluxes as well as vegetation properties between *Phragmites* and native vegetation zones along a salinity gradient, fluxes were measured via cavity ringdown spectroscopy in 3 New England coastal marshes, ranging from oligohaline to polyhaline. While daytime CH₄ emissions decreased predictably with increasing soil salinity, those from *Phragmites* zones were larger (15 to 1254 μmol m⁻² h⁻¹) than those from native vegetation (4–484 μmol m⁻² h⁻¹) across the salinity gradient. *Phragmites* zones displayed greater daytime CO₂ uptake than native vegetation zones (−7 to −15 μmol m⁻² s⁻¹ vs. −2 to 0.9 μmol m⁻² s⁻¹) at mesohaline-polyhaline, but not oligohaline, sites. Results suggest that vegetation zone and salinity both impact net emission or uptake of daytime CO₂ and CH₄ (respectively). Future research is warranted to demonstrate *Phragmites*-mediated impacts on GHG fluxes, and additional measurements across seasonal and diel cycles will enable a more complete understanding of *Phragmites*' net impact on marsh radiative forcing.

Keywords *Phragmites* · Coastal marsh · Methane · Carbon dioxide · *Spartina*

Introduction

Invasive plants can alter the structure and function of coastal wetlands. Exotic species invasions of coastal wetlands are known drivers of ecosystem-level change including impacts to vegetation (Bertness et al. 2002) and microbial (Ravit et al. 2003) community structure, trophic function (Levin et al. 2006), and biogeochemistry (Windham and Ehrenfeld 2003; Tong et al. 2012). Invasive plants can alter components of nitrogen (N), carbon (C), and water cycling via differences in productivity and rhizosphere conditions including nutrient uptake, soil oxygenation, and availability of C exudates relative to native plants (Ehrenfeld 2003).

In North American coastal wetlands, the presence of the invasive grass *Phragmites australis* has increased steadily in recent decades (Chambers et al. 1999; Meyerson et al. 2009) with potential implications for ecosystem function. *Phragmites* has been shown to outcompete native species by shading (Chambers et al. 1999), capitalizing on nutrient availability (Mozdzer and Zieman 2010), and rapidly spreading by both clonal replication (Amsberry et al. 2000) and seeding (McCormick et al. 2009). Although *Phragmites* invasion is known to exclude native high marsh vegetation (Minchinton et al. 2006) and therefore reduce species richness in the high marsh community (Silliman and Bertness 2004), ways in which ecosystem functions may be affected by *Phragmites* invasion are less well-understood.

The replacement of native vegetation with invasive *Phragmites*-dominated communities (hereafter *Phragmites* zones) can mediate significant shifts in net CO₂ and CH₄ fluxes. Generally, coastal wetlands emit minimal carbon dioxide (CO₂) and methane (CH₄) (Mitsch and Gosselink 2000; Poffenbarger et al. 2011; Madigan 2012). *Phragmites* may increase marsh CO₂ uptake in the short term due to its greater productivity relative to smaller native species (Windham

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1999). It may also contribute to decreased CH₄ emissions as a result of rhizosphere methanotrophy, since *Phragmites*' physiology often leads to a notable oxygenation of its rhizosphere (Armstrong 2000; Colmer 2003). However, invasive *Phragmites* also has the potential to exacerbate marsh CH₄ emissions relative to native vegetation (Mozdzer and Megonigal 2013). *Phragmites*' provision of labile organic C to its rhizosphere (Ravit et al. 2003; Lovell 2005; Armstrong et al. 2006) may result in increased methanogen presence or activity. *Phragmites* may also directly drive CH₄ emissions since its pressure-driven transport system is known to conduct rhizosphere-derived CH₄ (Brix et al. 2001) through the plants' massive aerenchyma and into the atmosphere (Armstrong et al. 1996; Grosse et al. 1996; Beckett et al. 2001; Colmer 2003). Characterization of CO₂ and CH₄ fluxes from marshes vegetated with invasive *Phragmites* and native vegetation could provide insight into potential impacts of *Phragmites* invasion on marsh GHG flux dynamics. However, few have performed such investigations (Emery and Fulweiler 2014), and no studies to date compare greenhouse gas (GHG) fluxes from *Phragmites* and the high marsh native perennials (such as *Spartina patens*, *Distichlis spicata* and *Juncus gerardii*) that *Phragmites* is likely to displace as it invades from upland borders and along creek banks (Chambers et al. 1999; Silliman and Bertness 2004).

Factors other than vegetation type also affect marsh GHG fluxes, and must be taken into account when attempting to discern impacts of changing plant communities. Salinity is known to be a major control on CH₄ fluxes in coastal wetlands (Poffenbarger et al. 2011) as frequent inundation with seawater replenishes sulfate to soil bacterial communities that out-compete methanogenic archaea (Mitsch and Gosselink 2000; Madigan 2012). Salinity also is understood to constrain *Phragmites* distribution (Burdick et al. 2001), and while *Phragmites* is capable of growing at marine strength salinities (Chambers et al. 2003), it often displays reduced vigor and success when exposed to increased seawater inundation (Hanganu et al. 1999). A comparison of GHG fluxes from *Phragmites* and native vegetation stands along a natural salinity gradient could begin to distinguish between biotic and abiotic controls on flux differences.

The objective of this research was to compare CH₄ and CO₂ fluxes from *Phragmites* and native high marsh vegetation zones during a growing season in three Southern New England coastal marshes that span a natural salinity gradient. Surface soil properties, plant variables and pore water sulfide also were measured and tested for their relationship to observed GHG fluxes. *Phragmites* zones were hypothesized to have higher CH₄ emissions but also higher rates of CO₂ uptake than native high marsh zones given the plant's greater gas transport and productivity rates. CH₄ fluxes were expected to decrease with increasing marsh salinity in both *Phragmites* and native high marsh zones.

Materials and Methods

Study Sites

Study sites were chosen to allow for comparison of GHG fluxes between *Phragmites* and native high marsh vegetation zones along a salinity gradient. Three *Phragmites*-invaded southern New England coastal wetlands were selected: two in lower Narragansett Bay, Rhode Island (Round Marsh and Fox Hill) and one in Waquoit Bay, Massachusetts (Sage Lot) (Table 1, Fig. 1). Sage Lot is located in a watershed with minimal development and minimal N loads (Valiela and Cole 2002), and Round Marsh and Fox Hill are located in lower Narragansett Bay where N concentrations from anthropogenic activities are estimated to be low (Wigand et al. 2003). Native vegetation consists primarily of *Spartina patens* and *Distichlis spicata* (see Table 1 for details), and *Phragmites* invasion encroaches from the upland edge of all marsh sites. Sites increase in growing season surface soil salinity from oligohaline levels in Round Marsh to polyhaline in Sage Lot, with Fox Hill being intermediate (Table 1). All sites experienced flooding with 32 ppt seawater in both vegetation zones during spring tides.

Experimental Design

At each site, GHG fluxes were compared between the *Phragmites* and native high marsh vegetation zones using three replicate plots per zone. At Round Marsh, three plots were selected in each vegetation zone with approximately 30 m of spacing between plots. At Fox Hill and Sage Lot, three plots were selected in the native high marsh zone, but in the *Phragmites* zone where pilot trials indicated high gas flux variability, three pairs of plots (with 0.3 m spacing between paired plots) were established (data from the paired plots were averaged prior to statistical analyses, as detailed below). In *Phragmites* zones, plots were established approximately 1 m from the leading, seaward edge of the stand, and in native vegetation zones plots were placed at random. *Phragmites*-mediated changes to edaphic conditions and microbial communities at the leading edge of the invasion have persisted for shorter duration than in older, interior portions of the stand. Therefore, comparisons between native and *Phragmites* zones represent conservative estimates of potential changes in GHG flux dynamics due to invasion.

For GHG flux measurements, bases were installed in each selected plot to support static flux chambers. Bases were installed in the early spring (at least 2 weeks prior to first measurements) so as to permit recovery of vegetation, and were left in place for the duration of the growing season to minimize soil disturbance. *Phragmites* zone chamber bases consisted of PVC rings (24 cm tall × 30 cm diameter), and native vegetation chamber bases consisted of stainless steel

Table 1 Study site characteristics and GHG flux measurement replication details

Site	Salinity Class	Native high marsh species	Replication	Months Measured
Round Marsh Jamestown, RI	oligohaline-mesohaline	<i>Spartina patens</i> <i>Distichlis spicata</i>	<i>Phragmites</i> : n = 3 Native: n = 3	May, June, July, August
Fox Hill Jamestown, RI	mesohaline-polyhaline	<i>Spartina patens</i> <i>Distichlis spicata</i>	<i>Phragmites</i> : n = 3 (3 pairs) Native: n = 3	April, May, June, July, August
Sage Lot Falmouth, MA	polyhaline	<i>Distichlis spicata</i>	<i>Phragmites</i> : n = 3 (3 pairs) Native: n = 3	May, June, July, August

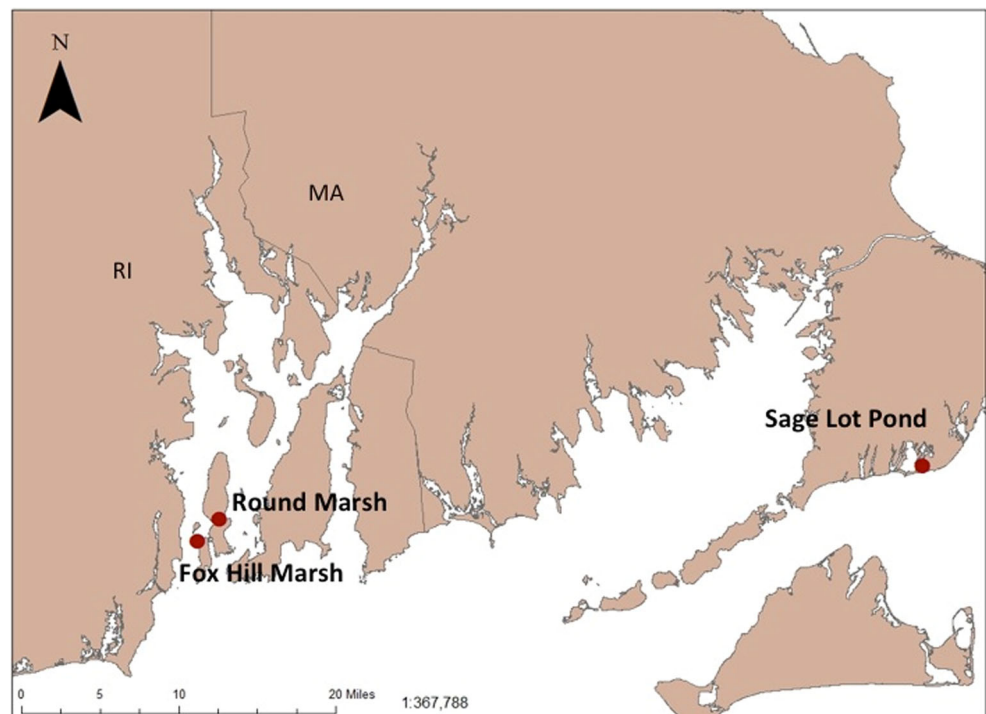
rings (9 cm tall × 30 cm diameter). *Phragmites* and native vegetation bases were inserted 8 cm into the soil and both types featured drainage holes positioned just beneath the soil surface to allow for lateral water movement after tidal inundation or rainfall.

Edaphic Variable and Plant Metrics

Surface soil (top 3 cm) salinities were measured at each plot within chamber bases once per month from April–August 2014 at the time of GHG flux measurements. Soil was pressed against paper filters using small syringes to extract water, which was analyzed for salinity using a handheld refractometer. Soil pore water was collected at each site in May, July and late August from each plot during GHG flux measurements using 15 cm Rhizon Soil Moisture Samplers (Ben Meadows, Janesville, WI), preserved using 1 M zinc acetate, and frozen until analysis. Pore water sulfide concentrations were

analyzed using standard colorimetric techniques (Cline 1969). Mid-growing season soil pH, oxidation-reduction potential, temperature and moisture point measurements were performed just outside each chamber base once each during June and July GHG flux measurements for a total of two measurements per plot. Soil oxidation-reduction (redox) potential (ORP) and pH were measured using an ORP probe and pH/ORP meter (Mettler Toledo, Greifensee, Switzerland) and pH meter (ExStick® Instruments, Nashua, NH). Soil temperature was measured with a digital thermometer inserted into soil at a depth of 15 cm, and soil moisture content was measured using a volumetric water content sensor (Decagon Devices, Pullman, WA) inserted 5 cm into soil. Soil for organic content analysis was collected from each plot in August. Using a cutoff syringe, approximately 10 mL of soil was collected. Soil was dried, weighed, and placed in a muffle furnace at 500 °C overnight. Change in weight was defined as loss on ignition (LOI), a proxy for soil organic content.

Fig. 1 Map of study sites in Narragansett Bay (Round Marsh and Fox Hill) and Waquoit Bay (Sage Lot Pond)



To characterize *Phragmites* vegetation at each site, densities of live and dead stems and average stem height within chamber bases were recorded during the growing season once plants were mature (July). For stem height, ten stems per plot were selected randomly and their heights were averaged.

GHG Flux Measurements

Daytime GHG flux measurements were performed during the early (April–May), mid- (June–July), and late (late August) growing season during 2014. Gas measurements were conducted for 6–10 min per plot, based on observed periods for linear rates of change. All GHG flux measurements were performed between 9:00 AM and 3:00 PM and within 3 h of low tide.

A cavity ring down spectroscopy (CRDS) analyzer (Picarro G2508) was used to measure CO₂, CH₄ and N₂O concentrations in real-time. The analyzer cavity, together with a flux chamber and connective tubing, creates a closed system within which gas concentration changes over time are measured with a flow rate of ~230 sccm and frequency of approximately 1 measurement/s. The gas analyzer simultaneously measures H₂O vapor concentrations and reports the dry mole fraction of the other target gases, and this corrected value was used for all flux calculations. H₂O vapor saturations never exceeded 2.5 % over the course of any measurements.

The analyzer was connected via nylon tubing to transparent polycarbonate chambers, which were placed into the previously-installed bases. Vegetation was left intact inside the chambers. A 0.02 m³ polycarbonate chamber was used for native species zone measurements following previously-described methods (Moseman-Valtierra et al. 2011). In order to accommodate tall (up to 2 m) *Phragmites* plants, a 2 m tall, 0.3 m diameter transparent polycarbonate tube (Rideout Plastics^R) was modified to extend the shorter polycarbonate chamber which was sealed to the extender using a polyethylene closed-cell foam collar with its channel filled with water (for a total chamber volume of 0.15 m³). Extender support bases were designed to create a gas-tight fit between base and extender. Two small fans attached to the inside of the polycarbonate chamber (10-cm fans) and extender (20-cm fans) ensured air mixing during measurements. A stainless steel 55 cm long, 0.8 mm diameter pigtail was used for pressure equilibration. Hobo[®] data loggers (Onset, Bourne, MA) were suspended within chambers during all flux measurements to monitor air temperature at 30 s intervals.

GHG fluxes were calculated using chamber size and footprint. The Ideal Gas Law ($PV = nRT$) was used to calculate changes in gas concentrations over time using field-measured air temperatures and atmospheric pressure. Cases in which no change in gas concentration over time was detectable for the duration of the measurement period were classified as having a flux of 0 (3.8 % of CO₂ and 7.6 % of CH₄ measurements).

When slopes had an R² value of less than 0.85, data were not included in the analysis (5.7 % of CO₂ and 1.9 % of CH₄ measurements). The relatively short time period of these greenhouse gas flux measurements are not designed to capture ebullitive fluxes, and thus may represent underestimates of total gas emissions, particularly for CH₄ (Tokida et al. 2005). However, our high resolution measurement of gas concentrations does enable detection of the rapid (often step-shaped) changes in gas concentrations that occur during ebullition to be very well resolved and distinguished from diffusive flux during the periods of chamber deployment (Middelburg et al. 1996). We did not detect ebullition from this dataset.

Statistical Analyses

When two sets of measurements were taken during a portion of the growing season ($n = 3$ seasonal stages: early, mid or late), averages for the two sampling dates were computed by plot. At Fox Hill and Sage Lot where *Phragmites* zone measurements were conducted in duplicate, averages of measurements from pairs of plots were used for statistical analyses. Therefore, for GHG flux, soil salinity and porewater sulfide data, each site had three data points per vegetation zone per growing season period for a total of 18 data points per site. CO₂ and CH₄ fluxes, soil salinity and porewater sulfide were compared between vegetation zones at each site using a two-factor ANOVA with vegetation type and growing season period (early, mid, late) as the two factors, and comparisons were drawn between sites using a one-factor ANOVA.

For edaphic variables, June and July data were averaged for the two sampling dates by plot. Edaphic and plant variable data collected from pairs of *Phragmites* plots were averaged and the means of the two values were used for statistical analysis. Therefore, for pH, redox potential, temperature, moisture, and soil organic C, each site had $n = 3$ data points per vegetation zone for the mid growing season only (for a total of six data points per site). Edaphic variables were compared using two-factor ANOVA with site and vegetation type as main effects. *Phragmites* vegetation characteristics (stem height, live and dead stem counts) were compared between sites using a one-factor ANOVA. Data were aligned then rank-transformed prior to ANOVA analyses (Salter and Fawcett 1993; Wobbrock et al. 2011) to account for deviations in normality while allowing for tests of effect interaction (Seaman et al. 1994). Tukey's HSD test was used for post-hoc pairwise comparisons when appropriate.

Potential relationships between edaphic and vegetation variables and GHG fluxes were investigated using Spearman's R Correlation Test.

All statistics were performed in R (R Core Team 2014) and interpreted at a significance level of 0.05.

Results

Edaphic Variables & Vegetation Characteristics

Confirming the expected salinity gradient, soil salinity differed significantly between all 3 sites and was highest at Sage Lot and lowest at Round Marsh, with Fox Hill intermediate (Table 2). Significant differences in salinity between vegetation zones (*Phragmites* and native) were present only at Fox Hill (Table 2), with salinity higher by several ppt in the native vegetation zone during the mid and late growing season stages.

Porewater sulfide concentrations ranged from 0 to approximately 250 μM , although one sample (from native vegetation at Sage Lot) had a sulfide concentration of over 1000 μM (Table 2). Concentrations did not differ significantly between vegetation zones at any site, but did display between-site differences when averaged across all dates, with Sage Lot sulfide concentrations (139.00 ± 17.77) significantly greater than those at Round Marsh (31.57 ± 16.31) (Table 2).

Surface soil pH averaged across vegetation zones at Sage Lot was significantly greater than at Round Marsh and Fox Hill (Table 3). Surface soil oxidation-reduction potential averaged across vegetation zones was significantly lower at Sage Lot than Round Marsh. Soil temperature (at 15 cm depth) averaged across vegetation zones was higher by approximately 3 °C at Sage Lot and Fox Hill than at Round Marsh (Table 3). Soil moisture (at 5 cm depth) averaged across vegetation zone differed between the three sites, decreasing from Sage Lot to Round Marsh with Fox Hill intermediate. Significant site \times vegetation zone interaction indicated that *Phragmites* zone soil moisture at Fox Hill was similar to Round Marsh, while native vegetation soil moisture at Fox Hill was similar to Sage Lot (Table 3). Soil organic content averaged between zones was significantly greater at Fox Hill than Round Marsh (Table 3).

Phragmites stand structure varied along the salinity gradient. Although not significant, trends in *Phragmites* stem height and live and dead stem counts were observed between sites (Table 3). Average *Phragmites* stem height displayed a trend of decrease with increasing site salinity. Live and dead *Phragmites* stem densities were generally greater at higher-salinity sites (Fox Hill and Sage Lot) than at Round Marsh.

GHG Fluxes

Daytime CH_4 fluxes were significantly greater (by up to several orders of magnitude) in *Phragmites* zones than in native vegetation zones at all sites (Fig. 2) and were orders of magnitude larger for both vegetation zones at oligo-mesohaline Round Marsh than polyhaline Sage Lot (Fig. 3). CH_4 emissions were highly variable and ranged from 0 to 4206 $\mu\text{mol m}^{-2} \text{h}^{-1}$. They increased after the early growing

season at meso-polyhaline Fox Hill (trend) and polyhaline Sage Lot (significantly); by contrast, however, oligo-mesohaline Round Marsh displayed a trend of larger CH_4 emissions during the early growing season, which declined later in the growing season (Fig. 2).

Daytime CO_2 fluxes ranged from $-37 - +7 \mu\text{mol m}^{-2} \text{s}^{-1}$, with significantly greater uptake (by 5–15 times during the mid growing season) in the *Phragmites* zone than in native vegetation at Fox Hill and Sage Lot, the higher-salinity sites (Fig. 2). The greatest *Phragmites* zone CO_2 uptake (approximately 2 \times as much as at Round Marsh and Sage Lot), as well as the greatest native vegetation zone CO_2 emission (positive fluxes), occurred at Fox Hill (intermediate salinity). CO_2 fluxes varied across the growing season at Round Marsh and Fox Hill, with the least CO_2 uptake occurring during the early growing season. For CO_2 fluxes at Fox Hill, interaction of vegetation type and seasonal stage were significant, indicating that greatest CO_2 uptake occurred in *Phragmites* zones during the mid growing season.

No detectable N_2O fluxes were observed (with a 30-s averaging period and minimal detection limit of approximately 1.4 $\mu\text{mol m}^{-2} \text{h}^{-1}$) (Brannon et al. *in prep*).

Across all sites, CH_4 emissions in *Phragmites* zones (but not native vegetation) were negatively correlated with salinity (Spearman's $r = -0.43$, $p = 0.04$). Soil redox potential was negatively correlated with CO_2 flux magnitude in native vegetation (Spearman's $r = -0.88$, $p < 0.01$), while soil temperature (Spearman's $r = 0.78$, $p = 0.01$), and soil moisture (Spearman's $r = 0.72$, $p = 0.04$) were positively correlated with CO_2 flux magnitude in that zone. No other significant relationships were found between GHG fluxes and edaphic and plant variables.

Discussion

Phragmites Zones Were Consistently Associated with Larger CH_4 Emissions Across the Salinity Gradient

Site histories prior to *Phragmites* invasions may vary. Therefore, experimental manipulations would be required in order to determine whether *Phragmites* invasion drove the observed consistent greater emission of CH_4 compared to native vegetation zones. However, the clear association between *Phragmites* presence and increased daytime CH_4 emissions during the growing season across sites suggests a role of this invasive species in driving GHG dynamics. These findings are consistent with *Phragmites*' known promotion of advective and diffusive fluxes of gases from soils to atmosphere (Armstrong et al. 1996; Brix et al. 1996; Colmer 2003), as well as potential greater C substrate provision (as a result of greater *Phragmites* biomass relative to native species) to

Table 2 Mean salinity (ppt) and pore water sulfide concentration \pm SE measured during the early, mid and late growing seasonal stages and results of ANOVA tests

	Early (Apr – May)	Mid (June – July)	Late (Aug)	Veg. Type	Season	Veg Type x Season Stage	Site
Average Surface Salinity (ppt) \pm SE							
Round Marsh <i>Phragmites</i>	4.00 \pm 1.26	5.15 \pm 1.36	– **	$F_{1,8} = 1.42, p = 0.26$	$F_{1,8} = 0.73, p = 0.41$	$F_{1,8} = 0.50, p = 0.50$	$F_{2,44} = 88.89,$ $p < 0.01^*$
Native Veg.	8.00 \pm 4.31	13.33 \pm 4.70	– **				Tukey HSD: RM ^c FH ^b SL ^a
Fox Hill <i>Phragmites</i>	7.13 \pm 1.04	28.00 \pm 3.30	24.33 \pm 3.93	$F_{1,12} = 16.68, p < 0.01^*$	$F_{1,12} = 12.46, p < 0.01^*$	$F_{1,12} = 1.17, p = 0.34$	
Native Veg.	10.67 \pm 0.44	34.17 \pm 1.59	33.6 \pm 1.83				
Sage Lot <i>Phragmites</i>	26.75 \pm 0.75	28.33 \pm 0.11	33.67 \pm 0.49	$F_{1,11} = 1.48, p = 0.25$	$F_{1,11} = 31.60, p < 0.01^*$	$F_{1,11} = 0.17, p = 0.85$	
Native Veg.	25.67 \pm 1.33	28.33 \pm 0.44	32.67 \pm 1.45				
Average Pore water sulfide (μ M) \pm SE							
Round Marsh <i>Phragmites</i>	106.97 \pm 71.04	0.00 \pm 0.00	17.51 \pm 15.21	$F_{1,9} = 0.62, p = 0.45$	$F_{1,9} = 1.96, p = 0.20$	$F_{1,9} = 1.14, p = 0.36$	$F_{2,44} = 6.96,$ $p < 0.01^*$
Native Veg.	20.95 \pm 13.98	0.00 \pm 0.00	50.83				Tukey HSD: RM ^b FH ^{abb} SL ^a
Fox Hill <i>Phragmites</i>	72.80 \pm 70.13	56.41 \pm 56.41	27.07 \pm 26.06	$F_{1,6} = 0.01, p = 0.90$	$F_{1,6} = 0.74, p = 0.50$	$F_{1,6} = 0.62, p = 0.57$	
Native Veg.	180.10 \pm 1.74	88.61 \pm 87.31	148.21 \pm 79.36				
Sage Lot <i>Phragmites</i>	0.00 \pm 0.00	14.16 \pm 7.70	103.53 \pm 74.55	$F_{1,12} = 1.73, p = 0.21$	$F_{1,12} = 1.53, p = 0.25$	$F_{1,12} = 0.62, p = 0.56$	
Native Veg.	73.13 \pm 66.20	91.58 \pm 59.12	514.07 \pm 410.39				

F statistics, degrees of freedom, and significance values are reported for 2-factor (Veg. Type x Seasonal Stage) and 1-factor (Site) ANOVA tests

*= Significant at $\alpha = 0.05$

**Salinity was measured on this date at an exceptionally high, late tide resulting in plot inundation and so is not included

Table 3 Edaphic and plant variable averages \pm SE measured during the mid growing season (June – July) and results of ANOVA tests

	pH	Redox potential (mV)	Soil Temp. (°C)	Soil Moisture (%)	Soil organic content (%)	Live stem height (cm)	Live stems	Dead stems
Round Marsh								
<i>Phragmites</i>	6.18 \pm 0.42	258.33 \pm 181.86	17.82 \pm 0.57	55.30 \pm 2.15	23.07 \pm 1.24	176.80 \pm 8.74	4.00 \pm 2.00	6.50 \pm 1.50
Native Veg.	6.47 \pm 0.40	217.22 \pm 156.16	17.88 \pm 0.62	55.52 \pm 3.18	26.09 \pm 2.66	–	–	–
Fox Hill								
<i>Phragmites</i>	6.95 \pm 0.16	39.00 \pm 53.76	20.15 \pm 0.50	56.71 \pm 2.28	52.28 \pm 13.60	134.09 \pm 19.18	8.67 \pm 1.15	16.00 \pm 2.16
Native Veg.	6.36 \pm 1.41	–29.50 \pm 98.17	20.68 \pm 0.48	63.71 \pm 0.84	47.61 \pm 3.13	–	–	–
Sage Lot								
<i>Phragmites</i>	7.46 \pm 0.14	0.08 \pm 101.98	21.15 \pm 0.77	66.25 \pm 0.81	45.77 \pm 4.18	123.13 \pm 7.62	9.67 \pm 0.33	15.67 \pm 3.86
Native Veg.	7.13 \pm 0.15	–83.83 \pm 24.06	20.82 \pm 0.83	64.55 \pm 0.85	25.74 \pm 6.00	–	–	–
Results of 2-factor ANOVA								
Veg. zone	$F_{1,11} = 0.19$, $p = 0.67$	$F_{1,12} = 0.94$, $p = 0.35$	$F_{1,12} = 3.00$, $p = 0.91$	$F_{1,12} = 2.89$, $p = 0.11$	$F_{1,11} = 2.68$, $p = 0.13$	–	–	–
Site	$F_{2,11} = 6.84$, $p = 0.01^*$	$F_{2,12} = 5.27$, $p = 0.02^*$	$F_{2,12} = 20.76$, $p < 0.01^*$	$F_{2,12} = 34.76$, $p < 0.01^*$	$F_{1,11} = 5.87$, $p = 0.02^*$	$F_{2,6} = 4.80$, $p = 0.06$	$F_{2,6} = 5.10$, $p = 0.05^*$	$F_{2,6} = 3.68$, $p = 0.09$
Veg. zone x Site	$F_{2,11} = 0.65$, $p = 0.54$	$F_{2,12} = 0.06$, $p = 0.94$	$F_{2,12} = 0.80$, $p = 0.47$	$F_{2,12} = 56.54$, $p = 0.01^*$	$F_{1,11} = 1.32$, $p = 0.30$	–	–	–
Tukey HSD for Site	Round Marsh ^b Fox Hill ^b Sage Lot ^a	Round Marsh ^b Fox Hill ^{ab} Sage Lot ^a	Round Marsh ^b Fox Hill ^a Sage Lot ^a	Round Marsh ^c Fox Hill ^b Sage Lot ^a	Round Marsh ^b Fox Hill ^a Sage Lot ^{ab}	–	Round Marsh ^a Fox Hill ^a Sage Lot ^a	–

F statistics, degrees of freedom, and significance values are reported for 2-factor (Veg. Type x Site) ANOVA tests

In the Tukey HSD row, sites not connected by the same letter are significantly different

*= Significant at $\alpha = 0.05$

methanogens in the form of rhizodeposition or litter (as reviewed in Lovell 2005).

In salt marshes, plant zonation follows strong gradients in multiple environmental conditions. Significantly larger emissions from *Phragmites* than from native vegetation zones at all sites along the salinity gradient may thus reflect a combination of edaphic and plant-driven factors. CH₄ emissions differed between zones despite similarity in mid-growing season surface soil variables (pH, redox, temperature, moisture, and organic content), a finding that may suggest direct CH₄ emission enhancement by *Phragmites*. However, the similarity of edaphic variables in surface soils (0–15 cm) does not rule out potential for significant differences in these and other factors between vegetation zones at depths greater than we sampled. *Phragmites*' ability to alter conditions in its rhizosphere environment is well-documented, with reported effects including decreased surface soil salinity (Windham and Lathrop 1999), oxygenation of the rhizosphere (Colmer 2003) and enhanced sediment accretion (Rooth et al. 2003). Given the plant's characteristic deep (up to 1 m) root system (Brix 1987; Moore et al. 2012), it is reasonable to suspect that *Phragmites* rhizosphere conditions may have contributed to the observed pattern of CH₄ emissions.

While this study found differences in CH₄ emissions between *Phragmites* and native high marsh vegetation zones, an

investigation comparing GHG fluxes between *Phragmites* and low marsh native *Spartina alterniflora* did not. Emery and Fulweiler (2014) measured GHG fluxes between January and September from *Phragmites* and *S. alterniflora* zones at Plum Island Estuary (mesohaline) and found that GHG fluxes (CO₂, CH₄ and N₂O) at this site did not differ between the two vegetation zones. The authors' reported growing season CH₄ fluxes were highly variable, but generally fall within the ranges of those we observed at higher-salinity sites. Their single exceptionally high *S. alterniflora* CH₄ flux of over 18,000 $\mu\text{mol m}^{-2} \text{h}^{-1}$, however, exceeds our greatest measured fluxes at any site by an order of magnitude. The discrepancy between our findings and those of Emery and Fulweiler are likely due a combination of methods differences, key ecophysiological differences in *S. alterniflora* and the high marsh species *S. patens* and *D. spicata*, and effects of the season during which measurements were conducted. In addition, the ability of CRDS technology to detect fluxes over much shorter periods than gas chromatograph-based methods (6–10 min vs. 60 min) may have allowed for better differentiation between vegetation zones.

In a mesocosm experiment, greater CH₄ emissions were attributed to more abundant biomass of invasive relative to native *Phragmites* (Mozdzer and Megonigal 2013). In our study, however, metrics indicative of *Phragmites* biomass

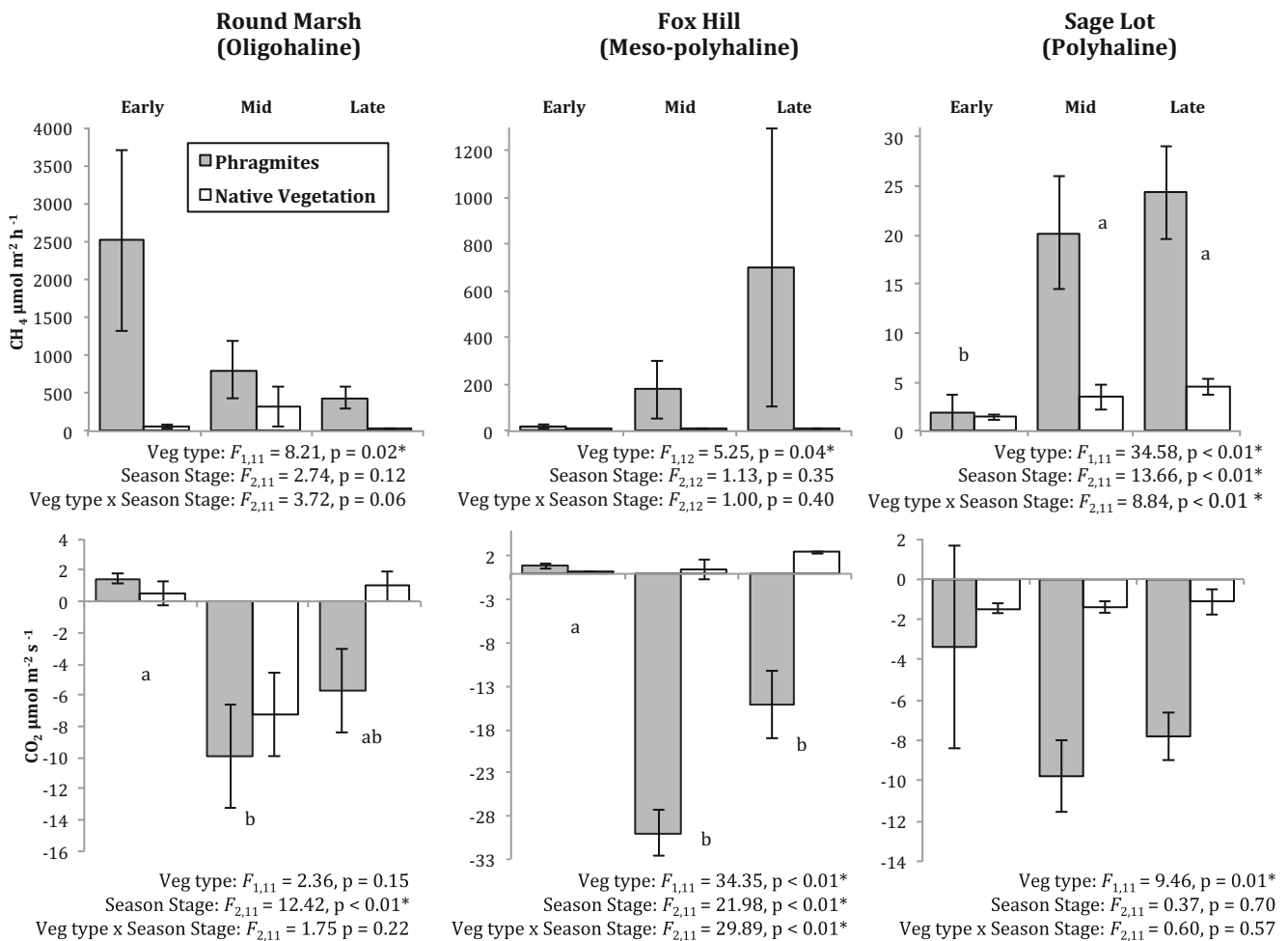


Fig. 2 Average CH₄ (top row) and CO₂ (bottom row) fluxes during the early (April–May), mid (June–July) and late (August) growing season stages at the three study sites. Standard error bars are shown. Lowercase letters indicate significant differences between growing

season periods; season flux measurements not connected by the same letter are significantly different. F statistics, degrees of freedom, and significance values are reported for two-way (Veg. Type x Seasonal Stage) ANOVA tests * = Significant at $\alpha = 0.05$

(stem density and height) did not correlate with CH₄ emissions, suggesting that differences in subsurface soil conditions or belowground biomass may instead be responsible for observed patterns of CH₄ fluxes.

Greater CO₂ Uptake by *Phragmites* Zones may Suggest Potential for Enhanced C Sequestration

Greater CO₂ uptake by *Phragmites* relative to native vegetation zones over the course of the growing season at Fox Hill and Sage Lot is reasonable given *Phragmites*' substantially greater biomass (Windham 2001) (and therefore more photosynthetic uptake) relative to smaller native high marsh species. At oligohaline Round Marsh, mid-growing season uptake by native vegetation greater than that measured at other sites could be due to greater aboveground biomass (which was not measured in this study) or to reduced salinity stress.

At Round Marsh and Sage Lot, mid-season *Phragmites* zone CO₂ uptake is similar to that reported by Emery and

Fulweiler (2014) (approximately 11 μmol m⁻² s⁻¹). Mid-growing season uptake at intermediate-salinity Fox Hill, however, averaged more than twofold greater at about 30 μmol m⁻² s⁻¹. Such difference in uptake magnitude between Fox Hill and Sage Lot is surprising since *Phragmites* live stem densities and heights were similar between these sites (Table 3), and may suggest an influence of soil-driven CO₂ emission that counters plant-mediated uptake at Sage Lot.

Although CH₄ fluxes in *Phragmites* zones were larger than in native vegetation zones, they were small compared to measured *Phragmites* zone CO₂ uptake rates on a gram-to-gram C basis. Therefore, based on daytime, low tide fluxes measured during this growing season study, net CH₄ emissions were not sufficient to offset net CO₂ uptake. However, CO₂ uptake is diminished (and emissions therefore increased) during the evening, and studies over annual or tidal cycles will likely exhibit reduced overall uptake of CO₂.

Phragmites' substantial increase in daytime CO₂ uptake relative to native vegetation, coupled with its known slow

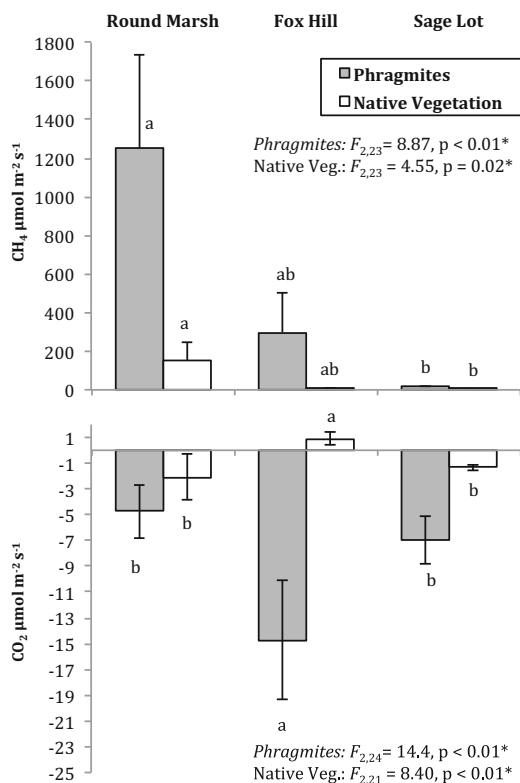


Fig. 3 Average CH₄ (top) and CO₂ (bottom) fluxes from *Phragmites* and native vegetation zones averaged over the growing season (Early, Mid and Late seasonal stages) for each site. *F* statistics, degrees of freedom, and significance values are reported for one-factor ANOVA tests for site differences. Lowercase letters represent the results of a Tukey HSD test. Bars within vegetation type not connected by the same letter are significantly different. * = Significant at $\alpha = 0.05$

rates of decomposition and high productivity rates relative to *S. patens* (Windham 2001) and its promotion of marsh accretion (Rooth et al. 2003), may suggest that its presence could ultimately enhance marsh C sequestration. However, such a conclusion must be based on more detailed temporal GHG flux measurements (seasonal and diel), including longer term gas ebullition studies, and coupled with measurements of long-term C sequestration rates.

Comparing GHG Emissions Across Seasonal Stages and Complex Environmental Gradients

Since *Phragmites* commonly invades marshes from the landward edge (Amsberry et al. 2000) and therefore displaces native high marsh species, GHG fluxes need to be characterized in order to assess ecosystem-scale response to a changing vegetation community. This study broadens understanding of growing season patterns of daytime CO₂ and CH₄ fluxes across the complex marsh landscape and over a growing season period.

Phragmites zones exhibited distinct temporal CH₄ flux trends along the salinity gradient, with fluxes increasing over the course of the growing season in the meso-polyhaline sites and decreasing at the oligohaline site. The observed increase in net CH₄ emissions from early to late seasonal stages in the more saline sites may imply a role of plant-mediated transport and/or an increase as the growing season progresses in microbial CH₄ production that is not being offset by increased microbial CH₄ oxidation. At the oligohaline site, observed temporal patterns of CH₄ fluxes may imply that vegetation presence decreases CH₄ emissions (potentially by soil oxygenation) and/or that microbial CH₄ production decreases as the growing season progresses.

The difference in CH₄ emissions between sites is consistent with the known control of salinity on marsh CH₄ emission (Bartlett et al. 1987; Mitsch and Gosselink 2000; Poffenbarger et al. 2011; Madigan 2012), but other variables (soil moisture, redox potential, and pore water sulfide concentration) also vary along the salinity gradient. CH₄ emissions were greatest at Round Marsh, the site of lowest soil salinity, moisture and porewater sulfide and least reduced conditions, and smallest at Sage Lot, which was characterized by greatest soil salinity, moisture and sulfide concentrations and most reduced conditions. Fox Hill's soil conditions were intermediate. These findings support known roles of salinity and sulfate availability as strong predictors of marsh CH₄ emission magnitude, but contradict known positive relationships between methanogenesis and anaerobic, reduced soil conditions. Given the difficulty in determining relative contributions of soil variable and plant-mediated effects on GHG fluxes, future research should be directed toward experimentation to discern biotic and abiotic feedbacks along these environmental gradients.

Conclusions

Phragmites-dominated zones were characterized by significantly larger daytime CH₄ emissions than native high marsh vegetation zones along the natural salinity gradient, and larger daytime CO₂ uptake rates were observed in *Phragmites* zones in meso-polyhaline marshes. Although this study is not able to discern relative impacts of physical and biological controls on observed CO₂ and CH₄ fluxes, it reveals differences between two marsh zones for which GHG fluxes had not previously been compared and therefore confirms a need for future manipulative experiments to test mechanisms driving flux differences. In order to determine whether *Phragmites* may affect marsh net GHG uptake and C sequestration in the long term, future studies should monitor GHG fluxes over annual and diel cycles and investigate how rates of *Phragmites*-zone C sequestration compare with rates in native vegetation zones.

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