

Carbon dioxide fluxes reflect plant zonation and belowground biomass in a coastal marsh

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Abstract. Coastal wetlands are major global carbon sinks; however, they are heterogeneous and dynamic ecosystems. To characterize spatial and temporal variability in a New England salt marsh, greenhouse gas (GHG) fluxes were compared among major plant-defined zones during growing seasons. Carbon dioxide (CO₂) and methane (CH₄) fluxes were compared in two mensurative experiments during summer months (2012–2014) that included low marsh (*Spartina alterniflora*), high marsh (*Distichlis spicata* and *Juncus gerardii*-dominated), invasive *Phragmites australis* zones, and unvegetated ponds. Day- and nighttime fluxes were also contrasted in the native marsh zones. N₂O fluxes were measured in parallel with CO₂ and CH₄ fluxes, but were not found to be significant. To test the relationships of CO₂ and CH₄ fluxes with several native plant metrics, a multivariate nonlinear model was used. Invasive *P. australis* zones (–7 to –15 μmol CO₂·m^{–2}·s^{–1}) and *S. alterniflora* low marsh zones (up to –14 μmol CO₂·m^{–2}·s^{–1}) displayed highest average CO₂ uptake rates, while those in the native high marsh zone (less than –2 μmol CO₂·m^{–2}·s^{–1}) were much lower. Unvegetated ponds were typically small sources of CO₂ to the atmosphere (<0.5 μmol CO₂·m^{–2}·s^{–1}). Night-time emissions of CO₂ averaged only 35% of daytime uptake in the low marsh zone, but they exceeded daytime CO₂ uptake by up to threefold in the native high marsh zone. Based on modeling, belowground biomass was the plant metric most strongly correlated with CO₂ fluxes in native marsh zones, while none of the plant variables correlated significantly with CH₄ fluxes. Methane fluxes did not vary between day and night and did not significantly offset CO₂ uptake in any vegetated marsh zones based on sustained global warming potential calculations. These findings suggest that attention to spatial zonation as well as expanded measurements and modeling of GHG emissions across greater temporal scales will help to improve accuracy of carbon accounting in coastal marshes.

Key words: biological invasion; blue carbon; emissions; global climate changes; *Juncus gerardii*; methane; nitrous oxide; sea-level rise; *Spartina alterniflora*.

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INTRODUCTION

Coastal salt marshes rank among the most productive ecosystems on the planet (Mcleod et al. 2011) and are valued for numerous services including habitat provision for wildlife, nutrient retention (Valiela and Cole 2002), water quality improvement (Valiela and Cole 2002), and coastal stabilization (Constanza et al. 2008). Along with seagrasses and mangroves, salt marshes have among the highest rates of biological carbon (C) sequestration of all ecosystems (Mcleod et al. 2011). The C sequestered in salt marshes and other coastal marine ecosystems is referred to as “blue carbon” (Mcleod et al. 2011). The unique combination of high rates of primary productivity by vascular plants and slow rates of decomposition in mostly anoxic soils creates major carbon dioxide (CO₂) sinks. Further, high salinities in coastal wetlands make them negligible methane (CH₄) sources (Poffenbarger et al. 2011), which is significant given that CH₄ has a sustained global warming potential of 45 times that of CO₂ (Neubauer and Megonigal 2015). However, intertidal marshes live in highly dynamic and heterogeneous environments. Salt marshes have been found to produce larger and more variable CH₄ and CO₂ fluxes than adjacent sandy intertidal zones (Hirota et al. 2007). They are defined by strong physical gradients in tidal flushing, salinity, and elevation along which major shifts in plant community composition occur (Nixon 1982, Bertness 1992). Therefore, rates of carbon exchange between the ecosystem and atmosphere may be highly variable across a marsh landscape.

Ecological interactions between plants and microorganisms drive greenhouse gas (GHG) fluxes. Thus, patterns in GHG fluxes may reflect patterns of vascular plant presence, plant species composition, and/or abiotic factors. In western Atlantic coastal marshes, productive cordgrasses (e.g., *Spartina alterniflora*) typically dominate the lowest, most inundated zones due to unique adaptations such as aerenchyma (internal gas-filled spaces) that enable them to tolerate frequent inundation by oxygenating roots and surrounding sediments (Maricle and Lee 2002, Colmer 2003). The aerenchyma facilitates bidirectional gas exchange and therefore may increase fluxes of GHGs between anoxic marsh

soils where microbes are active and the atmosphere. Historically, at the higher elevations, denser, more shallowly rooted species (*Distichlis spicata*, *Spartina patens*, *Juncus gerardii*) better competed for the least stressful habitats (Bertness 1992, Bertness and Leonard 1997). Their smaller stature and less extensive ventilation of marsh soils may translate into lower GHG fluxes. Drier, more oxic soils in the high marsh zone may also result in lower rates of GHG production. Both field and mesocosm studies have described positive relationships between marsh plant biomass and trace gas fluxes (Cheng et al. 2007, Hirota et al. 2007), potentially because plants fuel microbial respiration by exuding labile carbon into rhizospheres and/or due to their role as gas conduits. Meanwhile, unvegetated, permanently inundated ponds may offer physical barriers to gas diffusion and/or the soils underlying shallow ponds may be active sites of organic matter decomposition due to high temperatures and low burial rates. While ponds are naturally occurring in marshes, their presence is thought to be facilitated by human-derived impacts such as mosquito-ditching, drainage, and their prevalence may be increasing in response to sea-level rise.

Invasive species, such as *Phragmites australis*, are major agents of change in coastal New England marshes that alter historical plant-defined zonation gradients in marshes. Along terrestrial borders, shoreline development promotes invasion by the genetically diverse reed, *P. australis* (Chambers et al. 2003, Silliman and Bertness 2005, Kirk et al. 2011, Meyerson and Cronin 2013). *P. australis* is highly tolerant of waterlogging, in part due to minimal radial oxygen loss via the formation of tight apoplastic barriers in growing roots (Soukup et al. 2007). The introduction of *P. australis* has dramatically transformed New England native high marsh plant communities into dense, tall (2–4 m) monospecific stands (Weinstein and Balletto 1999, Parsons 2003). With massive aboveground and deeply rooting belowground structures (Mozdzer et al. 2013), invasive *P. australis* has exceptional potential to increase exchange of gases between wet soils and the atmosphere and may increase CO₂ uptake in coastal marshes through increased photosynthetic activity to a greater extent than the native species it often replaces (Martin and

Moseman-Valtierra 2015). In order to predict how GHG fluxes may shift in response to changes in plant community composition, including biological invasion by *P. australis*, key controls on GHG fluxes must be better understood.

The central goal of this research was to examine differences in GHG fluxes associated with contrasting plant-defined zones across a New England marsh landscape. Specifically, we compared GHG fluxes across native (high and low marsh), *P. australis*-invaded, and permanently inundated zones in a salt marsh at Sage Lot Pond in Waquoit Bay, Massachusetts. CO₂ and CH₄ fluxes were measured during summer months in two mensurative experiments that spanned from 2012 to 2014 by deploying laser-based absorption GHG analyzers. We compared daytime and nighttime fluxes in the two major native marsh zones on a subset of dates. We also measured primary production (above- and belowground), stem density, and plant height in the two native marsh zones and tested the relationships of CO₂ and CH₄ fluxes with these plant properties using a new data-analytics and modeling approach.

METHODS

Site description

Sage Lot Pond is a 34-acre shallow (1 m deep at low tide) estuary within the Waquoit Bay National Estuarine Research Reserve, Falmouth, Massachusetts, on the south shore of Cape Cod (Fig. 1). This site has very little surrounding housing development and thus receives a small anthropogenic nitrogen (N) load (average total N concentrations in groundwater are reported at 38 μM, Kroeger et al. 2006). Nitrogen loadings for Sage Lot Pond were estimated to be 9 kg N·ha⁻¹·yr⁻¹ (McClelland et al. 1997). Air temperatures ranged annually between 2013 and 2014 at Sage Lot Pond from -15° to 37°C and water temperatures ranged from -1° to 30°C (NERRS 2012). Sage Lot Pond experiences mean tidal amplitudes of approximately 0.3 m (Lever and Valiela 2005). Based on 2012 plant species distributions, the portion of Sage Lot Pond included in the study site area (Fig. 1) consists of *Spartina alterniflora*-dominated low marsh (42% by area), a mixed high marsh community (9% by area), permanently inundated zones (11% by area), and invasive *P. australis* (12%). Other

habitat types within the study site area, but not included in data collection, are comprised of sedges and cattails (2%), creeks (1%), and upland marsh borders (22%; J. Mora, unpublished data).

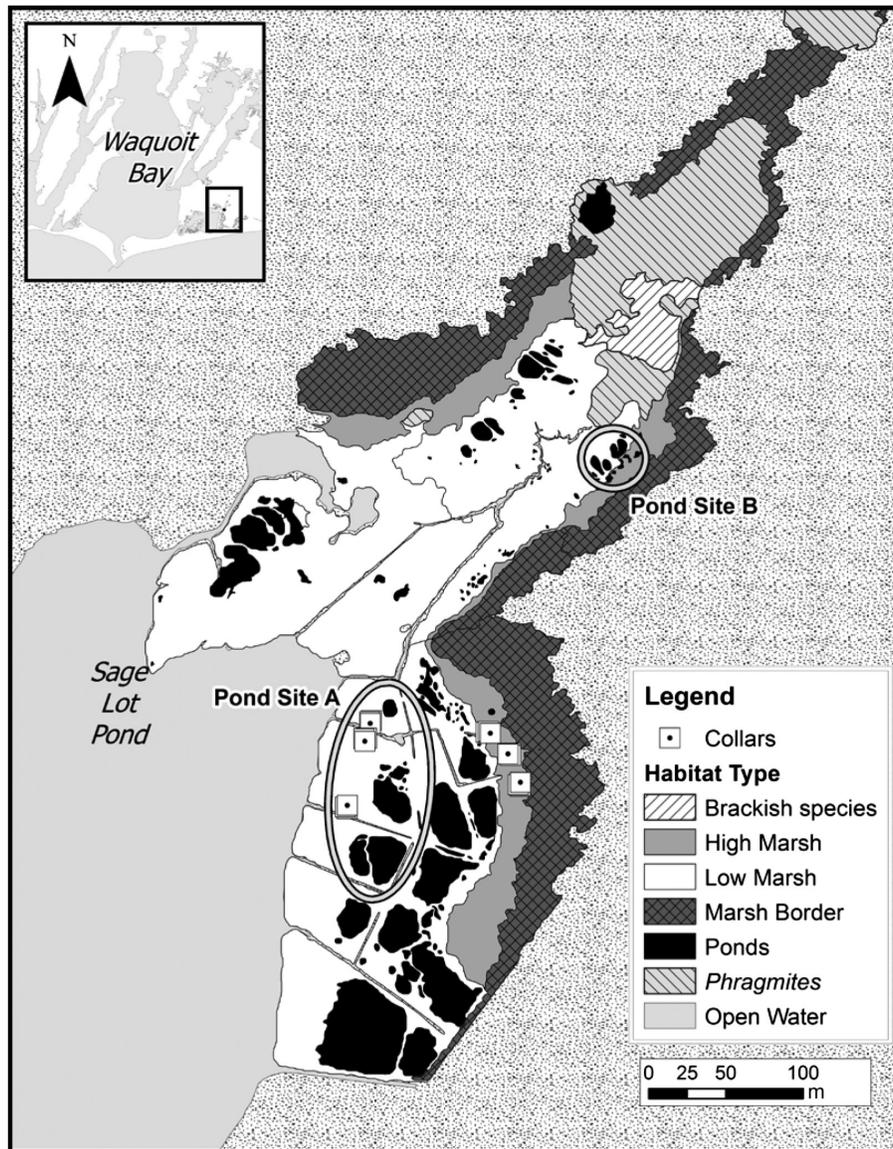
Greenhouse gas fluxes

CO₂ and CH₄ fluxes were compared across major plant-defined marsh zones (low marsh, high marsh, invasive *P. australis*, and permanently inundated zones) of Sage Lot Pond during summer months in 2012–2014. To draw comparisons of the zones at similar times, we divided our analyses into two mensurative experiments (Table 1). Mensurative Experiment 1 (2012–2013) focused on contrasts of the native low and high marsh zones (Table 1). Mensurative Experiment 2 (2013–2014) focused on comparisons of the high marsh zone with unvegetated ponds and invasive *P. australis* zones (Table 1). Although it was not generally feasible to analyze all zones on the same date, CO₂ and CH₄ fluxes were compared across all four plant zones (within approximately a 4-h period in total) on two dates (July 2013 and July 2014). On three dates, carbon flux measurements were repeated in both day- and nighttime in the native high and low marsh zones.

For mensurative Experiment 1, three plots were established in both the *S. alterniflora*-dominated low marsh zone and *J. gerardii* and *D. spicata*-dominated high marsh zone at Pond Site A for soil, plant, and GHG flux measurements (Fig. 1), except August 2012 when only two high marsh plots existed. Each plot consisted of three subplots (56 cm × 56 cm) arranged around the end of a boardwalk that stood approximately 0.5 m above the marsh surface, clustered within one meter of each nearest neighbor.

For mensurative Experiment 2, three plots were established in both the high marsh and *Phragmites australis*-invaded zones and in three permanently inundated areas at Pond Site B (Fig. 1). These high marsh plots were selected because they were closer to *P. australis* than those in mensurative Experiment 1. Three subplots existed in the high marsh (56 cm × 56 cm), and two subplots in the *Phragmites australis*-invaded zone (spaced 0.3 m apart, with 30 m between the three replicate plots).

Measurements were taken within 3 h of low tide to minimize variability in data brought on



Project funded by NERRS Science Collaborative. Map by J. Mora, Waquoit Bay NERR, Sept 2015. Habitat zones based on 2012 NIR aerial photographs (0.25-m resolution).

Fig. 1. Map of Sage Lot Pond field site in the Waquoit Bay National Estuarine Research Reserve. Squares mark an area for triplicate plots as detailed in the *Methods* section.

by tidal cycling. Different zones were measured as closely as possible to each other (alternating order of zones between dates) to maximize similarity of weather (light, temperature) and tidal conditions. All subplots were averaged prior to statistical analyses.

Gas fluxes were measured during daytime with a transparent chamber to reflect the net result of photosynthesis and respiration in the

marsh plots. To observe contrast between day- and nighttime fluxes, all plots in the low and high marsh zones were compared on three dates per zone during summer 2013 by repeating measurements in random sequence for each plot under light and dark conditions. On two dates, nighttime fluxes were measured approximately 1 h prior to sunset using a dark tarp covering the flux chamber for logistical expediency.

Table 1. Overview of Experiments 1 and 2 including the list of sampling dates and zones for greenhouse gas flux measurements.

Experiments	Date	Gas fluxes
Experiment 1	27-Aug-12	LM and HM
	†5-Jun-13	
	†19-Jun-13	
	†10-Jul-13	
	19-Jul-13	
Experiment 2	14-Aug-13	LM, HM, Phrag, Pond HM2, Phrag, Pond
	27-May-14	
	24-Jun-14	
	11-Jul-14	
	21-Aug-14	
	9-Jul-14	LM, HM, Phrag, Pond

Note: LM = low marsh, HM = high marsh, Phrag = *Phragmites australis*-invaded zones, pond = permanently inundated zone.
† Day- and nighttime measurements completed.

CO₂ and CH₄ fluxes were measured by connecting a cavity ring-down spectrometer (Model G2301; Picarro Inc., Santa Clara, California, USA) to a transparent acrylic chamber (60 cm × 60 cm ft × 60 cm) in a closed loop. N₂O fluxes were measured by also connecting a N₂O/CO gas analyzer (Los Gatos Research, Mountain View, California, USA) to the same chamber. The chamber contained two battery-powered fans to homogenize the air inside, pigtailed to prevent pressure accumulation (inner diameter of 0.71 mm), and four ports to connect to inlets and outlets of both analyzers in a closed loop system. Square steel collars (56 cm × 56 cm) sealed the base of the chambers and were preinstalled (at least 1 month prior to first measurements) to a depth of approximately 20 cm.

All gas fluxes were calculated from linear rates of change in gas concentrations in each chamber over time using the ideal gas law (as detailed in Martin and Moseman-Valtierra 2015). Changes in gas concentrations over time (dC/dt) were analyzed with linear regressions. We define positive fluxes as those in which gas concentrations increased over time within a chamber (representing vertical emission from the marsh surface to the atmosphere), and negative fluxes as those in which concentrations decreased (representing net uptake from the atmosphere to the marsh). Significant fluxes were defined based on R^2 values of 0.90 or greater and P -values of 0.05 or less. In cases in which both CH₄ and CO₂ fluxes

showed insignificant R^2 and P -values, the data were discarded (<5% of cases) as they were interpreted to indicate experimental errors (i.e., plot disturbance). The remainder of insignificant CH₄ fluxes (about 2%) in field plots with clear and significant CO₂ fluxes (i.e., not suggestive of any experimental error from plot disturbance) were defined as 0. No significant N₂O fluxes were detected during these experiments in approximately 90 measurements in low and high marsh zones across five dates and 63 measurements in high marsh, *Phragmites*, and pond zones across seven dates (all slopes were close to 0 ppm/s). Therefore, N₂O fluxes are not discussed further.

Plant properties

To test the potential relationships between ecological characteristics and gas fluxes, a suite of plant properties were examined. Native plant community composition and stem density were determined in June and August 2013 by identifying and counting plants in small quadrats (25 cm × 25 cm for the low marsh and 10 cm × 10 cm for the high marsh) within 1 m of each gas flux collar. Because marsh plant communities are uniform and homogenous within zones, it was not necessary to include flux collars in plant community composition surveys. Heights of 10 randomly selected shoots (of *S. alterniflora* in each of the low marsh quadrats and of *J. gerardii* in each of the high marsh quadrats) were measured in June and August 2013.

Native aboveground plant biomass was measured in June, July, and August 2013 in the low marsh zone via clipping of the ground and harvest of all material from the quadrats. In the high marsh zone, aboveground biomass was measured in June and August 2013 only in a 25 cm × 25 cm quadrat (placed around the smaller 10 cm × 10 cm quadrat for plant density). Live and dead aboveground biomass was separated prior to drying and weighing.

Native belowground plant biomass was determined by collecting cores (50 cm deep) within 1 m of each of the triplicate collars for gas flux measurements after clipping. In the low marsh, belowground biomass was determined in June and August 2013. For the high marsh, measurements were only taken in late summer due to logistical limitations. In the low marsh, a Russian peat corer was used (5 cm diameter), while in the high marsh,

a PVC core (5.08 cm diameter) was used. These coring devices were compared and found to not yield significantly different biomass estimates (data not shown). Cores were sectioned into 10-cm intervals and stored at -20°C until analysis. Each 10-cm section was washed through a 1-mm sieve to separate sediment, roots (<2 mm diameter), and rhizomes (>2 mm diameter). We did not distinguish between live and dead for the roots and rhizomes. All biomass samples (above- and belowground) were dried at 60°C for 48 h prior to weighing.

In *P. australis* (live and dead stems) and immediately adjacent high marsh zones (Pond Site A), stem density was measured inside of each flux collar at the time of gas flux measurements (0.068 m^2) in July 2013, May 2014, and July 2014. In 2014, average stem height of *P. australis* and the adjacent native high marsh plants was also quantified inside of the gas flux bases by measuring and averaging heights of 10 randomly selected stems. No biomass was measured for these plant communities due to logistical constraints.

Surface soil and pore water properties

Pore water sulfide, soil moisture, and salinity were measured within gas flux plots in each vegetated marsh zone. Pore water (at least 10 mL) was collected from each native zone plot on as many dates as possible (Table 1). Water was sampled within 1 h of gas flux measurements from 0 to 10 cm depths using Rhizon samplers (Soil Moisture Co., Goleta, California, USA) and preserved in equal volumes of 1 M zinc acetate and stored frozen (-17°C) for pore water sulfide analyses (following Cline 1969). Soil moisture content was measured (three times per plot in random locations between plant culms) by inserting an EC-5 soil sensor to a depth of 5 cm (Decagon Devices, Pullman, Washington, USA). Soil pH was measured by collecting a surface plug of soil (approximately 5 mL), adding to 10 mL of distilled water in a sterile centrifuge tube, and immediately measuring the pH of the resulting slurry (Orion Star A326 Multiparameter Meter; Thermo Scientific, Pittsburgh, Pennsylvania, USA). In all 2014 dates, soil pH methods were switched (for expediency) to use of a surface probe pH meter (Ex Stick Instruments, Nashua, New Hampshire, USA). Comparisons indicated that these probes were comparable (data not shown). Salinity of water (filtered and squeezed)

from surface (approximately top 2 cm) sediments was measured with a handheld refractometer.

Statistical analyses

Greenhouse gases.—For Experiment 1, a two-factor ANOVA was used to compare average GHG fluxes between native (high and low marsh) zones and across dates. To compare GHG fluxes between high marsh, *P. australis*, and pond zones, data were also analyzed using a two-factor ANOVA (factors = zone and date). For two dates (July 2014 and July 2013) with data from all four zones (including the low marsh), separate single-factor ANOVAs were applied on each date. Methane fluxes were generally not normally distributed, and thus, they were log-transformed prior to statistical analyses. Two anomalies were excluded from analyses of methane fluxes because they were orders of magnitude higher than the rest of the fluxes in this study (306 and $227\ \mu\text{mol CH}_4\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ in the high marsh in 2012 and low marsh in 2014, respectively). These anomalies likely reflected ebullition brought upon by plot disturbance and therefore excluded from methane flux analysis as inclusion would misrepresent fluxes and skew data.

To compare day- and nighttime fluxes of CO_2 and CH_4 from both marsh zones (in summer 2013), paired *t* tests were used due to limited data sets. Separate paired *t* tests were carried out for low marsh and high marsh due to differences in the specific dates on which the day-night comparisons were drawn.

Edaphic properties.—To test for temporal variation in salinity and moisture, two-factor ANOVAs were applied (factor 1 = date and factor 2 = zone). Separate analyses were performed for Experiments 1 and 2. Due to limited data sets, average pH and pore water sulfide were compared either between native plant zones (Experiment 1) or between *P. australis* and adjacent native high marsh (Experiment 2) across all dates using paired *t* tests.

Plant properties.—Aboveground plant biomass, height, total density, and percentage species composition were compared between high and low marsh zones (Pond Site B) using *t* tests with separate analyses in June and August 2013. Belowground root and rhizome biomass at the end of the growing season (August 2013) was compared for high and low marsh zones and

sampling depth intervals (0–10, 10–20, 30–40, 40–50 cm) using two-factor ANOVAs (marsh zone and sampling depth as the two factors).

Phragmites australis density was compared with that of adjacent high marsh native zones (Pond Site A) in July 2013. Heights were compared in May and July 2014 with separate *t* tests on each date.

For all ANOVAs, Tukey's HSD tests were used as post hoc tests to determine which groups significantly differed from each other.

Testing relationships of coastal marsh plant properties with GHG fluxes: modeling approach

To investigate the relative controls of different plant variables on CO₂ and CH₄ fluxes, a multivariate data-analytics framework, proposed by Ishtiaq and Abdul-Aziz (2015), was applied. The method included a Pearson correlation matrix, principal components analysis (PCA), factor analysis (FA), and explanatory multiple regression modeling. The following data were examined from high marsh and low marsh zones: daytime CO₂ and CH₄ fluxes (F_{CO_2} and F_{CH_4} , respectively), aboveground biomass (AGB), belowground biomass (BGB), stem density (SD), and plant height (PnH). While it is widely recognized that several environmental factors (light, temperature, salinity) affect carbon fluxes, our analyses focused only on those plant properties, in part due to the relatively limited environmental data set and also because our objective was to test the relationships of plant metrics with GHG fluxes. The analyses focused on native high and low marsh zones only in summer 2013 because it was the most complete subset of data for these factors. Data were filtered such that gaps for any participatory variable resulted in the exclusion of the corresponding data panel from the final data set. Further, three remotely outlying CH₄ observations were detected through visual inspections and the corresponding data panels removed from further analyses, leading to 16 instantaneous daytime observation panels for three dates (June, July, and August 2013). All data were log₁₀-transformed to incorporate the nonlinear process interactions. Further, log-transformed data for each variable were centered around the respective mean and normalized by the SD (i.e., obtaining Z-scores) to eliminate the disparity of units among the variables and bring all variables to a comparable reference scale.

The emergence of the overall outcomes from the entire data-analytics framework, rather than that of an individual analysis, can provide a complete and confirmatory representation of the relative linkages of predictors with the response (Ishtiaq and Abdul-Aziz 2015). Due to the multicollinear structure (e.g., mutual correlations of plant variables) of the data matrix, the correlation coefficients (*r*) alone provide a preliminary and an incomplete understanding on the dependency between the gas fluxes and plant variables. In contrast, the orthogonal (i.e., independent) component-based PCA resolves multicollinearity and unravels relationships hidden in the data, allowing interpretations that are difficult to achieve with a Pearson correlation matrix. For example, the PCA depicted the interrelation and grouping patterns of variables through biplots with the two major principal components (PCs) while corroborating the preliminary findings obtained through the correlation analysis. Factor analysis (FA) was applied to verify the findings from PCA and achieve further insights using transformation of the original variables to a small set of uncorrelated latent (i.e., unobservable) variables or factors. FA with an optimal number of orthogonal dimensions (i.e., factors) indicated the dominant variables in explaining the overall biological–ecological data variance. The optimal number of factors was extracted based on an initial eigenvalue criterion (eigenvalue > 1) to ensure that the extracted factors optimally explained the overall data-system variance. Further, a “varimax” orthogonal rotation was performed in the FA to maximize the loadings (i.e., correlation) of the variables on each extracted factor. Multiple nonlinear regression models were then estimated to quantify the relative linkages (i.e., weights) of different biological variables with the fluxes. Because data were log-transformed and standardized to Z-scores, only absolute values of the correlation coefficients, factor loadings, and regression coefficients (BETA) were considered when interpreting the results. More details on the data-analytics method can be found in Ishtiaq and Abdul-Aziz (2015).

RESULTS

Greenhouse gas fluxes: marsh zone comparisons

In Experiment 1, daytime CO₂ fluxes from the low marsh zone were significantly greater than

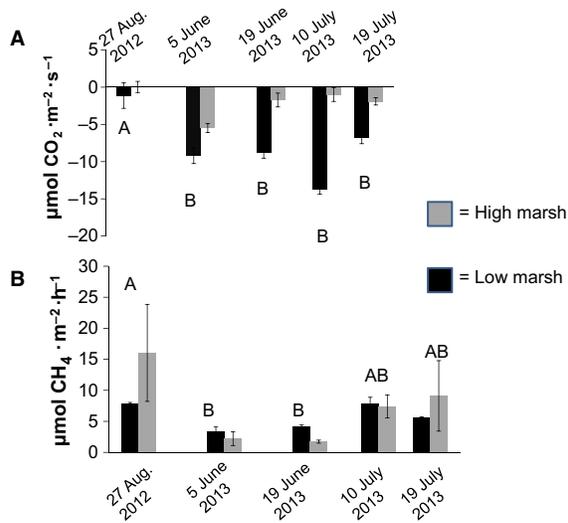


Fig. 2. Comparison of (A) average CO_2 fluxes ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and (B) average CH_4 fluxes with SE bars between high (dark bars) and low marsh zones (light bars) on a series of dates from summer 2012 to summer 2013 (Experiment 1).

in the high marsh zone at Pond Site A (Fig. 2A, Table 2). In both zones, CO_2 fluxes were generally negative, indicating that photosynthetic rates exceeded respiration rates in the daytime (Fig. 2A). However, daytime CH_4 fluxes did not significantly differ between native zones and were consistently positive, indicating net emission of the gas (Fig. 2B, Table 2).

In Experiment 2, CO_2 fluxes were significantly larger (and negative) for *P. australis* than for the high marsh or pond zones (Fig. 3A, Table 2). Ponds were unique among all zones in displaying positive fluxes (net emissions) of CO_2 on multiple dates rather than negative fluxes (net CO_2 uptake; Fig. 3A). CH_4 fluxes were also larger (and positive) for *P. australis* zones than for high

marsh or pond zones (Fig. 3B, Table 2). The high marsh zone did not significantly differ from unvegetated pond zones in terms of either CO_2 or CH_4 fluxes.

Overall, CO_2 fluxes were much larger than CH_4 fluxes for all zones, even for the *P. australis* zone. The largest CO_2 and CH_4 fluxes (average of $-15 \mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and $50 \mu\text{mol CH}_4\cdot\text{m}^{-2}\cdot\text{h}^{-1}$) were seen in the *P. australis* zone during July 2013 (Fig. 3). This was the first date (one of two) on which all four marsh zones were simultaneously measured. On that date, CO_2 fluxes were significantly larger in *P. australis* than in the two native marsh and pond zones ($F_{3,13} = 21.61$, $P < 0.001$), while CH_4 emissions were significantly greater from the *P. australis* zone than from the high marsh zone ($F_{3,13} = 4.36$, $P = 0.03$). In contrast, native marsh zones and ponds were similar in terms of both gases. On the second comparison of four zones (in July 2014), CO_2 fluxes remained largest in the *P. australis* zone and the low marsh had intermediate fluxes, while the high marsh and ponds remained lowest ($F_{3,10} = 46.85$, $P < 0.001$). Methane fluxes did not significantly vary between the four zones on that date ($F_{3,10} = 0.85$, $P = 0.51$).

Greenhouse gas fluxes: diel patterns in native marsh zones

In both the low and high marsh zones, daytime CO_2 fluxes were consistently negative, while nighttime fluxes were positive (Fig. 4). The magnitude of daytime CO_2 fluxes was significantly greater than the magnitude of nighttime fluxes in the low marsh ($t_2 = -4.35$, $P = 0.05$, Fig. 4). In contrast, the high marsh showed only a trend of larger CO_2 fluxes in daytime than in nighttime ($t_2 = -3.39$, $P = 0.08$, Fig. 4). There, highest average nighttime fluxes were 3.2

Table 2. Summary of statistical results for two-factor ANOVA testing differences in daytime CO_2 and CH_4 fluxes between marsh zone and sampling dates at Pond Site A (Experiment 1) and at Pond Site B (Experiment 2).

Experiments	Variables	Whole model	Zone effect	Date effect	Zone \times date interaction
1	CO_2 fluxes	$F_{17,54} = 30.21$, $P < 0.001$	$F_2 = 211.61$, $P < 0.001$	$F_5 = 4.90$, $P = 0.001$	$F_{10} = 3.29$, $P = 0.04$
	CH_4 fluxes	$F_{17,54} = 4.44$, $P < 0.001$	$F_2 = 17.14$, $P < 0.001$	$F_5 = 4.90$, $P = 0.001$	$F_{10} = 1.49$, $P = 0.18$
2	CO_2 fluxes	$F_{9,25} = 21.84$, $P < 0.01$	$F_1 = 81.73$, $P < 0.001$	$F_4 = 14.76$, $P < 0.001$	$F_4 = 9.84$, $P = 0.003$
	CH_4 fluxes	$F_{9,24} = 2.41$, $P = 0.06$	$F_1 = 1.30$, $P = 0.27$	$F_4 = 5.00$, $P = 0.008$	$F_4 = 0.26$, $P = 0.90$

Note: Significant effects and interactions (at $\alpha = 0.05$ levels) are highlighted in bold font.

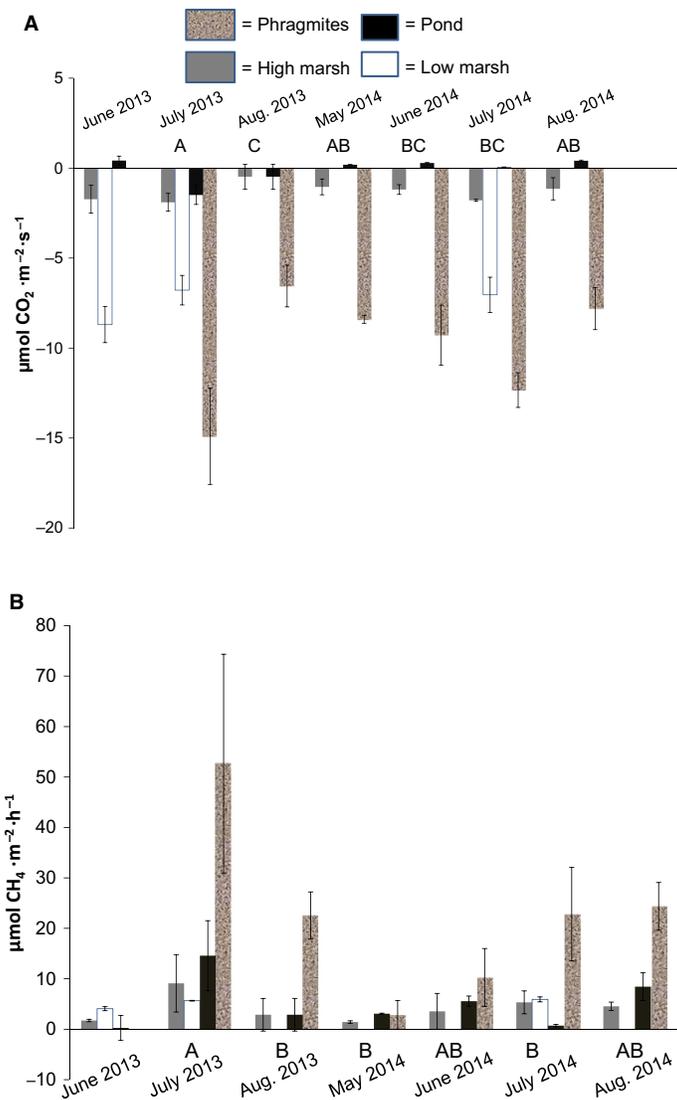


Fig. 3. Average daytime (A) CO_2 and (B) CH_4 fluxes from *Phragmites australis*, native high marsh, and pond zones in Sage Lot Pond during summer 2013 and summer 2014 (Experiment 2). Bars are SEs for fluxes from each zone and date. Letters denote significant differences between dates. Pond data from Site B are shown on 19 June 2013 only, while remaining pond data are from Site A.

(± 0.3) $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (in early July 2013), which were similar in magnitude, but opposite in direction to the largest average daytime fluxes ($-5.5 \pm 0.6 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$).

CH_4 fluxes did not differ between day- and nighttime in either native zone (low marsh: $t_2 = 0.97$, $P = 0.44$; high marsh: $t_2 = 0.24$, $P = 0.83$). CH_4 fluxes were positive in both day- and nighttime (Fig. 4) and showed more variability between dates.

Plant communities in contrasting marsh zones

The native high marsh plant community at Pond Site B was consistently dominated by *Juncus gerardii* and *Distichlis spicata*. At Pond Site B, *J. gerardii* and *D. spicata* comprised on average $79 \pm 4\%$ and $27 \pm 9\%$, respectively, of the high marsh plots, while the low marsh community was composed mainly of *Spartina alterniflora* ($92 \pm 3.9\%$), with minor components of *Spartina patens* ($4 \pm 0.3\%$). The high marsh

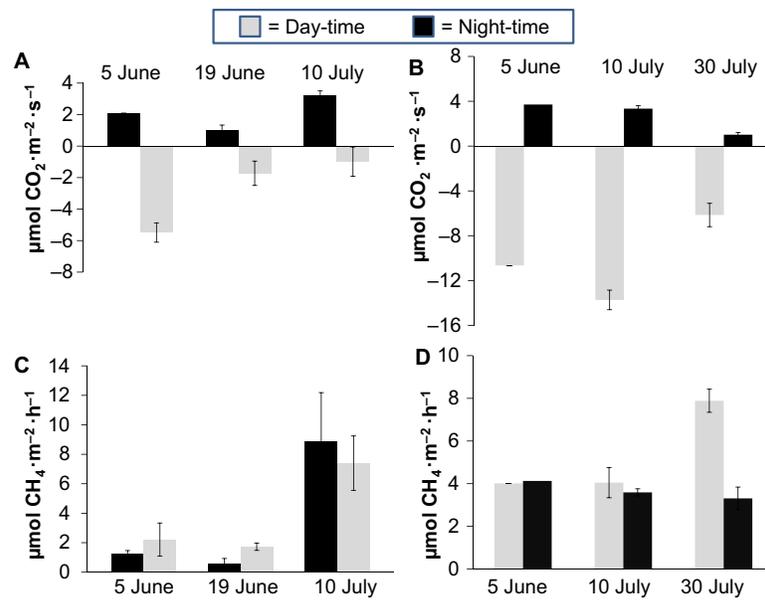


Fig. 4. Average daytime (in gray bars) and nighttime fluxes (in black bars) of (A, B) CO_2 and (C, D) CH_4 on three dates during summer 2013 of Sage Lot Pond. CO_2 and CH_4 fluxes from the high marsh zone are shown in parts A and C, respectively. CO_2 and CH_4 fluxes from the low marsh (*Spartina alterniflora*) zone are shown in parts B and D, respectively. Bars indicate SEs for fluxes on each date.

plant community at Pond Site A (adjacent to the *P. australis* zone) was dominated by *Distichlis spicata* (greater than 95% in the study plots).

High marsh (*J. gerardii*-dominated) plant communities were denser than the *S. alterniflora* low marsh plant communities (Table 3) in both early ($t_7 = -6.03$, $P = 0.005$) and late summer 2013 ($t_4 = -2.72$, $P = 0.05$). Average stem height of *S. alterniflora* in the low marsh was similar to that of *J. gerardii* in the high marsh, although there was a trend of taller *S. alterniflora* than *J. gerardii* by the end of the growing season (August 2013: $t_4 = 2.66$, $P = 0.06$; Table 3). In contrast, *P. australis* height consistently exceeded by as much as 100 cm that of native *Distichlis spicata* (May 2014: $t_3 = 14.86$, $P < 0.01$; July 2014: $t_4 = 12.51$, $P < 0.01$; Table 4). *P. australis* density was significantly lower than *D. spicata* density (July 2013: $t_4 = -13.83$, $P < 0.01$; Table 4).

Biomass was measured for native marsh plants only. Live aboveground live biomass was greater in the high marsh zone than in the low marsh during early summer (June 2013: $t_7 = -3.15$, $P = 0.02$), but this pattern reversed by the end of the growing season (August 2013:

$t_4 = 4.92$, $P = 0.008$) when aboveground biomass of *S. alterniflora* was 635 g/m^2 and was only 352 g/m^2 for the high marsh plants (Table 3).

Total belowground biomass in August 2013 was $5750 \pm 1800 \text{ g/m}^2$ and $2605 \pm 108 \text{ g/m}^2$ for the low and high marsh, respectively. Root biomass was greater in the low marsh than in the high marsh ($F_{9,29} = 3.90$, $P < 0.01$), but rhizome biomass did not differ ($P = 0.20$) between zones. There were no significant differences in root biomass between sampling depths ($P = 0.65$), but there was a significant interaction between zone and depth ($P = 0.01$). Highest root biomass was found in the low marsh zone at depths of 30–40 cm, while it was significantly lower in the high marsh zone at all depths except the top 0–10 cm (Fig. 5). Rhizome biomass was significantly different among depths ($F_{9,29} = 7.74$, $P < 0.01$), and there was a significant interaction between zones and depths ($P < 0.01$). In the high marsh, rhizome biomass was greatest in the top 0–10 cm depth interval and lowest at the deepest sampling interval (40–50 cm, Fig. 5). For the low marsh zone, rhizome biomass peaked at the 10–20 cm depth interval and was more consistent across depths (Fig. 5).

Table 3. Average \pm SE aboveground properties in early, mid-, and late summer for LM and HM zones of Sage Lot Pond in 2013 (Experiment 1).

Date	Variables	LM	HM
June 2013	Aboveground biomass (g/m ²)	261 \pm 23	466 \pm 85
	Stems (m ⁻²)	995 \pm 144	2171 \pm 248
	Avg. stem height (cm)	26.1 \pm 3.0	27.2 \pm 2.9
July 2013	Aboveground biomass (g/m ²)	565 \pm 65	N/A
	Stems (m ⁻²)	720 \pm 114†	N/A
	Avg. stem height (cm)	N/A	N/A
August 2013	Aboveground biomass (g/m ²)	635 \pm 36	352 \pm 35
	Stems (m ⁻²)	834 \pm 34	1910 \pm 476
	Avg. stem height (cm)	42 \pm 4	30 \pm 3

Note: Plant biomass in LM refers to *S. alterniflora* and to *J. gerardii* in the HM1 sites (Pond Site A).

† Signifies low replication (average of only three plots).

Soil properties in contrasting marsh zones

Soil moisture ($P = 0.002$; low marsh: 33.7 ± 3.8 to 66.7 ± 0.8 ; high marsh: 10.8 ± 1.2 to 64.8 ± 0.7) was greater in the low native marsh zone than in the high marsh zone in Experiment 1, but pH ($P = 0.64$; low marsh: 6.8 ± 0.1 to 7 ± 10.6 ; high marsh: $6.7\text{--}7.4$) and salinity ($P = 0.38$; low marsh: 23.2 ± 1.3 to 34.4 ± 0.6 ; high marsh: 22.7 ± 1.0 to 34.5 ± 0.5) did not significantly differ (Table 5). Further, significant interactions between dates and native marsh zones were observed for soil moisture ($P = 0.005$) such that moisture levels in August 2012 for the low marsh (65.8%) were among the greatest, while moisture levels for the high marsh in August 2012 were among the lowest levels observed in this study (10.8%). A trend of greater pore water sulfide concentrations was observed in the low marsh zone than in the high marsh zone across all dates (paired $t_3 = -2.03$, one-tailed $P = 0.07$; low marsh:

123.2 ± 52.0 to $2390 \pm 880 \mu\text{M}$; high marsh: 18.1 ± 4.8 to $1230 \pm 1137 \mu\text{M}$). Although similar between both native zones, salinity varied over time ($P < 0.001$), and there was an interaction between zones and time ($P = 0.003$), with highest salinities (39.8 ± 0.83 psu) in the high marsh during July 2012 (Table 5).

Soil moisture was significantly greater ($P = 0.03$) and there was a trend of higher soil pH ($P = 0.08$) in the *P. australis* zones than in adjacent native high marsh zones in Experiment 2 ($P = 0.03$, Table 6). Neither sulfide concentrations ($P = 0.32$) nor salinity ($P = 0.58$) significantly differed between *P. australis* and high marsh zones. Although salinity significantly varied over time at Pond Site B ($P < 0.001$), values were within the range of those observed at Pond Site A, and no significant interactions between zone and date were observed ($P = 0.36$).

Table 4. Average \pm SE aboveground properties in early, mid-, and late summer for *Phragmites*-invaded zones and HM2 zone of Sage Lot Pond in 2013–2014.

Date	Variables	HM2	Phrag
July 2013	Aboveground biomass (g/m ²)	N/A	N/A
	Stems (m ⁻²)	1750.5 \pm 126.5	205 \pm 42
	Avg. stem height (cm)	N/A	N/A
May 2014	Aboveground biomass (g/m ²)	N/A	N/A
	Stems (m ⁻²)	N/A	132 \pm 0
	Avg. stem height (cm)	16 \pm 1	70 \pm 4
July 2014	Aboveground biomass (g/m ²)	N/A	N/A
	Stems (m ⁻²)	N/A	83 \pm 20
	Avg. stem height (cm)	27 \pm 1	123 \pm 8

Notes: Phrag = *Phragmites australis*-invaded marsh zones. HM2 aboveground biomass consists of *D. spicata*, the dominant plant in that section of high marsh (Pond Site B; Experiment 2).

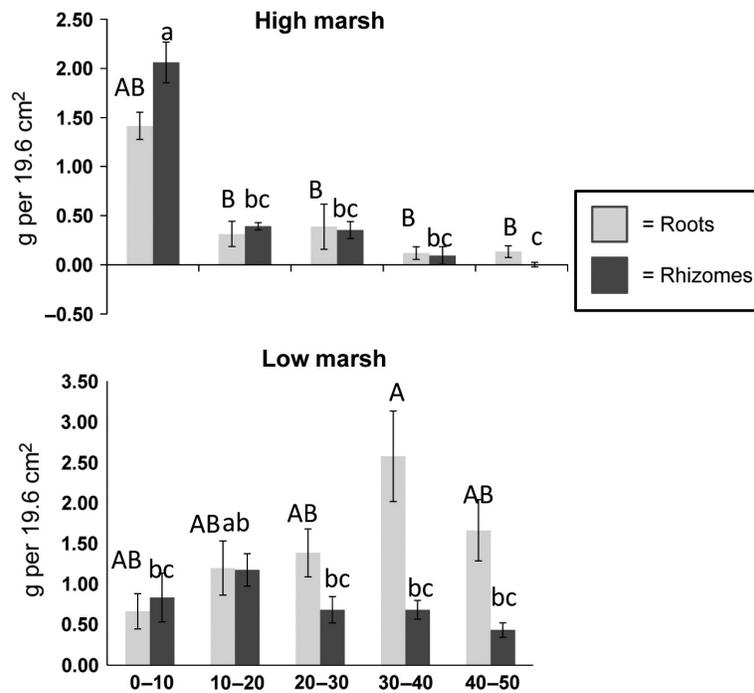


Fig. 5. Average (and SE) root and rhizome biomass from the high and low marsh zones at Sage Lot Pond. Lowercase letters denote depths with significantly different rhizome biomass, and capitalized letters denote depths with significantly different root biomass, from comparisons across both marsh zones and all sampling depths.

Relationships between native plant properties and GHG fluxes

To better understand the potential roles of plants in influencing CO_2 and CH_4 fluxes, a group of complementary and confirmatory data-analytics methods (correlation analysis, PCA and FA, and multiple nonlinear regression modeling) was applied. The 2013 data set was chosen for the analytics, because it represented a more complete information for fluxes and plant variables than that of the other years. The analytics focused on the low and high marsh zones to test the relative controls of the above- and below-ground biomass, stem density, and plant height. Because data were \log_{10} -transformed (to incorporate nonlinearity) and standardized to Z-scores (bringing all variables to a comparable scale), only absolute values of the correlation coefficients (r), factor loadings, and regression coefficients (BETA) were considered for interpreting the results.

Correlation (nonlinear, \log_{10} -transformed) analysis.— CO_2 fluxes (F_{CO_2}) were highly correlated

with the belowground biomass (BGB; $|r| = 0.76$) and were weak to moderately correlated with the stem density (SD; $|r| = 0.24$) and aboveground biomass (AGB; $|r| = 0.33$) (Table 7). In contrast, CH_4 fluxes (F_{CH_4}) showed moderate correlations with the SD ($|r| = 0.53$), BGB ($|r| = 0.47$), and plant height (PnH; $|r| = 0.44$). However, moderate to high correlations were observed between BGB and SD ($|r| = 0.37$), AGB and PnH ($|r| = 0.57$), and PnH and SD ($|r| = 0.70$), indicating significant relationships among the biotic variables and the presence of strong multicollinearity in the data matrix. AGB and BGB showed a weak correlation, which likely refers to a time lag between their synthesis processes.

Principal components analysis.—The first two PCs explained around 75% of the total variance (Fig. 6). Nonorthogonal (0° or 180°) orientations among F_{CO_2} , SD, AGB, and BGB suggested their moderate to high linkages. Because BGB had a much smaller angle with F_{CO_2} than that of SD and AGB with F_{CO_2} , BGB demonstrated by far the strongest linkage with F_{CO_2} . Nearly orthogonal

Table 5. Average \pm SE surface soil properties in the native marsh sites for Experiment 1.

Date	Variables	LM	HM
30 July 2012	pH	6.8 \pm 0.1	6.7 \pm 0.1
	Salinity (psu)	34.4 \pm 1.0	39.8 \pm 0.8
	†Moisture (%)	33.7 \pm 3.8	31.8 \pm 19.4
27 Aug. 2012	Sulfide (μ M)	2390 \pm 880	N/A
	pH	N/A	N/A
	Salinity (psu)	34.4 \pm 0.6	34.5 \pm 0.5
5 June 2013	†Moisture (%)	65.8 \pm 0.5	10.8 \pm 1.2
	Sulfide (μ M)	1823 \pm 1214	1.7 \pm 0.8
	pH	7.0 \pm 0.0	7.0 \pm 0.2
19 June 2013	Salinity (psu)	23.2 \pm 1.3	25.1 \pm 0.5
	†Moisture (%)	61.1 \pm 2.2	60.3 \pm 1.4
	Sulfide (μ M)	123.2 \pm 52.0	24.7 \pm 18.7
10 July 2013	pH	7.1 \pm 0.1	7.4 \pm 0.4
	Salinity (psu)	27.2 \pm 0.3	22.7 \pm 1.0
	†Moisture (%)	66.7 \pm 0.8	66.0 \pm 0.5
10 July 2013	Sulfide (μ M)	205.4 \pm 83.0	18.2 \pm 4.8
	pH	6.8 \pm 0.1	N/A
	Salinity (psu)	28.7 \pm 0.2	N/A
10 July 2013	†Moisture (%)	62.7 \pm 1.3	64.8 \pm 0.7
	Sulfide (μ M)	2700 \pm 108	1230 \pm 1137

Notes: LM = low marsh, HM1 = high marsh site 1. For all measurements, $n = 3$, except when two HM sites existed on 6-5-2013 and 6-19-2013.

† Indicates significant difference between zones across dates.

Table 6. Average \pm SE surface soil properties and gas flux measurements in the *Phragmites australis*-invaded sites (Phrag) and the native high marsh site (HM2) for Experiment 2.

Date	Variables	HM2	Phrag
19 July 2013	Salinity (psu)	24.0 \pm 2.0	24.3 \pm 0.7
	†Moisture (%)	61.6 \pm 2.9	65.8 \pm 0.5
14 Aug. 2014	pH	6.9 \pm 0.0	7.0 \pm 0.1
	Salinity (psu)	27.7 \pm 1.4	27.3 \pm 0.9
27 May 2014	†Moisture (%)	63.1 \pm 1.1	63.5 \pm 1.4
	pH	6.1 \pm 0.2	6.6 \pm 0.0
24 June 2014	Salinity (psu)	25.0 \pm 2.0	26.8 \pm 0.6
	Moisture (%)	63.3 \pm 0.3	64.5 \pm 0.4
	Sulfide (μ M)	7.2 \pm 7.2	0 \pm 0
11 July 2014	pH	7.1 \pm 0.2	7.5 \pm 0.1
	Salinity (psu)	31.7 \pm 0.3	29.8 \pm 0.2
21 Aug. 2014	†Moisture (%)	66.2 \pm 0.6	65.0 \pm 1.3
	Salinity (psu)	25.0 \pm 0.6	26.8 \pm 0.2
21 Aug. 2014	†Moisture (%)	62.8 \pm 0.5	67.5 \pm 0.2
	Sulfide (μ M)	91.6 \pm 6.0	14.2 \pm 7.7
21 Aug. 2014	Salinity (psu)	33.9 \pm 0.9	33.3 \pm 0.9
	Sulfide (μ M)	514 \pm 410	103 \pm 74

Notes: For high marsh, $n = 3$, and for *Phragmites australis* measurements, $n = 2$. Sulfide data are limited to two dates as listed in the table.

† Indicates significant difference between zones across dates.

Table 7. Pearson's correlation coefficients (r) of the participatory variables upon \log_{10} transformation, showing the nonlinear correspondences among the biomass, F_{CO_2} , and F_{CH_4} fluxes.

Variables	SD	AGB	BGB	PnH	F_{CO_2}	F_{CH_4}
SD	1.00					
AGB	-0.16	1.00				
BGB	-0.37	0.04	1.00			
PnH	-0.70	0.57	0.20	1.00		
F_{CO_2}	-0.24	-0.33	0.76	-0.11	1.00	
F_{CH_4}	-0.53	0.18	0.47	0.44	0.36	1.00

Note: F_{CO_2} = CO_2 sequestration flux, F_{CH_4} = CH_4 emission flux, SD = stem density, AGB = aboveground biomass, BGB = belowground biomass, PnH = plant height.

(90°) orientations between F_{CO_2} and PnH suggested their weak linkages.

Based on the orientations (angles), F_{CH_4} had a weak linkage with AGB and moderate linkages with BGB, SD, and PnH. However, relatively small loadings of F_{CH_4} on the second PC exhibited its small contributions to the overall data variance. Furthermore, the orientation between AGB and BGB was also nearly orthogonal, indicating their weak mutual linkage.

Factor analysis.—To identify dominant variables explaining variance in the data set, two orthogonal latent factors were extracted based on the initial eigenvalue criterion, eigenvalue > 1 (Table 8). The high loadings of F_{CO_2} and BGB on the second factor suggested their strong linkages, whereas the relatively small loadings of SD and AGB on this factor indicated their weak to moderate relations with F_{CO_2} . Although AGB, SD, and PnH showed moderate to high loadings on the first factor, F_{CO_2} loaded very weakly thereon; this suggested a moderate linkage among AGB, SD, and PnH, while indicating their weak linkages with F_{CO_2} . Loadings of F_{CH_4} on both factors were moderate, indicating moderate relationships of the methane fluxes with the plant variables.

Multiple nonlinear regressions (CO_2 and CH_4 fluxes).—The multiple nonlinear regression model for F_{CO_2} , as developed by using \log_{10} -transformed and standardized data, showed a high overall statistical significance ($F_{15} = 7.61$, $P = 0.003$, $R^2 = 0.73$). Only the BGB was statistically significant ($P < 0.01$) with a high value of regression coefficient ($|\text{BETA}| = 0.76$), confirming its high linkage with F_{CO_2} . Based on the regression coefficients, AGB ($|\text{BETA}| = 0.27$, $P = 0.22$), PnH

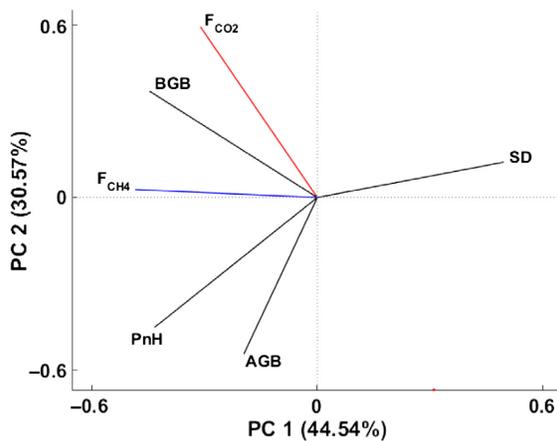


Fig. 6. Biplot showing relative orientations and interrelations of plant properties and GHG fluxes (CO_2 and CH_4). Percentage explained by each principal component (PC) is given in parentheses. F_{CO_2} = CO_2 flux, F_{CH_4} = CH_4 flux, SD = stem density, AGB = aboveground biomass, BGB = belowground biomass, PnH = plant height.

($|\text{BETA}| = 0.21$, $P = 0.48$), and SD ($|\text{BETA}| = 0.15$, $P = 0.57$) had low to moderate linkages with F_{CO_2} , although they were not statistically significant.

The multiple regression model for F_{CH_4} showed a weak overall statistical significance ($F_{15} = 1.73$, $P = 0.21$, $R^2 = 0.39$). The moderate R^2 indicated that plant properties had low to moderate relationships with methane emissions ($|\text{BETA}| = 0.33, 0.28, 0.17$, and 0.03 for BGB, SD, PnH, and AGB, respectively). All plant variables were statistically insignificant predictors of F_{CH_4} ($P = 0.22, 0.48, 0.71$, and 0.94 for BGB, SD, PnH, and AGB, respectively). However, BGB appeared

Table 8. Optimally extracted orthogonal latent factors.

Variables	Factor 1	Factor 2
SD	-0.71	-0.30
AGB	0.56	-0.29
BGB	0.23	0.79
PnH	0.99	0.03
F_{CO_2}	-0.08	0.99
F_{CH_4}	0.46	0.40

Notes: F_{CO_2} = CO_2 sequestration flux, F_{CH_4} = CH_4 emission flux, SD = stem density, AGB = aboveground biomass, BGB = belowground biomass, PnH = plant height. Bolded numbers indicate moderate to strong loadings.

to be the strongest predictor of F_{CH_4} , which is consistent with that of F_{CO_2} .

DISCUSSION

Zonation patterns of CO_2 fluxes

Complex zonation gradients in salt marshes, in which benthic community composition and soil edaphic properties covary, offer unique challenges in estimates of potential carbon sequestration rates. In this study of GHG fluxes across a plant-defined zonation gradient including unvegetated ponds in a New England coastal marsh, we found striking differences in CO_2 fluxes that reveal substantial spatial heterogeneity in coastal marsh carbon dynamics. While differences between bare, inundated ponds and vegetated marsh zones were expected (Fig. 5), the significant differences in CO_2 fluxes between two relatively similar native vegetated zones were more surprising (Fig. 3). This heterogeneity has important implications given growing interest in connecting tidal wetland restoration to voluntary carbon markets, as such efforts require accurate carbon accounting (Emmer et al. 2014).

Our findings illustrate the potential for CO_2 fluxes to mirror visible differences in plant communities across a coastal marsh landscape. Although multiple edaphic properties often vary across marsh zones (Nixon 1982, Bertness 1992), our zonation gradient in Sage Lot Pond was mainly characterized by relatively subtle differences in surface soil moisture and sulfide and no significant differences in other key variables (salinity, pH; Tables 5 and 6). In contrast, plant community composition and aboveground structural properties (Tables 3 and 4) and belowground biomass (Fig. 5) were markedly different. The differences in carbon dioxide fluxes between the dominant native zones in coastal New England marshes can be attributed to well-known characteristics of the dominant primary producers. The consistent pattern of greater CO_2 uptake in the *S. alterniflora* low marsh zone than in the *J. gerardii* and *D. spicata*-dominated high marsh (Fig. 2) mirrors higher total primary production (measured as aboveground biomass) in the former zone (Table 3) and likely higher rates of carbon fixation. *S. alterniflora*'s higher capability to tolerate inundation has been attributed to well-developed aerenchyma that facilitates

gas exchange between soils and the atmosphere (Bertness 1992). The most visible differences in plant zonation across the marsh landscape—at the upland border where invasive *P. australis* towers over native high marsh perennials—were also reflected by the largest contrasts in carbon fluxes. Surprisingly, high rates of CO₂ uptake by *P. australis* (between four and seven times greater than native high marsh zones, Fig. 3) may be attributed to the rapid growth rates and high photosynthetic capacity of this invasive species (Amsberry et al. 2000, Windham 2001). This finding may be a particular feature of meso- and polyhaline marshes, as CO₂ fluxes were larger in the native high zone of an oligohaline marsh and therefore more similar to *P. australis* zones (Martin and Moseman-Valtierra 2015). Salinity stress and low biomass may explain the relatively low rate of CO₂ uptake in the high marsh. We did not measure primary production of *P. australis* in this study, but the towering height of this plant relative to natives (more than four times taller, Table 4) is consistent with our qualitative observations of greater biomass and extensive documentation of such by several other marsh studies (i.e., Windham and Lathrop 1999, Windham 2001, Emery and Fulweiler 2014).

Significantly lower CO₂ uptake rates or (more frequent) emissions were observed in unvegetated ponds (Fig. 3) than in native or vegetated zones of the marsh at Sage Lot Pond. This was expected given the absence of photosynthetic macrophytes. Similar ponds in other New England marshes have displayed net heterotrophy (A. Spivak, *unpublished data*). Experimentally flooded plots in high salt marsh zones have shown reduced mean net carbon uptake relative to unflooded plots, although transitions to net carbon loss (heterotrophy) were observed only with additional *S. alterniflora* wrack deposition (Miller et al. 2001). Waterlogging is known to stress-dominant plant species in the high marsh, and although historically forbs have colonized waterlogged soils in some northern New England marshes, they have been reduced in number by regional marsh ditching (Ewanchuk and Bertness 2004). Waterlogging is contributing to the prevalence of unvegetated ponds and decline of vascular plant communities in high marsh zones, and potentially lowers C accumulation rates (Raposa et al. 2015, Watson et al. 2015).

Neither forbs nor *S. alterniflora* are readily able to colonize those spaces once other native species are lost (Ewanchuk and Bertness 2004). In ponds with more significant micro- and/or macroalgae and seagrasses, higher CO₂ uptake rates may be observed, and further work is needed to quantify the impacts of such species on potential GHG fluxes. Studies should also expand gas flux measurements across annual cycles. However, algal productivity will not likely contribute as much as marsh or seagrass to long-term carbon sequestration due to lower burial efficiency (Hill et al. 2015) and higher lability (Nguyen et al. 2005).

Similarity of CH₄ across marsh zones

In contrast to CO₂, the similarity of CH₄ emissions between native marsh zones (Fig. 2) as well as between ponds and vegetated marsh (Fig. 3) suggests that methanogens are more significantly influenced by physical variables (water level, salinity, temperature; Whiting and Chanton 1993, Poffenbarger et al. 2011) than by plants. The high salinity in coastal marshes is known to limit the overall magnitude of those emissions due to stronger competition of sulfate reducers for substrates than methanogens (Bartlett et al. 1987, Poffenbarger et al. 2011). In our study, most soil properties (including salinity) and weather factors were surprisingly similar across vegetated marsh and pond zones. Climatic and tidal variables were relatively constant for purposes of a “controlled” zone comparison, which limited our ability to explore the broader relationships of carbon fluxes with abiotic drivers. Nevertheless, small but significant differences in moisture between plant zones likely influenced the similarity of methane emissions between native marsh zones (Table 2, Fig. 2). For example, in July 2013—the date with the largest (approximately fivefold) difference in CH₄ emissions between *P. australis* and native high marsh zones (Fig. 3), higher moisture levels in the *P. australis* zone likely contributed to the higher emissions. Although native high marsh is generally at a lower elevation than *P. australis*, moisture levels may have been lower among the dense tussock-like structures formed near surface soils by *D. spicata* roots (the dominant native high marsh plant in HM 2 plots, Pond B, Fig. 1). However, this was only a 4.2% difference in average soil moisture values. Salinities were also similar in the adjacent high marsh plots

with lower methane (24 psu, Table 6). However, the high CH₄ emission in July 2013 from the *P. australis* zone occurred during the period of lowest salinity. The importance of salinity as a controlling factor of CH₄ emissions is well known (Poffenbarger et al. 2011). Air temperatures at Sage Lot Pond also reached 37°C in July 2013 (National Estuarine Research Reserve System [NERRS] 2012), and these warm temperatures very likely also contributed to the large fluxes on that date (Fig. 3). The hypothesis that abiotic controls exert stronger influence than plants on methane emissions is being tested in model efforts with more comprehensive and longer data sets in the New England region (e.g., O. I. Abdul-Aziz, K. S. Ishtiaq, J. Tang, S. Moseman-Valtierra, K. D. Kroeger, K. Morkeski, and J. Mora, *in preparation*).

Overall, CH₄ emissions only offset a small fraction of the CO₂ uptake rates in the vegetated marsh zones of Sage Lot Pond based on the sustained global warming potential of methane (Neubauer and Magonigal 2015). Based on the maximum average summer-time CH₄ emissions, CO₂ uptake rates could be only offset up to 0.2% in the low marsh, by 4% in the high marsh, and 1.5% in *P. australis* zones. These estimates take into account the latest estimates of radiative efficiency and atmospheric lifetime for CH₄ and they reflect an adjustment to the GWP to account for the larger impact of sustained emissions (rather than pulses), as appropriate for ecosystems (Neubauer and Magonigal 2015). Significant methane losses via ebullition (comparable to diffusive losses) have been reported from ponds (Negandhi et al. 2013), and as our method does not adequately quantify ebullition, our methane emissions are likely underestimates. Nonetheless, the significantly greater magnitude of CO₂ fluxes relative to CH₄ emissions, together with high rates of primary productivity, supports the current notion that coastal marshes are appropriate targets for efforts to maximize biological C sequestration.

Relationships of plant metrics with C fluxes

For both scientific and applied purposes, there is a need for accurate tools with which to predict carbon fluxes in coastal marshes. Our data-analytics methods including a series of complementary methods which all suggested that belowground biomass (BGB) was very strongly

linked to CO₂ fluxes. The significant (nonlinear) relationship of CO₂ fluxes with belowground biomass across the two native plant zones (Table 7) is consistent with a strong influence of rhizosphere interactions (between plants and microbes) on net carbon uptake. The strong connection of CO₂ fluxes with belowground biomass indicates a substantial influence of root respiration and/or root-associated microbial respiration on net CO₂ uptake. This may be expected, as continuous enrichment of the belowground carbon pool relies on active growth by vascular plants (Fontaine and Barot 2005). Nonetheless, observed moderate correlations between stem density and belowground biomass as well as the high correlation between stem density and plant height (Table 7) support a dependency between aboveground primary productivity and CO₂ fluxes. PCA and FA also showed a moderate relationship between some metrics of aboveground primary productivity (i.e., stem density and aboveground biomass) and the CO₂ fluxes (Fig. 6, Table 8); however, the relatively weak linkages of those aboveground properties with CO₂ fluxes compared with those of belowground biomass may be related to distinct timescales over which these properties are related as well as to differential responses to many environmental factors (Morris et al. 2013). While temporal variability certainly plays an important role in explaining relationships among primary productivity, belowground biomass, and CO₂ fluxes, it was not reflected in our analysis of connections between plant properties and GHG fluxes due to limited duration and frequency of the data set, particularly for plant biomass.

Given the relative simplicity of measuring belowground biomass, our findings suggest that it may represent a promising proxy by which coastal managers may ultimately estimate CO₂ fluxes. Given disturbance impacts of coring on marshes, there is a need to limit the overall coring activities, therefore this metric may be most promising in cases where biomass data have already been collected and/or can be reasonably limited. Importantly, our model still needs to be tested for applicability to *P. australis* or other plant species. However, removal of aboveground *P. australis* biomass (via clipping) rapidly switched CO₂ uptake to emission, suggesting that biomass of that species is also strongly linked to CO₂ flux rates (R. Martin and S. M. Moseman-Valtierra, *in revision*).

Although methane fluxes were not significantly related to any of the plant properties in this study, the different layers of data-analytics and regression modeling (e.g., Fig. 6, Table 8) indicate that belowground biomass and stem density were among the strongest predictors. Production of organic carbon exudates and oxygenation of rhizospheres by plant roots are likely involved in the moderate relationship between CH₄ fluxes and belowground biomass (Whiting and Chanton 1993, Cheng et al. 2007). This relationship may potentially be weaker than that between CO₂ and belowground biomass because methanogenic archaea in soils and rhizospheres are indirectly impacted by plant primary production (Whiting and Chanton 1993), with plants acting as conduits for either gas or substrate transport (Magonigal et al. 1999, Garnet et al. 2005), while root respiration is a direct and potentially major source of CO₂ (Hanson et al. 2000, Spivak and Reeve 2015). Future models for methane estimation may be developed using data-analytics approaches that include abiotic drivers with more comprehensive data sets. Also, the Marsh equilibrium model is now being amended to estimate CH₄ fluxes from brackish marshes (Morris et al. 2013).

Day–night variation in GHG fluxes

Diel cycles constitute a substantial element of temporal variation in the dynamic coastal marsh environment. Night CO₂ fluxes at Sage Lot Pond were a substantial portion of the daytime fluxes (Fig. 4) and on one occasion exceeded daytime CO₂ uptake in the high marsh zone. Such large respiration rates and generally small CO₂ uptake rates in the high marsh zone may lead to smaller long-term carbon accretion rates. This could potentially result in greater vulnerability of those zones to sea-level rise relative to other marsh zones. The observed nighttime CO₂ emissions were generally comparable to soil respiration rates (CO₂ emissions) that have been measured in the high marsh zones of Plum Island (3–6 μmol CO₂·m⁻²·s⁻¹, Moseman-Valtierra et al. 2011) and Narragansett Bay (Wigand et al. 2009). Given that soil respiration rates are based on methods that aim to exclude plants and are often positioned between plant culms (as used by Wigand et al. 2009, Moseman-Valtierra et al.

2011), the similarity of these fluxes suggests that attempts to minimize plant impacts on respiration simply by excluding aboveground biomass may require improvement.

The consistent lack of difference in day–night fluxes for methane was surprising, given previous reports of significant diel cycles in vegetated marshes and mesocosms (Van Der Nat et al. 1998, Zhang and Ding 2011). Diel cycles have been attributed to shifts in temperature and associated plant-driven conduction of gases. *S. alterniflora* has displayed diel variation in methane transport in coastal marsh mesocosms with ratios of minimum and maximum methane fluxes ranging from 1.3 to 1.8 (Zhang and Ding 2011). In our study, a wider range of ratios for day and night CH₄ fluxes was observed (from 0.8 to 3 in the high marsh zone and 1 to 2 in the *S. alterniflora* zone; Zhang and Ding 2011). The high variability in methane emissions in general contributed to the lack of a consistent difference between day and night in each of the native marsh zones (Fig. 4). Possibly, a comparison of day- and nighttime methane fluxes later in the plant growing season would have produced a stronger, more consistent contrast (Zhang and Ding 2011). However, the gas transport capacity of less massive high marsh species, *J. gerardii* and *D. spicata*, is also likely lower than for *S. alterniflora*. Therefore, the range in methane emissions in multiple plant zones across longer timescales warrants further study.

Dark emissions were not measured from *P. australis* zones in this study, but larger daytime CH₄ emissions were found than at night in a similar New England coastal marsh (Martin and Moseman-Valtierra, *in revision*). This suggests that nighttime CH₄ emissions may not be significant in these coastal wetlands. We did observe large variability in CH₄ emissions from *P. australis* zones (Fig. 3), which may in part be due to active methane transmission through these plants (Van Der Nat et al. 1998).

Implications for marsh conservation

Anthropogenic activities profoundly influence the structure, fate, and function of marshes, including whether they are sustained or lost over the next decade as sea level rises and biological invasions expand. Marsh restoration actions, such as return of tidal flushing, may limit the

spread of invasives such as *P. australis* and reduce methane emissions through increases in salinity. This research suggests, however, that direct removal of *P. australis* and/or failure to enhance *S. alterniflora* stands in coastal wetlands may result in the loss of a significant carbon sink at least over short terms within the marsh landscape. While several other ecosystem functions (i.e., habitat provision) may be impaired by *P. australis*, and similar invasive plants in coastal marshes, potential carbon sequestration should be included in the suite of services (and disservices) that coastal managers evaluate when determining trade-offs associated with various conservation strategies. Given the significant genetic diversity of *P. australis*, further studies are needed to test the applicability of these findings to the range of lineages that colonize North America (and other parts of the world; Kirk et al. 2011, Meyerson and Cronin 2013). Further, comparisons of GHG fluxes should be extended beyond the summer seasons in which our study was conducted, and data are needed to test whether *P. australis* invasion results in changes to long-term C sequestration rates. Significant production by *P. australis* is also known to occur belowground, even beyond 1 m depths (J. Meschter and T. Mozdzer, *unpublished data*), which suggests the potential for large root respiration rates to offset some of the CO₂ uptake and/or for rhizosphere exudates to stimulate decomposition. Although high accretion rates (Rooth and Stevenson 2000) and low lability (Windham 2001) suggest that most *P. australis* biomass will contribute to carbon accumulation in marshes, long-term carbon sequestration rates should be compared with those of native marsh macrophytes.

In cases where standing water leads to the loss of marsh vegetation, carbon sinks will be lost and marshes may become net carbon sources to the atmosphere. As organic carbon is essential for marsh accretion, this may produce a harmful feedback such that rising sea levels reduce marsh abilities to be sustained against further sea-level rise. Many factors influence the potential for such a feedback to occur, including mineral sediment inputs and accretion rates, which can vary between marsh zones (Kirwan and Megonigal 2015, M. Gonneea, *unpublished data*). High marsh zones, where net CO₂ uptake was smallest among vegetated plots and which are

currently hotspots for ponding, seem to be particularly susceptible to such a transformation by rising sea level.

The recent approval of the first methodology for coastal wetland restoration by Verified Carbon Standards (Emmer et al. 2014) is a prime opportunity for coastal restoration activities to receive funding for increasing carbon sequestration and/or minimizing GHG emissions from marshes. As policy frameworks expand for connecting coastal wetlands to carbon markets, efforts should continue to be made to continuing to develop models and proxies to make accurate accounting feasible. This study suggests that belowground plant biomass may be one key, cost-effective predictor in the models of carbon fluxes. Overall, these data support the potential for coastal marsh conservation and restoration to ameliorate anthropogenic impacts on climate change and they assert the need to protect these significant carbon sinks against complex global changes.

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