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LETTER

Spartina alterniflora has the highest methane emissions in a St. Lawrence estuary salt marsh

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Abstract

Salt marshes have the ability to store large amounts of 'blue carbon', potentially mitigating some of the effects of climate change. Salt marsh carbon storage may be partially offset by emissions of CH_4, a highly potent greenhouse gas. Sea level rise and invasive vegetation may cause shifts between different elevation and vegetation zones in salt marsh ecosystems. Elevation zones have distinct soil properties, plant traits and rhizosphere characteristics, which affect CH_4 fluxes. We investigated differences in CH_4 emissions between four elevation zones (mudflat, *Spartina alterniflora, Spartina patens* and invasive *Phragmites australis*) typical of salt marshes in the northern Northwest Atlantic. CH_4 emissions were significantly higher from the *S. alterniflora* zone (17.7 ± 9.7 mg C m^{-2} h^{-1}) compared to the other three zones, where emissions were negligible (<0.3 mg C m^{-2} h^{-1}). These emissions were high for salt marshes and were similar to those typically found in oligohaline marshes with lower salinities. CH_4 fluxes were significantly correlated with soil properties (salinity, water table depth, bulk density and temperature), plant traits (rhizome volume and biomass, root volume and dead biomass volume all at 0–15 cm) and CO_2 fluxes. The relationships between CH_4 emissions, and rhizome and root volume suggest that the aerenchyma tissues in these plants may be a major transport mechanism of CH_4 from anoxic soils to the atmosphere. This may have major implications for the mitigation potential carbon sink from salt marshes globally, especially as *S. alterniflora* is widespread. This study shows CH_4 fluxes can vary over orders of magnitude from different vegetation in the same system, therefore, specific emissions factors may need to be used in future climate models and for more accurate carbon budgeting depending on vegetation type.

1. Introduction

Salt marshes have high rates of carbon sequestration, which have the potential to reduce some of the impacts of climate change (Chmura *et al* 2003, McLeod *et al* 2011). The strength of the carbon sink resulting from carbon sequestration may be offset by emissions of the potent greenhouse gas (GHG), CH_4, which has a sustained-flux global warming potential 45 times higher than that of CO_2 over 100 years (Neubauer and Megonigal 2015). Salt marshes are often assumed to have negligible CH_4 fluxes (Chmura *et al* 2003, McLeod *et al* 2011), however, some studies have observed CH_4 fluxes from these environments (e.g. Chmura *et al* 2011, Roughan *et al* 2018, Yang *et al* 2021). Despite CH_4 emissions potentially switching salt marshes from net C sinks to net C sources (Bridgham *et al* 2006), understanding of the effect of how global change will affect CH_4 emissions from these systems remains inadequately quantified (McLeod *et al* 2011).

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Methane fluxes from salt marshes vary between elevation zones due to changes in soil properties, plant species composition, plant traits and rhizosphere characteristics (Burke *et al* 2002, Philippot *et al* 2009, Noyce and Megonigal 2021, Rosentreter *et al* 2021). The soil properties affecting CH_4 emissions include temperature, bulk density, redox conditions, hydrological regime and substrate supply (Boeckx *et al* 1997, Zhao *et al* 2020, Noyce and Megonigal 2021, Rosentreter *et al* 2021). Salinity (as a proxy for sulphate supply from tidal floodwaters) is a major control (Mitsch and Gosselink 2007, Poffenbarger *et al* 2011) and sulphate-reducing bacteria in the soil outcompete methanogenic archaea (Villa 2020). However, alternative methanogenic pathways have been observed recently, which enable significant CH_4 emissions even at high salinities (Kelley *et al* 2015, Yuan *et al* 2019, Villa 2020). CH_4 emissions may vary between vegetation zones due to changes in both production versus consumption and transport from the soil to the atmosphere (Villa *et al* 2020, Noyce and Megonigal 2021).

A key mechanism of CH_4 transport is through pore spaces within the aerenchyma system of rhizomes, roots and stems, which can account for 80%–90% of total GHG emissions from some wetlands (Schutz *et al* 1991). Aerenchyma provide a direct channel between anoxic soils and the atmosphere, allowing CH_4 to be released without oxidation, therefore, increasing emissions (Brix *et al* 1992, Verville *et al* 1998). The transport mechanism and capacity can vary greatly depending on plant species and composition and so is expected to vary with marsh elevation zone (Laanbroek 2010, Villa 2020). Stomatal conductance may also be responsible for some plant-mediated transport, however, conflicting results of both higher CH_4 emissions and no effect of stomatal conductance have been observed (e.g. Whiting and Chanton 1996, Garnet *et al* 2005).

Salt marshes are under threat from changes in many environmental factors including sea level rise and invasive vegetation (Kirwan and Megonigal 2013, Martin and Moseman-Valtierra 2015). Environmental change effects on salt marsh vegetation include landward shifts in vegetation zones, transitions from native to invasive vegetation and vegetation dieback (e.g. Kirwan and Megonigal 2013, Martin and Moseman-Valtierra 2015). This may result in changes in the size or species composition of different elevation zones and conversion of vegetated salt marshes to tidal flats. The effect of shifting vegetation zones due to sea level rise on GHG fluxes and the understanding of the dominant controls on GHG fluxes remain critical knowledge gaps (Moseman-Valtierra *et al* 2016, Villa 2020).

In this study we examine whether fluxes of CH_4 vary with different elevation zones of a northern salt marsh, particularly considering differences in vegetation as a key driver of CH_4 fluxes. We considered all four of the major elevation zones present in the region: mudflat, *Spartina alterniflora, Spartina patens* and invasive *Phragmites australis*, therefore, incorporating marsh zones that may shift with both sea level rise and invasion of non-native species. We measured soil and plant properties to determine the environmental factors driving high CH_4 emissions and controlling differences observed between zones.

2. Materials and methods

2.1. Study site

This study was conducted in a salt marsh on the St. Lawrence estuary near La Pocatière, Quebec, Canada (47°22′24.7″ N 70°03′26.3″ W, figure 1(a)). The St. Lawrence estuary is mesohaline at this location (Gauthier 1980) with soil porewater salinities measured in this study ranging between 13 and 23 PSU. The average tidal range at this location is ∼4.3 m. The climate is cool and wet with an average annual temperature and precipitation of 4.5 °C and 933 mm, respectively (Environment Canada, 2020). The salt marsh is approximately 160 m wide, with extensive mudflat, and is bordered on the landward side by a dyke. The salt marsh deposits are 1.8–2.R. Devel4 m deep (van Ardenne 2016).

The zonation of salt marsh vegetation found here reflects that of the St. Lawrence estuary and is common across salt marshes of Eastern Canada and the Northeast U.S. (figure 1(b)). An extensive mudflat, exposed at low tides, is bordered by *S. alterniflora*, which is replaced at higher elevations by *S. patens*. Here, the *S. patens* zone also contains *Bolboschoenus maritimus, Plantago maritima, Triglochin maritima*, and *Salicornia europaea* in minor abundance. *Solidago sempervirens* and *Spartina cynosuroides* are found as elevation continues to increase, followed by a transition into terrestrial species along the dyke (Gu *et al* 2020). An invasive genetic strain of *P. australis,* widespread across the US and Canada (Saltonstall 2002), was observed at this study site in 2006 and has replaced the native vegetation in the transition zone from high marsh to terrestrial species, creating tall, dense monospecific stands (Gu *et al* 2020).

2.2. Field sampling

Six sampling locations were identified in each of the four elevation zones: mudflat, *S. alterniflora, S. patens,* and *P. australis* (*S. patens*/*P. australis* transition zone with 20% aerial coverage of *P. australis*). The sampling locations were chosen to capture similar elevation and species composition within each zone. The average

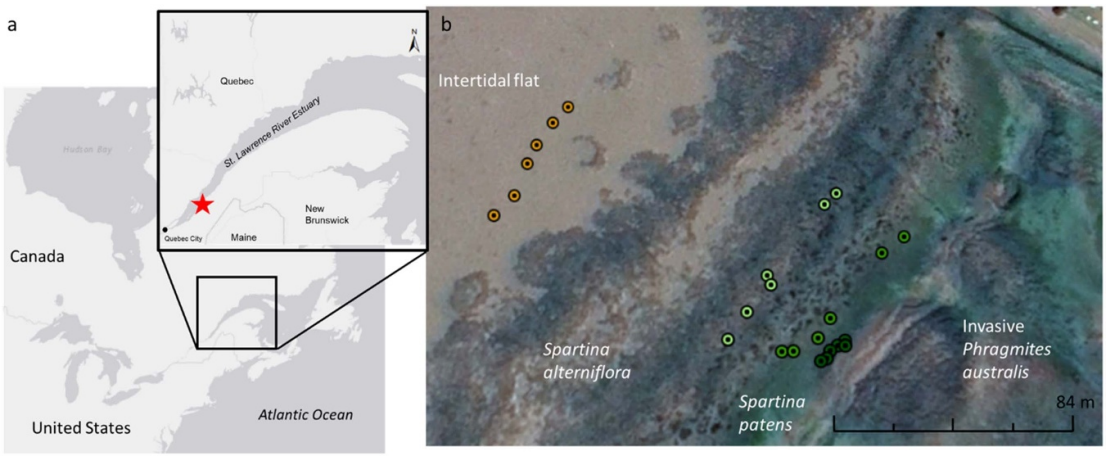


Figure 1. (a) The location of the study site along the St. Lawrence River Estuary in the Kamouraska Region of Quebec, Canada (gadm.org) and (b). A Google Earth image of the studied salt marsh showing sampling locations within the four elevation zones (Google Earth 7.3.3 (2020) *Salt marsh at La Pocatière, Quebec, 47° 22′ 24.7″ N 70° 03′ 26.3″ W.*). These zones are indicated by the different colours where orange indicates mudflat, pale green indicates *Spartina alterniflora*, green indicates *Spartina patens* and dark green indicates *Phragmites australis* mixed with *Spartina patens.*

elevations of sampling locations in the *S. alterniflora, S. patens* and *P. australis* were 1.8, 2.5 and 2.7 m higher than the mudflat, respectively.

2.3. Gas sampling

GHG fluxes (CH_4 and CO_2) were measured using a dark, static chamber method designed to enclose both soil and vegetation (Magenheimer *et al* 1996). Chambers were made of 18 l, 26 cm diameter polycarbonate bottles, which were wrapped with bubble wrap and aluminium foil to insulate and block sunlight. Chambers were fitted with a 12 V, battery-powered computer fan (Sunon, Brea, California, U.S.) to ensure mixing of the air within the chamber and a venting tube was wrapped once around the outside of the chamber to minimise pressure differences (Hutchinson and Mosier 1981, Rochette 2011). The air temperature (HOBO Temperature Data Logger, Onset, Bourne, Massachusetts, U.S.) inside and outside of the chambers was measured during gas flux measurements. The average outside air temperature was 28.2 °C, with temperatures inside the chambers <4 °C below this.

Gas samples were taken on the 23rd of August 2020 from all sites, and gas fluxes presented here should represent the growing season fluxes. Gas samples were taken between 12:30 and 17:40, 5.5–10.5 h after high tide. In the vegetated sites, the chambers were deployed onto PVC collars (10 cm high) inserted 2.5 cm into the salt marsh three days before sampling. Chambers were fitted with a sampling assembly that was inserted into the chamber opening before the chambers were placed into the collar rim. The collar rim was filled with ambient water, taken from a nearby pool, to ensure an air-tight seal without altering porewater characteristics if any water overflowed onto the soil. Care was taken to ensure no vegetation was broken during installation of the chambers. The sampling assembly was long enough to minimise disturbance during sampling and had a 35 ml volume, therefore, during sampling, 35 ml of gas was extracted and discarded before a 25 ml sample representing gas inside the chamber was extracted. Five millilitres was expelled through the stopcock and needle of the syringe to minimise cross-contamination between samples and 20 ml was injected into a pre-evacuated 12 ml exetainer (Labco, U.K.). Gas samples were taken at 0, 20, 40 and 60 min. In the mudflat, chambers were carefully inserted directly into the mudflat to approximately 3 cm. Chambers were allowed to equilibrate with the air for 10 min after installation to minimise the effect of any disturbance during installation on initial GHG concentrations (Hamilton *et al* 2020). After this time, sampling assemblies were gently inserted into the chamber opening and sampled as described for the vegetated zones, except that gas samples were taken at 0, 20 and 40 min. Soil temperature was measured during chamber deployment at 10 cm depth within 10 cm of the collars using a soil thermometer (DeltaTrak 11050, Pleasanton, USA).

Soil and vegetation samples were collected from within the collar locations from the 24 to 26 August 2020 and the 19 and 20 September 2020. Vegetation was clipped at the soil surface and two 0–15 cm soil cores were collected, one for bulk density, total organic carbon (TOC) and total nitrogen (TN) analysis, and one for extractable nutrients, dissolved organic carbon (DOC) and total dissolvable nitrogen (TDN). Soil cores for bulk density/TOC/TN were collected using a 2.5 cm dia. Dutch gouge corer, sliced at 0–15 cm, then wrapped in plastic wrap. Soil cores for extractable nutrients were collected using the same corer, except in the mudflat where the top 3 cm were collected into a plastic bag using a metal spoon. Water table depth (WTD) was

measured as in Yu and Chmura (2009). Porewater was collected to measure salinity at 0–15 cm using a porewater sipper or extracted with a syringe from core holes (Yu and Chmura 2009). Neither of these methods were successful in the *S. alterniflora*, therefore, at these locations sub-samples of the extractable nutrient cores were centrifuged to release porewater. Tidal water was sampled for mudflat salinity measurements and salinity was measured using a portable ATC refractometer. All soil cores were collected with minimal compaction and all samples were transported cool and in the dark to the laboratory and stored at 4 °C.

2.4. Analyses

2.4.1. Bulk density and TOC/TN

Bulk density/TOC/TN cores were dried at 60 °C to constant weight, finely ground and analysed for TOC/TN. The bulk density was determined by dividing the dry soil weight by the core volume. TOC and TN samples were processed and analysed by the Soil Ecology Research Group, McGill University. Samples of ∼0.5 g were weighed into a crucible and 1–2 ml of HCl was added to eliminate inorganic C. The samples were then dried at 50 °C for 48 h to remove all HCl. TOC and TN were measured by direct combustion at 900 °C with an Elemental Analyser (ThermoFinnigan Flash EA 1112 CN analyser, Carlo Erba, Milan, Italy). Results were obtained with an accuracy of ±5% for N and ±1% for C, and a limit of detection of 0.05% for both N and C.

2.4.2. Extractable nitrate and ammonium

Nitrate and ammonium samples were processed and analysed by the Soil Ecology Research Group, McGill University. Nitrate was measured as nitrate + nitrite and is referred to as nitrate from here on. A volume of 25 ml of 2 M KCl was added to 5 g of field-moist soil, shaken for 1 h at 200 rpm and then centrifuged for 20 min at 4000 rpm within 48 h of sample collection. The extractant was then filtered (0.45 μm) and analysed following the method of Sims *et al* (1995) on a microplate reader with a limit of detection of 0.1 ppm and an accuracy of ±5%.

2.4.3. Extractable DOC and TDN

To extract DOC and TDN 25 ml of ultrapure water (18.2 MΩ) was added to 5 g of field-moist soil, shaken for 1 h at 200 rpm and then centrifuged for 20 min at 4000 rpm. The extractant was then filtered (0.45 μm) and analysed on a TOC/TDN analyser (TOC VCSn + TMN-1, Shimadzu, Kyoto, Japan), with a 50 mg C l^{-1} standard resulting in an accuracy and precision of 3.0 and ±4.4 mg l^{-1}, respectively.

2.4.4. GHG fluxes

Gas samples were analysed for CH_4 and CO_2 on a gas chromatograph (GC-14, Shimadzu, Kyoto, Japan) fitted with a flame ionisation detector at 250 °C. CO_2 was methanised to CH_4 for analysis. Standards of CH_4 (5.1 ppm) and CO_2 (5000 ppm) resulted in an accuracy and precision of 6.6 ± 1.5 and 0.4 ppm, and 5324 ± 324 and 78 ppm, respectively, for CH_4 and CO_2. GHG fluxes were calculated from the change in headspace gas concentration over time using a linear regression of the linear portion of the flux, which prevented data from being excluded due to low r^2. Where fluxes were below the minimum detectable concentration difference (MDCD) of the GC, fluxes were set to zero (Sgouridis and Ullah 2017).

2.4.5. Statistical analysis

Due to the relatively small sample size the non-parametric Kruskal–Wallis rank sum was used to test for significant differences ($p < 0.05$) in GHG fluxes between sites using R (R Development Core Team 2011). If significant differences were found, a post-hoc Dunn test with Bonferroni correction was performed to determine which groups were significantly different from each other. Spearman's R correlation, which is a non-parametric correlation analysis able to find linear or non-linear relationships, was performed in R (R Development Core Team 2011) to investigate potential relationships between CH_4 fluxes and environmental variables.

3. Results

3.1. CH_4 fluxes

CH_4 emissions were significant (above the MDCD) from the *S. alterniflora* locations resulting in a net CH_4 flux of 17.7 ± 9.7 mg C m^{-2} h^{-1} (figure 2). Only two locations in the *P. australis* zone and one in each of the *S. patens* and mudflat zones had CH_4 fluxes above the MDCD, which were all small at <0.3 mg C m^{-2} h^{-1}. This resulted in significant differences in CH_4 fluxes between zones ($p < 0.01$, Kruskal–Wallis rank sum test).

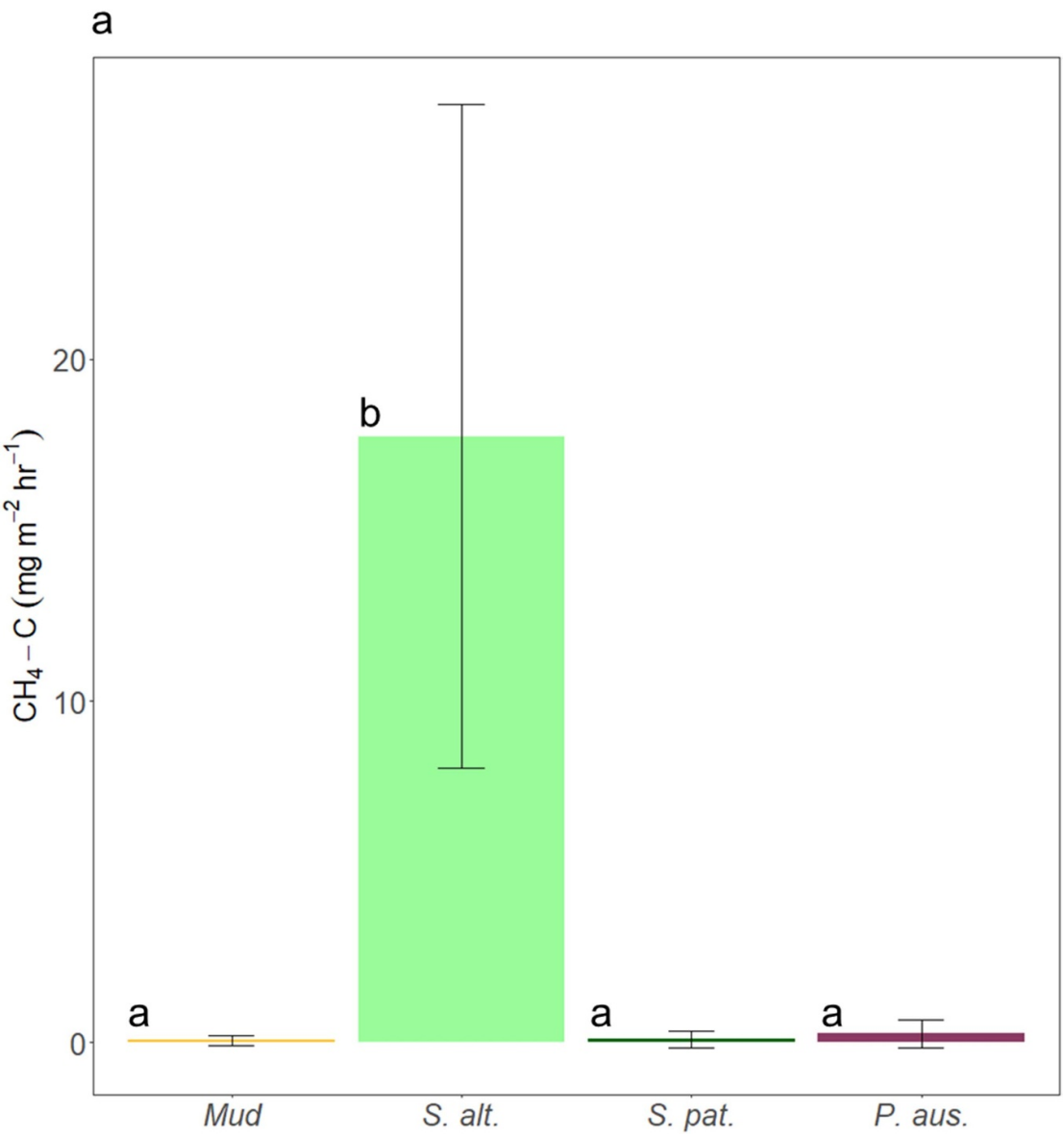


Figure 2. Zone-averaged CH_4 fluxes in mg C m^{-2} h^{-1} from four salt marsh elevation zones (mudflat, *S. alterniflora, S. patens* and invasive *P. australis*). Significant differences in fluxes between zones are indicated with different letters and the error bars represent one standard deviation.

Fluxes were significantly higher from the *S. alterniflora* zone compared to all three of the other zones (mudflat $p < 0.01$, *S. patens* $p < 0.01$, *P. australis* $p = 0.01$, Dunn test).

3.2. Relationships between GHG fluxes and environmental parameters

Zone-averaged environmental parameters are shown in table 1 and include further data from a companion study at this site, which were collected at the same time as the sampling of this study (Ampuero Reyes and Chmura 2022). Spearman correlation analysis on the whole dataset (table 2, figures 3 and S1 (available online at stacks.iop.org/ERE/1/011003/mmedia)) revealed that CH_4 fluxes were significantly related to multiple parameters with highest correlations found with salinity ($r = 0.72$, adjusted $p < 0.01$), WTD ($r = 0.72$, adjusted $p < 0.01$), CO_2 ($r = 0.64$, adjusted $p < 0.01$), rhizome volume at 0–15 cm ($r = 0.62$, adjusted $p < 0.01$), bulk density ($r = 0.61$, adjusted $p = 0.01$) and temperature ($r = 0.60$, adjusted $p = 0.01$). Rhizome biomass, root volume and dead volume at 0–15 cm were also significantly related to CH_4 with Spearman's r correlation coefficients between 0.48 and 0.51 (adjusted $p < 0.04$, table 2). Spearman correlation analysis on the *S. alterniflora* dataset revealed no significant relationships between CH_4 fluxes and environmental parameters.

Table 1. Environmental variables from four elevation zones at La Pocatière on the St. Lawrence River Estuary, August–September 2020. Included are data from this study and from a comparison study conducted at the same time (Ampuero Reyes and Chmura 2022).

	Zone			
Variable	Mudflat	*S. alterniflora*	*S. patens*	*P. australis*
CH_4–C (mg m^{-2} h^{-1})	0.1 ± 0.2	17.7 ± 9.7	0.1 ± 0.2	0.3 ± 0.4
CO_2–C (mg m^{-2} h^{-1})	59.7 ± 49.4	333.9 ± 67.7	156.7 ± 48.3	279.2 ± 100.7
NO_3^- (μg N g wet $soil^{-1}$)	0.7 ± 0.2	0.6 ± 0.2	0.6 ± 0.1	0.6 ± 0.1
NH_4^+ (μg N g wet $soil^{-1}$)	2.6 ± 0.7	3.4 ± 2.1	3.0 ± 0.7	1.7 ± 0.1
DOC (μg C g wet $soil^{-1}$)	32.5 ± 15.9	48.7 ± 11.4	43.5 ± 11.1	35.5 ± 5.0
TDN (μg N g wet $soil^{-1}$)	13.3 ± 2.4	8.5 ± 2.5	9.4 ± 5.4	7.3 ± 3.2
Salinity	13.0 ± 0.0	20.3 ± 2.0	14.5 ± 0.8	15.2 ± 0.4
Temp. (°C)	19.6 ± 0.2	19.9 ± 0.0	16.9 ± 0.7	16.8 ± 0.3
Depth of water table (cm)	0.0 ± 0.0	7.0 ± 0.0	1.5 ± 0.7	5.0 ± 0.0
TOC (%)	1.5 ± 0.1	3.0 ± 0.3	3.6 ± 0.4	3.5 ± 3.0
TN (%)	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0
OC:N	13.9 ± 1.7	15.7 ± 1.8	16.6 ± 1.1	14.8 ± 0.7
Bulk density (g cm^{-3})	0.6 ± 0.0	0.8 ± 0.0	0.6 ± 0.1	0.6 ± 0.1
Aboveground biomass (g m^{-2})	NA	26.1 ± 5.0	28.6 ± 8.7	62.2 ± 12.2
Rhizome volume 0–15 cm (cm^3)	NA	25.9 ± 11.9	11.3 ± 6.2	9.9 ± 1.2
Rhizome biomass 0–15 cm (g m^{-2})	NA	3.2 ± 1.4	2.3 ± 0.9	2.9 ± 0.5
Root volume 0–15 cm (cm^3)	NA	27.8 ± 13.1	23.1 ± 13.8	7.6 ± 1.4
Root biomass 0–15 cm (g m^{-2})	NA	2.7 ± 1.5	3.0 ± 1.3	0.9 ± 0.3
Dead volume 0–15 cm (cm^3)	NA	47.5 ± 14.9	29.5 ± 15.5	57.0 ± 28.3
Dead biomass 0–15 cm (g m^{-2})	NA	3.2 ± 0.9	2.3 ± 1.1	4.1 ± 1.5
Rhizome volume 15–30 cm (cm^3)	NA	10.5 ± 5.5	7.4 ± 2.4	14.3 ± 10.4
Rhizome biomass 15–30 cm (g m^{-2})	NA	1.2 ± 0.7	0.9 ± 0.3	2.4 ± 1.7
Root volume 15–30 cm (cm^3)	NA	12.2 ± 4.9	22.2 ± 9.3	20.6 ± 15.2
Root biomass 15–30 cm (g m^{-2})	NA	1.6 ± 0.5	2.2 ± 0.4	3.2 ± 2.8
Dead volume 15–30 cm (cm^3)	NA	23.3 ± 16.2	12.0 ± 4.0	52.3 ± 50.8
Dead biomass 15–30 cm (g m^{-2})	NA	2.2 ± 1.6	1.3 ± 0.4	3.4 ± 2.2

Table 2. Spearman's correlation (r) and adjusted p-values for the variables found to be significantly correlated with CH_4 fluxes.

Gas	Variable	Spearman's correlation (r)	Adjusted p (FDR)
CH_4	CO_2	0.64	<0.01
CH_4	Salinity	0.72	<0.01
CH_4	Temp.	0.60	0.01
CH_4	Water table depth	0.72	<0.01
CH_4	BD	0.61	0.01
CH_4	RZ vol. 0–15 cm	0.62	<0.01
CH_4	RZ bio. 0–15 cm	0.51	0.03
CH_4	Root vol. 0–15 cm	0.51	0.03
CH_4	Dead vol. 0–15 cm	0.48	0.04

4. Discussion

4.1. Comparison of CH_4 fluxes from *S. alterniflora* to other salt marshes

CH_4 fluxes observed from the *S. alterniflora* were much higher than those observed from other Northern salt marshes with *S. patens* and *S. alterniflora* as dominant vegetation (Magenheimer *et al* 1996, Chmura *et al* 2011, 2016, Roughan *et al* 2018). When compared to fluxes from other *S. alterniflora* marshes these results aligned with one study in China at a site with low salinity (Yang *et al* 2021) but were higher than most other fluxes previously observed (e.g. Bartlett *et al* 1985, Roughan *et al* 2018, Tong *et al* 2018). Annual *S. alterniflora* fluxes found here (upscaled for the period that the salt marsh is not frozen) were almost 140 times those expected for polyhaline marshes, with fluxes similar to the highest emitting oligohaline marshes (Poffenbarger *et al* 2011). This is especially surprising given that the study salt marsh is typically frozen from November to April i.e. no expected fluxes during this period and average annual temperatures are much lower than those found in other salt marshes. As gas fluxes were only measured once here, the annual fluxes calculated are estimates that should be refined with more annual data points, however, this upscaling suggests that CH_4 fluxes were much higher than those expected for polyhaline marshes.

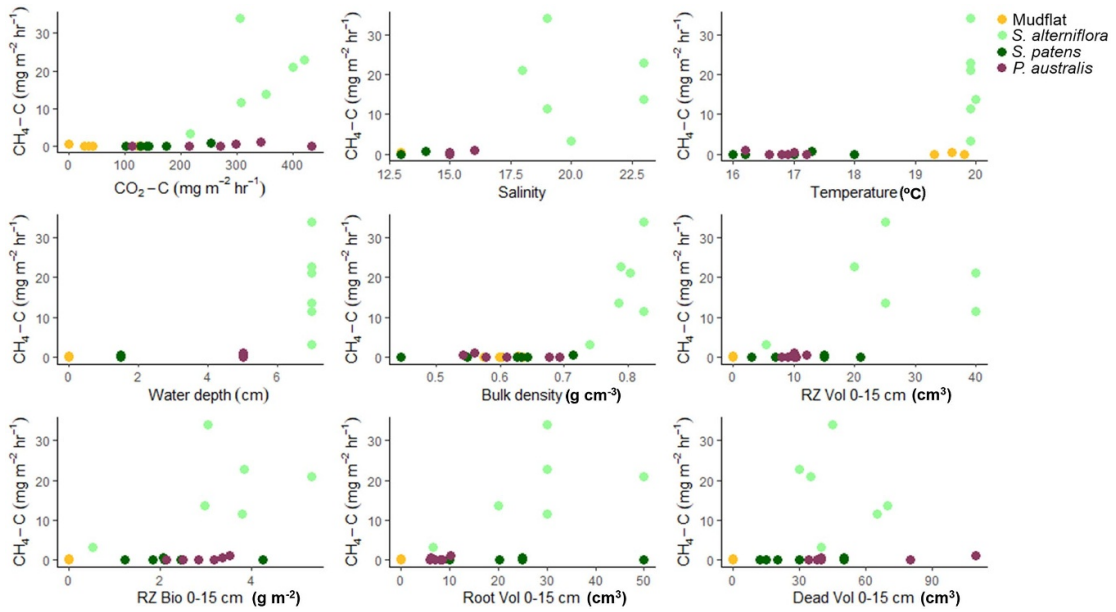


Figure 3. Bivariate plots of CH_4 fluxes versus significantly correlated environmental variables.

4.2. Fluxes between zones

To our knowledge, CH_4 fluxes from all four marsh zones studied here have not been previously investigated, however, differences between marsh zones have been observed. Previously, higher CH_4 emissions from *S. alterniflora* than from bare mudflat, *S. patens* and *P. australis* (Yuan *et al* 2015, Roughan *et al* 2018, Liu *et al* 2019, Yang *et al* 2021), as well as other salt marsh species including, *Cyperus malaccensis* and *Suaeda salsa* have been observed (Zhang *et al* 2010, Yuan *et al* 2015). However, similar emissions between *S. alterniflora* and invasive *P. australis*, and *S. alterniflora* and *S. patens,* as well as higher emissions from invasive *P australis* than native *S. patens/Distichlis spicata* have also been measured (Emery and Fulweiler 2014, Martin and Moseman-Valtierra 2015, Moseman-Valtierra *et al* 2016, Mueller *et al* 2016). Here, emissions of invasive *P. australis* and *S. patens* were similar. Species-specific comparisons are critical, therefore, to estimate correct emission factors for GHG budgets of salt marshes for the use in future climate models and for more accurate carbon budgeting depending on vegetation type.

4.3. Environmental controls

Differences in CH_4 emissions observed between elevation zones can be explained by differences in plant traits (such as root and rhizome biomass and volume) and plant-associated microbial assemblages, which can affect CH_4 production and consumption, and transport of CH_4 from anoxic soils to the atmosphere (Moseman-Valtierra *et al* 2016, Noyce and Megonigal 2021). Distinct differences between microbial communities of *S. alterniflora* and *P. australis* have previously been found (Ravit *et al* 2003).

Belowground or total biomass may be positively correlated with CH_4 emissions or porewater concentrations (Cheng *et al* 2007, Mozdzer and Megonigal 2013, Martin and Moseman-Valtierra 2017a, Noyce and Megonigal 2021) or have no significant relationship (Moseman-Valtierra *et al* 2016). Additionally, lower CH_4 emissions with higher belowground biomass from *S. patens* has been attributed to increased methane oxidation in the rhizosphere (Martin and Moseman-Valtierra 2017a). These conflicting results indicate that the controls of the rhizosphere on CH_4 emissions requires further exploration and stage in the growing season, among other factors, may be affecting these relationships. This may be due to the interplay between root exudates promoting methanogenesis and diffusion of O_2 through roots suppressing methanogenesis (Fritz *et al* 2011, Waldo *et al* 2019), which are two processes among many others, which require further investigation.

Vascular plants promote gaseous exchange between the atmosphere and the subsurface with the dominant CH_4 emissions pathway in wetlands being through aerenchyma (Megonigal *et al* 1999, Villa 2020). *S. alterniflora, S. patens* and *P. australis* all have the ability to create extensive aerenchyma in their rhizome and root systems with the extent of aerenchyma formation dependent on abiotic factors affecting soil oxygenation, such as water logging (e.g. Armstrong and Armstrong 1991, Armstrong *et al* 1999, Maricle and Lee 2002, Granse *et al* 2022). In salt marshes of the Northern Northwest Atlantic, *S. alterniflora* is subject to

the longest hydroperiod of any species, therefore, more extensive aerenchyma are expected compared with the *S. patens* and *P. australis*.

The relationship of CH_4 emissions with rhizome volume, rhizome biomass and root volume at 0–15 cm suggests this could be a key metric in predicting high CH_4 emissions and that CH_4 was transported through aerenchyma. An increase in CH_4 emissions where aerenchymous plants are present (e.g. Ford *et al* 2012) and at sites with higher stem densities (Chmura *et al* 2016) have been observed previously in salt marshes. The relationship with both rhizome metrics but only the root volume is likely due to the rhizome system being particularly important in these gaseous transport mechanisms (Armstrong and Armstrong 1991, Brix *et al* 1992).

Higher plant-mediated transport from *S. alterniflora* than *P. australis* has been observed previously, supporting the higher CH_4 emissions found here from the *S. alterniflora* (Tong *et al* 2012). Furthermore, the removal of *P. australis* aboveground biomass has no effect on CH_4 emissions indicating that plant transport is less important than abiotic factors or microbial production (Martin and Moseman-Valtierra 2017b). CH_4 fluxes from *S. alterniflora* have been found to be significantly correlated with porewater CH_4 concentrations (Zhang and Ding 2011) suggesting that the high emissions from this zone may be due to both high CH_4 production and high gas transport, which was found by Tong *et al* (2012).

An inverse relationship between salinity and CH_4 emissions, with negligible CH_4 emissions above a threshold salinity of 18 is widely assumed (Bartlett *et al* 1987, Poffenbarger *et al* 2011). Here, a positive correlation was observed between salinity and CH_4 fluxes contradicting both the inverse relationship between salinity and CH_4 emissions, and the salinity threshold of 18 for negligible CH_4 emissions (Poffenbarger *et al* 2011). Similar observations of highest CH_4 emissions at study sites with highest salinities and high CH_4 emissions at salinities >18 have been reported previously (e.g. Chmura *et al* 2011, 2016, Martin and Moseman-Valtierra 2017a, Emery and Fulweiler 2017), indicating that the assumption of low or negligible CH_4 emissions at high salinities is not valid across all environmental conditions. This may be due to other confounding environmental factors playing a more dominant role in CH_4 production and subsequent transport, for example, temperature being a more dominant control on CH_4 emissions than salinity (Abdul-Aziz *et al* 2018) or higher stem densities in areas of high salinity increasing transport (Chmura *et al* 2016).

High salinity is assumed to result in low CH_4 production due to substrate-competition between sulphate-reducing bacteria and methanogens (King and Wiebe 1980, Villa 2020). Methanogenesis can occur through three different pathways, acetoclastic, hydrogenotrophic and methylotrophic (Villa 2020). Methylotrophic methanogens preferentially use methylated substrates and are not in direct competition with sulphate-reducers (Oremland *et al* 1982, Villa 2020). This is the primary pathway for CH_4 production in salt marshes (Oremland *et al* 1982), therefore, despite high salinities salt marshes may be sources of CH_4 to the atmosphere. A transition from hydrogenotrophic to methylotrophic methanogenesis has been observed after *S. alterniflora* invasion into a tidal flat, further supporting the hypothesis that methanogens were not competing with sulphate-reducing bacteria (Yuan *et al* 2014, 2019). Additionally, salinity is not always a good indicator of sulphate concentrations as local depletion of sulphate in soil microzones may occur independently of salinity (King and Wiebe 1980, Poffenbarger *et al* 2011).

Higher water table or flooding is generally associated with higher CH_4 emissions although there may be a lag between higher water table and higher CH_4 emissions (Turetsky *et al* 2008, Zhao *et al* 2020, Calabrese *et al* 2021, Knox *et al* 2021). The highest CH_4 emissions observed here from the *S. alterniflora* zone where the water table was deepest below the surface were, therefore, unexpected. However, lower water level has been observed to have both no control on and increased rates of CH_4 fluxes from salt marshes indicating that other factors may be more important drivers in these ecosystems (Cheng *et al* 2007, Abdul-Aziz *et al* 2018).

Decomposition of dead vegetation is a likely source of carbon for methanogenesis explaining the significant relationship between dead volume at 0–15 cm and CH_4 fluxes. Additionally, the significant relationship between CH_4 and rhizome volume and biomass and root volume suggest that root-allocated organic carbon is an important source of fresh substrate for methanogenic bacteria. The lack of a significant relationship between CH_4 fluxes and DOC perhaps indicates that exudation by the dense rhizome of *S. alterniflora* was driving high rates of methanogenesis. Methanogenesis tends to occur in deeper, more anoxic soil layers so that dead vegetation at greater depths likely promotes methanogenesis (Conrad 1996, Villa 2020), however, CH_4 production has been observed up to ten times higher in oxic compared to anoxic soils (Angle *et al* 2017), supporting the relationship with dead volume in the upper soil layer observed here.

High temperature and bulk density may promote increased rates of biogeochemical reactivity and methanogenesis over methanotrophy (Dunfield *et al* 1993, Boeckx *et al* 1997). Higher temperatures are well known to increase reaction rates and have previously been observed to drive increased CH_4 emissions in salt and brackish marshes, as well as other wetlands (e.g. Hirota *et al* 2007, Noyce and Megonigal 2021). Despite this, conflicting relationships have been reported including no effect of temperature on CH_4 emissions, lower

CH_4 emissions at higher temperatures and increased CH_4 emissions with temperature in *P. australis* but not *S. alterniflora* (Ford *et al* 2012, Martin and Moseman-Valtierra 2017a, Liu *et al* 2019). Soils with higher bulk densities tend to facilitate more anoxic conditions, which may lead to methanogenesis and limit CH_4 oxidation (Boeckx *et al* 1997, del Grosso *et al* 2000). CH_4 emissions were also correlated with CO_2 emissions, indicating that the *S. alterniflora* zone was characterised by high rates of both aerobic and anaerobic respiration.

CH_4 transport by plant diffusion alone is slower than active exchange mechanisms (Brix *et al* 1992), which occur in the presence of light. Measuring fluxes in dark chambers excludes the active pumping mechanism of GHGs through plants (e.g. Whiting and Chanton 1996) resulting in potential underestimation of GHG fluxes. The relationships observed here between belowground biomass and CH_4 emissions indicate that diffusive plant processes, at least, are still important, supporting previous suggestions of diffusive transport of CH_4 through the aerenchyma of *S. alterniflora* (Zhang and Ding 2011). Additionally, plant community composition determines the extent to which light may alter rates of CH_4 emissions, with both large and negligible effects observed (Bartlett *et al* 1987, van der Nat and Middelburg 2000, Poffenbarger *et al* 2011).

4.4. Effect of sea level rise and invasive vegetation on CH_4 emissions

The relatively high CH_4 emissions from the *S. alterniflora* zone suggest that the strength of the carbon sink of salt marshes vegetated with *S. alterniflora* is greatly reduced. This has large implications for the blue C value of salt marshes, as *S. alterniflora* distribution is widespread and rapidly invading some coastal ecosystems. The patterns of CH_4 fluxes between elevation zones suggest that conversion of *S. alterniflora* to mudflat from sea level rise will significantly reduce CH_4 emissions, by 99.4%. If *S. patens* converts to *S. alterniflora* due to sea level rise this will lead to a large increase in CH_4 emissions (17 600%). Here, where the transition between *S. patens* and *P. australis* was studied, the effect of the invasive *P. australis* on the strength of the carbon sink appears to be minimal. CH_4 fluxes from within the monospecific *P. australis* stands are required to assess how the complete replacement of *S. patens* with invasive *P. australis* may affect the strength of the carbon sink.

5. Conclusions

Methane emissions were dependent on elevation zone with the highest emissions from the *S. alterniflora* while fluxes from the other elevation zones were negligible. These findings indicate that species-specific emission factors should be considered in carbon budgeting and to refine modelling of the strength of the carbon sink in salt marshes.

Methane emissions were high for salt marshes and were similar to those typically found in oligohaline marshes with lower salinities. Methane fluxes were significantly correlated with soil properties, plant traits and CO_2 fluxes. The control of root and rhizome volume on CH_4 fluxes indicates the importance of aerenchyma in transporting CH_4 directly from anoxic soils or porewater into the atmosphere, without being oxidised.

Highest CH_4 emissions from the zone of highest salinity provides further evidence that high salinity may not be a good predictor of low CH_4 emissions. This may be due to evidence that the methanogenic pathway in salt marshes and particularly in *S. alterniflora* does not directly compete with sulphate reducers. Further investigation is required to determine the microbial production versus emissions of CH_4 in these zones, as well as on constraining the methanogenesis mechanism in major salt marsh zones to allow the effect of salinity to be better constrained.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: https://doi.org/10.5281/zenodo.6500188 (Comer-Warner *et al* 2022). Data will be available from 03 January 2023.

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