CONTROLS AFFECTING METHANE FLUXES IN RESTORED AND NATURAL TIDAL WETLANDS

BY

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ABSTRACT OF THE DISSERTATION

Controls affecting methane fluxes in restored and natural tidal wetlands

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Natural wetlands emit one third of global methane (CH_4), the second most important greenhouse gas after carbon dioxide (CO_2). However, there is a huge uncertainty about regional and global CH_4 emission estimates, because of the estimation of CH_4 emissions for large areas based on the CH_4 flux measurement made in highly heterogeneous, poorly mapped small areas. But, within a small area of wetland, there can be a huge spatial variation in CH_4 flux due to spatial heterogeneity. Therefore, for better understanding of CH_4 dynamics of a wetland, CH_4 flux measurement should be made in a variety of microsites of a wetland covering different scales, vegetation, and heterogeneity of the sites. Our two-year CH_4 flux measurements from two microsites from each of three wetlands of New Jersey Meadowlands will help to refine CH_4 budget of low salinity marshes, which have a large uncertainty about their CH_4 budget. The annual CH_4 flux in a restored high marsh site varied from 1.8 (*Spartina patens* marsh) - 26.6 (*Phragmites*

australis marsh) g CH_4 m^{-2} yr^{-1}. The *S. alterniflora* marsh and mud flat area of another restored low marsh, emitted 15.6 and 7.5 g CH_4 m^{-2} yr^{-1}, respectively. The annual emission of CH_4 for a *S. patens* marsh and a *P. australis* marsh at a natural high marsh site were 2.7 and 12.6 g CH_4 m^{-2} yr^{-1}, respectively. We also investigated relationships between CH_4 flux and various physical factors including air and soil temperature, net radiation, and vapor pressure deficit (VPD). Presence of most of the belowground biomasses close to the soil surface suggests that most of the effect of belowground biomass on CH_4 dynamics occurs close to soil and atmosphere interface. Investigations of belowground biomass distribution, root and rhizome characteristics as well as leaf area index (LAI), in this study aid modeling CH_4 and other greenhouse gas transport. There was higher CH_4 emission during incoming tide than during outgoing tide in a mud flat microsite; however, we did not find a relationship between tidal water depth difference and CH_4 flux in vegetated areas. The weak, but positive relationship between CH_4 flux and VPD in vegetated areas suggest stomatal control on CH_4 flux.

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Dedicated to my parents

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Introduction

Methane (CH_4) is the second most important greenhouse gas after carbon dioxide (CO_2) and it is 28 times more potent than CO_2 for global warming on a mass basis over a period of a century [*Stocker et al.,* 2013]. Natural wetlands are the largest source of global CH_4 emission as one third of the CH_4 is emitted from them [*Solomon et al.*, 2007]. There is a large uncertainty about regional and global CH_4 emission estimates, since the CH_4 emission estimate for large areas are extrapolated based on a few CH_4 flux measurements carried out in poorly mapped and highly heterogeneous wetland environments [*Bridgham et al.*, 2013]. Studies have pointed out that there could be a large variation in CH_4 emission within small area due to the spatial heterogeneity caused by variations in species composition and water table position [*Forbrich et al.*, 2011]. Therefore it is important to have CH_4 flux measurement from both natural and restored wetland covering a range of spatial scales with differences in vegetation, hydrology and mircrosite topography within a wetland to better understand spatial and temporal CH_4 dynamics. Also, a better understanding of the relationships between various biological as well as physical factors with CH_4 flux aid to get better insight on CH_4 dynamics of a wetland that can help better planning of CH_4 emission mitigation. The plants growing in a wetland is an important factor that affect CH_4 dynamics of a wetland by impacting production, consumption and transport of CH_4 [*Laanbroek*, 2010]. In the oxygen deprived reduced environment of a wetland, CH_4 producing microbes use decaying roots, rhizomes, and aboveground plant parts as well as root exudates as substrate for CH_4 production [*Le Mer and Roger*, 2001]. The plant parts do not only play a role in CH_4 production, they also

play a role in the consumption and transport of CH_4. Some of the CH_4 produced in the reduced soil of wetlands is oxidized into CO_2 by oxygen leaked from roots. Part of the CH_4 produced in reduced wetland sediment is transported to atmosphere via root, rhizome and aboveground plant parts including stem and leaf [*Laanbroek*, 2010; *Lai*, 2009]. The CH_4 dynamics in wetlands depend not only on wetland plants, it also depends on various physical factors including hydrology, soil and air temperature, net radiation, and oxidation-reduction potential.

Hydrology of the wetland is a key determinant of CH_4 dynamics [*Altor and Mitsch*, 2006; 2008; *Roulet et al.*, 1993; *Sass et al.*, 1992; *Yagi et al.*, 1997] as hydrology largely determines the availability of oxygen in a wetland soil. Temperature stimulate activity of both CH_4 producing and CH_4 oxidizing bacteria, but the production of CH_4 become greater than oxidation due to higher sensitivity of CH_4 producing bacteria to temperature than CH_4 oxidizing bacteria [*Inglett et al.*, 2012; *Moosavi and Crill*, 1998]. The increase in temperature does not only impact CH_4 dynamics directly by affecting activities of the bacteria, but also affect the dynamics indirectly by impacting other factors such as CH_4 dissolution in the water column [*Casper et al.*, 2000], photosynthesis and supply of root exudation [*Hatala et al.*, 2012; *Laanbroek*, 2010]. Studies have also found the effect of light on CH_4 emission, which is due to increase in stomatal conductance [*Frye et al.*, 1994], photosynthesis [*Chanton et al.*, 1995], and sediment temperature [*Mikkela et al.*, 1995] with increasing light. Likewise, salinity is another factor that affects salt marsh CH_4 dynamics. A recent review of CH_4 emission from 31 salt marshes with a salinity range of 0.05 to 18 ppt showed that CH_4 emissions decrease with increasing salinity [*Poffenbarger et al.*, 2011].

We investigated CH_4 flux, above- and belowground biomass distributions, and the relationship between CH_4 flux and various environmental factors that include hydrology, air and soil temperature, VPD, net radiation, and oxidation-reduction potential for two microsite each in two restored and one natural wetland of the New Jersey Meadowlands. We also measured diameter of rhizomes and roots, the number of primary roots per node and the root surface area to volume ratio for four dominant marsh plants and tested following four hypotheses: 1) Natural wetlands emit more CH_4 than restored wetlands because more organic material is available for CH_4 production in the natural wetland due to the longer time period for organic carbon accumulation, and 2) within the same wetland type (natural vs. restored), areas of invasive *Phragmites australis* emit more CH_4 than areas of native *Spartina patens*, since *P. australis* is located at lower elevations having a shallower water table and have a more efficient CH_4 transport mechanism, convective through-flow [*Armstrong and Armstrong*, 1991]. *S. patens* is located at higher elevations with a lower water table, and does not have a convective through-flow mechanism. 3) Both rhizome and root biomass are higher near the soil surface for all the species. 4) Diameter of rhizomes and roots, the number of primary roots per node, and the root surface area to volume ratio are higher in *P. australis* than native *S. patens* and *D. spicata* as the *P. australis* marsh has been shown to emit more CH_4 than marshes of *S. patens*. Our measurement of CH_4 flux and the investigation of the relationship between the flux and various biotic and environmental factors will help better understand CH_4 flux dynamics of a wetland and contribute to refine global CH_4 emission estimates. The investigated aboveground and belowground biomass distribution as well as root and rhizome characteristics will aid modeling CH_4 and other greenhouse gas transport.

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Chapter 1

Methane emission from urban temperate wetlands: Temporal and spatial variations[1]

Abstract

Variation in methane (CH_4) flux was investigated using static chambers over a two-year period in two microsites in each of two restored and one natural tidal wetland sites in the New Jersey Meadowlands. Within the same marsh, there was a large variation in CH_4 emissions between marsh areas covered by different species even though the aboveground biomasses of the studied species were not significantly different. Also, the year-to-year variation in CH_4 emissions varied with species. The annual CH_4 flux in 2013 in a restored high marsh site varied from 1.8 g CH_4 m^{-2} yr^{-1} for a *Spartina patens* marsh to 26.6 g CH_4 m^{-2} yr^{-1} for a *Phragmites australis* marsh. The *Spartina alterniflora* marsh and a mud flat area of another restored low marsh emitted 15.6 g CH_4 m^{-2} yr^{-1} and 7.5 g CH_4 m^{-2} yr^{-1}, respectively. The annual emission of CH_4 for a *S. patens* marsh and a *P. australis* marsh at a natural high marsh site were 2.7 g CH_4 m^{-2} yr^{-1} and 12.6 g CH_4 m^{-2}

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[1] Manuscript by R. Tripathee, H.J. Renninger, Kristen Tomasicchio, M.C. Reid, P. R. Jaffé and K.V.R. Schäfer (under review, *Journal of Geophysical Research-Biogeosciences*)

yr^{-1}, respectively. Most of the belowground biomass was found close to the soil surface suggesting that a majority of belowground biomass effect on CH_4 dynamics happens at a shallower soil depth. However, the presence of roots at 55 cm below the soil surface indicated that the effect of belowground biomass on CH_4 dynamics extends well below the soil surface.

Introduction

On a per mass basis, methane (CH_4) is 28 times more potent than carbon dioxide (CO_2) as a radiative forcing greenhouse gas, over a 100-year period [*Stocker et al.*, 2013]. Atmospheric CH_4 concentrations have been increasing due to anthropogenic as well as natural sources. Agriculture, natural gas distribution pipelines and landfills are the main human activities contributing to increasing CH_4 in the atmosphere, whereas wetlands are the biggest natural sources of CH_4 [*Solomon et al.*, 2007]. CH_4 emissions from wetlands may have contributed to the increased global warming that has been observed since the 1990s [*Fletcher et al.*, 2004; *Wang et al.*, 2004; *Zhuang et al.*, 2004]. Wetland plants absorb atmospheric carbon dioxide (CO_2) during photosynthesis. Because of anaerobic waterlogged condition in soil, the carbon absorbed during photosynthesis is stored in soil as organic material results in wetland as a significant carbon sink [*Bridgham et al.*, 2006; *McLeod et al.*, 2011]. However, due to anoxic conditions, CH_4 is produced by the decomposition of organic materials by methanogenic bacteria in wetland soils [*Mitsch and Gosselink*, 2007].

Once CH_4 is produced in wetland soils, it is released into the atmosphere through three major pathways: 1) transport through vascular plants, 2) diffusion along a concentration gradient, and 3) release in the form of gas bubbles (ebullition) [*Le Mer and Roger*, 2001]. Concurrently, some of the produced CH_4 is oxidized into CO_2 by methanotrophs within and above the soil [*Bubier and Moore*, 1994] and in the oxic rhizosphere of wetland plants. Thus, emission of CH_4 from wetlands into the atmosphere is the net result of production and consumption of the gas by microbes. In peatlands, where the water table lays below the soil surface, diffusion is the major CH_4 transport mechanism; whereas

plant mediated transport and ebullition are key transport mechanisms of CH_4 in peatlands with a water table at or above the surface [*Bubier and Moore*, 1994]. Ebullition is the main transport process in the non-vegetated area of a wetland [*Van der Nat and Middelburg*, 1998]. Aquatic plants contain aerenchymatous tissue (tissue with large gas space between cells), which can act as a conduit for CH_4 transport, by means of diffusion or pressurized ventilation, from the zone of production to the atmosphere [*Brix et al.*, 1992; *Dacey*, 1981]. The same aerenchymatous tissue transports oxygen from the atmosphere to the roots and some of this oxygen can escape into the root zone (rhizosphere). The methanotrophic bacteria present in the rhizosphere use the oxygen and consume some of the CH_4 produced in the anaerobic zone of the wetland soil [*Le Mer and Roger*, 2001]. In some wetland ecosystems, the oxygen supply by plant roots at the rhizospheric region is so effective that it enables CH_4 consuming microbes to oxidize all the CH_4 produced in the soil, resulting in zero emission even if a significant amount of methane is being produced in the soil [*Fritz et al.*, 2011]. However, when CH_4 is transported through plants, soil surface oxidation of CH_4 by aerobic methanotrophic bacteria is bypassed. Plant transport of CH_4 is a very important mechanism since 50 to 90% of the total flux of CH_4 in wetlands is transported through plants into the atmosphere [*Hanson and Hanson*, 1996; *Reid et al.*, 2013]

Studies carried out in saline marshes have shown that marshes having salinity less than 18 ppt emit significantly greater CH_4 than marshes having salinity more than 18 ppt [*Poffenbarger et al.*, 2011]. Therefore, it is likely that if wetlands are restored in the area of low salinity level, they will emit higher amounts of CH_4. Millions of hectares of freshwater and salt-water wetlands are restored every year around the world in an effort

to regain important ecosystem services (e.g., carbon storage, biodiversity conservation, flood attenuation, recreation) that were lost due to wetland degradation. Previous studies have shown that CH_4 emissions from restored wetlands change slowly over time after restoration and remain different from natural wetlands because they emit less CH_4 for many years following restoration [*Tuittila et al.*, 2000; *Waddington and Day*, 2007]. The speed of change depends on factors including management practices, vegetation before and after the restoration and water table height of the restored wetland [*Droesler et al.*, 2008; *Herbst et al.*, 2011].

Low soil organic matter (SOM) in restored and created wetlands can limit establishment of plants and their growth as well as important ecosystem function such as nutrient cycling [*Groffman et al.*, 1996; *Sutton-Grier et al.*, 2009; *van der Valk et al.*, 1999; *Zedler and Langis*, 1991]. Therefore, in some cases, organic matter is added at the beginning of wetland restoration/creation to mitigate low SOM conditions and facilitate the restoration of functional equivalency to a similar level as natural wetlands [*Ballantine and Schneider*, 2009; *Ballantine et al.*, 2012; *Bruland et al.*, 2009; *Sutton-Grier et al.*, 2009]. Wetlands restored without the addition of organic materials should have less CH_4 emissions than wetlands restored with organic materials for at least a few years after restoration, as organic matter is the substrate for CH_4 production.

Studies have shown large variation in CH_4 emission within a small area due to spatial heterogeneity of source areas caused by differences in species composition or water table position [*Forbrich et al.*, 2011]. However, CH_4 emissions for large areas are extrapolated based on a few CH_4 flux measurement made in highly heterogeneous and poorly mapped wetlands leading to major uncertainties about regional and global CH_4 emission estimates

[*Bridgham et al.*, 2013]. In order to better understand spatial and temporal heterogeneous CH_4 emissions, CH_4 flux measurements need to be conducted in both natural and constructed/restored wetlands covering a range of microsites within a wetland. Therefore, our study of two microsites in each of three mesohaline (salinity between 5 to 18 ppt) wetlands will contribute to refining global methane budgets, and increase understanding of CH_4 emissions from low salinity marshes which have larger uncertainties in their CH_4 budget [*Poffenbarger et al.*, 2011].

We investigated CH_4 fluxes from two restored wetlands and one natural mesohaline wetland in New Jersey. Flux measurements were made in two microsites within each of the sites. Microsites at one restored wetland are a non-vegetated mud flat and a vegetated area with *Spartina alterniflora*. Areas dominated by *Phragmites australis* and *S. patens* were selected at one natural and another restored site. We tested two hypotheses in this study: 1) Natural wetlands emit more CH_4 than restored wetlands because more organic material is available for methane production in the natural wetland due to the longer time period for organic carbon accumulation, and 2) within the same wetland type (natural vs. restored) areas of invasive *P. australis* emit more methane than areas of native *S. patens*, since *P. australis* is located at lower elevations having a shallower water table and has a more efficient CH_4 transport mechanism, convective through-flow [*Armstrong and Armstrong*, 1991]. *S. patens* is located at higher elevations with a lower water table, and does not have a convective through-flow mechanism.

Materials and Methods

Study site

The New Jersey Meadowlands (NJM) has many typical urban tidal wetlands surrounded by high-density urban areas. Two restored wetland sites, Marsh Resource Meadowlands Mitigation Bank (MRMMB) and Secaucus High School (SHS), and one natural wetland, Hawk Property (HP), were located within the estuarine ecosystem and selected for this study. The MRMMB is located in Carlstadt, Bergen County, New Jersey (40.82N, 74.03W). The total area of the site is 83.4 hectare. The site was restored by planting native *S. alterniflora* after removing invasive *P. australis* in 1999. However, new small patches of *P. australis* appear every year despite application of chemicals to eliminate this species. The MRMMB has been described in a previous study [*Reid et al.*, 2013]. The SHS site is located in Secaucus, Hudson County, New Jersey (40.80N, 74.04W). The total area of this high marsh site is 17.4 hectare. This site was restored in 2007 by removing the monoculture of *P. australis*. *S. patens* and *Distichlis spicata* are dominant at higher elevations of this marsh. *P. australis* is also invading these marshes again mainly, and more vigorously, at lower elevations. CH_4 fluxes were measured at the height of 1.01 MASL (meter above sea level) for *S. patens* and at a height of 0.74 MASL for *P. australis*. Areas with *P. australis* have a shallower water table than areas with *S. patens*. The HP site, which is 9 hectares in size, is also located in Secaucus, New Jersey (40.70N, 74.04W). This is a natural, mesohaline marsh currently being invaded by *P. australis* (approximately 53% of the area). However, there is still one large (> 3,000 m^2) and a few small (<200 m^2) remnant patches dominated by native *S. patens* (about 6 % of the area, mixed with *D. spicata*, the remainder being non-vegetated mudflat areas) surrounded by

P. australis. There is also a mixed vegetation patch of *S. patens* and *P. australis* between *S. patens* dominated areas of higher elevation/deeper water table (0.91 MASL), and pure areas of *P. australis* at low elevation/shallow water table (0.83 MASL). The salinity of the study sites ranges from 7.6-13.9 ppt (**Table 1**, *Pal et al.* unpublished).

CH_4 flux measurements were made in pure vegetation of *S. alterniflora* and a non-vegetated area (mud flat) at the MRMMB site, and pure vegetation patches of *P. australis* and of *S. patens* (mixed with *D. spicata*) at SHS site and HP site. We measured fluxes from January 2012 to December 2013 at the MRMMB and from August 2012 to December 2013 at all the three sites. The measurements of CH_4 fluxes were made every 4-6 week during low tide at MRMMB in 2012. At all three sites, every 4-6 weeks, measurements of CH_4 flux were made from August 2012 to December 2013, whereby monthly measurements of CH_4 flux were made during summer 2013 (June to August). In October, 2012, Hurricane Sandy flooded the research areas to a depth of 1.6m above high tide, uprooting some vegetation and removing sediment along the shorelines of the Hackensack River in the New Jersey Meadowlands. Thus, differences in fluxes between 2012 and 2013 may be due, in part, to the disturbance the sites underwent.

Chamber construction and sampling of CH_4

Chamber construction and installation were based on *Klinger et al.* [1994], *Livingston and Hutchinson* [1995] and *Altor and Mitsch* [2006]. Three chambers were installed in each vegetated and non-vegetated (mud flat) area of the marsh at the MRMMB site. At the HP and SHS sites, three chambers each were installed in a *S. patens* patch and a *P. australis* patch. Chambers were installed by inserting a cylindrical plastic bucket, 30 cm in diameter and 35 cm in height (five US gallon), into the soil after removing the base of

the bucket. Thirty cm of the basal part (20 cm at SHS site and HP site) of the bucket was placed into the marsh soil. Bags made from clear plastic (Husky plastic sheeting, 0.09 mm thick) were attached to the exposed upper edge of the bucket along with supports made with PVC pipes (1.3 cm in diameter) during each sampling time. During non-sampling periods, the PVC frame and bags were removed. The chambers were vented with a 1m long, 3 mm inner diameter tube to prevent pressure build up inside the chamber over the sampling period. Samples were collected using a syringe (30 ml) through a bulkhead fitting with septum every 15 min over a period of 1.25 hrs for a total of six samples. The sampling procedure was repeated once more during low tide from each microsite at each site, except at the MRMMB site in May and August of 2012. The chambers were 1.06 m tall for vegetated areas when there was no vegetation or vegetation was short (January through May) and the mud flat area. When vegetation was taller (June to December), 1.6 m tall chambers at the MRMMB site and 2 m tall chambers at the SHS site and HP site were used. To mix the gas inside the chamber, a small fan for 1.06 m tall chambers and 2 small fans for 1.6 m and 2 m tall chambers were run by battery inside the chambers. The 30 ml gas samples collected with a syringe were injected into evacuated serum vials (20 ml) that were then over pressurized and taken to the lab for further analysis using gas chromatography (Shimadzu GC-2014, Shimadzu Corporation, Tokyo, Japan) within a week of sampling. Gas samples were stored in a freezer until analysis. Measurements of CH_4 concentration was made on a gas chromatograph equipped with a flame ionization detector (FID).

Analysis of gas sampling

Linear regression of CH_4 concentration vs. sampling time was used to calculate CH_4 flux. Linear regression P values ≤0.1 were considered significant. Regression slopes were used to calculate CH_4 flux by multiplying with the volume of the measurement chamber and dividing by the area of the chamber to derive fluxes per unit area. When the P-value for the regression line was >0.1 and individual measurements used for the regression line varied by less than 1 ppm, the slope of the regression line, and therefore the CH_4 flux, was considered equal to zero. If $P > 0.1$ and CH_4 concentration varied more than 1 ppm over the sampling period, an outlier detection was run by which one point was removed from the regression line, and if the P-value of the regression line improved to 0.05, the slope of the regression line was used for flux calculation; otherwise the regression line was not used for the calculation of the fluxes. Annual CH_4 fluxes were estimated by integrating the curve connecting averages of replicate measurements following *Van der Nat and Middelburg* [2000]. An average hourly flux for 2013 was calculated by dividing annual flux by total number of hours in the year.

Above- and belowground biomass harvest, and root density and rhizome density

The aboveground and belowground biomass harvest was carried out within 2-3 meter distance from the CH_4 flux measurement chambers to represent the biomass that was affecting the CH_4 flux within the chamber. For aboveground biomass, three plots of 50 x 50 cm were harvested from each of the vegetation types measured except in a *P. australis* patch at the SHS site because there was no living patch of *P. australis* during our harvesting time (last week of July to first week of August, 2013). To eliminate invasive

P. australis patches of these restored sites, plants are killed by applying chemicals, which was done in the fall of 2012 and the fall of 2013. During aboveground biomass harvest, all the plants present in the 50 cm x 50 cm were cut at the soil surface and brought back to the lab. All leaf and stem material connected to the dead and decaying stems were considered previous year(s) biomass and all leaf (green and dead) and stem material connected to green stems were considered current year biomass. Only current year biomass was considered aboveground biomass in this study. The aboveground biomass was dried in a commercial drying oven (Thermo Scientific Precision 3050 Series premium oven, Thermo Fisher Scientific, USA) for a week at 60 °C and weighed. Within the same plots where aboveground biomass harvest was carried out, a 25 cm x 25 cm area was marked and all belowground biomass (root and rhizome) along with soil was dug out using a shovel to a depth of 55 cm below the soil surface. The belowground harvest was portioned into three soil blocks; the first block = 0-25 cm deep, the second block = 25-40cm deep, the third block = 40-55cm deep. This soil depth was sufficient for the restored sites to capture the majority of the roots (>95%). In order to be consistent, we applied the same depth to the natural wetland sites, whereby approximately 90% of the roots and rhizomes were captured. Belowground samples were returned to the lab and washed with tap water to remove the soil. Belowground biomass was separated into rhizome and root. Dry weights of rhizome and root were recorded for each depth from each of the harvested plots, after drying in a commercial drying oven as described above. Root volume was estimated by the displacement method in water for nine root samples from the top soil section (0-25 cm) from each plot and then their dry weight was determined. Root density was calculated as the ratio of dry weight to root volume.

Soil organic C (%) and nitrogen (N %)

Soil organic matter is a potential substrate for methanogens, thus soil cores were taken to determine soil organic matter (SOM) using the Loss on Ignition (LOI) technique following a similar protocol as in *Craft et al.* [1991]. SOM samples were collected from all locations and microsites except the *P. australis* microsite at the SHS site. Soil samples were extracted from sites with a soil corer in 0.5 m sections to a depth of 1 m. Three replicates of each vegetation type and two replicates for the mud flat area were extracted. In the lab, the core sections were cut into 5 cm sections and plant material was removed and set aside for another study. The 5 cm sections were dried in a 105°C oven overnight, weighed, and then burned in a 450°C furnace for 8 h [*Craft et al.*, 1991]. In order to test for burning time a subsample (n=12) was first subjected to 8 h burning time, weighed, then burned an additional 8h [*Craft et al.*, 1991]. The resulting weight after 16 h did not differ significantly from 8 h of burning (paired t-test, P=0.8), thus a burning time of 8 hours was deemed appropriate to determine LOI. Pre-burn weight minus post-burn weight divided by pre-burn weight resulted in the organic matter burned off (LOI in %). To derive the organic carbon content (in %) and total nitrogen content (in %), equations derived by *Craft et al.* [1991] were used.

Statistical analyses

Analysis of variance (ANOVA) was used to test whether a) species, b) sites, c) season, and d) years were different from each other, with associated two- and three-way interactions. The CH_4 flux data were not normally distributed, thus a $\log_{10}$ transformation was performed after a value of 1 was added to remove zeros. Negative numbers were eliminated, as the objective of the study was to determine methane efflux. In 2012, one

such value was eliminated at the MRMMB site for a *S. alterniflora* patch, and in 2013, eight out of nine values occurred in *S. patens* patches at the SHS and HP sites and one *P. australis* patch at the HP site, thus resulting in removal of ten values in two years. As these values also occurred in the wintertime, they were deemed spurious. The log-transformed data were normally distributed and thus an ANOVA with Tukey HSD multiple comparison of means was used on the log-transformed values. P-values ≤ 0.05 were considered significant. All statistical analyses were done using R version 2.15.3 (The R Foundation for Statistical Computing, http://www.r-project.org/).

Results

Temporal variation of CH_4 flux during low tide

CH_4 flux to the atmosphere from vegetated and non-vegetated areas (mud flat) at all sites showed strong seasonality in both 2012 and 2013 with the majority of emissions occurring from June to November and little or no emission during winter ($P < 0.00001$; **Fig. 1, Table 2**). The seasonal CH_4 flux measurements from all three sites showed that most of the flux occurred during the summer season (June to August) (**Fig. 1**). CH_4 fluxes did not differ during the winter in 2012 and 2013 ($P = 0.6$), nor between the summer of 2012 and 2013 (season and year interaction, $P = 0.34$). However, 2012 and 2013 were significantly different from each other ($P = 0.03$) with 2013 exhibiting slightly higher fluxes than 2012.

Spatial variation in CH_4 flux during low tide

CH_4 flux differed between the marsh zones (vegetated vs. non-vegetated, zones dominated by either *P. australis* or *Spartina spp*) in either year ($P<0.00001$; **Table 2**). In

2012, within the same study site, the marsh dominated by native *S. patens* emitted less CH_4 than the marsh with invasive *P. australis* during the growing season ($P<0.00001$) when the emission of CH_4 from the marshes was high. In general, the CH_4 flux from *P. australis* microsite was greater than the other microsite, except for *S. alterniflora*. CH_4 flux from the *P. australis* marsh at the SHS site was 26.13 ± 5.26 mg m^{-2} hr^{-1} whereas the flux from the *P. australis* marsh at the HP site was 27.48 ± 2.99 mg m^{-2} hr^{-1} in August 2012 and over the course of the measurement period they are not different from each other ($P = 0.08$; **Fig. 1**). For the same month (August 2012), CH_4 fluxes were 0.19 ± 0.12 mg m^{-2} hr^{-1} for the *S. patens* marsh at the SHS site, 1.46 ± 1.51 mg m^{-2} hr^{-1} for the mud flat at the MRMMB site, 1.59 ± 0.37 mg m^{-2} hr^{-1} for the *S. patens* marsh at the HP site, and 1.79 ± 1.18 mg m^{-2} hr^{-1} for the S. *alterniflora* marsh at the MRMMB site. The *S. alterniflora* marsh at the MRMMB site (2.86 ± 1.004 mg m^{-2} hr^{-1}) and *P. australis* marsh at the HP site (2.89 ± 0.45 mg m^{-2} hr^{-1}) emitted significantly greater CH_4 than the *S. patens* marsh at SHS site (0.27 ± 0.17 mg m^{-2} hr^{-1}) and the HP site (0.60 ± 0.24 mg m^{-2} hr^{-1}) in August of 2013. The *P. australis* marsh at the SHS site emitted 4.56 ± 2.09 mg m^{-2} hr^{-1} in August of 2013. The SHS site was not significantly different from the other two sites in any year (interaction of site and season $P=0.01$, but not site $P=0.17$, **Table 2**). Likewise, CH_4 emission from *S. patens* marsh at the SHS site and the HP site were not significantly different ($P = 0.7$), but *S. alterniflora* was different from both HP and SHS *S. patens* ($P < 0.0001$ and $P = 0.01$, respectively). Overall, the sites did not differ in their CH_4 emissions ($P = 0.17$), yet the within site variation is great (site – species interaction $P = 0.0002$). Therefore, there was no difference between natural and restored site methane emissions, despite one site having only *S. alterniflora* and a mudflat being measured.

The annual flux estimated by integrating the curve connecting averages of replicate measurements of 2013 varied from 1.8 g CH_4 m^{-2} yr^{-1} for the *S. patens* marsh at the SHS site to 26.6 g CH_4 m^{-2} yr^{-1} for the *P. australis* marsh at the same site. The *S. alterniflora* marsh and the mud flat area of the MRMMB site emitted 15.6 g CH_4 m^{-2} yr^{-1} and 7.5 g CH_4 m^{-2} yr^{-1}, respectively, in 2013. The annual emission of CH_4 for the *S. patens* marsh and the *P. australis* marsh at the HP site were 2.7 g CH_4 m^{-2} yr^{-1} and 12.6 g CH_4 m^{-2} yr^{-1}, respectively.

Aboveground and belowground biomass, root density and rhizome density

Aboveground biomass of the studied marshes were not significantly different from each other (P = 0.52; **Fig. 2**). Mean aboveground biomass varied from 1.29 ± 0.15 kg m^{-2} to 1.90 ± 0.20 kg m^{-2}, respectively, for *S. patens* marsh and *P. australis* marsh at the HP site. Aboveground biomass for the *S. alterniflora* marsh at the MRMMB site and the *S. patens* marsh at the SHS site were 1.72 ± 0.38 kg m^{-2} and 1.56 ± 0.34 kg m^{-2}, respectively.

Belowground biomass was different among the microsites (**Fig. 2**, P = 0.0001) and most of the belowground biomass was close to the soil surface (**Fig. 3**) for all the studied species. Belowground biomass of *P. australis* (13.21 ± 1.49 kg m^{-2}) and *S. patens* (15.15 ± 1.44 kg m^{-2}) at the HP site were higher than the belowground biomass of *S. alterniflora* (3.73 ± 0.05 kg m^{-2}) at the MRMMB site and *S. patens* at the SHS site (2.42 ± 1.40 kg m^{-2}). Root density did not differ significantly with microsite (p = 0.06), however rhizome density varied significantly (**Fig. 4**, P<0.0001). Rhizome density of *S. patens* at the SHS site (0.27 ± 0.03 gm cm^{-3}) was higher than the rhizomes of plant species growing at other sites. Rhizome density of *P. australis* at the HP site (0.15 ± 0.009 g cm^{-3}) was higher than

S. alterniflora at the MRMMB site (0.09 ± 0.006 g cm^{-3}), but the rhizome density of *P. australis* and *S. patens* (0.14 ± 0.008 g cm^{-3}) at the HP site were not significantly different.

Soil organic C (%) and nitrogen (N %)

Soil organic C and N were higher at the MRMMB site and the SHS site than in the HP site (**Fig. 3**). On average, soil organic C (%) and N (%) at MRMMB site (45.49 ± 2.48 %C and 1.86 ± 0.11 %N at *S. alterniflora* marsh and 55.95 ± 1.99 %C and 2.16 ± 0.07 %N for mud flat) and SHS site (45.05 ± 2.17 %C and 1.81 ± 0.08 %N for *S. patens* marsh) are more than twice that at the HP site (21.94 ± 2.12 %C and 0.93 ± 0.08 %N for *S. patens* marsh, and 14.78 ± 1.83 %C and 0.61 ± 0.08 %N for *P. australis* marsh).

Discussion

Monthly CH_4 flux during low tide

May to September is the active growing season for wetland plants at the study site. Substrate availability for methane production should be greater in the wetland during this time, as plants release organic carbon into the soil during the active growing season as root exudates [*Laanbroek*, 2010], which can be used by microbes to produce CH_4. Higher temperatures during the growing season stimulate more CH_4 production [*Moosavi and Crill*, 1998]. Thus, higher temperature and higher substrate availability for CH_4 production as well as plant-mediated transport should have contributed to the higher emission from June to November from the vegetated area. Likewise, CH_4 emission from the mud flat area is similar to the vegetated area at the MRMMB site during the entire period, indicating sufficient lateral organic carbon transport into the mud flat area [*Reid*

et al., 2013]. Wetland plants transport oxygen from the atmosphere to the roots and some of this oxygen escapes to the surrounding root zone. Methanotrophic bacteria use this oxygen and consume some of the CH_4 in the vegetated area [*Le Mer and Roger*, 2001]. In the mudflat area, due to the lack of plant transported oxygen, methane consumption as found in the vegetated area is not present [*Laanbroek*, 2010]. Also, at our site, the water table at the vegetated area falls 15 to 20 cm below the soil surface during low tide whereas the water table remains above the soil surface at the mudflat area even during the low tide period *[Reid et al., 2013]*. Due to the lowered water table position, the vegetated sediment above the water table becomes oxygenated, and in turn, some of the CH_4 becomes oxidized in this sediment layer [*Lai*, 2009]. Therefore, it is likely that, even if the mud flat area has a lower amount of substrate availability for CH_4 production, it can emit either more than or as much as the vegetated area due to the consumption of some CH_4 around roots or in the oxygenated sediment layer close to the surface. There can be a lag of up to two months between production and emission of CH_4 *[Kelley et al., 1995; Reid et al., 2013]*. CH_4 emissions during October and November, during the non-growing season month, might be due to this lag effect. Alternatively, CH_4 producing microbes get organic material from senescing plant parts rather than root exudates as plants start to senesce in October. Sulfate, which is another pathway for methane to be oxidized, was not crucial in our study [see *Reid et al.* 2013].

Comparison of CH_4 flux between microsites

Our CH_4 flux measurements at three different sites in 2012 and 2013 showed that marshes with the dominant invasive plant *P. australis* emit more CH_4 than marshes dominated by the native plant *S. patens*. The native *S. alterniflora* marsh emitted less

CH_4 than *P. australis* in 2012 but both *S. alterniflora* and *P. australis* marsh emitted a similar amount of CH_4 in 2013. This has also been found in a New England Marsh, whereby *S. alterniflora* and *P. australis* exhibited similar CH_4 flux [*Emery and Fulweiler*, 2014]. Thus inundation rather than species *per se* may play a larger role since *S. patens* is located in high marsh areas that, by definition, are more elevated and thus experience more oxygenation at the soil surface and have smaller water table fluctuations than *S. alterniflora* or *P. australis*. The higher dissolved organic C (DOC) and pore water CH_4 in the sediment vegetated by *P. australis* and *S. alterniflora* than in the sediment vegetated by *S. patens* (**Table 1**, *Pal et al.* unpublished) should have contributed to relatively higher CH_4 flux from the *P. australis* and *S. alterniflora* marsh.

Studies have reported both negative and positive impacts of *P. australis* invasion in wetland ecosystems of United States. Reduction in plant diversity [*Odum*, 1984], reduction of habitat quality due to accumulation of more sediment and alteration of water flow [*Weinstein and Balletto*, 1999], decrease in bird richness [*Benoit and Askins*, 1999], and reduction of recruitment of juvenile fish [*Able et al.*, 2003] are some of the notable negative consequences of *P. australis* invasion. However, other studies have shown that invasion of *P. australis* in North America has positive impacts as well. The benthic organisms found in most of the *P. australis* dominated marshes are as diverse and abundant as found in *S. alterniflora* marshes. Moreover, the food value of *P. australis* detritus is comparable to that of native *S. alterniflora*, and detritus is an important component of the estuarine food web [*Weis and Weis*, 2003]. *Kiviat* [2013] has reviewed the studies related to *P. australis* impact on US and Canadian ecosystems and concluded that *P. australis* has, in fact, provided various important ecosystem services. The notable

services include sequestration of nutrients, carbon and heavy metals, stabilization of soil, habitat function for other organisms, and supply of products for human use.

Our study showed that, within the same marsh, the area covered by *P. australis* emits more CH_4 than the adjacent area covered by *S. patens*. The higher emission from marsh area covered by *P. australis* is partly due to the more reduced conditions, which are a consequence of the shallower (closer to the soil surface) water table than at the *S. patens* area. We do not know the extent that water table level has played to increased CH_4 emission from the *P. australis* marsh. To ascertain whether invasion of *P. australis* in *S. patens* marsh increases CH_4 emissions, the CH_4 flux should be measured from the *S. patens* marsh and *P. australis* marsh having similar water table position. If *P. australis* marsh and *S. patens* marsh have similar water table position and *P. australis* marsh still emits more CH_4 emission, then it is likely that the invasion of *P. australis* might cause another negative impact: more CH_4 emission since invasion by this species in US wetlands is continuing [*Chambers et al.,* 1999]. In our study, we measured CH_4 flux for two years and CH_4 emissions from the *P. australis* marsh was higher than emission from the *S. alterniflora* marsh in one year (2012) but emissions from both the *S. alterniflora* and the *P. australis* marshes were similar in another year (2013). As in our 2013 measurement, *Emery and Fulweiler* [2014] also reported similar CH_4 emission from *S. alterniflora* and *P. australis* marsh of New England, USA. In China, many ecosystems dominated by *P. australis*, which is a native plant for Chinese ecosystems, have been invaded by *S. alterniflora* (native to US) [*An et al.,* 2007]. Interestingly, contrary to what we found in this US ecosystem, in China, the *S. alterniflora* marsh emits more CH_4 than the *P. australis* marsh [*C. Tong et al.,* 2012]. Our results also show that within the same

marsh, there can be huge variation in CH_4 emissions between the marsh areas dominated by different species. Also, the year to year variation in CH_4 emissions for one species might be greater than another as shown for *S. patens* and *P. australis* marshes emphasizing the importance of measuring CH_4 flux for several years considering the area covered by different species for a better estimate of CH_4 source strength of a wetland.

Studies have reported a positive correlation between CH_4 emission and plant biomass [*Chanton et al.*, 1993; *Whiting and Chanton*, 1993]. The positive relationship between CH_4 emissions could have arisen for different reasons. Plants having more biomass can provide more root exudates as substrate for CH_4 production. In addition, plants having more biomass could have more roots, which ultimately decay and provide organic carbon for CH_4 production. Larger root biomass in plants having higher biomass, provide more conduits for CH_4 transport from the sediment to the atmosphere. Some of the aboveground biomass also contributes to CH_4 production when it decays at the end of growing season. Thus, a higher amount of root exudates, decaying organic materials and CH_4 transporting conduits in plants having higher biomass might have contributed to higher emissions from the area having higher biomass [*Noyce et al.*, 2014]. However, the exudates of some plants are very labile and can be easily utilized by CH_4 producing microbes leading to higher CH_4 production. The same is true for the decaying organic matter [*Laanbroek*, 2010]. Also, a significant part of CH_4 produced in marsh sediment is transported from sediment to atmosphere via root, rhizome and aboveground plant parts [*Ding et al.*, 2005; *Whalen*, 2005]. In a similar way, oxygen is transported from aboveground plant parts to the rhizomes and roots. Some of the oxygen leaks from the roots and can oxidize CH_4. If this rhizospheric (region around the roots) CH_4 oxidation is

strong, there will be lower or no emission into the atmosphere from vegetation even if CH_4 is produced belowground [*Fritz et al.,* 2011]. Therefore, more roots do not necessarily result in more CH_4 emission. It is the interplay between the ability of roots to transport CH_4 and its capacity for oxidation in the rhizospheric region. Thus, the great variation between plant species in the amount and quality of root exudates they produce, the quality of organic carbon formed from decaying above and belowground biomass, the ability of roots to transport CH_4 from the sediment to the atmosphere and the ability to oxidize CH_4 in the regions around the roots (rhizosphere) are likely the culprit to the differences in CH_4 emission between species even if the species are not different in their aboveground biomass production as we found in our study. Furthermore, in our study, *S. alterniflora* was present in a low marsh and *S. patens* and *P. australis* were present in high marsh. The low marsh is flooded twice daily but high marsh is flooded only around periods of full moon and new moon when highest tides are formed. Even within the high marsh, *S. patens* was growing at higher elevation with deeper water table and *P. australis* was located at lower elevation with shallower water table and closer to the tidal channel. Due to differences in elevation, some of the intermediated tides that flood areas of *P. australis* do not flood the areas of *S. patens*. Due to shallower water table and more frequent flooding, the areas of *P. australis* have more reduced conditions favorable to CH_4 production. Thus, differences in reduced conditions between *S. patens* and *P. australis* zones at high marsh and *S. alerniflora* zones at low marsh might also have masked the expected positive relationship between CH_4 emission and aboveground biomass in our study. Similar to our findings *Ding et al.* [2004; 2003] also found significant differences in CH_4 emissions between areas vegetated by different plant

species (*Carex lasiocarpa*, *C. meyeriana* and *Deyeuxia angustifolia*, fresh water marshes, Sanjiang plain, north-eastern China) even though aboveground biomass produced by these species were not significantly different from each other [*Ding et al.*, 2005; 2003]. *Bhullar et al.* [2014] also found no relationship between plant biomass and CH_4 emissions at a restored wetland in Switzerland. For all the species in our study, most of the root biomass is located close to soil surface, which suggests that most of the root effect on CH_4 production, oxidation and transport is likely to be close to the soil surface. However, roots are distributed to at least 55 cm below the soil surface indicating that root effects on CH_4 dynamics might extend well below the soil surface. The plants adapted to the reduced soil conditions of wetlands have loosely arranged cells forming aerenchymatous tissue in root and rhizome, and the degree of this aeration depends on species [*Jackson and Armstrong*, 1999]. The loosely arranged cells facilitate oxygen transport necessary for growth of below ground tissue in the reduced wetland soil environment [*Mitsch and Gosselink*, 2007]. Through the same loosely arranged tissue, CH_4 is also transported from soil to atmosphere. Differences in rhizome density between species suggest that the degree of looseness of the cells present in the rhizome varies between species suggesting that CH_4 transport capacity of the tissue also varies between species in our study. The organic %C and %N indicate that there is sufficient substrate in wetland soil for colonization by microbes [*Bruland et al.*, 2009]. The total organic C (%) in *P. australis* marsh was similar to *S. patens* marsh at the HP site, but *P. australis* marsh emitted greater amounts of CH_4 than *S. patens* marsh. Likewise, the total organic C (%) at the MRMMB site is higher than at the HP site, but CH_4 emission from *P. australis* marsh at the HP in 2013 is similar to CH_4 emission from *S. alterniflora* at MRMMB site. Total

organic C include both labile and recalcitrant C, and the recalcitrant organic C plays only a minor role as substrate for CH_4 production [*Chanton et al.*, 1995; *Joabsson et al.*, 1999] Therefore, if proportion of labile C is greater in soil, it is likely that more CH_4 is produced. It is likely that the proportion of labile C is higher at a *P. australis* marsh, which leads to relatively higher CH_4 emission from the *P. australis* marsh.

Comparison of CH_4 emissions from *Spartina* and *Phragmites* dominated wetlands across the world

Past studies showed huge variation in CH_4 flux between marshes of same species (**Fig. 5**) across the world. CH_4 flux reported by *DeLaune et al.* [1983] for *S. patens* marsh having salinity 1.8 ppt at Barataria Basin, Louisiana, was 97.3 g CH_4 m^{-2} yr^{-1} whereas for the marsh of the same species located at Fundy, New Brunswick, Canada with salinity of 31.6 ppt, *Magenheimer* [1996] reported CH_4 flux of only 0.18 g CH_4 m^{-2} yr^{-1} indicating much lower fluxes from a marsh with high salinity. A review of CH_4 fluxes from tidal marshes [*Poffenbarger et al.*, 2011] showed that CH_4 emissions from marshes having salinity above 18 ppt is very low and that marshes having a salinity below 18 ppt emit a greater amount of CH_4 although emissions are highly variable. The salinity of our sites varies from 5 ppt to 9 ppt and annual CH_4 emission for the *S. patens* marsh in our study (2.72 g CH_4 m^{-2} yr^{-1} at HP site and 1.82 g CH_4 m^{-2} yr^{-1} at SHS site) is slightly higher than the annual flux reported by *Magenheimer* [1996]. Studies conducted in various *S. alterniflora* marshes have reported huge variation in CH_4 emission between the marshes. In a study carried out in a salt marsh in Sapelo Island, Georgia, *King and Wiebe* [1978] found annual CH_4 emissions of 0.44 g CH_4 m^{-2} yr^{-1} from the area vegetated by tall *S. alterniflora* (length of plant stalk more than 1 m), whereas the emission was 5.79 g CH_4

m^{-2} yr^{-1} and 53 g CH_4 m^{-2} yr^{-1} from areas of mid-marsh and short *S. alterniflora* marsh (length of plant stalk less than 0.5 m). The reduced CH_4 emission from tall *S. alterniflora* marsh was attributed to higher sulfate concentration in the marsh. The presence of sulfate can cause competition between sulfate reducers and methane producers for substrates, hydrogen and acetate, leading to reduced CH_4 production due to limitations of substrate for methane producer [*Bartlett et al.*, 1987; *Wang et al.*, 1996]. In the *S. alterniflora* marsh we studied, the suppressive effect of sulfate on methanogenesis is likely to be small and limited to within the top 10 cm from the soil surface [*Reid et al.*, 2013]. CH_4 fluxes of 15.62 g CH_4 m^{-2} yr^{-1} from *S. alterniflora* marshes from our study (salinity 2 - 8 ppt) is similar to a salt marsh with the same species (16.94 g CH_4 m^{-2} yr^{-1}) at Queen's Creek, Virginia, USA, with salinity 8-12 ppt [*Bartlett et al.*, 1987]. *Magenheimer* [1996] reported CH_4 fluxes of only 0.18 g CH_4 m^{-2} yr^{-1} from *S. alterniflora* marshes at Fundy, New Brunswick, Canada indicating significantly lower fluxes in a high salinity marsh (salinity 31.6 ppt).

CH_4 emissions in August 2012 from the *P. australis* marsh at the SHS (26.13 ± 5.26 mg m^{-2} hr^{-1}) and the HP (27.48±2.99 mg m^{-2} hr^{-1}) sites were fairly high, but are similar to CH_4 emissions (27.08 mg m^{-2} hr^{-1}) reported for late summer CH_4 fluxes measured using the eddy covariance technique in a *Phragmites* dominated, freshwater prairie marsh in Nebraska, United states [*Kim et al.*, 1999], indicating a reduced impact of salinity on the CH_4 emissions of *Phragmites* in the New Jersey Meadowlands. The yearly flux estimate of the prairie marsh was 80 g CH_4 m^{-2} yr^{-1} [*Kim et al.*, 1999]. *Van der Nat and Middleburg* [2000] found similar CH_4 fluxes from a tidal freshwater marsh of the Scheldt estuary, Netherlands (75.2 g CH_4 m^{-2} yr^{-1}). The peak value of CH_4 emission for *P.*

australis vegetation of lake Vesijarvi, Finland, was fairly high (85.42 mg m^{-2} hr^{-1}) but there was large interannual variation in the emissions [*Kankaala et al.*, 2004]. The average CH_4 emissions from the vegetation of the lake were 22, 58, 40 g CH_4 m^{-2} yr^{-1} for 1997, 1998, 1999, respectively. *Tong et al.* [2010] measured CH_4 emissions from tidal *P. australis* marshes at Mid River estuary, South China, at different tidal stage and found a large variation in CH_4 emissions depending on tidal stage. Average values of CH_4 emissions before flooding, during flooding and ebbing process and after ebb were 5.13, 2.08 and 5.06 mg m^{-2} hr^{-1} respectively. For the pre-flood measurement, the peak value of CH_4 emission was recorded in July (11.9 mg m^{-2} hr^{-1}) whereas for the measurement done after ebb, the peak value of CH_4 emission was recorded in June (12.7 mg m^{-2} hr^{-1}). The annual flux estimations for *P. australis* marshes in our study (26.6 and 12.6 g CH_4 m^{-2} yr^{-1}, respectively, at the SHS and HP sites) are similar to the lower range of the lowest annual flux estimations reported in previous studies. Low CH_4 emissions in our sites might be the result of higher salinity, and less reduced conditions caused by infrequent flooding in the high marsh area.

Conclusions

Our study of CH_4 flux for two years in three wetlands shows large variations in the flux between marsh zones having different species even within the same wetland. Likewise, inter-annual variation in CH_4 flux differs between marsh species underlining the importance of measuring CH_4 fluxes across marsh types, plant species and years for a better estimation of a wetland's CH_4 source strength. CH_4 flux shows strong seasonality, emitting most of the CH_4 during the warm growing season and little or no emission during winter. For *S. patens* and *S. alterniflora* marshes, annual CH_4 flux estimates are

within the range of flux estimates from various past studies for marshes of the same species around the world. However, annual CH_4 flux estimations for *P. australis* marshes in our study is close or the lower end of the lowest annual CH_4 flux estimates from past studies of *P. australis* marshes. Aboveground biomass of the studied species is not significantly different but CH_4 emissions from marshes covered by each species were different suggesting that other factors like water table position, rhizospheric effect and quality of substrate between marshes covered by different species may be masking the expected positive relationship between CH_4 emissions and plant biomass. Presence of most of the belowground biomass close to the soil surface indicates that the effect of belowground biomass on the production, oxidation and transportation of CH_4 should be higher at the soil profile closer to its surface. The belowground biomass distribution in soil depth profile also suggests that the effect of belowground biomass on CH_4 dynamics should be prevalent, at least to a depth of 55 cm from the soil surface. The presence of higher total organic C (%) in a wetland does not necessarily mean higher CH_4 flux as CH_4 producing bacteria mostly use labile forms of C and most of the organic C in some soil can be recalcitrant even if there is a large amount of organic C.

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Figures and tables

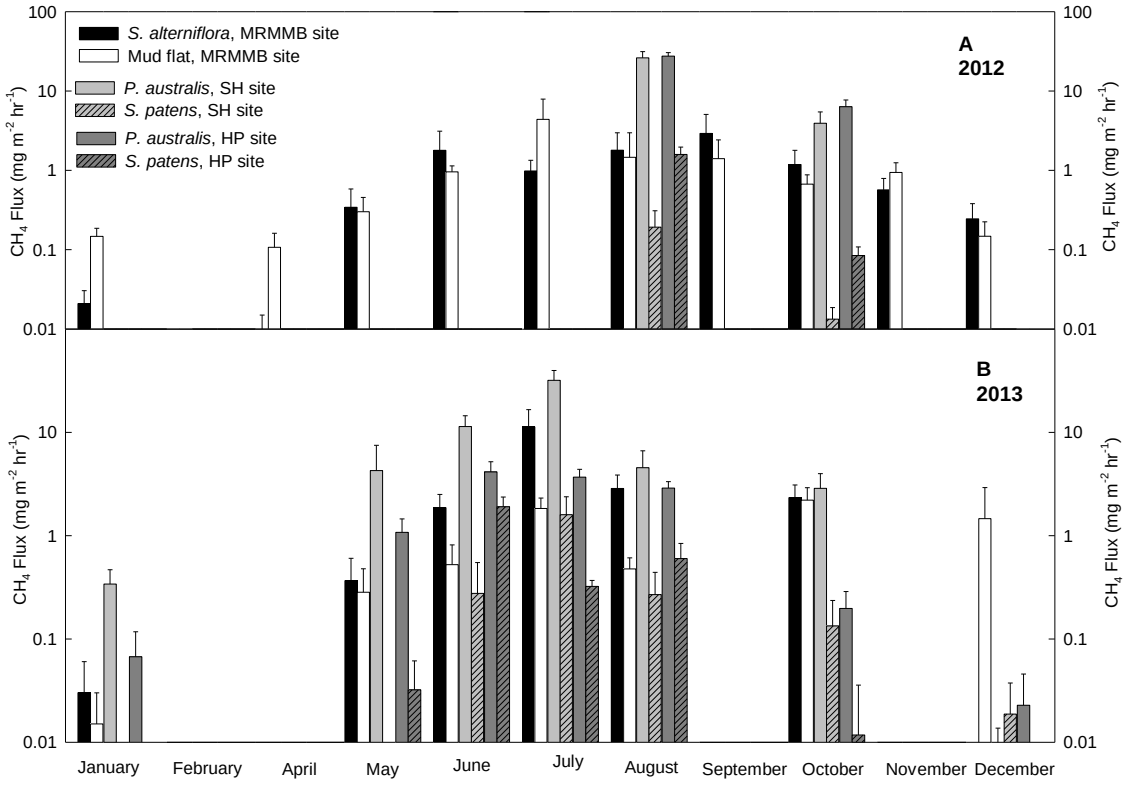

Figure 1 CH_4 fluxes (note the $\log_{10}$ scale) in different areas of MRMMB, SHS and HP sites for 2012 (A) and 2013 (B). Error bars are standard error of 3-6 measurements. Sampling was performed during low tide.

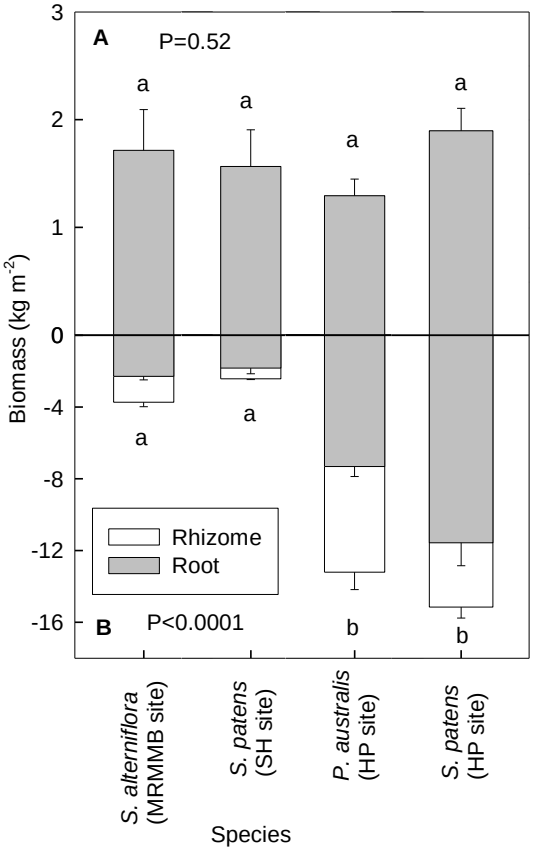

Figure 2 Aboveground (panel A) and belowground (panel B) (rhizome plus root) biomass for various species/site combinations. Error bars are standard error of three samples. For each panel, biomasses represented by the same letter are not significantly different from one another. $P \leq 0.05$ is considered significant. Note that panel A and Panel B have different scales.

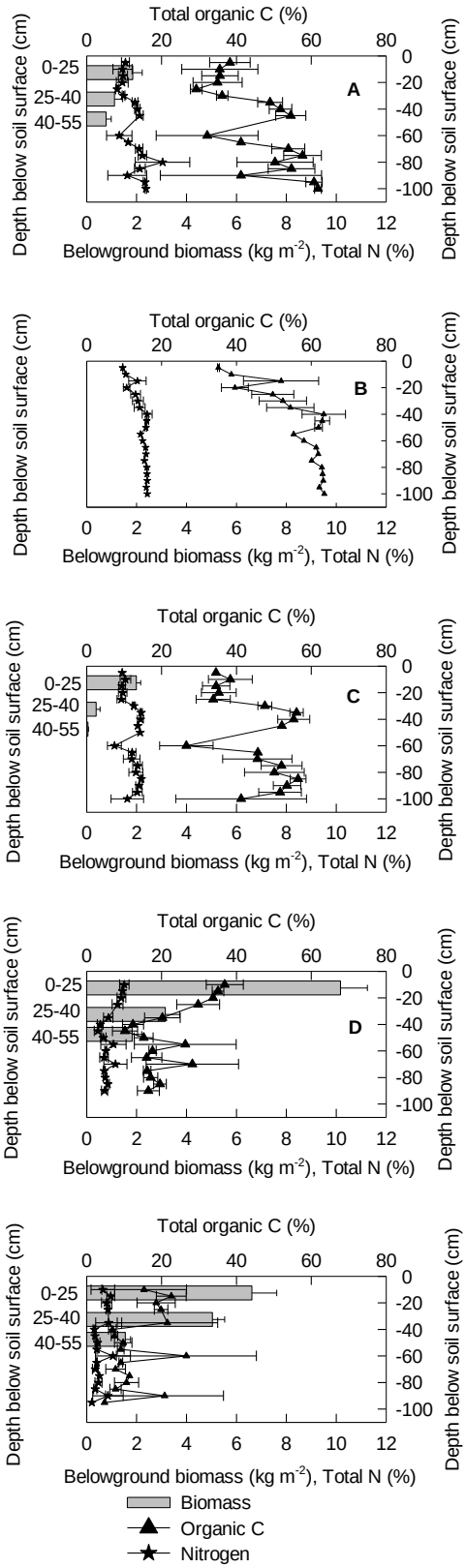

Figure 3 Belowground biomasses (rhizome plus root) at different soil depth of various species as well as % organic C and %N at different soil depths. Error bars are standard error of three samples. A: *S. alterniflora* (MRMMB site), B: Mud flat (MRMMB site), C= *S. patens* (SH site), D: *S. patens* (HP site), E=*P. australis* (HP site).

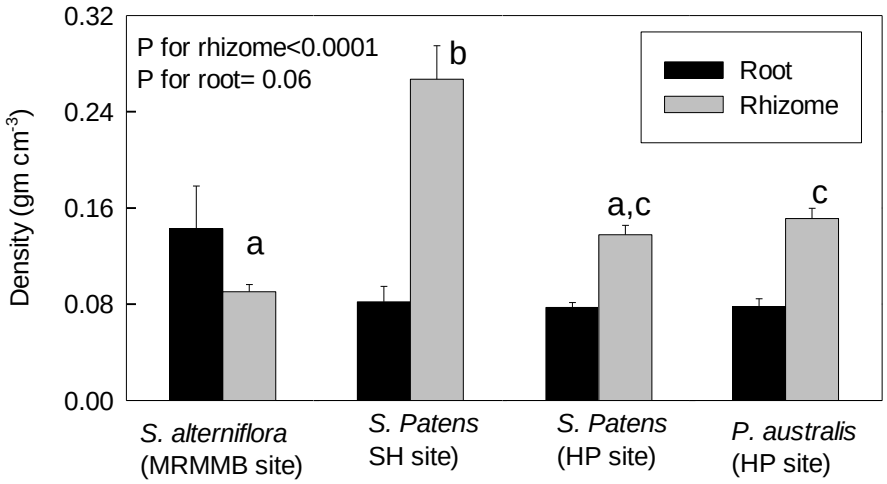

Figure 4 Root and rhizome density of various species. Error bars are standard error of nine samples. Rhizome densities represented by the same letter are not significantly different from one another. Root densities are not different across sites/species. $P \leq 0.05$ is considered significant

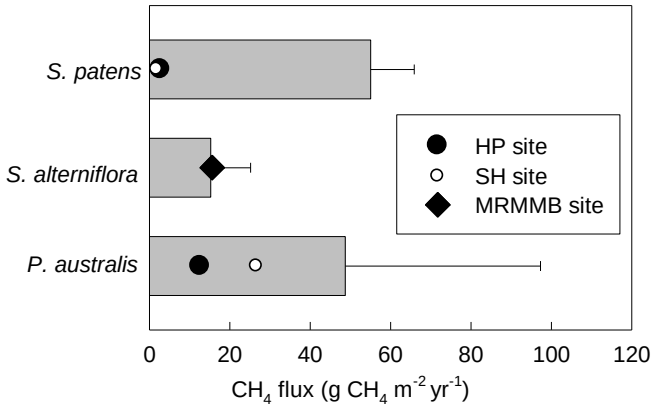

Figure 5 Comparison of CH_4 flux of previous studies (bar diagram, mean±SE) with the flux of this study (symbols, circle and diamond). Previous studies include *DeLaune et al.* [1983], *Magenheimer* [1996] for *S. patens* (n=2); *King and Wiebe* [1978], *Bartlett et al.* [1987], *Magenheimer* [1996] for *S. alterniflora* (n=5); and *Kim et al.* [1999], *Van der Nat and Middleburg* [2000] and *Kankaala* [2004] for *P. australis* (n=5).

Table 1 Site characteristics of three wetlands examined in this study. Salinity, dissolved organic carbon and pore water CH_4 measurements were made in January and February 2013 (*Pal et al.* unpublished)

Site	**Marsh type**	**Area sampled**	**Salinity (ppt)**	**Dissolve organic carbon (DOC) (mg m^{-2})**	**Pore water CH_4 (mg m^{-2})**
MRMMB	low	mud flat	7.6	3013.3	114.9
MRMMB	low	*S. alterniflora*	10.5	1650.5	3.7
SHS	high	*P. australis*	9.3	3036.9	192.8
SHS	high	*S. patens*	9.4	539.3	0.6
HP	high	*P. australis*	12.1	6422	53
HP	high	*S. patens*	13.9	3900.4	16.3

Table 2 Analysis of Variance (ANOVA) for log-transformed data in 2012 and 2013 with the year, season, site and species as explanatory variables and their respective two-way and three-way interactions denoted by ":". Significant p-values (<0.05) are denoted by bold font. Details see text.

	DF	F	P
Year	1	4.38	**0.03**
Season	1	148.11	**<0.0001**
Site	2	1.75	0.17
Species	2	68.24	**<0.0001**
Year : Season	1	0.88	0.34
Year : Site	2	23.00	**<0.0001**
Season : Site	2	4.01	**0.01**
Year : Species	2	13.00	**<0.0001**
Season : Species	2	16.63	**<0.0001**
Site : Species	2	8.45	**0.0002**
Year : Season : Species	2	1.42	0.24
Year : Site: Species	1	0.03	0.85
Year : Season : Site	2	1.06	0.34
Season : Site : Species	1	0.56	0.45
Year : Season : Site : Species	1	0.26	0.43
Residuals	399		

Chapter 2

Above- and belowground biomass allocation in four dominant salt marsh species of the Eastern United States[2]

Abstract

Measurements of aboveground and belowground biomass allocations are important for characterization of structure and function of a marsh ecosystem as various processes such as carbon sequestration, gas transport, nutrient cycling, and ecosystem resilience are affected by the allocations. Therefore, aboveground and belowground biomass, root and rhizome characteristics, leaf area index (LAI), and carbon to nitrogen (C/N) ratio of various tissues of four tidal marsh species in New Jersey were measured by harvesting biomass during peak growing season. The aboveground biomasses for *Spartina patens*, *S. alterniflora, Phragmites australis,* and *Distichlis spicata* were 2.3, 2.2, 1.7 and 1.2 kg m^{-2}, respectively. The ratio of belowground to aboveground biomass for *S. alterniflora* and *D. spicata*, harvested from a recently restored wetland were lower than in previous studies. LAI for *S. alterniflora, D. spicata, P. australis,* and *S. patens* were 8.4, 6.8, 4.8 and 3.7 m^2 m^{-2}, respectively. Diameter of rhizome and root, number of primary roots per

[2] Manuscript by R. Tripathee and K.V.R. Schäfer (submitted after revision, *Wetlands*)

node, root surface area to volume ratio, and C/N of various tissues varied with species. The measured above- and belowground biometric traits are crucial for a better understanding of carbon dynamics, and modeling greenhouse gas transport of a marsh.

Introduction

Salt marshes are highly productive and one of the most valuable carbon sinks on the planet (McLeod et al. 2011; Townend et al. 2011). Flooded or saturated conditions limit oxygen availability in marsh soils causing slow decomposition of plant material (Solomon et al. 2007), resulting in the accumulation of significant amounts of organic carbon over time (Chmura et al. 2003). The addition of organic carbon to marsh soil serves as a carbon sink and also contributes to vertical accretion of marsh sediment (Nyman et al. 2006; Langley et al. 2009; Deegan et al. 2012; Kirwan and Mudd 2012; Langley et al. 2013). If vertical accretion is slower than sea level rise, shallow open water could replace tidal marshes (Roman et al. 1997; Orson et al. 1998). Thus, production of plant material in marsh ecosystems is important both for carbon sequestration and the persistence of marshes with rising sea level. Therefore, accurate measurements of both above- and belowground biomass are necessary to improve estimates of the carbon sequestration potential of salt marshes.

Accurately quantifying belowground biomass of wetland plants is also important because production, consumption, and transport of greenhouse gases such as carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) depend largely on the amount of root biomass belowground. When roots die, they serve as substrate for the production of these gases, and exudates supplied by roots are important substrates for CH_4 production (Chanton et al. 1989). The CH_4 and N_2O produced in a hypoxic wetland soil environment are transported to the atmosphere via roots and aboveground tissue. In addition to transporting CH_4 and N_2O to the atmosphere, roots also transport oxygen (O_2) from the atmosphere to the soil via aboveground tissue (Le Mer and Roger 2001). This oxygen can

be used by microbes for decomposition of organic compounds or to oxidize CH_4, both resulting in the production of CO_2 (Mitsch and Gosselink 2007). Therefore, the diameter and length of the roots are likely to affect the transport of O_2 and greenhouse gases between the atmosphere and the soil (Segers and Leffelaar 2001). Knowledge of the vertical distribution and amount of roots as well as their length and diameter are important in order to better understand the role of roots in the production and transport of greenhouse gases from marsh soils to the atmosphere.

Belowground biomass production plays a key role in the accumulation of organic carbon in a wetland environment (Nyman et al. 2006; Neubauer 2008). However, usually, only aboveground biomass is used to calculate salt marsh net primary productivity (NPP), because roots and rhizomes are difficult to measure (Fahey and Knapp 2007). Even when belowground biomass estimates are made, there is a significant variation among measurements, partly due to natural variability, but also due to measurement error in terms of small core diameters and inconsistency in technique used by investigators during processing and sorting of samples (Good et al. 1982; Fahey and Knapp 2007). Previous studies have shown that variation in belowground biomass estimations were significantly larger when core diameters of 10 cm or less were used, leading to biases in the estimation of belowground production (Singh et al. 1984; Fahey and Knapp 2007). Therefore, harvesting larger volumes results in better estimates of belowground biomass. Estimates of aboveground biomass are relatively easy to obtain via harvesting, but can also be estimated via remote sensing methods (Lefsky et al. 2002). Thus, more accurate estimates of aboveground to belowground biomass ratios can be used to improve estimates of overall plant biomass production.

In this study, we characterized above- and belowground biomass as well as diameter and length of primary roots of four marsh plant species in coastal North America: *Spartina alterniflora* (Loisel.), *S. patens* ((Aiton) Muhl), *Distichlis spicata* ((L.) Greene), and *Phragmites australis* ((Cav.) Trin. ex Steud.). Comparison of allocation of biomasses in aboveground and belowground tissues for the four dominant marsh species will help to better understand carbon dynamics of marshes. The measurements of distribution of leaf area at various canopy heights as well as root and rhizome parameters can aid in modeling greenhouse gas flux (Beckett et al. 2001, Dai et al. 2004). In low marsh areas of the Eastern United States, *Spartina alterniflora* is a dominant native grass. Whereby, *Spartina patens* is also a native to the Eastern United States and found in high marsh areas. *Distichlis spicata* is found in high marsh areas along with *S. patens*. *Phragmites australis* is an invasive species in the Eastern United States and typically outcompetes native vegetation resulting in monocultures. We hypothesized that both rhizome and root biomass are higher near the soil surface as the main nutrient source in these marshes comes from the surface water, the supply of most of the nutrients to the soil profile is therefore close to its surface, and thus stimulate most of the belowground biomass growth there (Valiela et al. 1976, Shin et al. 2013). Also, because *P. australis* marsh has been shown to emit more CH_4 than marshes of *S. patens* (Tripathee et al. in preparation), we hypothesized that the diameter of rhizomes and roots, the number of primary roots per node and the root surface area to volume ratio are higher in *P. australis* than native *S. patens* and *D. spicata*.

Materials and Methods

Study sites

This study was conducted in the New Jersey Meadowlands (NJM), which covers most of the Hudson Raritan estuary ecosystem and is comprised of about 35,000 ha of wetlands including tidal marshes and water bodies. These wetlands are surrounded by intense urban activities. We selected two restored (Marsh Resource Meadowlands Mitigation Bank, MRMMB; and Secaucus High School, SH) and one natural (Lyndhurst Riverside Marsh, LRM) wetland sites within this estuarine ecosystem for this study. The MRMMB site (site #1) is located in Carlstadt, Bergen County, New Jersey (40.82^{o}N, 74.03^{o}W). This 83.4 ha site was restored by removing *P. australis* and planting *S. alterniflora* in 1999. Despite the application of herbicides to eliminate *P. australis*, new patches have continued to appear annually. The herbicide application has limited the coverage of *P. australis* to approximately 15% of the total coverage of this wetland, and there were no *P. australis* plants within a few meters of harvested plots. Therefore, there was no or minimal biological interaction between *S. alterniflora* and *P. australis* in the harvested area. The *P. australis* in our site is likely to be the Eurasian haplotypes as it is the most common in the region and has the most widespread distribution in North America among the haplotypes of *P. australis* (Saltonstall 2002; Howard et al. 2008). We harvested above- and belowground biomass of *S. alterniflora* from this site. The SH site (site #2) is located in Secaucus, Hudson County, New Jersey (40.80^{o}N, 74.04^{o}W). This 17.4 ha site was restored in 2007 by removing the monoculture of *P. australis*. Currently, *S. patens* and *D. spicata* are dominant in this high marsh system. We harvested above- and belowground biomass of *D. spicata* from this site. The LRM site (site #3) is located in

Lyndhurst, Bergen County, New Jersey (40.78^{o}N, 70.09^{o}W) and spans 12.5 ha. This site is a natural (or non-mitigated) wetland with invasive *P. australis* as the dominant species although some remnant patches of native *S. patens* can also be found. We harvested above- and belowground biomass of both *P. australis* and *S. patens* from this site.

Above- and belowground biomass harvest and rhizome and root biomass at various depths

For each study species, three 25x25 cm plots were randomly selected in monospecific stands of *S. alterniflora* (site #1), *D. spicata* (site #2), *S. patens* and *P. australis* (site #3). Beginning at ground level, we harvested aboveground biomass in 10 cm height increments. For every 10 cm, biomass was separated into different components: florescence, green leaves, dead leaves, leaf sheath and stem. Harvested biomass was dried in a commercial drying oven (Thermo Scientific Precision 3050 Series premium oven, Thermo Fisher Scientific, USA) for one week at 60 °C and weighed.

In conjunction with aboveground sampling, we harvested belowground biomass by excavating up to 55 cm below the soil surface using a shovel. At each sampling point, the harvested blocks were partitioned into 0-25 cm, 25-40 cm and 40-55 cm depth from the soil surface. These blocks were rinsed with tap water and belowground biomass for each portion was separated into rhizomes and roots. Belowground biomass was dried and weighed as above.

Measurements of root and rhizome characteristics

From the uppermost belowground sampling block (25x25x25 cm), we randomly selected three average-sized plants and measured the diameter of the rhizome and the length and diameter of every root at every node of the plant using a digital caliper for diameter

measurement and a ruler for length measurements (± 1 mm accuracy). Root diameter was measured around the midsection of the root to account for slight variations in diameter along the root. Root surface area to volume ratio was also calculated assuming roots were approximately cylindrical.

Leaf area distribution and leaf area index

Total leaf area per plot was calculated by multiplying specific leaf area (SLA, leaf area per unit dry mass) by total leaf dry weight. In order to determine SLA, two mature green leaves were taken from canopy mid-height from each harvested plot. We cut 15 cm long pieces from the mid portion of each harvested leaf and determined its area using a commercial scanner (Epson Perfection V30, Epson America, Inc, Long Beach, CA) and Image J software (http://rsbweb.nih.gov/ij/, National Institutes of Health). The leaves were dried as above and weighed. We calculated leaf area index (LAI, m^2 leaf area m^{-2} ground area) for various heights of the canopy by multiplying SLA with leaf weight of each particular canopy height.

%N and total C in leaves; C/N in roots, rhizomes and leaves

To estimate %C and %N of leaves, roots and rhizomes, dried biomass samples from each species and plot were finely ground into a powder using a ball bearing mill (8000D Dual Mixer/Mill, Metuchen, NJ, USA). The ground samples (2.5- 3.5 mg each) were placed in tin capsules and sent to the UC Davis Stable Isotope Facility, Department of Plant Sciences, Davis, California, USA, for analysis. The facility used a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) for the analysis of %C and %N.

Statistical analyses

Comparisons between species were made for total aboveground, total belowground, total rhizome and total root biomasses. For each soil depth (0-25, 25-40 and 40-55 cm from the soil surface) and each belowground biomass type (root and rhizome), comparisons were made between species. We also compared belowground to aboveground biomass ratio, root length, root diameter, root surface area to volume ratio, rhizome diameter, leaf %N, leaf total C content and C/N for each tissue type and LAI between species. For each species, we also compared C/N of leaves, roots and rhizomes. Analysis of Variance (ANOVA, Tukey HSD test) was performed for all comparisons using MATLAB (MATLAB R2012a, Mathworks, Natick, MA). A P value ≤ 0.05 was considered significant.

Results

Total above- and belowground biomass

Total biomass, aboveground biomass, and belowground biomass varied between species (**Table 1, 4**). For each of the biomass categories, *S. patens* had the *highest* and *D. spicata* had the lowest value (**Fig. 1**). The belowground biomasses of *S. patens* and *P. australis* were more than four times greater than their respective aboveground biomasses, whereas for *S. alterniflora* and *D. spicata*, the belowground biomasses were less than twice that of aboveground biomasses (**Fig. 1**). The belowground to aboveground biomass ratios were 1.7±0.1, 1.0±0.25, 4.9±0.2 and 4.9±0.9 for *S. alterniflora*, *D. spicta*, *S. patens* and *P. australis*, respectively (**Table 1**).

Rhizome and root biomass at various depths

For all species, the majority of the rhizome and root biomass was found close to the surface (0-25 cm below the soil surface; **Fig. 2, 3**). *P. australis* had significantly greater rhizome biomass than the other three species at greater depths (40-55 cm below the soil surface). The ratio of rhizome biomass to root biomass varied with species (**Table 2**). For *S. alterniflora* and *D. spicata,* the ratios were greater than one, whereas the ratios were below one for *S. patens* and *P. australis*.

Root and rhizome characteristics

The number of primary roots at a rhizome node varied from 2 to 5 and the highest number was found in *S. alterniflora* (**Table 2**). Similarly, rhizome diameter was largest in *P. australis* followed by *S. alterniflora*. Mean root diameters varied from 0.5 to 1.1 mm (**Table 2**). The surface areas to volume ratios of roots were significantly different from one another and varied from 44.5 to 109.7 cm^{-1}.

Leaf area distribution and LAI

For each investigated species, LAI varied with species and the majority of leaf area was found at canopy mid-height, although species differed significantly in their overall canopy height (**Fig. 4**). The highest LAI was found in *S. alterniflora,* which was more than twice that of the lowest LAI found in *S. patens* (**Table 1**).

%N and total C in leaves; C/N in roots, rhizomes and leaves

The %N in leaf tissue differed significantly among the studied species and was highest in leaf tissue of invasive *P. australis* (**Table 3**). For every species, C/N ratio was higher in rhizomes than in leaves (**Table 3, 4**). *D. spicata* had a higher C/N ratio than *S.*

alterniflora and *S. patens* in root tissues (**Table 3**). The C/N ratio in root tissues of *D. spicata* and *P. australis* were not significantly different. For rhizomes, *S. alterniflora* and *P. australis* had higher C/N ratios than *D. spicata* and *S. patens* (**Table 3**). For leaves, *P. australis* had a lower C/N ratio than all other study species. When total carbon content in roots was compared between species, *S. patens* had the highest amount, followed by *P. australis*, *D. spicata*, and *S. alterniflora* (**Table 3, 4**). Likewise, rhizomes of *D. spicata* had the smallest total carbon content, compared to the other species. Total Carbon content in green leaves was less than 1 kg m^{-2} for all the species (**Table 3**).

Discussion

Aboveground biomass

Aboveground biomass estimation can vary depending on the method employed. For example, Shew et al. (1981) estimated a range of 0.2 to 1.0 kg of aboveground biomass per m^2 per year for *S. alterniflora* in a North Carolina marsh, depending upon the method used. This variation arises because certain methods may not take into account one or more components that affect biomass estimation. For example, in the Peak Standing Crop Method, net aboveground primary production is the single largest value of aboveground living biomass present during a one-year growth period. In the Milner and Hughes (1968) Method, all positive changes in live biomass over time are summed up, thereby including a time element that is not included in the Peak Standing Crop Method. The Peak Standing Crop Method does not take into account decomposition, mortality or growth occurring after peak growth and the Milner and Hughes Method does not take into account decomposition or dead material. Likewise, another method, the Smalley Method (1959),

does not account for decomposition, but records changes in live and dead plant material over time.

For a given species, the variation in productivity between various studies is not solely the result of differences in methodology, as other factors also determine productivity levels. Marshes of lower latitude are generally more productive than marshes of higher latitude, due to longer growing seasons and warmer climates in lower latitudes (Turner 1976). Reviews of past studies regarding aboveground biomass showed great variation depending upon harvest method, location of marsh, and year of harvest (**Table 5**). Aboveground biomass varied from 0.2-3.7, 0.1-3.7, 0.5-0.9, and 1.1-3.7 kg m^{-2} yr^{-1} for *S. alterniflora*, *S. patens*, *D. spicata*, and *P. australis*, respectively. The highest aboveground biomasses for *S. alterniflora* and *D. spicata* were recorded in Louisiana (Pezeshki and Delaune 1991), which could be due to a longer growing season as well as nitrogen enrichment (Turner 1976; Valiela et al. 1976; Goolsby et al. 2001). Year to year disparity in productivity of the same marsh is due to changes in physical and chemical properties of marsh sediment caused by variation in climate and tidal events that vary from year to year (Mendelssohn and Morris 2000).

Aboveground biomass for *S. alterniflora*, *D. spicata*, *S. patens* and *P. australis* in our study were 2.2±0.23, 1.2±0.09, 2.3±0.21, and 1.7±0.14 kg m^{-2}, respectively. Except for *D. spicata*, the biomass estimates for different species in our study falls within the range of the biomass estimates in other studies (**Table 5**).

Belowground biomass, root and rhizome characteristics

Generally, belowground biomass estimates are made by harvesting biomass many times a year throughout the season. Net belowground primary productivity is calculated by subtracting minimum recorded biomass from maximum recorded biomass (Roman and Daiber 1984; Darby and Turner 2008). However, our biomass harvest occurred during the mid-growing season (July).

Estimates of belowground biomass using a range of core diameters have shown that cores with a smaller diameter underestimate belowground biomass (Gross et al. 1991). In comparison to the area and depth harvested in many studies (Smith et al. 1979; Roman and Daiber 1984; Kirwan and Mudd 2012), greater area (25 cm by 25 cm plot) and greater depth (up to 55 cm down from soil surface) were reached in our study. Therefore, we assume that our harvest is giving a better estimate for belowground biomass than the belowground biomass estimates performed using a smaller core reaching only to a shallower soil depth.

As in aboveground biomass, review of past studies showed large variation in belowground biomass productivity depending on the location of the marsh and the year of harvest (**Table 5**). In these past studies, the belowground biomasses for *S. alterniflora*, *S. patens* and *P. australis* were 3.5-17, 2.5-7.3 and 1.2-6.4 kg m^{-2} yr^{-1}, respectively. In our study, belowground biomasses for *S. patens* and *P. australis*, were greater than the biomasses reported in the past studies. The belowground biomass was estimated from a single harvest during the peak growing season, instead of estimating the belowground productivity by subtracting minimum recorded biomass from maximum recorded biomass from harvests done at different times of the year. This could have contributed to

the high belowground biomass estimates for the two species in our study. We do not know how much belowground biomass is retained year to year in the marshes we studied, but in some other marshes, about 12-70% of maximum belowground biomass is retained annually (Roman and Daiber 1984). The aboveground and belowground biomass estimates for *S. alterniflora* and belowground biomass for *P. australis* in our study are higher than estimates done in a different marsh of the NJM a decade earlier by Windham et al (2003). They harvested the biomasses from a mixed patch of the same two species reaching only up to 30 cm below the soil surface using a smaller corer. Conversely, we harvested *S. alterniflora* from a pure patch of a restored wetland and *P. australis* from a natural high marsh of the NJM. Also, we reached greater depth covering a greater area for belowground biomass estimates. Therefore, differences in location, species composition, depth and size of the harvested area, and the year of harvest between their and our study could have contributed for the differences in biomass estimates between the two studies. Except Windham et al (2003), in all the other studies we reviewed (**Table 5),** biomasses were harvested from pure patches of a particular species. When our harvest data were compared with the biomass harvested from pure patches, belowground biomass in our study was at the lower end of the range reported in past studies for *S. alterniflora.* Belowground biomass of *D. spicata* was similar to aboveground biomass (**Table 5**). *Spartina alterniflora* and *D. spicata* were harvested from wetlands restored in 1999 and 2007 respectively. We expected that the plants growing in these recently restored wetlands have not had as much time as natural wetlands to accrue belowground biomass, resulting in lower belowground biomass for the species. Due to lower belowground biomass, the ratios of belowground to aboveground biomass were also

lower for *S. alterniflora* and *D. spicata* in comparison to *S. patens* and *P. australis* harvested from a natural wetland in our study, as well as various past studies. We harvested belowground biomass up to 55 cm below the soil surface and found that most of the belowground biomass (both root and rhizome) was present closer to the soil surface (0-25 cm soil profile). This was also found by Darby and Turner (2008) for all the species, thus confirming our first hypothesis. The presence of the majority of the belowground biomass close to the soil surface suggests that most of the root effect on production, consumption and transport of CH_4 takes place at the wetland sediment to atmosphere interface. Porewater CH_4 measurements from one of our sites (site # 1; Reid et al. 2013) showed higher CH_4 concentration in deeper soil layers confirming that the root effect on methane oxidation and/or transportation should be lower in deeper soil due to a decreased root biomass in this region.

P. australis had more belowground biomass in the deeper soil region than any other species. Thus, the effect of belowground biomass on CH_4 dynamics should be greater for *P. australis* than the other plant species in the deeper soil profile. Our second hypothesis was that the diameters of rhizome and root, number of primary roots per node, and root surface area to volume ratio would be higher in *P. australis* than native *S. patens* and *D. spicata*. This hypothesis was partially confirmed. The number of primary roots per node was higher in *P. australis* than in *D. spicata* and *S. patens* but lower than in *S. alterniflora*. For rhizome and root diameters, *P. australis* was not different from *S. alterniflora,* but diameters were higher in *P. australis* than in *D. spicata* and *S. patens*. Davey et al. (2011) measured root and rhizome diameter of *S. alterniflora* at a marsh in Jamaica Bay, New York and found higher rhizome and root diameter in a deteriorating

marsh than in a stable marsh in 10-20 cm soil depth. In 10-20 cm soil depth, only rhizome diameters were higher in a deteriorating marsh than in stable marsh. The rhizome diameter of *S. alterniflora* in our study was similar to the deteriorating marsh but root diameter in our study was smaller than in the marsh of Jamaica Bay.

In this study, root surface area to volume ratios were higher in *P. australis* than in *S. alterniflora,* but lower than in *D. spicata* and *S. patens*. Variation in rhizome and root diameters and number of primary roots per node of rhizome and root surface area to volume ratio could cause differences in surface area availability for CH_4 and O_2 exchange between wetland sediment and plant tissue. Differences in surface area might be one of the contributing factors that causes variation in production and release of CH_4 from wetlands that are dominated by different species (Emery and Fulweiler 2014), while the root and rhizome parameters can be useful for modeling CH_4 flux from the plant (Beckett et al. 2001).

Leaf area distribution and LAI

The leaf area distribution at various heights of canopy showed that most of the leaves were found at the mid-height of canopy in all studied species. A significant part of CH_4 produced in wetland sediment is transported by root and rhizome and released either from leaves or stems into the atmosphere (Van der Nat et al. 1998). The presence of most of the leaf area at canopy mid-height suggests that the leaf mediated CH_4 release from plant to atmosphere occurs mainly from mid-height of the plant canopy. The highest LAI in *S. alterniflora* and the lowest LAI in *S. patens* indicate that the former species has higher leaf area for CH_4 and other greenhouse gases release per unit ground area than the latter.

Leaf area distribution at various heights of the canopy can be useful for modeling stomatal mediated greenhouse gas flux (Dai et al. 2004).

%N and total C in leaves; C/N in roots, rhizomes and leaves

Quality of decomposing plant materials, as indicated by C/N ratio and C/lignin ratio, is an important factor affecting the affinity of decomposers to litter, which then affects CH_4 production as methanogens prefer litter low in C/N and C/lignin (Valentine et al. 1994; de Neiff et al. 2006). Higher C/N ratios in rhizomes than in leaves of the studied species suggests that methanogens prefer leaf litter over rhizomes. Although the nitrogen concentrations in leaf tissue of *S. alterniflora* and *P. australis* were similar to a previous study carried out in a different marsh of the NJM (Windham et al. 2003), they exhibited the opposite trend with *S. alterniflora* having higher N than *P. australis*. In a previous study, it was shown that *P. australis* decomposes more slowly than *S. alterniflora*, thus building up more litter and sediment over time (Windham et al. 2004). In our study, the opposite response may be expected due to a lower C/N ratio in *P. australis* than *S. alterniflora*.

Conclusion

The aboveground biomass of *S. alterniflora*, *S. patens* and *P. australis* in this study were within the range of biomasses reported in the literature from various locations. *D. spicata* had higher aboveground biomass than earlier studies. Likewise, belowground biomass for *S. patens* and *P. australis*, which were harvested from natural wetlands, were greater than previously estimated. This higher biomass could be due to harvesting belowground biomass from a single harvest in peak season, rather than estimating belowground productivity by subtracting minimum recorded biomass from maximum recorded

biomass by harvesting the biomass multiple times a year. However, *S. alterniflora* and *D. spicata*, which were harvested from recently restored wetlands, have had low belowground biomass, resulting in a lower belowground to aboveground biomass ratio than previous studies indicate. Recently restored wetlands do not have as much time as natural wetlands to accrue belowground biomass, likely contributing to the low belowground to aboveground biomass ratio in *S. alterniflora* and *D. spicata*. The majority of the belowground biomass (both root and rhizome) were found in the region close to the soil surface, suggesting that most of the effect of belowground biomass on production, consumption and transport of CH_4 and other greenhouse gases takes place in the soil close to its surface. In a deeper soil region, the effect of belowground biomass on CH_4 dynamics is likely to be greater under *P. australis* than under other species, as *P. australis* had more belowground biomass than the other species at this soil region. For all species, most of the leaf area was found at canopy mid-height, suggesting that most of the leaf-mediated greenhouse gas emission occurs in this region. Variation in rhizome and root diameter, number of primary roots per node of rhizome, and root surface area to volume ratio between species may be some of the contributing factors that lead to variations in CH_4 release from wetlands of different species as root and rhizome characteristics affect CH_4 and O_2 exchange between wetland sediment and plant tissue. Above- and belowground tissues of the species differ in substrate quality, suggesting that different species can have different effects on methanogenic activity, even if they have the same amount of a particular tissue. More importantly, the belowground plant characteristics as well as LAI we reported in this study can be useful for modeling CH_4 and other greenhouse gas transport.

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Figures and tables

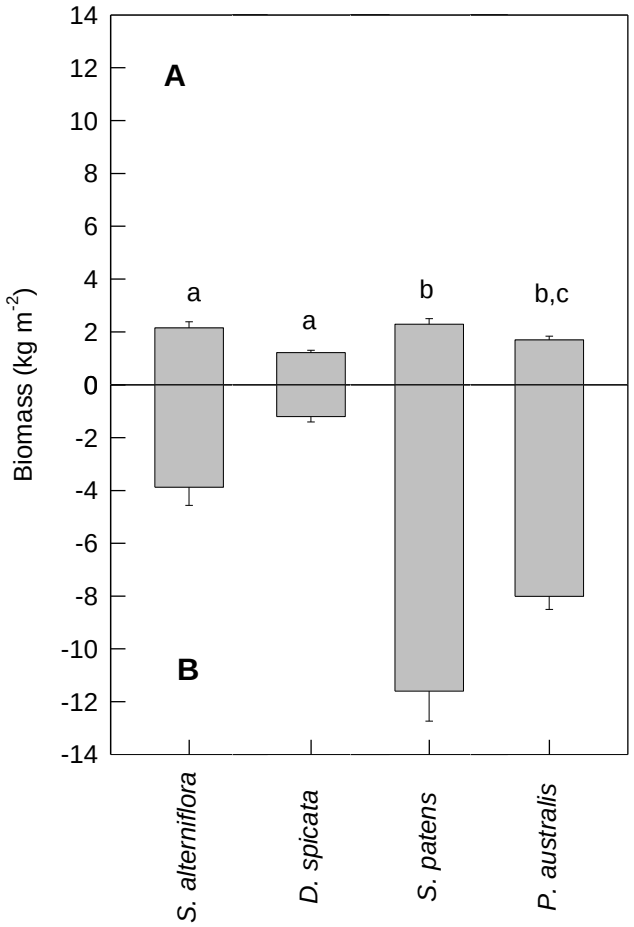

Fig. 1 Mean total biomass for different species. Positive values are for aboveground biomass (panel **A**) and negative values are for belowground biomass (both rhizome and root) (panel **B**). Significant differences ($P \leq 0.05$) between the total biomass of different species are indicated by different letters. The error bars are standard errors of 3 replicates

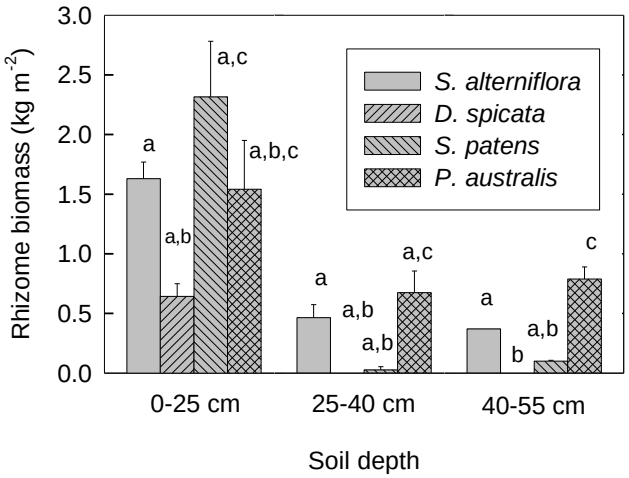

Fig. 2 Mean rhizome biomass at various depths for each species. For each depth, significant differences ($P \leq 0.05$) between the biomass of different species are indicated by different letters. The error bars are standard errors of 3 replicates

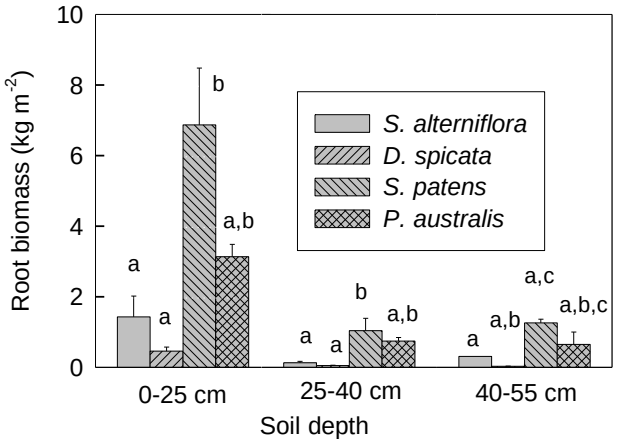

Fig. 3 Mean root biomass at various depths for each species. For each depth, significant differences ($P \leq 0.05$) between the biomass of different species are indicated by different letters. The error bars are standard errors of 3 replicates

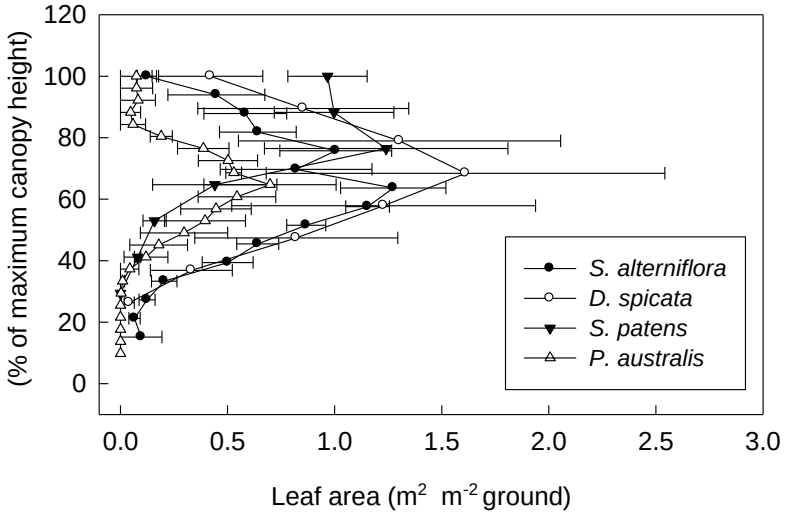

Fig. 4 Leaf area distribution of different species within their canopies (% of maximum canopy height for each 10 cm interval in height of canopy). The error bars are standard errors of 3 replicates

Table 1 Contribution of different components of above- and belowground biomass (kg m^{-2}) to the total above- and belowground biomass (kg m^{-2}), and leaf area index (LAI, m^2 m^{-2} ground area) for different species. Values are mean and standard error of three replicates. Significant differences ($P \leq 0.05$) between biomass and LAI of different species are indicated by different letters

	S. alterniflora	***D. spicata***	***S. patens***	***P. australis***
Florescence	0	0.02±0.01	0.01±0.01	0
Green leaf	0.7±0.1	0.4±0.07	0.5±0.05	0.4±0.04
Dead leaf	0.1±0.01	0.1±0.01	0.1±0.01	0.1±0.01
Green leaf sheath	0.3±0.04	0.2±0.08	0.1±0.1	0.2±0.07
Stem	0.5±0.08	0.5±0.1	1.3±0.00	1.1±0.09
Litter	0.4±0.09	0.1±0.04	0.2±0.19	0
Total aboveground	2.2±0.23^{c}	1.2±0.09^{b}	2.3±0.21^{a,c}	1.7±0.14^{a,b,c}
Root	1.7±0.52^{a,d}	0.5±0.11^{d}	9.2±1.42^{b,c}	5.2±0.61^{a,b,c}
Rhizome	2.2±0.21^{a}	0.6±0.11^{b}	2.4±0.48^{a}	2.8±0.11^{a}
Total belowground	3.9±0.69^{a}	1.2±0.20^{a}	11.6±1.14^{b}	8.0±0.5^{b}
LAI	8.4±0.9^{a}	6.8±1.3^{a,b}	3.7±2.1^{b}	4.8±0.4^{a,b}

Table 2 Ratio between rhizome biomass and root biomass, number of primary roots per node, rhizome diameter, primary root diameter and root volume for different species. Values are mean and standard error of three (ratio of rhizome and root biomass), 40-90 (number of primary roots per node), 9-31 (rhizome diameter), and 118-187 (primary root diameter) replicates. For surface area to volume ratio of a root, values are mean and standard error of 197 (*S. alterniflora)*, 117 (*D. spicata*), 143 (*S. patens*) and 185 (*P. australis*) roots. Significant differences ($P \leq 0.05$) between each of the parameters of different species are indicated by different letters

	S. alterniflora	***D. spicata***	***S. patens***	***P. australis***
Rhizome biomass/Root biomass	1.5±0.33[a]	1.2±0.17[a,b]	0.3±0.1[b]	0.6±0.09[a,b]
No. of primary root per node	4.9±0.44[a]	1.8±0.15[b]	1.6±0.13[b]	2.8±0.23[c]
Diameter of rhizome (mm)	5.5±0.2[a]	1.9±0.09[b]	2.2±0.14[b]	6.7±0.78 [a]
Diameter of primary root (mm)	0.9±0.07[a]	0.5±0.02[b]	0.6±0.02[b]	1.1±0.03[a]
Surface area to volume ratio of a root (cm^{-1})	29.1±0.92[a]	109.7±4.83[b]	83.0±3.41[c]	44.5±1.35[d]

Table 3 %N and total C in leaves and C/N ratio in roots, rhizomes and leaves of different species. Values are mean and standard error of three replicates. Significant differences ($P \leq 0.05$) between each of the parameters of different species (lower case, superscript), and C/N of various tissues within species (upper case, subscript) are indicated by different letters.

	S. alterniflora	***D. spicata***	***S. patens***	***P. australis***
Root (C/N)	$53.8\pm6.66^{a,}{}_{A,B}$	$81.9\pm6.37^{b,c,}{}_{A}$	$46.4\pm5.81^{a,}{}_{A}$	$65.9\pm4.4^{a,c,}{}_{A}$
Root (C, kg m^{-2})	$0.7\pm0.39^{a,c}$	0.2 ± 0.14^{a}	4.1 ± 2.38^{b}	$2.2\pm1.29^{d,c}$
Rhizome (C/N)	$85.4\pm16.64^{a,b,}{}_{B}$	$64.6\pm4.72^{a,}{}_{A}$	$58.6\pm4.32^{a,}{}_{A,B}$	$130.4\pm12.83^{a,b,}{}_{B}$
Rhizome (C, kg m^{-2})	0.9 ± 0.52^{a}	0.3 ± 0.17^{b}	1.1 ± 0.63^{a}	1.1 ± 0.65^{a}
Green leaf (%N)	1.5 ± 0.09^{a}	1.3 ± 0.02^{a}	1.4 ± 0.1^{a}	2.5 ± 0.07^{b}
Green leaf (C/N)	$32.5\pm2.55^{a,}{}_{A}$	$32.8\pm1.41^{a,}{}_{B}$	$31.0\pm2.91^{a,}{}_{A,C}$	$19.3\pm1.2^{b,}{}_{C}$
Green leaf (C, kg m^{-2})	0.3 ± 0.02^{a}	0.1 ± 0.02^{b}	$0.2\pm0.01^{a,b}$	0.2 ± 0.01^{b}

Table 4 Analysis of Variance (ANOVA) for all the plant tissues measured of the different species. Comparisons within the species are indicated by "*". Comparisons without "*" are between species. *P* values ≤ 0.05 are considered significant.

	DF	***F***	***P***
Aboveground biomass	3	7.49	0.01
Total root biomass	3	21.11	0.0007
Total rhizome biomass	3	9.99	0.05
Belowground biomass	3	31.44	0.0002
Total Biomass	3	19.17	0.002
Belowground/aboveground	3	15.51	0.003
Rhizome biomass, 0-25 cm	3	4.53	0.04
Rhizome biomass, 25-40 cm	3	9.8	0.005
Rhizome biomass, 40-55 cm	3	45.11	0.0005
Root biomass, 0-25 cm	3	23.91	0.004
Root biomass, 25-40 cm	3	6.86	0.01
Root biomass, 40-55 cm	3	5.92	0.03
LAI	3	5.43	0.03
Rhizome biomass/root biomass	3	7.31	0.01
No. of primary root per node	3	39.86	<0.0001
Diameter of rhizome (mm)	3	61.3	<0.0001
Diameter of primary root (mm)	3	28.34	<0.0001
Surface area to volume ratio of a root	3	3.69	0.01
Root (C/N)	3	6.98	0.01
Root (Total C)	3	23.53	0.003
Rhizome (C/N)	3	8.77	0.006
Rhizome (Total C)	3	10.89	0003
Green leaf (%N)	3	45.84	<0.0001
Green leaf (C/N)	3	9.03	0.006
Green leaf (total C)	3	7.98	0.009
***C/N (root, rhizome, leaf, *S. alterniflora*)**	2	6.47	0.03
***C/N (root, rhizome, leaf, *D. spicata*)**	2	28.73	0.008
***C/N (root, rhizome, leaf, *S. patens*)**	2	9.4	0.01
***C/N (root, rhizome, leaf, *P. australis*)**	2	50.31	0.002

Table 5 Comparison of aboveground and belowground biomasses of our studies with past studies

Marsh and/or location	Aboveground ($kg\ m^{-2}\ yr^{-1}$)	Belowground ($kg\ m^{-2}\ yr^{-1}$)	References
S. alterniflora			
Great Sippewissett Salt Marsh, Cape Cod	0.4-0.7	NA	(Valiela et al. 1975)
Great Sippewissett Salt Marsh, Cape Cod	0.4	3.5	(Valiela et al. 1976)
New Jersey marsh	0.4-0.5	11.0	(Smith et al. 1979)
Brunswick County, North Carolina	0.2 to 1.0	NA	(Shew et al. 1981)
Canary Creek Marsh and Black Bird Creek Marsh, Delaware Bay	0.5-1.5	4.3-7.7	(Roman and Daiber 1984)
Louisiana Gulf Coast	2.0 -3.7	NA	(Pezeshki and Delaune 1991)
Narragansett Bay, various sites	0.3-2.4	3.5-17	(Wigand 2008)
New Jersey Meadowlands (*S. alterniflora* and *P. australis* were intermingling on the site)	0.7	0.6	(Windham et al. 2003)
MRMMB site, New Jersey Meadowlands	2.2±0.23	3.9±0.69	Our study
S. patens			
Great Sippewissett Salt Marsh, Cape Cod	0.5-0.7	NA	(Valiela et al. 1975)
Great Sippewissett Salt Marsh, Cape Cod	0.6	2.5	(Valiela et al. 1976)
Canary Creek Marsh and Black Bird Creek Marsh , Delaware Bay	0.1-1.4	2.5-7.3	(Roman and Daiber 1984)
Louisiana Gulf Coast	3.7	NA	(Pezeshki and Delaune 1991)
Narragansett Bay, various sites	0.2-1.1		(Wigand 2008)
LRM site, New Jersey Meadowlands	2.3±0.21	11.6±1.14	Our study
D. spicata			
Canary Creek Marsh, Delaware Bay	0.5-0.9	NA	(Roman and Daiber 1984)
SHS site, New Jersey Meadowlands	1.2±0.09	1.2±0.2	Our Study
Phragmites australis			
Black Bird Creek Marsh, Delaware Bay	1.7-3.7	5.1-6.4	(Roman and Daiber 1984)
New Jersey Meadowlands (*S. alterniflora* and *P. australis* were intermingling on the site)	1.1	1.2	(Windham et al. 2003)
LRM, New Jersey Meadowlands	1.7±0.14	8.0±0.5	Our study

Chapter 3

Sources and biophysical control of methane emission from urban temperate wetlands[3]

Abstract

One third of total global methane (CH_4), a greenhouse gas that is 28 times more potent than carbon dioxide (CO_2) on a mass basis, is emitted from wetlands. Hydrology, air temperature, soil temperature, net radiation, and vapor pressure deficit (VPD) are some of the main factors that affect CH_4 flux in a wetland. Therefore, a better understanding of the relationship between these components and CH_4 flux in a wetland is necessary for understanding CH_4 flux dynamics, and formulation of CH_4 emission mitigation strategies. We investigated CH_4 flux and its relationship with various physical factors in two microsites in each of two restored, and one natural tidal wetland of the New Jersey

[3] Manuscript by R. Tripathee B. Mortazavi, P. R. Jaffé and K. V. R. Schäfer (submitted, *Global Change Biology)*

Meadowlands. We found a positive relationship between water depth difference (water depth difference at the end and the beginning of the measurement period) and CH_4 flux showing greater flux during incoming tide than during outgoing tide in the non-vegetated mud flat microsite. However, there is no correlation between the water depth difference and CH_4 flux in the vegetated areas. Even though the relationship is weak (R^2= 0.15 to 0.44), a positive relationship exists between vapor pressure deficit and CH_4 flux in the vegetated area indicating stomatal control of CH_4 emission. In addition, pore-water and chamber $\delta^{13}C - CH_4$ measurements in a non-vegetated mud flat and a vegetated area of a restored marsh indicate that methanogenic acetate fermentation is the possible process contributing to CH_4 emission.

Introduction

Although the absolute quantity of methane (CH_4) being emitted globally is smaller than the total emission of CO_2, the contribution of CH_4 to global warming is 28 times more effective than CO_2 (on a mass basis) over a period of 100 years (Stocker *et al.*, 2013), making CH_4 the second most important greenhouse gas after carbon dioxide (CO_2). Wetlands are a major source of CH_4 emission since they emit one third of total global CH_4 emission (Solomon *et al.*, 2007). Furthermore, approximately one third of terrestrial soil carbon is stored in wetland soil globally (Bridgham *et al.*, 2006). This is because during flooding or water logged conditions, anaerobic conditions are formed in wetland soil. Under such oxygen deprived conditions, methanogens (methane producing microbes) utilize wetland soil carbon and produce CH_4 (Mitsch & Gosselink, 2007). When soil redox potential drops below -100 mV, due to shortage of oxygen, a significant CH_4 production occurs. Two major pathways of CH_4 formation in a wetland are acetate formation and CO_2 reduction (Conrad, 1999). Carbon isotope signatures have been used as an indicator of the CH_4 production pathway. When CH_4 is produced by acetate fermentation, it produces CH_4 with $\delta^{13}C$ ranging from about -65 to -50‰, whereas the CO_2 reduction pathway produce CH_4 with $\delta^{13}C$ values ranging from about -110 to -60‰ (Whiticar *et al.*, 1986). The CH_4 formed in water saturated soil migrates from the soil into the atmosphere by three major pathways: diffusion, ebullition and via plant aerenchyma (Le Mer & Roger, 2001). Diffusion is the primary CH_4 transport pathway when the water table is below the soil surface, whereas ebullition and plant mediated transport are the primary mechanism for CH_4 transport from wetland soil to the atmosphere when the water table is at or above the soil surface (Bubier & Moore, 1994). Studies have shown

huge variations in plant mediated CH_4 flux, ranging from approximately 30-100% of total CH_4 flux (Dorodnikov *et al.*, 2011, Van der Nat & Middelburg, 1998, Whiting & Chanton, 1992). In the vegetated areas of wetlands, some of the CH_4 is oxidized into CO_2 in the rhizospheric region by oxygen leaked from the roots (Laanbroek, 2010). The CH_4 oxidizing bacteria preferentially consume lighter isotope of CH_4 that results in residual CH_4 being enriched in $\delta^{13}C$ (Chanton *et al.*, 1997). Thus, $\delta^{13}C$ of emitted CH_4 can indicate the extent of CH_4 oxidation in a wetland.

Temporal variation of CH_4 fluxes from a wetland depend on various biotic and physical factors including the type of vegetation, soil and air temperature and hydrology (Whalen, 2005). Soil temperature is an important factor impacting CH_4 production by increasing activities of both methanotrophic (methane oxidizing) as well as methanogenic (methane producing) microbes. Because methanogenic bacteria are more sensitive to temperature than methanotrophic bacteria, the CH_4 production becomes greater than CH_4 oxidation, leading to increase in net CH_4 emission with increasing temperature (Inglett *et al.*, 2012, Moosavi & Crill, 1998). Increased temperature not only affects CH_4 emission directly by impacting microbial activities, but also affects CH_4 emission indirectly by impacting other factors like photosynthesis (Oquist & Svensson, 2002) and CH_4 dissolution in the water column (Casper *et al.*, 2000). Altered rate of photosynthesis can change the supply of root exudates, an important substrate for methanogenesis in vegetated areas, leading to altered CH_4 emission (Hatala *et al.*, 2012, Laanbroek, 2010). Likewise, salinity is another factor that affects CH_4 emission in salt marshes. A recent review of CH_4 emission from 31 salt marshes with salinity from 0.05–18 ppt showed that CH_4 emissions decrease with increasing salinity on a log-linear scale (Poffenbarger *et al.*, 2011) confirming the

relationship reported based on the study of three sites more than two decades ago (Bartlett *et al.*, 1987).

In many vegetated wetlands, CH_4 emission rates are higher in high light condition than during dark periods, due to increased stomatal conductance (Frye *et al.*, 1994) and increased photosynthesis in light (Chanton *et al.*, 1995). The higher CH_4 emission during the day than during the night has also been attributed to increased sediment temperature (Mikkela *et al.*, 1995), light intensity (Chanton *et al.*, 1993) and transpiration (Chanton *et al.*, 1997). If CH_4 emission from a vegetated wetland is mostly controlled by transpiration, the emission can be increased with vapor pressure deficit (VPD), as transpiration increases with increase in VPD (Chanton *et al.*, 1997).

Hydrology of the wetland is another key determinant of the production of CH_4 (Altor & Mitsch, 2006, Altor & Mitsch, 2008a, Altor & Mitsch, 2008b, Bubier & Moore, 1994, Hernandez & Mitsch, 2006) as oxygen availability in wetland soils is largely determined by hydrology. A peatland study showed that a decrease in the water table by 25 cm changed the peatland from a CH_4 source to a CH_4 sink due to an increase in oxidation of methane in the ecosystem (Roulet *et al.*, 1993). Likewise, CH_4 flux in a rice field can also be decreased by water table manipulation. Intermittent, short-term drainage reduces the CH_4 flux from these ecosystems (Sass *et al.*, 1992, Yagi *et al.*, 1997). A study conducted in a created riparian marsh (Altor & Mitsch, 2006) showed that a considerably higher amount of CH_4 is released from water-saturated soil, but the emission of CH_4 progressively decreased with a falling water table. When the water table dropped 20 cm below the soil surface, the marsh no longer releases CH_4 to the atmosphere (Altor & Mitsch, 2006).

However, most of the studies, which have looked at the effect of water table changes on CH_4 emission were conducted in ecosystems where water table fluctuation occur over a longer time period (e.g., over a month or a season). However, in tidal marshes, the water table fluctuations happen on an hourly time scale as low tide and high tide alternate in about six hours. Thus, the water table fluctuations can range from a few centimeters to more than a meter within a short period of time. Low marshes are flooded twice daily, while high marshes are flooded less frequently, usually during spring tide and neap tide (Pennings & Bertness, 2001). The effects of the incoming and outgoing tides with frequent fluctuations of the water table on CH_4 emission from these tidal systems is not well understood, as studies observing the effects of tide on CH_4 emission found contradictory results. Kelly *et al.* (1995) and Van der Nat & Middelburg (2000) showed an effect of tidal stage on CH_4 emission. In both of these studies, the CH_4 emission was greatest when water level was close to the soil surface during high tide. However, other studies found no effect of tidal stage on CH_4 emission (Chmura *et al.*, 2011, Magenheimer *et al.*, 1996).

We measured CH_4 emission from one low marsh and two high marshes capturing different tidal stages of incoming and outgoing tides during the summer of 2013. We hypothesized that the CH_4 emission increases at the beginning of incoming tide because the incoming tidal water is pushing CH_4 out, which is present in the form of bubbles in the marsh sediment. Over time, most of the bubbles of CH_4 are pushed out by the incoming tide, some of the CH_4 is oxidized in an oxic tidal water column (Deangelis & Scranton, 1993, Kelley *et al.*, 1995), while some of the CH_4 is also dissolved in the tidal water (Bartlett *et al.*, 1985), resulting in a lower rate of CH_4 emission at a later stage of

the increasing tide as well as all the stages of decreasing tide. Hence, this study seeks to examine the physical drivers of CH_4 emissions in restored and natural wetlands in an urban tidal estuary in the Meadowlands of New Jersey. In addition, we examined the processes and potential substrate use in two different microsites in a restored wetland via $\delta^{13}C$ analysis of porewater CH_4 and chamber emissions of CH_4.

Materials and Methods

Study site

This study was conducted in three tidal wetlands located in the New Jersey Meadowlands (NJM). The NJM covers the majority of the Hudson Raritan estuary ecosystem and has an area of about 35,000 hectares that is surrounded by high urban activities of northeast New Jersey, USA. The NJM was highly impacted by land use practices in the last century that shrank areas of wetlands and water bodies thereby decreasing the area of the Meadowlands into half of its original size. The three sites selected in this study were the Marsh Resource Mitigation Bank site (MRMMB), the Secaucus High School site (SHS) and the Hawk Property site (HP). The MRMMB and SHS sites are restored sites and the HP site is a natural wetland site (see Figure 1). The MRMMB site is located in Carlstadt, Bergen County, New Jersey (N 40.82 and W 74.03) and was restored in 1999. The SHS site covers 17.4 hectares and is located in Secaucus, Hudson County, New Jersey (N 40.80 and 74.04 W). The restoration of this site was done in 2007. The natural HP site is also located in Secaucus, New Jersey (N 40.70 and 74.04 W) and has an area of 9 ha. This site is dominated by *Phragmites australis* (Cav.) Trin. ex Steud. with a few remnant patches dominated by native *Spartina patens* (Aiton) Muhl (mixed with *Distichlis spicata* (L.) Greene). CH_4 fluxes were measured from pure vegetation of *Spartina alterniflora* Loisel and a mud flat area at the MRMMB site, whereas fluxes were measured from a pure vegetation patch of *P. australis* and a heterogeneous patch of *S. patens* (mixed with *D. spicata*) at the SHS site and the HP site, respectively.

Chamber construction and sampling of CH_4

The chambers were constructed based on Klinger et al. (1994) and Altor & Mitsch (2006). For the construction of the chambers, five cm at the base (15 cm for SHS and HP sites) of the 35 cm height and 30 cm in diameter bucket was removed and inserted into the soil of the studied marsh. Each measured micro-site (mud flat and *S. alterniflora* marsh at MRRMMB site; and *S. patens* and *P. australis* marsh at SHS site and HP site) had three chambers. A clear bag made out of 0.09 mm thick plastic (Husky plastic sheeting) was used for sampling of the CH_4 gas from the headspace of the bag. To support the bag while sampling, frames were made using PVC pipes. The plastic bag was snuggly fitted to the supporting frame. The height of the frame of the chambers were 1.06 m, 1.6 m and 2 m depending upon height of the vegetation, since as the growing season progressed, the vegetation became taller for sampling at *S. alterniflora* and *P. australis* marshes. However, 1.06 m tall frames were always used for sampling at the *S. patens* patch. After correcting for the height of the collar above the soil surface and the volume occupied by the PVC frames, the inner volumes of chambers were 74 L at the mud flat site, 78 L for the short vegetation chamber, 116 L for the intermediate vegetation chamber and 144 L for the tall vegetation chamber. At the mud flat area, the chamber with 1.06 m tall frame was used during low tide only. Small fans powered by batteries were used to mix the gas inside the chamber. The 30 ml of gas collected using a syringe were injected into 20 ml evacuated serum vials and stored. Within a week of collection, the gas samples were analyzed using gas chromatography equipped with FID Flame ionization detector (Schimadzu GC-2014, Shimadzu Corporation, Chiyoda-ku, Tokyo, Japan).

During high tide (for the entire tidal cycle measurements), sampling at the mud flat micro-site was done with floating chambers. The floating chambers were constructed with plastic buckets. Height and diameter of the floating chamber were 0.19 m and 0.23m (~ 8 liters), respectively. A tube with sampling port was inserted inside the bucket through a hole on the bottom. Foam was attached at the top part of the bucket encircling it. The buckets were placed in an inverted position during sampling time. The foam provided buoyancy to the bucket and the sampling port remained at the top of the chamber when it was inverted. In the vegetated area, the same chambers were used during both high and low tide. Sampling procedure was the same for both high and low tide samplings. When chambers were flooded during high tide at the vegetated area, only the volume of chamber that is not occupied by water was used for the flux calculations.

Measurements of environmental variables

Measurements of potential environmental drivers for CH_4 flux in the study site were made with different sensors. Net radiation (R_n) was measured using a net radiation sensor (NRLite, Kipp & Zonen, Delft, NL). Air temperature (T_A) and relative humidity (RH) were measured using a HMP45C probe (Vaisala, Helsinki, Finland). Air temperature and relative humidity were used to calculate vapor pressure deficit (VPD) according to Goff and Gratch (1946). The atmospheric sensors were all located on a tower approximately 2.5 m above the ground, thus capturing the micro-environmental conditions at each site, where chamber CH_4 flux measurements were done. Soil temperature (T_s) was measured using TVC probes (TL107, Campbell Scientific Inc, Logan, UT). Oxidation-reduction potential probes (E_h, Wedgwood analytical ORP probes, Campbell Scientific Inc, Logan, UT) were installed at approximately 30 cm

depth, one in each of the microsites at all three locations. All the sensors were measured every 30 seconds, and half hourly averaged data were stored in a data logger (CR3000 Micrologger, Campbell Scientific Inc, Logan, UT). The water temperature data collected at the River Barge Park by the Meadowlands Environmental Research Institute (Environmental monitoring data, http://meri.njmeadowlands.gov/) in the Hackensack River was used to gap fill soil temperature data of the study sites. The River Park is close to the MRMMB site at approximately 1.6 km due southwest of the tower where the meteorological parameters were measured. All the sites are flooded by the Hackensack River (see Figure 1). Along with water temperature, this water quality monitoring station at the River Barge records dissolved oxygen, conductivity and salinity, water depth, and turbidity of the river water. Likewise, missing data for $T_{A,}$ RH and R_n for our study sites were gap-filled based on air temperature, relative humidity and solar radiation data collected at the Meadowlands Environmental Research Institute (MERI) weather station (Environmental monitoring data, New Jersey Meadowland commission, http://meri.njmeadowlands.gov/).

Measurements of porewater and chamber $\delta^{13}C - CH_4$

In June 2013, during a short measurement campaign, a multi-inlet Los Gatos Inc. cavity ringdown absorption spectroscopy laser (LGR, Los Gatos Research Inc., Mountain View, CA, USA) was installed measuring isotopic $\delta^{13}C - CH_4$ flux at the MRMMB site at the two microsites (Mortazavi *et al.*, 2013). The chambers that were used for the experiment were those used previously at the site, made of a bucket that is cut off at the bottom and inserted into the sediments and a pump connected to the chamber that drew in air from the chamber into the instrument at 2 liters per minute. Multiple fans mixed the air within

the chamber, and the air drawn by the pump and directed to the LGR was replaced with outside air. A multi-inlet unit was used to alternate air coming in from the chamber, outside air, and a standard. The procedure used is similar to what we have previously described (Mortazavi *et al.*, 2013). For the application at the Meadowlands, measurements of the low standard (2 ppm CH_4) for 10 minutes were made, switched to a high standard (~10ppm CH_4) for 10 minutes, outside air for 15 minutes and then chamber measurements for 20 minutes. For all the runs the first 6, and 13 minutes of the standards and outside air or chamber were discarded and the rest of the data was used for further calculations as described previously (Mortazavi *et al.*, 2013). When the concentration of methane from the outside air and chamber air coming into the LGR were less than 0.15 ppm different, we assumed that concentrations were not different enough to determine a flux. The short $\delta^{13}C - CH_4$ flux measurement campaign resulted in 31 half hourly values for the vegetated area and 4 values for the mudflat area for analysis. In addition, porewater samples were collected from the "peepers" installed at the site (Reid *et al.*, 2013) and sent for analysis to Florida State University, where they were analyzed for $\delta^{13}C - CH_4$ and $\delta^{13}C - CO_2$ in the porewater using an Isotope Ratio Mass Spectrometry (IRMS).

Analysis of gas sampling and statistical tests

For calculating CH_4 flux within each of the sampling chamber, CH_4 concentration was graphed against sampling time to obtain a linear regression. The product of the slope and the volume of the chamber divided by the area of the chamber resulted in CH_4 flux per unit area and time. Criteria for accepting and rejecting the slope for the calculation of the

CH_4 flux have been described earlier {Reid, 2013 #7531}. All statistical analyses were done using MATLAB (MATLAB R2012a, Mathworks, Natick, MA).

Results

Effect of Environmental variables on CH_4 flux

Linear models were fitted between various environmental variables and CH_4 flux (Figure 2, Table 1). With exception to the *S. alterniflora* microsite at the MRMMB site, there were positive relationships between air temperature and CH_4 flux at all of the vegetated areas, although the relationships were weak (explaining 16% to 45% of the variation in CH_4 flux, depending upon microsites, Table 1). Likewise, the mud flat area at the MRMMB site and *P. australis* marsh at the HP site showed a weak, but positive relationship between soil temperature and CH_4 flux (Table 1, Figure 2). Air and soil temperature explained most of the variation in CH_4 fluxes at the *P. australis* microsites (Table 1). There was no relationship between soil temperature and CH_4 fluxes in the *S. patens* microsite at the HP site and *S. alterniflora* marsh at the MRMMB site. There was a weak, but positive relationship between net radiation and CH_4 flux in the *P. australis* marsh at the SHS, and *P. australis* and *S patens* marsh at the Hawk Property site (explaining 13 to 33 % of the variation in CH_4 flux). There was no relationship between net radiation and CH_4 flux in either microsites at MRMMB. The relationship between relative humidity and CH_4 fluxes was subsumed in the relationships between VPD and CH_4 fluxes and thus not further explored. Although the relationship was weak, explaining 15% to 44% of the variation in CH_4 flux, VPD showed a positive relationship with CH_4 fluxes except at the mud flat microsite at the MRMMB site (Table 1, Figure 2). Oxidation-reduction potential showed a positive relationship at the mud flat microsite at

the MRMMB and *P. australis* marsh at the HP site (explaining 19 % and 16% CH_4 flux variation for mud flat and the *P. australis* microsite, respectively) but there was no relationship between oxidation-reduction potential and CH_4 flux at other microsites of MRMMB, HP site and the SHS site.

Effect of tide on CH_4 flux

The tidal amplitude varies in all the sites, whereby higher tidal amplitude is observed at the MRMMB site compared with the SHS and HP site (Figure 3). In all the sampled vegetated microsites, there was no relationship between CH_4 flux and tidal water depth difference (difference between water depth at the end of a 1.25 hrs measurement cycle and at the start of the measurement, Figure 4). In the mud flat microsite, there was a positive relationship between CH_4 flux and the water depth difference showing higher emission during incoming tide than during the outgoing tide. However, the relationship between CH_4 flux and the water depth difference was weak (explaining less than 30% CH_4 flux variation).

Analysis of $\delta^{13}C - CH_4$ porewater and chamber flux

The porewater $\delta^{13}C - CH_4$ measurements values for the vegetated and mudflat microsites at the MRMMB site were similar (Table 2, P=0.8). Likewise, the $\delta^{13}C - CO_2$ in the porewater were not different (P=0.8, Table 2). For the $\delta^{13}C - CH_4$ chamber flux measurements, the results were similar (Table 2, P=0.3) as well. For reference, the isotopic value of the two plant species that are found at the site, *S. alterniflora* and *P. australis* are given that were measured in 2009. The porewater $\delta^{13}C - CO_2$ values clearly

resemble C_4 plant carbon (Table 2), thus are derived from *S. alterniflora*. Average $\delta^{13}C$ of the CH_4 fluxes and porewater CH_4 were – 45 ‰ to – 52 ‰, respectively.

Discussion

Effect of Environmental variables on CH_4 flux

Temperature is an important environmental variable that determines CH_4 from a wetland because it affects both CH_4 production and oxidation. Many studies have reported positive correlations between CH_4 emission and temperature (Bartlett *et al.*, 1992, Kankaala *et al.*, 2004, Van der Nat & Middelburg, 2000); however, there are studies that have reported no correlation (Klinger *et al.*, 1994) or a negative correlation (Macdonald *et al.*, 1998) between CH_4 emission and temperature. Tong *et al.* (2012) reported significant but weak (R^2 varies from 0.04 to 0.4) relationships between CH_4 emission and temperature in a tidal estuarine wetland of China. In our study, the mud flat microsite showed no relationship between CH_4 emission and neither soil nor air temperature ($P > 0.05$) but all the vegetated areas showed a positive relationship between CH_4 fluxes and air temperature ($P< 0.05$) except the *S. alterniflora* marsh. A positive relationship between soil temperature and CH_4 flux was found only in the *P. australis* marsh at the natural wetland site. In a peatland ecosystem, Forbrich *et al.* (2011) evaluated temperature-based CH_4 flux models using soil temperature at various depths of peat sediment and found that the soil temperature at 50 cm soil depth is the best predictor for CH_4 flux aboveground. In our study, soil temperature was measured at 0-10 cm depth. It is probable that if we had temperature measurements at a deeper depth, the temperature would be a better explanatory variable for the CH_4 flux. Reid *et al* (2013) evaluated temperature-based CH_4 flux models using time lagged soil temperature at 0-10 cm depth

and found that the time lagged exponential temperature model best described the CH_4 flux in the vegetated area of the MRMMB site. The better prediction of CH_4 flux by time lagged soil temperature at 0-10 cm soil depth than the soil temperature of the depth during the measurement time, may be indicative of the lag in temperature that can be similar and representative of soil temperature of deeper soil.

There was a positive relationship between vapor pressure deficit (VPD) and CH_4 flux in the vegetated areas covered by different species even though the relationship was weak (explaining 15% to 44% of the variation in CH_4 flux) suggesting a limited amount of stomatal control on CH_4 flux. As VPD increases the transpiration rate increases (Oren *et al.,* 1999) and increased transpiration can lead to increased CH_4 emission resulting in a positive relationship between in CH_4 flux and VPD (Chanton *et al.,* 1997). The weak or no relationship of CH_4 flux with net radiation suggests that light was not a primary driver of the CH_4 flux in the studied marshes.

Significant CH_4 emission occurs in wetlands when soil redox potentials are lower than approximately -100 mV, while emission rates increase with decreasing oxidation-reduction potential (Hou *et al.,* 2000), showing a negative relationship between oxidation reduction potential and CH_4 flux. Contrary to our expectation, we found either a positive or no relationship between oxidation-reduction potential and CH_4 fluxes. Our probe measured oxidation-reduction potential in a shallower soil region (about 30 cm from the soil surface) of the marsh soil. But, production of most of the emitted methane occurs in deeper soil layers (Reid *et al.,* 2013). Therefore, it is reasonable to assume that the probes may have not captured the oxidation-reduction potential of the region where most of the

CH_4 production occurs, leading to unexpected positive or no relationships between oxidation-reduction potential and CH_4 flux.

Studies have reported both no effect and an effect of tidal inundation on CH_4 fluxes. Chmura *et al*. (2011) found no effect of soil water depth on CH_4 fluxes in a tidal wetland of *S. patens* in New Brunswick, Canada. Likewise, Magenheimer *et al*. (1996) measured CH_4 flux from a tidal marsh having different vegetation and found no relationship between water table position and CH_4 flux in the same region. However, some other studies showed an effect of the tide on CH_4 emission. In a tidally flooded river margin of the White Oak River estuary, North Carolina, Kelly *et al*. (1995) reported the greatest CH_4 fluxes when the water table was close to the soil surface both during increasing and receding tide. Van der Nat & Middelburg (2000) reported higher CH_4 emission during low tide than during high tide. In a *P. australis* tidal marsh of the Mid River estuary, South China, Tong et al (2010) found a huge variation in CH_4 emission depending on tidal stage with higher emission before flooding, and after ebb than during the flooding and ebbing process. In our study, we looked at the relationship between tidal height differences (the water level at the end of the 1hr 15min sampling period minus the water level at the beginning of the sample cycle) and found that there is no relationship between the water level difference and CH_4 flux in all the vegetated areas. However, there was a positive relationship between the water level difference and CH_4 flux in the mud flat area, with higher CH_4 flux during increasing tide. This difference in CH_4 emission between vegetated and non-vegetated mud flat could be due to differences in the CH_4 reservoir between the two marsh zones. The mud flat areas contain more CH_4 belowground than in vegetated area, and a part of the belowground CH_4 is stored in the form of bubbles (Reid

et al., 2013). When tidal water enters the marsh, it exerts pressure releasing more bubbles and non-bubble from CH_4 to atmosphere and that can be more pronounced in the mud flat micro-site where more CH_4 is present belowground. Thus, higher CH_4 release from the mud flat micros-site shows the effect of water depth differences in the mud flat areas but not in the vegetated areas. Likewise, the mudflat areas experience higher tidal amplitude than the vegetated areas. In particular, in the high marsh areas (*S. patens*), inundation only occurs during neap and spring tides, thus CH_4 fluxes are not influenced by the tidal amplitude.

$\delta^{13}C$ – CH_4 porewater and chamber flux

Acetate fermentation and CO_2 reduction are the two major pathways of CH_4 formation in wetlands (Conrad, 1999). Each of the CH_4 production pathways yields CH_4 with distinct carbon isotopic signature. The CH_4 produced from acetate fermentation pathway is enriched in ^{13}C ($\delta^{13}C$ ~ -65 to -50‰) relative to CO_2 reduction pathway ($\delta^{13}C$ ~ -110 to -60‰) (Whiticar *et al.*, 1986). Carbon isotopic measurements of the CH_4 fluxes and porewater resulted in an average value of -45 ‰ to -52 ‰, respectively, in our study, suggesting that acetate fermentation pathway was dominant in both vegetated and non-vegetated areas of our site. Since the mud flat area and the vegetated area at the MRMMB site, where the measurements were taken, are not different, either in their carbon isotopic signature for CH_4 or CO_2, it is suggested that similar substrates were used for methanogenesis. Presumably, as the $\delta^{13}C$ value of the porewater CO_2 suggest, recently respired CO_2 was derived from *Spartina* – a C_4 plant, then from *Phragmites* – a C_3 plant, which was used as a fill when the site was mitigated in 1999 and 2001 (USACE, 2004). Similar $\delta^{13}C$ value for tissues of *S. alterniflora* and CO_2 also suggests that the CO_2

was produced through non-fractionating pathways such as aerobic respiration, high-molecular weight organic matter fermentation, and other electron acceptor such as humics, nitrate, iron, and sulphate reduction (Corbett *et al.*, 2013). In the vegetated area of a wetland, methanotrophs are likely to utilize the oxygen leaked from roots and oxidize some of the produced CH_4 into CO_2 that in turn results in residual CH_4 being enriched in $\delta^{13}C$ relative to non-vegetated mud flat microsites without roots. But, in our study we saw similar $\delta^{13}C - CH_4$ values for vegetated area and non-vegetated mud flat suggesting that CH_4 oxidation due to the presence of roots was not significant in our system, at least, during mid growing season (June). Instead of oxidizing CH_4, the oxygen leaked from roots might have been used for other processes such as oxidation of sulphide to sulphate, Fe (II) to Fe (III), and ammonium to nitrate (Begg *et al.*, 1994, Reddy *et al.*, 1989, Wind & Conrad, 1997). Kruger *et al* (2001) reported in a rice field that CH_4 oxidation activity is important only at the beginning of the growing season for a short period of time. Since the porewater and the chamber CH_4 fluxes differ by < 5 ‰, it may suggest that the plants do not have a convective flow through system, as is the case in *Spartina alterniflora* (Chanton & Whiting, 1996, Chanton, 2005). Overall, this research suggests that the different microsites do not only differ in their overall fluxes, but also exhibit different drivers and thus pose a challenge to be able to model methane fluxes. However, due to similar substrate use and methanogenic processes, it may allow easier characterization of the belowground processes.

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Figures and tables

Figure 1: Study sites: Marsh Resource Meadowlands Mitigation Bank (circle, MRMMB), Secaucus High School marsh (diamond, SHS) and Hawk Property (pentagon, HP)

Figure 2: Relationship between CH_4 emission and various environmental factors, whereby in A) relationship with air temperature is displayed, in B) soil temperature at 10 cm depth, in C) net radiation and D) vapor pressure deficit (see Table 1 for statistics). Regression lines are shown when significant.

Figure 3: High (bottom panel) and low tide (top panel) of the Meadowlands Resource Mitigation Bank (left panels), the Secaucus High School site (middle panels) and the Hawk Property (right panels). Maximum water level for high tide (denoted in red) at the Meadowlands Resource Mitigation Bank is 1.95 m, at the Secaucus High School site is 1.65 m and at the Hawk Property 2.1 m.

Figure 4 Relationship between CH_4 flux and water depth difference (difference between water depth at the end of a 1h 15 min measurement cycle and at the beginning of the measurement) at the different microsites – A) and B) are at the Marsh Resource Mitigation Bank, C) and D) are at the Secaucus High School Marsh and E) and F) are at the Hawk Property. The negative and positive values for water depth indicate decreasing and increasing water depth, respectively. Note that scales on the y-axis are different for each graph.

Table 1: Coefficient of determination and P value for linear regressions of CH_4 flux with environmental parameters, whereby T_A – air temperature, T_S – soil temperature, VPD – vapor pressure deficit, R_n – net radiation and E_h – reduction-oxidation-potential.

Microsite	Site	T_A		T_S		VPD		R_n		E_h	
		R^2	P	R^2	P	R^2	P	R^2	P	R^2	P
S. alterniflora	MRMMB		0.08		0.08	0.15	0.04		0.08		0.54
mudflat	MRMMB		0.27		0.32		0.1		0.41	0.19	0.05
P. australis	SHS	0.36	0.002			0.44	0.0003	0.13	0.05		0.31
S. patens	SHS	0.16	0.04			0.17	0.03		0.08		0.42
P. australis	HP	0.45	<0.0001	0.39	<0.0001	0.23	0.01	0.33	0.003	0.16	0.02
S. patens	HP	0.18	0.01		0.06	0.20	0.03	0.27	0.02		0.54

Table 2: Methane and carbon dioxide $\delta^{13}C$ values for porewater, chamber air and plant parts measured in 2013 and 2011, respectively.

		$\delta^{13}C - CH_4$ ‰	$\delta^{13}C - CO_2$ ‰	$\delta^{13}C$ ‰
Porewater Vegetation		-52.9 (5.6)	-13.2 (2.8)	
	Mudflat	-52.2 (1.6)	-12.9 (0.3)	
Spartina	**Root/rhizome**			-13.5 (0.13)
	Leaves			-13.8 (0.26)
Phragmites **Root/rhizome**				-27.0 (0.21)
	Leaves			-27.3 (0.96)
Chamber Vegetation		-44.5 (0.98)		
	Mudflat	-47.5 (1.17)	-10.7*	

* measured in Jan 2010

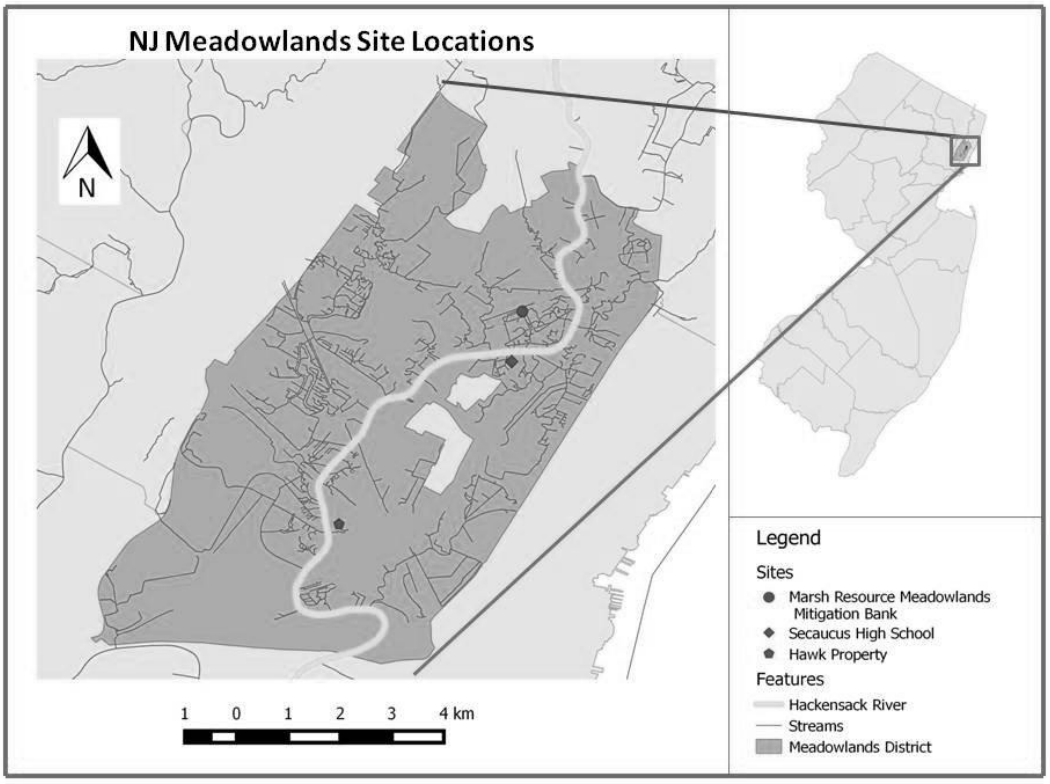
NJ Meadowlands Site Locations
N
1 0 1 2 3 4 km
Legend
Sites
Marsh Resource Meadowlands Mitigation Bank
Secaucus High School
Hawk Property
Features
Hackensack River
Streams
Meadowlands District

Figure 1

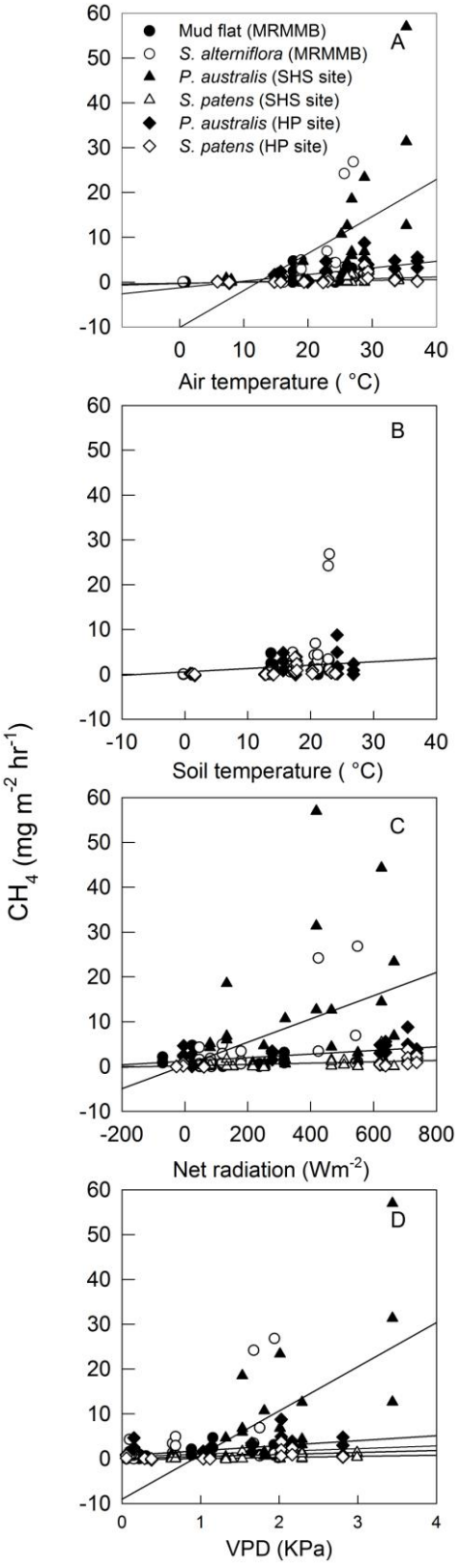
Mud flat (MRMMB)
S. alterniflora (MRMMB)
P. australis (SHS site)
S. patens (SHS site)
P. australis (HP site)
S. patens (HP site)
A
B
C
D
CH4 (mg m-2 hr-1)
Air temperature (°C)
Soil temperature (°C)
Net radiation (Wm-2)
VPD (KPa)

Figure 2

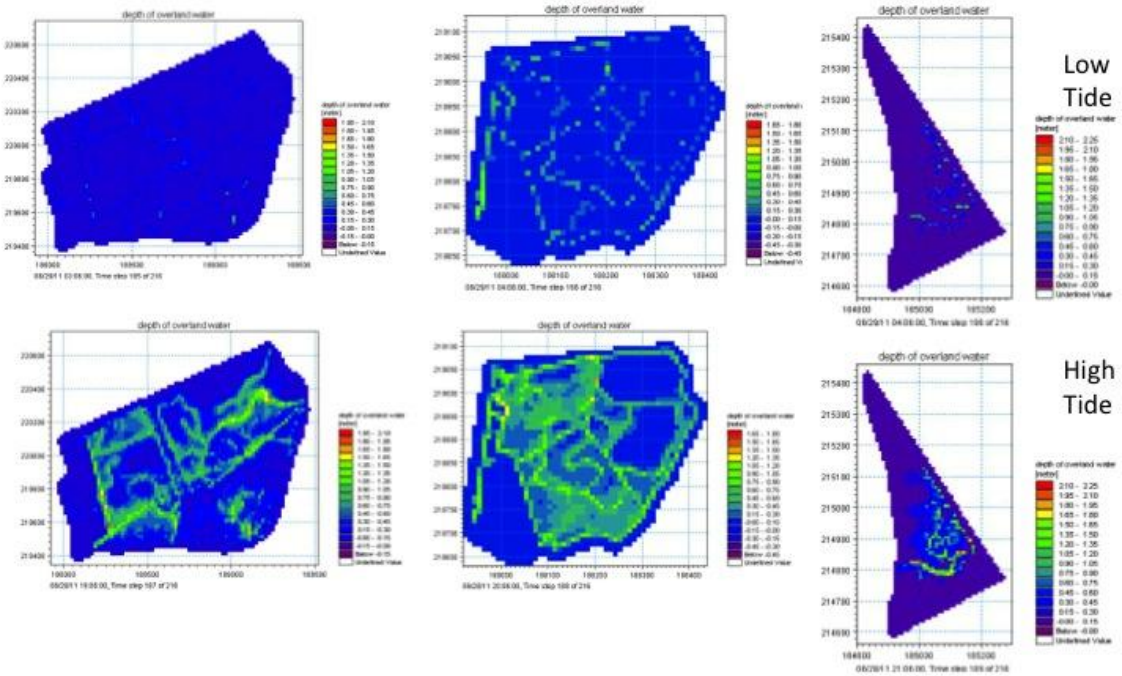
Low
Tide
High
Tide
Marsh Resource Mitigation Bank
Mitigated 1999
Secaucus High School Marsh
Mitigated 2007
Hawk Property
Natural

Figure 3

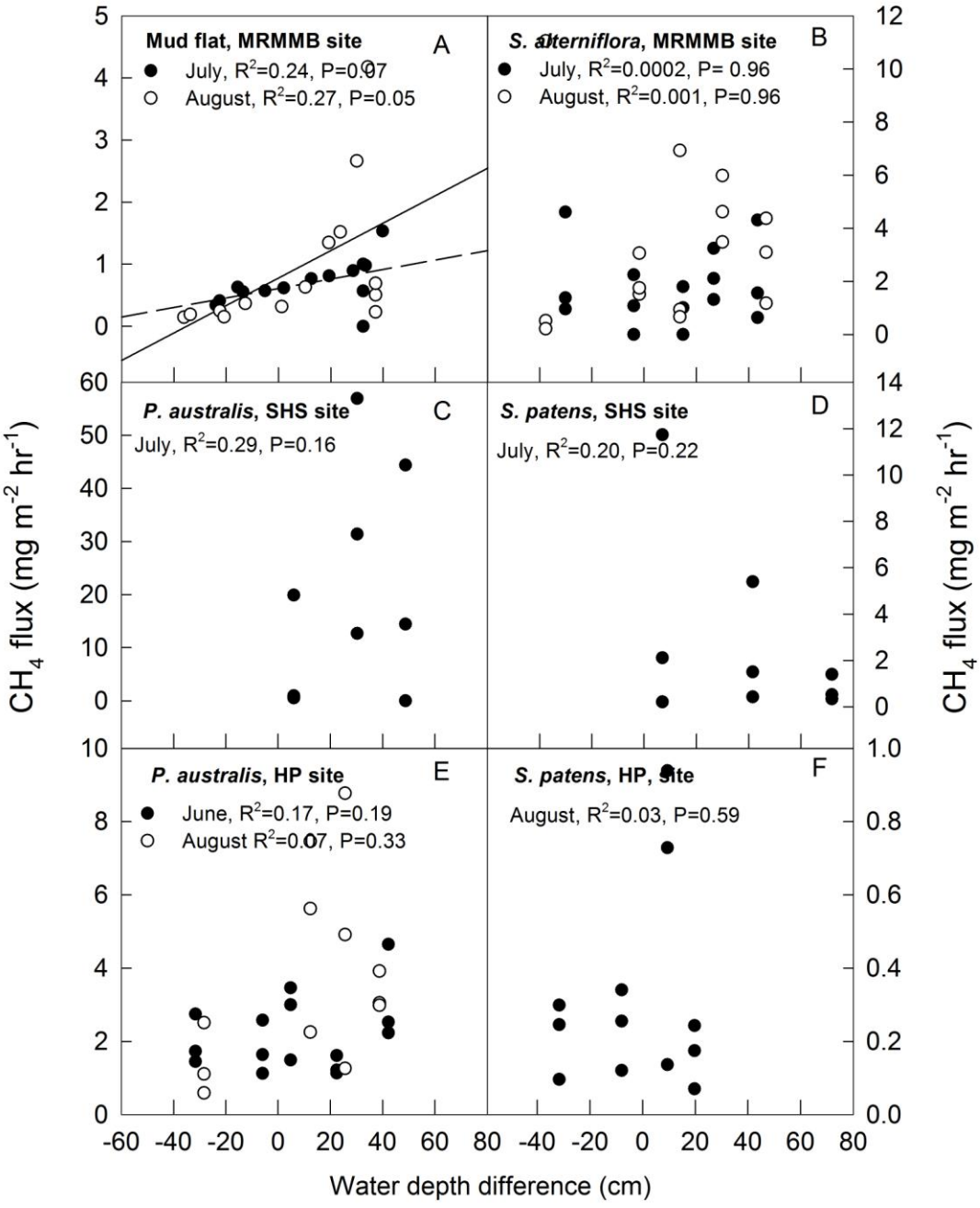
Mud flat, MRMMB site
A
July, R2=0.24, P=0.07
August, R2=0.27, P=0.05
S. alterniflora, MRMMB site
B
July, R2=0.0002, P= 0.96
August, R2=0.001, P=0.96
P. australis, SHS site
C
July, R2=0.29, P=0.16
S. patens, SHS site
D
July, R2=0.20, P=0.22
P. australis, HP site
E
June, R2=0.17, P=0.19
August R2=0.07, P=0.33
S. patens, HP, site
F
August, R2=0.03, P=0.59
CH4 flux (mg m-2 hr-1)
CH4 flux (mg m-2 hr-1)
Water depth difference (cm)

Figure 4

Summary

This study demonstrated CH_4 fluxes of two microsites in each of two restored and one natural wetlands of New Jersey Meadowlands reported on in chapter 1, have large variations associated with it. This study will thus, contribute to refining global CH_4 budgets, and increase our understanding of CH_4 emissions from low salinity mesohaline (salinity between 5 to 18 ppt) marshes, which have larger uncertainties in their CH_4 budget estimates [*Poffenbarger et al.*, 2011]. The study showed that even within the same marsh there can be large variation in CH_4 flux between the marsh zones having different species. And, year-to-year variation in CH_4 flux can be different depending upon marsh and species highlighting the importance of measuring CH_4 flux across marsh type, species for at least more than one year for better estimates of CH_4 source strength of a wetland. We saw strong seasonality in CH_4 emissions as expected, with most of the emission during warm growing season and little or no emission during winter. For *S. patens* (1.8- 2.7 g CH_4 m^{-2} yr^{-1}) and *S. alterniflora* (15.6 g CH_4 m^{-2} yr^{-1}) marshes, annual CH_4 flux estimates are within the range of flux estimates from various past studies for marshes of the same species around the world. However, annual CH_4 flux estimations for *P. australis* (12.6-26.6 g CH_4 m^{-2} yr^{-1}) marshes in our study is close or towards the lower end of the lowest annual CH_4 flux estimates from past studies of *P. australis* marshes. Even though, aboveground biomasses of the studied species were not significantly different from each other as demonstrated in chapter 1, the CH_4 flux from the marshes covered by the species were significantly different from each other suggesting that the difference in factors like water table position, rhizospheric effect and

quality of organic substance between the marsh areas covered by different species should have masked the expected positive relationship between plant biomass and CH_4 fluxes.

Both aboveground and belowground biomasses are the important factors impacting CH_4 flux in a wetland by affecting production and/or consumption of CH_4 (Laanbroek 2010). Therefore, accurately quantifying biomass of wetland plants is important to better understand CH_4 dynamics of a wetland. Root exudates and decaying above- and belowground biomasses can act as substrate for CH_4 production (Lai 2009). The CH_4 produced in oxygen (O_2) deprived wetland sediment is transported via aerenchymatous belowground tissue and finally released from leaves and stems into the atmosphere [*Van der Nat et al.,* 1998]. The aerenchymous tissue which transport CH_4 from wetland sediment to atmosphere also transport O_2 from atmosphere into soil resulting into oxidation of some of the CH_4 produced in sediment into CO_2 [*Le Mer and Roger*, 2001; *Mitsch and Gosselink,* 2007].

In chapter 2, we measured, aboveground and belowground biomass, root and rhizome characteristics, leaf area index (LAI), and carbon to nitrogen (C/N) ratio of various tissues of four tidal marsh species in New Jersey by harvesting biomass during peak growing season. Recently restored wetlands do not have as much time as natural wetlands to accrue belowground biomass that could be the reason why we found lower belowground to aboveground biomass ratios for *S. alternniflora* and *D. spicata* that were harvested from recently restored wetlands. Most of the leaf area was found at mid-height of the canopy suggesting that most of the leaf mediated greenhouse gas emission occurs from this region. The information about distribution of leaf area at various canopy heights can be useful for modeling stomatal mediated greenhouse gas emissions [*Dai et al.*,

2004]. Presence of most of the belowground biomass close to soil surface suggests that the effect of belowground biomass on CH_4 production, consumption and transport likely to be greater at the wetland sediment close to the soil-to-atmosphere interface. However, the presence of roots at least up to 55 cm below the soil surface indicates that the root effect of CH_4 dynamics occurs well below the soil surface. Variation in rhizome and root diameter, number of primary roots per node of rhizome, and root surface area to volume ratio between species may be some of the contributing factors that lead to variation in CH_4 emissions from wetlands covered by different species as the parameters related to root and rhizome affect exchange CH_4 as well as O_2 between underground plant tissue and wetland sediment. More importantly, the belowground plant characteristics as well as leaf area distribution at various canopy heights can be useful for modeling CH_4 and other greenhouse gas transport.

Not only do biological factors affect CH_4 dynamics of a wetland, but also various physical factors including hydrology [*Altor and Mitsch*, 2006; 2008a; b; *Bubier and Moore*, 1994; *Hernandez and Mitsch*, 2006] , air temperature, soil temperature [*Kankaala et al.*, 2004; *Klinger et al.*, 1994; *Macdonald et al.*, 1998; *Van der Nat and Middelburg*, 2000], net radiation [*Van der Nat et al.*, 1998], and vapor pressure deficit (VPD) [*Chanton et al.*, 1997] affect CH_4 flux. A better understanding of the relationships between CH_4 flux and factors affecting this flux is necessary to gain a better insight into CH_4 flux dynamics, and formulating CH_4 emission mitigation strategies for a wetland.

In chapter 3, we investigated CH_4 flux and its relationship with various physical factors. We found higher CH_4 flux during incoming tide than during outgoing tide in a mud flat as indicated by a positive relationship between water depth difference (water depth at the

end of 1.25 hrs measurement cycle and at the start of measurement) and CH_4 fluxes. But there was no relationship between CH_4 flux and water depth difference in vegetated areas. The effect of incoming tide on CH_4 release, due to downward force of incoming tide, should be more pronounced in mud flat area because of presence of higher amount of dissolved and bubble form of CH_4 in mud flat area than in vegetative area leading to higher CH_4 releasing during incoming tide than during outgoing tide from a mud flat area. The weak but positive relationship between VPD and CH_4 flux from vegetated areas indicate stomatal control on the flux. In addition, porewater and chamber $\delta^{13}C$-CH_4 measurements indicate that substrate used in the two microsites of a restored area was similar and methanogenic acetate fermentation is the possible process contributing to CH_4 emission.

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