

Complex invader-ecosystem interactions and seasonality mediate the impact of non-native *Phragmites* on CH₄ emissions

Peter Mueller · Rachel N. Hager · Justin E. Meschter ·
Thomas J. Mozdzer · J. Adam Langley · Kai Jensen ·
J. Patrick Megonigal

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Abstract Invasive plants can influence ecosystem processes such as greenhouse gas (GHG) emissions from wetland systems directly through plant-mediated transfer of GHGs to the atmosphere or through indirect modification of the environment. However, patterns of plant invasion often co-vary with other environmental gradients, so attributing ecosystem effects to invasion can be difficult in observational studies. Here, we assessed the impact of *Phragmites australis* invasion into native shortgrass communities on methane (CH₄) emissions by conducting field measurements of CH₄ emissions along transects of invasion by *Phragmites* in two neighboring brackish marsh sites and compared

these findings to those from a field-based mesocosm experiment. We found remarkable differences in CH₄ emissions and the influence of *Phragmites* on CH₄ emissions between the two neighboring marsh sites. While *Phragmites* consistently increased CH₄ emissions dramatically by $10.4 \pm 3.7 \mu\text{mol m}^{-2} \text{min}^{-1}$ (mean \pm SE) in our high-porewater CH₄ site, increases in CH₄ emissions were much smaller ($1.4 \pm 0.5 \mu\text{mol m}^{-2} \text{min}^{-1}$) and rarely significant in our low-porewater CH₄ site. While CH₄ emissions in *Phragmites*-invaded zones of both marsh sites increased significantly, the presence of *Phragmites* did not alter emissions in a complementary mesocosm experiment. Seasonality and changes in temperature and light availability caused contrasting responses of CH₄ emissions from *Phragmites*- versus native zones. Our data suggest that *Phragmites*-mediated CH₄ emissions are particularly profound in soils with innately high rates of CH₄ production. We demonstrate

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Phragmites invasion.

Peter Mueller and Rachel N. Hager have contributed equally to the manuscript.

P. Mueller (✉) · K. Jensen
Applied Plant Ecology, Biocenter Klein Flottbek,
University of Hamburg, Ohnhorststr. 18, 22609 Hamburg,
Germany
e-mail: peter.mueller@uni-hamburg.de

R. N. Hager
Ecology Center and Department of Watershed Sciences,
Utah State University, 5210 Old Main Hill, Logan,
UT 84322, USA

J. E. Meschter
Department of Environmental Science and Technology,
University of Maryland, College Park, MD 20742, USA

J. E. Meschter · J. P. Megonigal
Smithsonian Environmental Research Center, 647
Contees Wharf Rd, Edgewater, MD 21037, USA

R. N. Hager · T. J. Mozdzer
Department of Biology, Bryn Mawr College, 101 N.
Merion Ave, Bryn Mawr, PA 19010, USA

J. A. Langley
Department of Biology, Villanova University, Villanova,
PA 19085, USA

that the effects of invasive species on ecosystem processes such as GHG emissions may be predictable qualitatively but highly variable quantitatively. Therefore, generalizations cannot be made with respect to invader-ecosystem processes, as interactions between the invader and local abiotic conditions that vary both spatially and temporally on the order of meters and hours, respectively, can have a stronger impact on GHG emissions than the invader itself.

Keywords *Phragmites* · Methane emissions · *Spartina patens* · Blue carbon · Tidal wetlands

Introduction

Wetland ecosystems as landscape sinks are thought to be particularly susceptible to plant invasions (Zedler and Kercher 2004). Invasive wetland plants often form monocultures with cascading consequences for wetland biodiversity, food webs, biogeochemistry, and entire habitat structure (Zedler and Kercher 2004). Given the increasingly recognized function of tidal wetlands as a long-term carbon sink (Duarte et al. 2005; Mcleod et al. 2011), there is a growing body of research focused on the impact of invasive species on tidal wetland carbon sequestration and greenhouse gas (GHG) emissions, particularly with respect to changes in the balance of sequestration and methane (CH₄) emissions (e.g. Valéry et al. 2004; Emery and Fulweiler 2014; Yuan et al. 2015).

Under anoxic conditions and depending on the availability of alternative electron acceptors (e.g. nitrate, iron or sulfate), large amounts of GHGs such as CH₄ and nitrous oxide can be produced in tidal wetland soils. Previous work has shown that particularly CH₄ emissions have the potential to offset even high rates of carbon sequestration in low-salinity systems that experience low inputs of sulfate through seawater intrusion (Poffenbarger et al. 2011). Besides the availability of electron acceptors, also plant activity and certain plant traits (like aerenchyma formation) can greatly influence CH₄ emissions by affecting the three processes that contribute to net CH₄ emissions: microbial CH₄ production, microbial CH₄ oxidation, and plant-supported ventilation of CH₄ directly to the atmosphere, bypassing soil surface CH₄ oxidation (Armstrong et al. 1996; Colmer 2003; Sutton-Grier and Megonigal 2011).

Perhaps the most comprehensive research on the impact of an invasive wetland species on GHG emissions comes from the invasion of non-native *Spartina alterniflora* in East Chinese coastal wetlands where native plant communities are dominated by *Phragmites australis*, *Suaeda salsa* or *Scirpus mariqueter*. Here, in-situ closed-chamber quantification of CH₄ emissions (Tong et al. 2012; Yuan et al. 2015) and mesocosm experiments (Cheng et al. 2007; Zhang et al. 2010) suggest *S. alterniflora* invasion increases CH₄ emissions in comparison to the native communities.

North American wetlands have been rapidly invaded by a non-native lineage of the common reed, *P. australis* (hereafter *Phragmites*). In tidal wetlands, the introduced Eurasian lineage outcompetes the native lineage (Mozdzer and Zieman 2010; Mozdzer et al. 2013), increases CH₄ emissions (Mozdzer and Megonigal 2013), and also expands into historically novel habitats (Chambers et al. 1999). Examples of native plant communities susceptible to *Phragmites* invasion in North America are high marshes dominated by *Spartina patens* (Chambers et al. 1999; Windham and Lathrop 1999; Mozdzer et al. 2013), low marshes dominated by *S. alterniflora* (Chambers et al. 1998), and brackish marshes dominated by *Schoenoplectus americanus* (McCormick et al. 2010). Replacement of native communities by *Phragmites* results in altered soil properties (redox potential, nitrogen pools), porewater chemistry (salinity, nitrogen fluxes), and biomass production (Chambers et al. 1998; Windham and Lathrop 1999; Windham-Myers 2005; Mozdzer et al. 2010). Recent studies comparing in-situ emissions of CH₄ from different native communities and *Phragmites* in North America have reported contrasting outcomes: Emery and Fulweiler (2014) found no differences in CH₄ emissions from low marsh *S. alterniflora* and *Phragmites* stands in a New England salt marsh, while Martin and Moseman-Valtierra (2015) found consistently higher CH₄ emissions from *Phragmites* stands compared to *S. patens*-dominated high marsh communities in three New England tidal wetlands along a salinity gradient.

Previous studies that investigated invader-ecosystem effects on GHG emissions have generally used the approach of space-for-time substitution which assumes that areas supporting invasive species would be ecologically and biogeochemically identical to areas that presently support native communities if they

had not been invaded. Although this approach is insightful, knowledge of the effect of invasion on GHG emissions (and other processes) is limited by the fact that conclusions drawn from field measurements are rarely coupled to experimental support.

Invasive-species establishment commonly requires distinct environmental conditions within an ecosystem, e.g. low-salinity or high-elevation environments as suggested for the establishment of *Phragmites* (Bart et al. 2006; Mozdzer et al. submitted to this issue). Patterns of invasion are likely to follow gradients in environmental variables like salinity, elevation, and flooding frequency that have an impact on GHG emissions irrespective of the dominant plant community (Megonigal et al. 2004; Poffenbarger et al. 2011; Olsson et al. 2015). Furthermore, contrasts between sites in spatial patterns of invasion, establishment histories (Bart et al. 2006), or pre-invasion biogeochemical cycles may result in different responses of GHG emissions upon invasion. In order to develop conceptual models that explain invasion effects on GHG emissions, it is necessary to assess the extent to which we can generalize across study sites.

In this study, we assess the impact of *Phragmites* invasion on CH₄ emissions using a space-for-time substitution approach along transects of invasion by *Phragmites*. We conducted the study in two neighboring Chesapeake Bay brackish marsh sites that differ in geomorphic setting, porewater chemistry, invasion history, and *Phragmites* stature, assuming that these differences will indicate the extent to which our results can be generalized. Finally, we compare our field results to those from a field-based mesocosm experiment in order to isolate the factors that influence *Phragmites*-driven changes in CH₄ emission from other invasion-independent factors that may co-occur along natural transects of *Phragmites* invasion.

Materials and methods

Field study

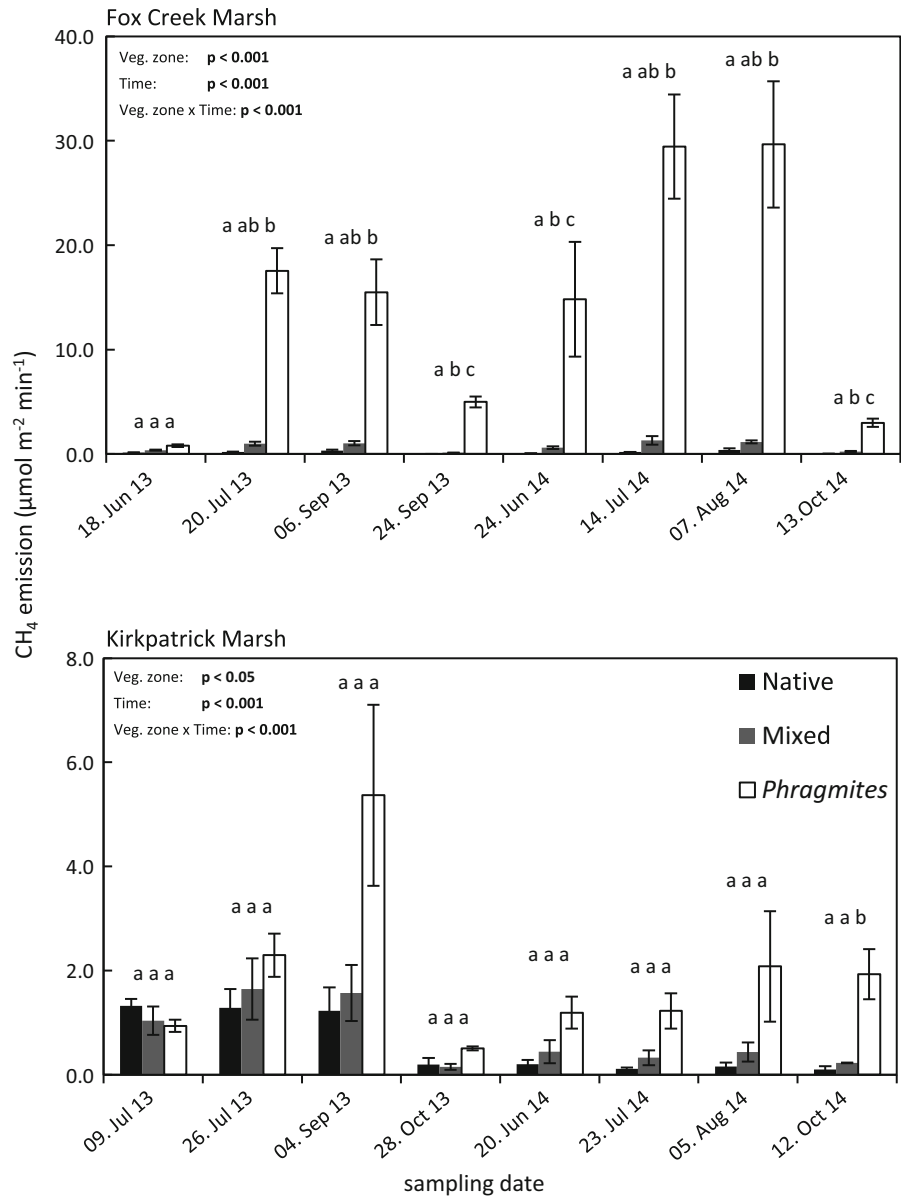
The field study was conducted in two *Phragmites*-invaded brackish, tidal wetland systems, Fox Creek Marsh and Kirkpatrick Marsh, home to the Smithsonian Global Change Research Wetland (GCREW) operated by the Smithsonian Environmental Research Center (38°53'N, 76°33'W) in Edgewater, Maryland,

USA. The study took place between June 2013 and October 2014. Both sites are located within the Rhode River, a sub-estuary of the Chesapeake Bay, but are separated by the Muddy Creek and a distance of approximately 800 m. These sites were selected based on aerial photos and remote sensing (unpublished data) that indicated they were uniformly covered by native grasses (dominated by *S. patens* with small contributions of *Distichlis spicata*, *Panicum virgatum* and *S. americanus*) and *Iva frutescens* until at least 1972. However, these two sites differ with respect to mechanisms of *Phragmites* establishment, and therefore represent different invasion patterns: At Fox Creek Marsh, *Phragmites* first established at the wetland-upland interface and has been spreading toward the marsh edge. In contrast, at Kirkpatrick Marsh, *Phragmites* established on the creek bank and has been spreading along the marsh edge and toward the marsh interior. In both sites, three vegetation zones representing different stages of invasion by *Phragmites* were classified: (1) a dense, monotypic *Phragmites* stand, (2) a mixed zone of native grasses (>90 % cover) and few clonally integrated shoots of *Phragmites* (approx. 10 per plot) and (3) a native zone dominated by *S. patens*. Replicated 50 × 50 cm aluminum collars (n = 4) were inserted 20 cm into the soil surface in each of the three zones at each site, and small boardwalks were installed to minimize disturbances during repeated sampling over 2 years.

CH₄-flux measurements

To examine the effect of *Phragmites* invasion on CH₄ emissions, CH₄ fluxes in *Phragmites*-, mixed-, and native-vegetation zones were measured approximately monthly between June and October of 2013 and 2014 (Fig. 1) using closed chambers. Measurements were conducted during day light under non-inundated conditions. As the main focus of this work is the relative comparison of CH₄ emissions between different vegetation zones and sites, we used an easily replicable closed-chamber design without temperature control. Depending on vegetation zone and site, absolute values of CH₄ emission presented here may be overestimated and should therefore be interpreted with caution (see “Results” for detail). Flux chambers were constructed of an aluminum frame and covered with transparent polyester film (Melinex 071, ICI, DE, USA) with topside sampling tubing from which to

Fig. 1 CH₄ emissions ($\mu\text{mol m}^{-2} \text{min}^{-1}$) from three vegetation zones representing different stages of invasion by *Phragmites australis* into native shortgrass communities measured on 8 sampling dates at Fox Creek Marsh (top) and Kirkpatrick Marsh (bottom). *P* values represent results of repeated-measures ANOVA. Lowercase letters represent results of a Tukey's HSD test at the given sampling date within a marsh site. Bars not connected by the same letter are significantly different ($p < 0.05$). Presented are mean values \pm standard errors; $n = 4$



extract gas samples. Chambers were equipped with thermometers on the inside to record chamber-temperature development during measurements. Chamber volumes were manipulated to accommodate the three vegetation-zone heights by using stackable 70 and 120 cm sections, resulting in a chamber headspace between 200 to 1025 L. During each flux measurement, 20 mL gas samples were collected from the chamber headspace every 30 min for 2 h and transferred to 12 mL gas sampling vials (Labco Ltd, High Wycombe, UK). Gas samples were analyzed on a

Shimadzu GC-14A gas chromatograph equipped with a flame ionization detector (Shimadzu Corporation, Kyoto, Japan) during measurements 1–3 in 2013; all subsequent gas analyses were performed on a Varian 450 gas chromatograph (Agilent Technologies, Santa Clara, CA, USA). CH₄ fluxes were calculated by linear regression analysis of the change in headspace gas concentration in the chamber versus time following the ideal gas law, assuming ambient pressure and chamber temperature at a given measuring point. Only fluxes with $r^2 \geq 0.80$ were used (applied to >95 % of

measurements). Annual CH₄ emissions for each experimental unit were calculated by linear interpolation between emission of single sampling dates and integrating those over time. Annual CH₄ emissions are likely overestimated because measurements were only conducted during daytime (Van Der Nat et al. 1998) and no flux measurements were conducted during winter and early growing season (Nov–May) when CH₄ emissions were presumably lower.

Solar-radiation and air-temperature data corresponding to the dates and times of our field measurements were acquired from a nearby (<2 km) meteorological tower (Photobiology and Solar Radiation Lab, SERC, MD, USA) on the campus of the Smithsonian Environmental Research Center. Solar radiation (W/m²) was measured using an Eppley model PSP precision spectral pyrometer (The Eppley Lab, Inc., New Port, RI, USA), which measures radiation from 285 to 2800 nm. Temperature was measured with a Vaisala HMP45AC probe (Vaisala, Helsinki, Finland).

Biomass assessment

Biomass was assessed in order to characterize differences in biomass between sites and vegetation zones that have previously been shown to influence CH₄ emissions (e.g. Mozdzer and Magonigal 2013). In June, August, and October 2014, we measured the density and height of *Phragmites* ramets within the *Phragmites*-zone flux collars. *Phragmites* biomass within the flux collars was estimated with an exponential allometric equation derived from 30 plants collected from outside the collars in June and August, corresponding to the gas flux sampling dates (June: $y = 0.6318e^{0.0151x}$; $R^2 = 0.945$, August: $y = 1.0596e^{0.0126x}$; $R^2 = 0.948$). In October 2014 *Phragmites* biomass and dead standing mass were estimated using the August allometric equation. Native vegetation biomass was assessed sampling three replicate clip plots (100 cm²) within each collar. Samples were separated into dead and live material, dried to constant weight at 60 °C, and weighed.

Porewater analyses

To evaluate the influence of porewater chemistry on CH₄ emissions, porewater was extracted from 30 cm below the soil surface at both sites in all three vegetation zones (n = 5) using “sipper” wells (Keller

et al. 2009). To directly compare the two sites, porewater for the different analyses (described below) was always sampled at low tide and within a 2 h period at both sites in all three vegetation zones. On 13 July 2013 porewater was extracted for dissolved sulfide, dissolved CH₄, and salinity analyses. Sulfide and dissolved CH₄ were analyzed within 4 h of sampling following Keller et al. (2012). Briefly, 3 mL of porewater were added to 3 mL of sulfide antioxidant buffer, and the solution was measured with an ion-selective electrode connected to a millivolt meter (ORION Research, Beverly, MA, USA). For dissolved CH₄ analysis, 15 mL of porewater was stripped by introducing a headspace of 15 mL of ambient air and vigorously shaking the syringe for 30 s. The water was then expelled and the 15 mL headspace was analyzed for CH₄ using a Shimadzu GC-14A gas chromatograph equipped with a flame ionization detector (Shimadzu Corporation, Kyoto, Japan). Porewater salinity was measured using a hand-held refractometer. On 22 October 2015 porewater was extracted for sulfate and chloride analyses, following Keller et al. (2009). Porewater samples were fixed with 5 % zinc acetate and filtered through preleached syringe filters (0.45 μm). Filtered samples were measured for SO₄²⁻ and Cl⁻ on a Dionex ICS-2000 RFIC ion chromatography system (Dionex Corporation, Sunnyvale, CA, USA) with an auto sampler. Sulfate depletion was calculated based on the porewater SO₄²⁻:Cl⁻ ratio (Keller et al. 2009).

Mesocosm experiment

In order to isolate *Phragmites*-driven changes in CH₄ emission from other invasion-independent factors, CH₄ emissions were also measured on mesocosms situated in a tidal creek of Kirkpatrick Marsh that were planted with *Phragmites* and native vegetation. The design of the mesocosm experiment has previously been described in Langley et al. (2013) and Mozdzer et al. (submitted to this issue). The mesocosm experiment was originally designed to assess effects of elevation relative to the marsh platform (as a proxy for relative sea level) and treatments of elevated CO₂ and nitrogen (N) fertilization on plant growth. All plants used in this experiment were planted in spring 2010 into 70 cm-deep mesocosms constructed from 10 cm-diameter PVC, filled with commercial sedge peat (Baccto, Michigan Peat Company, Houston, TX,

USA). For the purpose of this study, we only compared CH₄ emissions between *Phragmites*- and *S. patens*-dominated mesocosms set at the highest relative elevation (reference marsh platform (GCREW) +35 cm), which matches best the species composition in the native zones of our two high marsh field sites. For the comparison of CH₄ emissions between native- and *Phragmites*-planted mesocosms, we evaluated CH₄ emissions in the mesocosms grown at ambient CO₂ and N only (n = 4). After two seasons of growth, CH₄-flux measurements were conducted in July 2011. Mesocosms were removed from the tidal creek and placed into 120 L containers filled with tidal creek water corresponding to the mean water level of the respective elevation treatment and left to equilibrate overnight. Clear acrylic chambers (10.2 cm i.d. acrylic tube) were put onto the mesocosms and sealed with a rubber fitting. Headspace gas samples were taken every 20 min over a period of 2 h and analyzed for CH₄ on a Varian 450 gas chromatograph (Agilent Technologies, Santa Clara, CA, USA).

To assess the impact of light on CH₄ emissions, the clear flux chambers were covered in aluminum foil and measurements were made in the dark. The effect of the presence or absence of light was tested on four *S. patens*-dominated mesocosms from the highest elevation (two of which were ambient CO₂/ambient N treatments and two of which were ambient CO₂/N fertilized treatments), and on four *Phragmites*-planted mesocosms, all of which were ambient CO₂/ambient N treatments. Our N treatment did not influence CH₄ emissions from native mesocosms (unpublished data).

Statistical analyses

Factorial repeated-measures ANOVAs were used to test for effects of site, vegetation zone, and time on CH₄ emissions and to test for effects of site and time on *Phragmites* biomass. Factorial ANOVAs were conducted to test for effects of vegetation zone and site on October 2014 biomass (biomass and dead standing mass), and on porewater CH₄, sulfide, sulfate, sulfate depletion, and salinity. One-way ANOVA was used to test for the effect of vegetation type on CH₄ emissions from the experimental mesocosms. Tukey's HSD tests were conducted for pairwise comparisons, and data were log-transformed if Levene's test indicated heterogeneous variances (in situ CH₄ emission-, porewater CH₄-, and porewater sulfide data). A two-

tailed, paired *t* test was used to test for a light/dark effect on CH₄ emissions from the experimental mesocosms. To test for the effect of radiation and temperature on CH₄ emissions from the different vegetation zones and sites, the Homogeneity-of-Slopes GLM procedure was conducted. Linear and non-linear regression was used to further explore significant relations between radiation and CH₄ flux. Statistical analyses were conducted in STATISTICA 10, (StatSoft Inc., Tulsa, OK, USA).

Results

In-situ CH₄ emissions

CH₄ emissions significantly differed between Fox Creek and Kirkpatrick Marsh ($p < 0.01$). Emissions were an order of magnitude greater from the *Phragmites* zone of Fox Creek versus Kirkpatrick Marsh ($p < 0.01$; Fig. 1) However, there were no significant differences in CH₄ emissions between the sites when comparing the mixed- and the native zones ($p > 0.1$ and $p > 0.4$, respectively). CH₄ emissions were higher from *Phragmites*- than from native zones at both sites (Fig. 1). However, this difference in CH₄ emissions between the *Phragmites*- and the native zone was far greater at Fox Creek than at Kirkpatrick Marsh (Fig. 1): At Fox Creek Marsh, CH₄ emissions varied significantly between vegetation zones with emissions from the *Phragmites* zone often exceeding those from the mixed- and the native zone by an order of magnitude ($p < 0.001$; Fig. 1). CH₄ emissions from the *Phragmites* zone were significantly greater every sampling date except June of 2013, whereas CH₄ emissions from the mixed zone were significantly higher than from the native zone only at three sampling dates (Fig. 1). In contrast, at Kirkpatrick Marsh, although CH₄ emissions were also higher from the *Phragmites* zone, this effect of *Phragmites* was only significant at one sampling date (October 2014; Fig. 1).

Sampling date had a significant effect on CH₄ emissions at both marsh sites ($p < 0.001$), and was significantly more pronounced for CH₄ emissions from the *Phragmites* zones at both sites ($p < 0.001$; Fig. 1).

The linear Homogeneity-of-Slopes (HOS) model indicated that solar radiation had a significant effect on

CH₄ emissions ($p < 0.05$) which differed between vegetation zones ($zone \times radiation$, $p < 0.05$), but did not differ between sites ($site \times radiation$, $p > 0.8$; $site \times zone \times radiation$, $p > 0.1$). Solar radiation significantly increased CH₄ flux from *Phragmites* zones (exponential $R^2 = 0.425$; $p < 0.001$), but had no effect on CH₄ flux from the mixed- ($p > 0.05$) and the native zones ($p > 0.4$) of both sites. Also chamber temperature had a significant effect on CH₄ emissions ($p < 0.001$) which differed between vegetation zones ($zone \times temperature$, $p < 0.001$) and also between sites ($site \times temperature$, $p < 0.001$; $site \times zone \times temperature$, $p < 0.001$). Chamber temperature increased CH₄-emissions from the *Phragmites*- (exponential $R^2 = 0.709$; $p < 0.001$) and the mixed zone (exponential $R^2 = 0.589$; $p < 0.001$) of Fox Creek Marsh, but neither influenced CH₄ emissions from the native zone of Fox Creek Marsh ($p > 0.8$), nor CH₄ emissions from any vegetation zone of Kirkpatrick Marsh (all $p > 0.2$).

Chamber temperature was significantly correlated with radiation ($R^2 = 0.577$; $p < 0.001$) and weakly but still significantly correlated with outside temperature as acquired from the meteorological tower ($R^2 = 0.062$; $p < 0.01$). At most sampling dates, chamber temperature was considerably higher than outside temperature ($\Delta T = 8.8 \pm 0.7$ K). However, differently sized chambers, as used for the three vegetation zones, showed no significant difference in ΔT ($p > 0.4$). Based on temperature-CH₄ emission regressions, higher chamber- versus outside temperatures could have caused overestimation of temperature-sensitive CH₄ emissions from the *Phragmites*- and mixed zone of Fox Creek Marsh by 51 ± 36 % and 25 ± 28 %, respectively.

Biomass

Phragmites aboveground biomass was significantly greater at Fox Creek than at Kirkpatrick Marsh ($p < 0.05$; Table 1). Differences in biomass were evident in the height of the plants which were up to 3.85 m at Fox Creek Marsh versus 2.85 m at Kirkpatrick Marsh. At both sites, end of season aboveground biomass was significantly greater in the *Phragmites* zone than the native zone; however, at Kirkpatrick Marsh this result applied to dead standing mass but not to live biomass (Table 1).

Porewater chemistry

Dissolved porewater CH₄ was an order of magnitude higher at Fox Creek than at Kirkpatrick Marsh in all three vegetation zones (Fig. 2). Similarly, porewater sulfide was significantly higher at Fox Creek Marsh (Fig. 2). At both sites, porewater sulfide decreased significantly from the native to the *Phragmites* zone (Fig. 2). Porewater sulfate was higher and sulfate-depletion was marginally lower at Kirkpatrick than at Fox Creek Marsh with no differences between vegetation zones (Fig. 2). Porewater salinity in October 2015 was higher at Kirkpatrick (10.4 ± 0.3) than at Fox Creek Marsh (9.5 ± 0.3 ; $p < 0.05$) with no significant differences between vegetation zones ($p > 0.2$). Porewater salinity in July 2013 was 9.7 ± 0.2 and did not differ between sites ($p > 0.6$) and vegetation zones ($p > 0.7$).

Experimental-mesocosm CH₄ emissions

CH₄ emissions from *Phragmites* mesocosms were higher, but not significantly, than those from native mesocosms ($p > 0.2$; Fig. 3). CH₄ emissions decreased in each case after darkening ($n = 4$) in *Phragmites* (-65 ± 9 %; $p < 0.05$), whereas the opposite was true in native, where CH₄ emissions increased in each case ($n = 4$) after darkening of the flux chamber by 35 ± 15 % ($p < 0.1$).

Discussion

Spatial variability of CH₄ emissions

Our study demonstrates that the effects of invasive species on ecosystem processes such as GHG emissions may be predictable qualitatively but highly variable quantitatively. While *Phragmites* invasion tended to increase CH₄ emissions at both sites, the difference in emissions between native- and invaded zones ranged from dramatic (an order of magnitude) at one site to occasionally significant at a site located nearby. The data illustrate that generalizations cannot always be made with respect to invader-ecosystem processes, as interactions between invader and local abiotic conditions that vary on the order of meters in wetland ecosystems can have a stronger impact on GHG emissions than the invader itself.

Table 1 Aboveground biomass (g m^{-2}) within *Phragmites* gas-flux measuring collars in June and August 2014, as well as aboveground biomass and dead standing mass (g m^{-2}) within *Phragmites*- and native collars in October 2014

Site	Veg. zone	June	August	October live	October dead
Kirkpatrick	Native			61 ± 21^a	64 ± 15^a
	<i>Phragmites</i>	379 ± 184^a	380 ± 149^a	140 ± 149^{ab}	628 ± 200^b
Fox Creek	Native			92 ± 35^a	129 ± 24^a
	<i>Phragmites</i>	1122 ± 280^b	565 ± 120^a	338 ± 76^b	600 ± 166^b

Lowercase letters represent results of a Tukey's HSD test. Values within one column not connected by the same letter are significantly different ($p < 0.05$). Presented are mean values \pm standard deviations ($n = 4$)

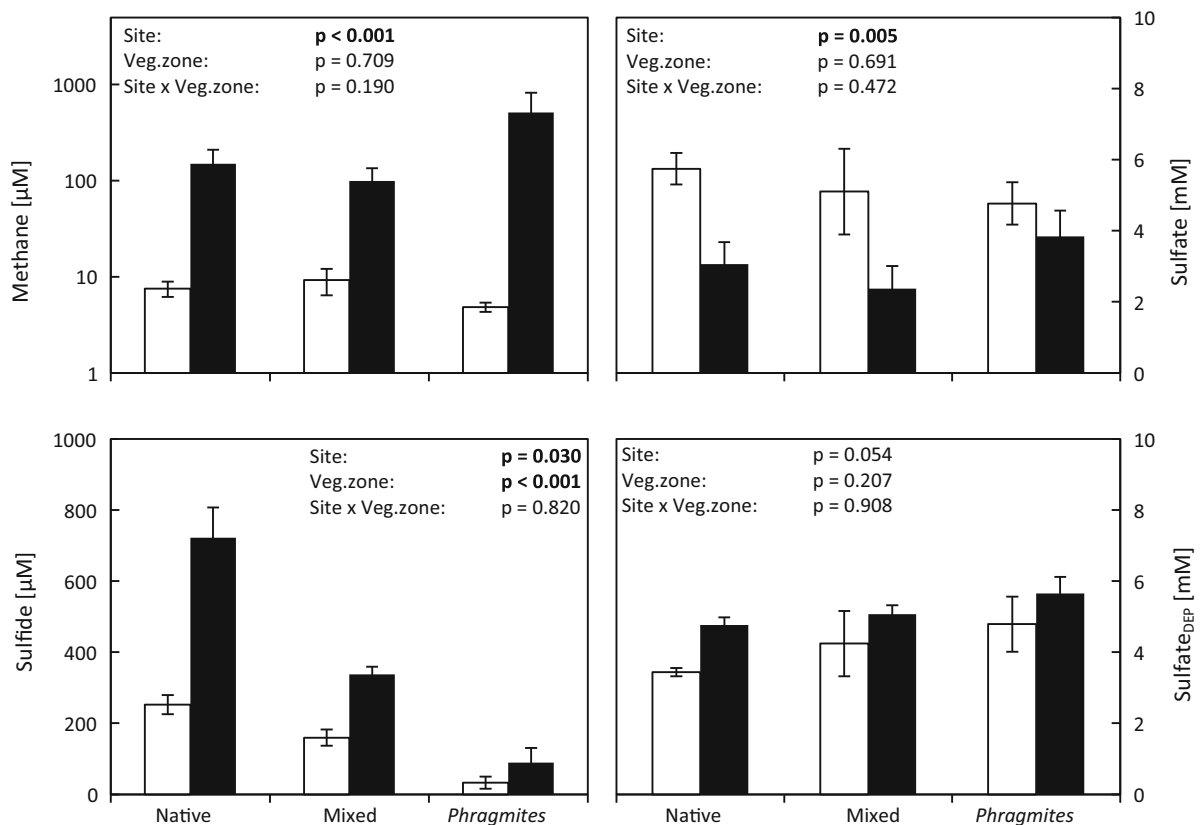


Fig. 2 Porewater CH_4 (μM), sulfide (μM), sulfate (mM) and sulfate depletion (Sulfate_{DEP}, mM) sampled from 30 cm soil depth in three vegetation zones representing different stages of invasion by *Phragmites australis* into native shortgrass

communities at Fox Creek Marsh (black bars) and Kirkpatrick Marsh (white bars). Presented are mean values \pm standard errors; $n = 5$

Porewater data didn't provide evidence that contrasting pre-existing biogeochemical gradients along the invasion transects (e.g. in salinity or [sulfate]) exist between our two sites (Fig. 2) that represent different invasion patterns of *Phragmites* into native shortgrass communities. Consequently, different invasion

patterns don't explain the large differences in CH_4 -emission change after *Phragmites* invasion between our two sites. Greater *Phragmites* biomass at Fox Creek than Kirkpatrick Marsh could help explain the observed differences in CH_4 emissions and CH_4 -emission change after invasion between sites

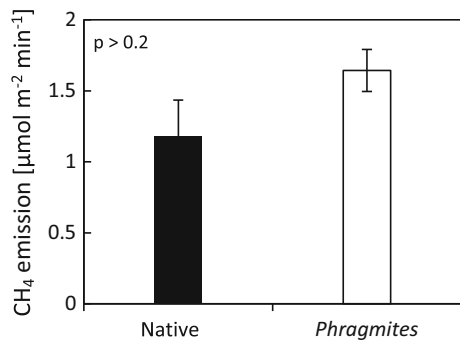


Fig. 3 CH₄ emissions (µmol m⁻² min⁻¹) from native- and *Phragmites*-planted experimental field mesocosms. Presented are mean values ± standard errors; n = 4

(Table 1). However, the fact that differences in biomass were only significant in the early growing season, as compared to order of magnitude differences in CH₄ emissions observed throughout the season, does not support differences in plant biomass as the main driver of the observed differences in CH₄ emissions.

Clear and consistent effects of *Phragmites* on CH₄ emissions were found at our high-porewater CH₄ site only, where dissolved porewater CH₄ concentrations exceeded those at Kirkpatrick Marsh by more than an order of magnitude in all three vegetation zones. Although we measured porewater CH₄ only once, our findings suggest that an increase in CH₄ emissions after *Phragmites* invasion is particularly important in soils with high rates of microbial CH₄ production. In such sites, CH₄ emissions may be enhanced at the earliest stages of *Phragmites* invasion, as illustrated in our mixed zone that contained only few plants clonally integrated into the native zone, accounting for relatively little *Phragmites* biomass (Fig. 1). Thus, the influence of *Phragmites* on CH₄ emissions is likely to vary depending on salinity and other factors that influence tidal marsh CH₄ biogeochemistry.

This conclusion—that relative increase in CH₄ emissions caused by *Phragmites* invasion increases with soil CH₄ production rates—is consistent with results from three New England marsh sites arranged across a salinity gradient: As expected from the well-established inverse relationship between salinity and CH₄ emissions (Poffenbarger et al. 2011), emissions from the native zones increased in the order of polyhaline < mesohaline < oligohaline (Martin and Moseman-Valtierra 2015). In each salinity zone,

Phragmites invasion into native (*S. patens*- or *D. spicata*-dominated) systems increased CH₄ emissions; however, the relative increase in CH₄ emission at the oligohaline site, where CH₄ production was presumably higher, was considerably larger than the relative increase at the polyhaline site, where CH₄ production was presumably lower (Martin and Moseman-Valtierra 2015).

The CH₄-emission rates we measured from the *Phragmites* zone at Fox Creek Marsh are similar to their oligohaline site, while our Kirkpatrick Marsh site is similar to their meso-polyhaline site (Martin and Moseman-Valtierra 2015). Differences in salinity and porewater sulfate (Fig. 2) between our sites could explain certain features of our data, including the relatively high CH₄ emissions and high porewater CH₄ concentrations at Fox Creek versus Kirkpatrick Marsh. However, particularly between the *Phragmites* zones, differences in salinity (<1) and porewater sulfate (Fig. 2) were small, suggesting that mechanisms other than site salinity per se are responsible for differences in the effect of *Phragmites* invasion on CH₄ emissions in the present study.

A potential weakness of any study that uses space-for-time substitution is the possibility that the sites were not identical before the change in question occurred. In both the present study and that of Martin and Moseman-Valtierra (2015) it is possible that *Phragmites* invaded areas of relatively high CH₄ emissions. Such a conclusion is consistent with our mesocosm-study results in which *Phragmites* did not significantly increase CH₄ emissions compared to native species planted in the same soils (Fig. 3). Evidence that higher CH₄ emissions in the *Phragmites* zones were due to the presence of *Phragmites* and not differences in pre-invasion soil biogeochemistry is the fact that porewater CH₄ concentrations were an order of magnitude higher in all Fox Creek Marsh plots compared to all Kirkpatrick Marsh plots. This is a clear example of pre-existing soil biogeochemical differences that might cause different emissions even in the absence of *Phragmites*. However, differences in CH₄ emissions between Fox Creek and Kirkpatrick Marsh were only present between the *Phragmites* zones of the two sites, and not the native zones. Because both sites have supported the same native plant species since at least 1972 and CH₄ emissions from the native zones of both sites were similar despite order of magnitude differences in porewater CH₄, we

conclude that higher emissions in the *Phragmites* zones are due to changes induced by *Phragmites* itself.

While we demonstrated a plant-species effect on CH₄ emissions at both marsh sites (Fig. 1), this result was not confirmed by our experimental data in a mesocosm experiment (Fig. 3). However, there were similarities between the mesocosm- and Kirkpatrick Marsh results that suggest that a longer term mesocosm study may have produced significant effects of *Phragmites* on CH₄ emissions. Namely, mesocosm CH₄ emissions were within the range of in-situ emissions from native areas with similar vegetation in Kirkpatrick Marsh, and likewise *Phragmites* effects on CH₄ emissions in Kirkpatrick Marsh were only occasionally statistically significant.

Temporal variability of CH₄ emissions

Seasonality and the changing influence of plant-mediated effects on ecosystem processes also influence CH₄ emissions. Sampling date had a significant impact on CH₄ emissions from the *Phragmites* zone at both sites, but a less pronounced influence in the native zones (*zone x time* interaction at both sites, $p < 0.001$). This result could be interpreted as a diverging impact of seasonality, such as the time course of biomass development, on CH₄ emissions from different vegetation zones. Similar effects were reported by Martin and Moseman-Valtierra (2015). Although greater *Phragmites* biomass at Fox Creek Marsh could help explain differences in CH₄ emissions between sites, we don't have sufficient biomass data over the course of the season to determine if changes in biomass parameters explain changes in CH₄ emissions over time.

Light-driven convective gas flow significantly influenced CH₄ emissions in *Phragmites* only. The effects of solar radiation differed between vegetation zones, increasing CH₄ emissions from *Phragmites*- but not the native zones. The relationships between radiation and CH₄ emissions we observed in the field were even clearer in the experimental mesocosms planted with *Phragmites*. We interpret the contrasting responses of CH₄ emission from *Phragmites* and native grasses such as *S. patens* to light as a result of differences in mechanisms of gas transport through the different plant species, as previously demonstrated in studies comparing *Phragmites* with species of the genus *Scirpus* (Van Der Nat et al. 1998; Arkebauer

et al. 2001). *Phragmites* is one of few wetland plants known to support light-enhanced convective gas flow, which increases O₂ delivery to the rhizosphere and emissions of CH₄ and H₂S (hydrogen sulfide) to the atmosphere (Mitsch and Gosselink 1993; Brix et al. 1996). Given the lack of convective gas flow, CH₄ emissions are insensitive to light in the *S. patens* dominated community.

As the flux chambers used in this study were not equipped with a cooling system, radiation also led to increases in chamber temperature. CH₄ emissions increased with chamber temperature; however, this was only true in the presence of *Phragmites* (mixed- and *Phragmites* zone) and only at our high-porewater CH₄ site. Different responses of CH₄ emissions between vegetation zones to temperature are consistent with the responses to radiation and can be attributed to the temperature sensitivity of convective gas flow in *Phragmites* (e.g. Brix et al. 1996; Minke et al. 2014). Along with the large differences in relative CH₄-emission change after invasion between our two sites (discussed above), contrasting responses between the sites to temperature indicate that pre-existing biogeochemical site conditions determine the extent to which temperature- and light-sensitive plant traits like convective gas flow can influence GHG emissions from wetland soils.

At most sampling dates, chamber temperature was considerably higher than outside temperature. However, because outside temperature was measured at a nearby meteorological tower and not on site, we cannot precisely determine the extent to which chamber temperature actually differed from outside temperature of the surrounding. Further, we cannot account for potential microclimatic differences between vegetation zones, although those differences are likely to be expected (Báldi 1999). Therefore, it is possible that *Phragmites*-induced changes of the microclimate have an impact on temperature- and humidity-sensitive CH₄ emissions from *Phragmites* stands.

The design of our closed-chamber system limits our ability to separate temperature- from light induced changes in CH₄ emission. Further studies applying improved methodology (as for instance presented in Minke et al. (2014) or Martin and Moseman-Valtierra (2015)) are needed to evaluate the role of seasonal changes in light availability, diurnal (light) effects,

and temperature in order to assess the net impact of plant invasions on GHG emissions from wetlands.

Mechanisms influencing CH₄ emissions after *Phragmites* invasion

Changes in CH₄ emissions after plant invasion in wetland ecosystems must be caused by one of three processes that contribute to net CH₄ emissions: (1) microbial CH₄ production, (2) microbial CH₄ oxidation, and/or (3) plant-supported ventilation of CH₄ directly to the atmosphere, bypassing soil surface CH₄ oxidation. However, there is a small existing literature on the mechanisms by which invasive plants change CH₄ cycling that can be used to develop hypotheses about the mechanisms that are likely responsible for increased CH₄ emissions after *Phragmites* invasion (Mozdzer and Megonigal 2013).

An increase in plant-supported CH₄ production (mechanism 1) does not seem to be an important driver of increased CH₄ emissions in our study. Otherwise we would have expected a stronger plant-species effect on CH₄ emissions from our low-porewater CH₄ site and also from our mesocosm experiment. We do not have soil redox profiles, O₂ profiles, or CH₄ oxidation rate data to address the possibility that *Phragmites* changed CH₄ oxidation rates at the soil surface (mechanism 2). However, such an effect may occur if *Phragmites* invasion increases soil surface elevation as suggested by Rooth et al. (2003), or *Phragmites* increases root O₂ loss in the soil profile (Tanaka et al. 2007). Evidence of increased root O₂ loss is the fact that porewater sulfide concentrations were lower in *Phragmites*-invaded zones (Fig. 2). Increased sulfide oxidation rates are one possible explanation for this pattern because there were no corresponding patterns in porewater sulfate concentration or sulfate depletion across vegetation zones (Fig. 2). However, lower porewater sulfide concentrations in the *Phragmites*-invaded zones can also result from H₂S removal through increased plant ventilation of gases to the atmosphere (mechanism 3).

Higher concentrations of dissolved porewater CH₄ and sulfide, and higher sulfate depletion (Fig. 2) at Fox Creek versus Kirkpatrick Marsh indicate higher rates of anaerobic decomposition in Fox Creek Marsh. As discussed above, the dramatic difference in porewater CH₄ concentrations between the two sites did not translate into differences in CH₄ emissions in the

native zone. In contrast, the presence of *Phragmites* produced dramatic differences in emissions that reflect porewater CH₄ concentrations. Thus, we hypothesize that *Phragmites* stimulates CH₄ emissions primarily via mechanism 3, in which increased plant ventilation routes soil CH₄ past oxidizing soil layers. *Phragmites* has vastly deeper root systems (>1 m deep in our study sites; J. Meschter et al., unpublished data) than the native grasses it is replacing, and can more efficiently transport CH₄ via pressurized ventilation.

GHG-balance implications

If the reported changes in CH₄ emissions from our field sites are primarily *Phragmites*-induced, as our data suggest, *Phragmites* invasion increased GHG emissions by 34 (Global Warming Potential) or 47 (Sustained Global Warming Potential; Neubauer and Megonigal 2015) Mg CO₂-equivalents ha⁻¹ year⁻¹ in our high-porewater CH₄ site, and by 3.3 or 4.7 Mg CO₂-equivalents ha⁻¹ year⁻¹ in our low-porewater CH₄ site (Table 2). However, it is not possible to interpret the impact of *Phragmites* invasion on radiative forcing without also determining whether soil carbon sequestration rates have also increased as one study suggests (Rooth et al. 2003). An increase in soil carbon sequestration of 47 and 4.7 Mg CO₂eq ha⁻¹ year⁻¹ at Fox Creek Marsh and Kirkpatrick Marsh, respectively, would relate to 254 % of the peak aboveground biomass (18.5 Mg CO₂eq ha⁻¹ year⁻¹) at Fox Creek Marsh and 75 % at Kirkpatrick Marsh (Table 1). Even under the assumption of a 3:1 ratio of belowground to aboveground production, it seems unlikely that soil carbon sequestration rates have entirely offset the increase in CH₄ emissions. Future research needs to show if higher rates of biomass production, carbon sequestration and potential reduction in N₂O in *Phragmites* versus native shortgrass communities can counterbalance increases in CH₄ emissions.

Conclusion

In contrast to previous studies that have focused on invader-ecosystem effects on GHG emissions, we found that invader-ecosystem effects are site-specific. We found remarkable differences in total CH₄ emissions and the influence of the invader on CH₄

Table 2 Annual estimates of CH₄ emissions and CO₂-equivalents calculated based on a CH₄- global warming potential (GWP) of 32 and a sustained global warming potential (SGWP) of 45 over a 100-year time horizon (Neubauer andMagonigal 2015) from three vegetation zones representing different stages of invasion by *Phragmites australis* into native shortgrass communities measured in two brackish Chesapeake Bay marsh sites

Site	Type	Annual CH ₄ emission (g m ⁻² year ⁻¹)				GWP-CO ₂ eq (Mg ha ⁻¹ year ⁻¹) Mean	SGWP-CO ₂ eq (Mg ha ⁻¹ year ⁻¹) Mean
		Mean	SD	Min	Max		
Kirkpatrick	Native	3.1	1.8	0.4	5.5	1.0	1.4
	Mixed	4.5	2.7	1.2	8.3	1.4	2.0
	<i>Phragmites</i>	13.5	4.6	6.4	18.7	4.3	6.1
Fox Creek	Native	1.0	0.4	0.6	1.5	0.3	0.5
	Mixed	5.2	2.2	3.2	8.8	1.7	2.3
	<i>Phragmites</i>	105.5	39.3	66.7	164.8	33.8	47.5

emissions at two adjacent marsh sites of similar salinity and species composition. Furthermore, seasonality and changes in temperature and light availability can cause contrasting responses of CH₄ emissions from different vegetation types. Therefore, we suggest that generalizations regarding invader-ecosystem processes should be drawn with caution, as interactions between invader and local abiotic conditions that vary both spatially and temporally on the order of meters and hours, respectively, can have a stronger impact on GHG emissions than the invader itself.

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