11-24-2016

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Author Manuscript

This is a pre-publication author manuscript of the final, published article.

Recommended Citation

Lawrence, Beth A.; Lishawa, Shane; Tuchman, Nancy; Hurst, Nia; and Castillo, Buck T.. Wetland Invasion by Typha×glauca Increases Soil Methane Emissions. Aquatic Botany, 137, : 80-87, 2016. Retrieved from Loyola eCommons, School of Environmental Sustainability: Faculty Publications and Other Works, http://dx.doi.org/10.1016/j.aquabot.2016.11.012

Wetland invasion by *Typha* × *glauca* increases soil methane emissions

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Highlights:

- *Typha* × *glauca* invasion increased CH_4 emissions from experimental mesocosms
- *Typha*-invaded field soils had greater CH_4 production potential than native soils
- Biomass production, soil C, and N were positively correlated with CH_4 emissions
- Large scale invasion by productive macrophytes could alter regional CH_4 fluxes

Abstract

Wetland invasion by monotypic dominant plants can alter the physicochemical and biological properties of soils that affect methane emissions, a potent greenhouse gas. We examined the effects of *Typha* × *glauca* invasion on soil methane using laboratory incubation and controlled mesocosm experiments. *Typha*-invaded soils collected from three Midwestern (USA) wetlands had greater methane production potential during laboratory incubation than soils dominated by native wet meadow vegetation. Ten years post-invasion of native plant-dominated mesocosms, *Typha* increased methane emissions at least three-fold (native: 15.0 ± 10.5 mg CH_4-C m^{-2} h^{-1}, median: 6.1 mg CH_4-C m^{-2} h^{-1}; *Typha*: mean: 45.9 ± 16.7 mg CH_4-C m^{-2} h^{-1}, median: 26.8 mg CH_4-C m^{-2} h^{-1}) under high (+10 cm) water levels, though methane emissions were negligible under low (-10 cm) water levels. Methane emissions were positively correlated with soil carbon, nitrogen, and aboveground biomass, all of which were greater in *Typha*-invaded mesocosms. Together, our data suggest that replacement of large tracts of native wetlands throughout eastern North America with monocultures of invasive *Typha* could alter regional methane emissions.

Keywords: Great Lakes; methane emissions; plant invasion; *Typha*; wetland

1. Introduction

Wetlands provide many beneficial ecosystem services such as flood mitigation, biodiversity, water filtration, and carbon (C) storage (Zedler and Kercher 2004), but they are also key sources of methane, a potent greenhouse gas, with a global warming potential (GWP) 28 times that of CO_2 on a 100-year time horizon (Ciais et al. 2013). A newly developed metric ("sustained-flux global warming potential") suggests that the standardly used GWP may be too conservative however, as it assumes a single pulse emission rather than continuous emissions (Neubauer and Megonigal 2015). Worldwide, wetlands emit 177-284 Tg CH_4 yr^{-1}, accounting for an estimated ~35-50% of the global flux to the atmosphere (Ciais et al. 2013), and the contribution from herbaceous plants to global methane flux is emerging as an import component of global methane flux (Carmicheal et al. 2014).

A primary mechanism by which plants regulate methane emissions from wetlands is by providing the methanogen community with C substrates for anaerobic respiration (Sutton-Grier and Megonigal 2011). Biomass turnover and root exudation provide microbial communities with labile C, as many studies have found greater methane emissions with biomass production (Cheng et al. 2007; Kao-Kniffin et al. 2011; Updegraff et al. 2001; Whiting and Chanton 1993; Zhang et al. 2010). Nitrogen (N) availability can also stimulate methane emissions by enhancing plant productivity (Granberg et al. 2001; Zhang et al. 2010) and/or by directly stimulating the microbial community (Cai et al. 2007; Mozdzer and Megonigal 2013).

Plant invasion by monotypic dominant species can alter both wetland soil physicochemical (e.g., organic matter, N, pH) and biological (e.g., microbial community) properties, which in turn can influence C emissions. Many invaders have a suite of traits, including higher capacity to acquire resources and ability to grow rapidly, which can lead to enrichment of C and N pools (Ehrenfeld

2010; Liao et al. 2008; Vilà et al. 2011). Thus, wetland invasion by productive macrophytes could provide labile C substrates from root exudates and decomposing biomass as well as increased N availability to stimulate methanogenesis in anaerobic sediments.

Invasive hybrid cattail (*Typha angustifolia* × *Typha latifolia*: *Typha* × *glauca*; hereafter *Typha*) is considered one of the most problematic wetland invaders in the Laurentian Great Lakes region (Freeland et al. 2013). *Typha*'s high aboveground biomass production coupled with its relatively slow decomposition rate (due to a prolonged standing dead phase; Davis and Van der Valk 1978; Vaccaro et al. 2009), results in thick accumulations of litter that inhibit light penetration to the soil surface, reduce soil temperatures, reduce native plant species richness and abundance, and increase soil C and N (Farrer and Goldberg 2009; Larkin et al. 2012a; Mitchell et al. 2011; Vaccaro et al. 2009). Surface litter can accumulate rapidly when *Typha* invades; litter mass doubled within 10 years of *Typha* invasion in a Lake Michigan coastal wetland (Mitchell et al. 2011), and soil organic matter increased from <1% to 80% after 60 years of *Typha* invasion in a Lake Huron coastal wetland (Lishawa et al. 2013). *Typha* invasion has also been positively correlated with increased soil microbial biomass and diversity (Angeloni et al. 2006), as well as denitrification rates (Lishawa et al. 2014). Changes in soil microbial communities and the addition of labile C and available N from decomposing *Typha* litter could stimulate methane production in inundated, *Typha*-invaded wetlands.

Great Lakes coastal wetlands are dynamic ecosystems with significant intra- and inter-annual water level variability due to wind-driven seiche events and regional climatic patterns. Great Lakes water levels are predicted to decline (Kling et al. 2003; Angel and Kunkel 2010) as a result of more winter ice-free days, higher summer temperatures (Sousounis and Grover 2002), and evaporation

exceeding precipitation basin-wide (Magnuson et al. 1997; Sellinger et al. 2008). Compared with the last 100 years, the recent low-water period (2001-2013) was of anomalously long duration and low variability (Sellinger et al. 2008), though lake levels rebounded during the 2014-16 growing seasons. Thus, understanding how methane emissions vary under different hydroperiods is critical.

We tested the effects of *Typha* invasion on soil methane using an incubation study of field-collected soils and a controlled mesocosm experiment. During an incubation experiment, we compared the methane production potential of soils collected from *Typha*-invaded and native wet meadow stands from three Midwestern wetlands (USA); we expected greater methane production from *Typha*-invaded soils and that production rates would be positively correlated with soil C and N. To examine methane emissions under experimental conditions, we took advantage of an ongoing mesocosm experiment to compare methane emissions from native and *Typha*-invaded communities under high and low water levels. We predicted that *Typha* would enrich soils with C and N due to greater biomass production and result in greater methane emissions than native species. We also expected high water tables to promote methane due to anoxic soils.

2. Material and Methods

2.1 Incubation Experiment

We incubated field-collected wetland soil from *Typha*-invaded and native-dominated habitats to quantify methane production potential in a laboratory experiment. We collected surface soils from three wetlands in the south-western Great Lakes region (Pheasant Branch, Dane County, WI; 43°7’13” N, 89°29’12.43” W; Gardner Marsh, Dane County, WI; 43°3’18” N, 89°24’14” W; Prairie Wolf Slough, Lake County, IL; 42°12’23” N, 87°51’39” W) that had stands of *Typha* as well as native wet meadow communities. *Typha* spreads via rhizomes and creates dense thickets

with clear boundaries delineating *Typha* and native vegetation zones (i.e., the "invasion front"). At each wetland, we ran transects along the invasion front and collected five samples from *Typha*-invaded areas (>50% of vegetative cover) and native-dominated (*Carex stricta* and *Calamagrostis canadensis* composed >50% of vegetative cover) soils, for a total of 10 composite samples per wetland site. Samples were collected from randomly determined locations 15-30 m perpendicular to either side of the invasion front; at each location, we composited three soil cores (2 cm diameter to 20-cm depth). To reduce the confounding effect of hydrology, we sampled from areas that had similar elevation and water depth. Soil samples were stored in plastic bags at 4°C until further processing.

We removed large (> 2 mm) pieces of organic matter and roots and homogenized samples by hand. We placed 25-35 g of soil into plastic sample cups (125 mL), added 25 mL of distilled water, and stirred with a glass rod. We also dried subsamples to assess their water content gravimetrically, and then pulverized them with a ball grinder to quantify C and N content using a Flash EA 1112 C-N elemental analyzer (CE Instruments, Wigan, UK) at DePaul University.

Sample cups were placed inside 946 mL glass incubation chambers (quart-sized canning jars). Chambers were sealed with lids fitted with rubber septa and flushed with N_2 for five minutes to create anaerobic conditions. We randomly placed sample jars in a dark growth chamber set at 22.5 °C which approximates maximum soil temperatures of wetland soils in the region (Lawrence et al. 2013). Thus, the methane production rates we measured likely represent maximum field values and are considered production "potentials."

We sampled the chamber headspace on five days (day: 3, 7, 17, 22, 35) during the 5 week-long experiment and used the change in concentration over time to estimate CH_4 production potentials

(mg C g dry soil^{-1} day^{-1}). Prior to gas sampling (15 mL), jars were manually swirled for 30 seconds and the headspace was mixed three times with a 15 mL nylon syringe. To maintain atmospheric pressure within the chamber, we injected 15 mL of N_2 immediately after collecting each sample. We stored gas samples in syringes and analyzed CH_4 concentration within an hour of sample collection using an SRI 8610 gas chromatograph with flame ionization detector (SRI Instruments, Torrence, CA, USA) at DePaul University. Rates of CH_4 production were calculated from gas concentration differences between gas sampling periods.

Similar to Morse et al. (2012), we determined concentrations of certified gas standards and estimated the minimum detectable concentration difference (MDCD) for each sample date (Yates et al. 2006, Matson et al. 2009; MDCD= $\mu + (2\theta)$; where μ is the average difference between sample pairs of standard gas analyzed during each analytical run and θ is the standard deviation between sample pairs). We calculated the MDCD on replicate gas standards and used the initial linear portion of CH_4 concentration vs. time to estimate methane production potential. In many replicates, CH_4 concentrations plateaued after day 17 when high concentrations in the headspace likely inhibited additional production; thus we used the change in concentration during the first 3 samplings to estimate methane production potentials.

2.2 Mesocosm Experiment

We tested how soil methane flux differed among two vegetation communities (*Typha* vs. native) under two water levels (low, high) using 20 experimental mesocosms at the University of Michigan Biological Station (Pellston, Michigan, USA; 45°33'30.44"N, 84°40'37.25"W). We summarize pertinent elements of the experimental design here, but see Larkin et al. (2012a) for further details.

In 2003, mesocosms (2-m long, 1-m wide, and 1-m deep) were countersunk into the ground, lined with pond liner, and filled with a hydric soil/sand mixture to approximate nutrient and organic matter concentrations found in a nearby reference wetland (Cheboygan Marsh). Cheboygan Marsh is a ~23 ha lacustrine, open-embayment wetland (Albert et al. 2005) located on the shores of Lake Huron in northern lower Michigan and ~20 km from the Biological Station; the site's invasion by *Typha* × *glauca* has been well documented (Angeloni et al. 2006; Larkin et al. 2012a; Lishawa et al. 2014; Tuchman et al. 2009). All mesocosms (n = 20) were planted during the 2003 growing season with a mixture of 10 native species from 4 genera (*Carex aquatilis*, *C. hystericina*, *C. viridula*, *Eleocharis* spp., *Juncus alpinoarticulatus*, *J. balticus*, *J. nodosus*, *Schoenoplectus acutus*, *S. pungens*, and *S. tabernaemontani*,) at mean densities estimated from the native vegetation zone at Cheboygan Marsh (Larkin et al. 2012a).

In 2004, half of the mesocosms (hereafter referred to as the "*Typha"* treatment) were invaded by planting 16 *Typha* × *glauca* rhizomes and adding ~400 g m^{-2} of the previous season's *Typha* leaf litter collected from Cheboygan Marsh (Larkin et al. 2012a). Similar amounts of leaf litter were collected from the field and added to *Typha* replicates annually during the 2006-2012 growing seasons to simulate a more advanced stage of invasion, as litter density increases both with time since invasion (Mitchell et al. 2011) and *Typha* density (Tuchman et al. 2009) with typical field litter mass values of ~2000 g m^{-2} (Tuchman et al. 2009; Vaccaro et al. 2009). In contrast, uninvaded areas dominated by native sedges and rushes have minimal litter accumulation, typically <500 g m^{-2} (Tuchman et al. 2009). We quantified litter mass in *Typha* replicates in 2012 by collecting all senescent material on the mesocosm soil surface in 16 x 16-cm quadrats, drying, weighing, and scaling to 1 m^2; *Typha* replicates averaged 2114 g m^{-2} ± 169 (1 S.E.) of litter, which was similar to litter mass in areas of Cheboygan Marsh that had been invaded with *Typha* for at least 30 years

(1893 g m^{-2} ± 292 (Lishawa, unpublished results), and to litter densities observed by Vaccaro et al. (2009) in *Typha*-invaded coastal Lake Erie wetlands. In a related study, we also quantified belowground biomass density (roots and rhizomes) in 2013 to 10-cm depth in the *Typha*-invaded mesocosms (0.023 g/cm^3 ± 0.004) and found that it was comparable to estimates from nearby *Typha*-invaded Cheboygan Marsh (0.017 g/cm^3 ± 0.002 (Lawrence, unpublished results). These litter and belowground biomass data indicate that our *Typha* treatments reasonably simulated *Typha*-invaded wetlands that are common in the Laurentian Great Lakes region of North America.

During the 2012 growing season, we estimated methane emissions from two vegetation treatments (native, *Typha*) that had been randomly assigned to either low (-10 cm below soil surface) or high (+10 cm above soil surface) water levels. Mesocosms were subjected to similar water levels (high, low) during the peak of the growing season (June through August) from 2003-2012, and were flooded at the soil surface during the rest of the year (September through May). The water table in "low" treatments was maintained 10 cm below the soil surface by filling mesocosms up daily with low-nutrient water from a nearby well until water spilled out of holes drilled 10 cm below the soil surface. "High" water levels were watered daily as needed to maintain the water level 10 cm above the soil surface. A ground water well supplied low-nutrient water. Each treatment combination (native-low, native-high, *Typha*-low, *Typha*-high) was replicated five-fold for a total of 20 replicates.

2.2.2 Estimating Gas Flux

We used closed-cover chambers to compare soil CH_4 flux between vegetation and water level treatments. Static chambers (white plastic, 3.8 L Letica bucket with the base removed) were placed in the center of each mesocosm without any growing plant stems (but litter was present) and

inserted 10 cm into the soil to maintain a gas-tight seal. To avoid plant mediated transport, any stems that grew into chambers were clipped at the soil surface prior to flux measurements. Chambers were installed several days before the first gas sampling campaign and remained in place throughout the growing season. During sampling campaigns, chambers were capped with air-tight lids fitted with a rubber stopper. A needle inserted into a septa in the chamber lid equilibrated air pressure in the chamber with atmospheric pressure. Sediment disturbance and ebullition of methane was presumed to be minimal, as researchers were outside of the mesocosms during sampling. A 30 mL syringe was used to mix air in the headspace (3×) and draw a 30 mL sample. We collected gas samples at 0, 10, 20, and 30 minutes after lid placement, and transferred them to glass vials that were flushed and then overpressurized with sample gas. Gas samples were analyzed for CH_4 within three days using a Finnigan trace gas chromatograph equipped with an FID detector at the University of Michigan Biological Station. We collected gas samples between 1700 and 2000 hours on July 2nd, July 27th, and August 13th, 2012.

Under ideal conditions during static chamber incubations, gases accumulate or are consumed linearly and flux rates are calculated using the slope of the CH_4 concentration over time and then correcting for the ideal gas law and scaling for the size of the chamber (Livingston and Hutchinson, 1995). To estimate gas flux, the slope of the concentration vs. time line was used when $r^2 > 0.85$. When the accumulation rate was non-linear ($r^2 < 0.85$) and the change in concentration between time intervals was greater than the MDCD, we used the rate during the initial linear portion of the incubation. Incubations during which there was no detectable concentration change were assigned a flux rate of zero. We eliminated three fluxes which had elevated initial concentrations or measurements in which concentrations increased substantially (greater than MDCD) and then decreased substantially, which indicated possible ebullition during sample collection.

2.2.3 Environmental variables

Soil and air temperature, and soil reduction-oxidation potential (redox) were also measured during gas sampling campaigns. Soil redox was measured in a subset of mesocosms (3 replicates per treatment combination, n = 12) using platinum-tipped redox electrodes installed in the soil to 10-cm depth, a calomel reference electrode (Accumet, Fisher Scientific), and a multimeter.

We buried iButton thermochron temperature sensors (iButtonLink, Whitewater, WI) 5-cm below the soil surface in two randomly selected mesocosm for each vegetation and water level treatment combination. We averaged hourly temperatures within treatments to estimate daily temperatures.

Soil cores to 10-cm depth were collected from each mesocosm after the final gas sampling campaign in mid-August 2012, dried at 105°C, and then sieved with a 2 mm standard sieve. Sub-samples were pulverized using a ball mill and analyzed for C and N content on a Costech Elemental Analyzer (Valencia, CA, USA) at the University of Michigan Biological Station. We also estimated soil pH by inserting a standard pH meter into slurries of 15 g of dry soil and 30 mL of deionized water.

2.2.4 Vegetation sampling

During July 2011 the number, height, and species of all stems were measured, and heights were converted to biomass using mesocosm-specific height-to-biomass regressions for each species (M. Freyman and K. Jankowski, unpublished data). We summed these values to estimate total aboveground biomass (g m^{-2}) per mesocosm. In August 2012 we visually estimated the percentage

cover of each species in each 2-m^2 mesocosm. We added the cover values of all native species together to estimate native species cover.

2.3 Statistical analysis

We used two-way Analysis of Variances (ANOVA) to test for differences in soil methane production and soil parameters (%C, %N, C:N) among wetland sites and habitats in the incubation experiment. We made post-hoc pair-wise comparisons among sites with Tukey HSD ($\alpha < 0.05$), and used linear regressions to investigate correlative relationships between soil parameters and methane production potential.

We collected multiple gas samples from each mesocosm during the 2012 growing season, thus we used a repeated measures to compare methane flux among vegetation, water level, and sampling date. Because flux rates were non-normal, we relativized by the minimum value (due to some flux rates being negative or zero) by adding the lowest value + 1 to each flux estimate, and then log-transformed data to improve homoscedasticity. Two-way ANOVAs were used to test for differences between vegetation and water level treatments among environmental variables: soil %C, %N, C:N, pH, redox potential, aboveground biomass, native species cover, and leaf litter cover. We used linear regression analyses to evaluate correlations between soil variables (%C, %N, C:N, redox potential, pH), aboveground biomass, and average methane emissions.

Data were log-transformed when necessary to promote homoscedasticity. Means are presented ± 1 S.E. All statistical analyses were conducted using RStudio Version 0.98.501 (RStudio 2013).

3. Results

3.1 Incubation Experiment

Soil methane production potential varied between habitats ($F_{1,23} = 6.14$, $p = 0.021$) and was greater in *Typha*-invaded stands than native-dominated wet meadows (Fig. 1). Methane production was similar across the three sites ($F_{2,22} = 1.44$, $p = 0.257$; Fig. 1), with no interaction between site and habitat ($F_{2,\ 22} = 0.27$, $p = 0.767$).

Soils from the incubation experiment did not differ between *Typha* and native vegetation zones in C, N, or C:N ratios ($p > 0.05$), so we averaged values across vegetation zones (Table 2). We observed differences across sites in soil C ($F_{2,24} = 447.8$, $p < 0.0001$), N ($F_{2,24} = 20.0$, $p < 0.0001$) and C:N ratios ($F_{2,24} = 492.8$, $p < 0.0001$; Table 2), but found no correlations between measured soil parameters and methane production potential ($p > 0.05$).

3.2 Mesocosm experiment

Repeated measures ANOVA revealed that methane flux differed among vegetation treatments ($F_{1,15} = 4.55$, $p = 0.048$) and water levels ($F_{1,15} = 9.89$, $p = 0.007$), but not among sampling dates ($F_{2,15} = 1.11$, $p = 0.353$). Two- and three-way interactions were not significant ($p > 0.05$). Across water levels and sampling dates, soils from *Typha*-invaded mesocosms (mean = 21.5 ± 8.6 mg CH_4-C m^{-2} h^{-1}; median = 2.3) emitted more methane than those dominated by native species (mean = 0.4 ± 5.5 mg CH_4-C m^{-2} h^{-1}; median = 0.0). Inundated soils from the high water level treatment had much larger methane fluxes (mean = 29.7 ± 10.1 mg CH_4-C m^{-2} h^{-1}; median = 15.3) than those in the drier low water levels, which did not emit methane (-3.8 ± 3.3 mg CH_4-C m^{-2} h^{-1}; median = 0.0). Under high water levels, average methane emissions from *Typha*-invaded soils (46.0 mg CH_4-C m^{-2} h^{-1} ± 16.7; median = 26.8) were three times greater than native soils (15.0 mg CH_4-C m^{-2} h^{-1} ± 10.5; median = 6.1; Fig 2).

Average daily soil temperatures (± S.D) for the vegetation and water level treatments were: native-low: 22.0°C ± 1.6, native-high: 21.0°C ± 1.1, *Typha*-low: 20.6°C ± 1.2, *Typha*-high: 20.2°C ± 1.1.

Typha-invaded soils were richer in C ($F_{1, 16}$ = 15.8, p = 0.001) and N ($F_{1, 16}$= 11.3, p = 0.004) than native vegetation (Table 1), but C:N ratios, soil pH, and redox potential did not differ between vegetation treatments (p > 0.5). Redox measurements did not differ significantly among sampling dates, so data were averaged across sampling dates. Soils subjected to high water levels had greater C ($F_{1, 16}$ = 5.9, p = 0.027), lower pH ($F_{1, 1 6}$ = 8.8, p = 0.009), and lower redox ($F_{1,8}$=132.9, p < 0.0001) compared to low water levels (Table 1). Water level treatments had similar soil N and C:N ratios (p > 0.1). There were no significant interactions (p > 0.05) between vegetation and water level treatments for any of the soil parameters tested.

Typha-invaded mesocosms had twice as much aboveground biomass (1104 g m^{-2} ± 89) than native treatments (549 g m^{-2} ± 47; $F_{1,16}$= 35.72, p < 0.001), with *Typha* stems contributing over 80% of the aboveground biomass (897 g m^{-2} ± 91). High water levels tended to have more aboveground biomass than low water levels (924 g m^{-2} ± 134 vs. 730 g m^{-2} ± 86; $F_{1,16}$= 4.35, p = 0.054). *Typha*-invaded mesocosms also had less cover by native species than native treatments (15.6% ± 0.9 vs. 26.8% ± 2.9; $F_{1,16}$= 7.6, p = 0.014).

Several parameters were correlated with average mesocosm CH_4 flux (averaged across three sampling dates); soil %C ($F_{1,18}$= 5.58, p = 0.030; Fig. 3a) and soil %N ($F_{1,18}$= 4.57, p = 0.047; 3b) were positively associated with CH_4 flux, and redox potential was negatively associated with CH_4 flux ($F_{1,11}$ = 5.30, p = 0.044; Fig. 3c). Methane emissions were not correlated with soil pH or C:N ratio (p > 0.10). CH_4 flux was also positively correlated with aboveground biomass ($F_{1,18}$= 4.43, p = 0.049; Fig. 3d).

4. Discussion

Wetland invasion by productive macrophytes may promote methanogenesis by increasing the availability of C sources via root exudation, biomass turnover, and litter input (Whiting and Chanton 1993) and/or by altering the methanogen community. We observed greater methane production potential of field-collected soils from *Typha*-invaded than native sedge meadow soils. In an experimental mesocosm study, we observed a three-fold increase in soil methane emissions when *Typha* × *glauca* invaded native-dominated wetland soils. Together, our results suggest that *Typha* invasion increases methane production relative to native-dominated marshes in the Great Lakes region.

In our study, aboveground biomass doubled with *Typha* invasion and was positively correlated with methane emissions. This corroborates several recent studies (Cheng et al. 2007; Mozdzer and Megonigal; Zhang et al. 2010) that have found greater productivity and methane emissions with wetland invasion by dominant macrophytes. In Chinese coastal marsh mesocosms, greater biomass and higher stem density of invading *Spartina alterniflora* were correlated with increased methane emissions compared to native communities dominated by *Phragmites australis* or *Suaeda salsa* (Cheng et al. 2007; Zhang et al. 2010). Increased methane emissions were observed from an invasive vs. native strain of *P. australis* in North America; the invasive strain had greater plant density, root mass, and leaf area than the native lineage, which correlated with greater CH_4 emissions (Mozdzer and Megonigal 2013). Atmospheric CO_2 enrichment increased biomass production of several *Typha* species (Kao-Kniffin et al. 2011; Sullivan et al. 2010), which was positively correlated with methane flux from *Typha angustifolia*, one of the parental species of *T.* × *glauca* (Kao-Kniffin et al. 2011).

Our work suggests that *Typha* invasion increases soil methane emissions because it is more productive than the native species it replaces, but it is possible that elevated greenhouse gas emissions are offset by enhanced soil C sequestration. Similar to several studies in Great Lakes coastal wetlands (Farrer and Goldberg 2009; Tuchman et al. 2009; Lishawa et al. 2010), we observed soil %C more than doubled in *Typha*-invaded mesocosms relative to native plant-dominated controls, though our litter additions to the *Typha* treatment likely elevated soil C . To simulate a more advanced stage of *Typha* invasion under controlled soil and water levels, we added *Typha* litter, which is the primary mechanism by which *Typha* invasion alters wetland communities (Farrer and Goldberg 2009; Larkin et al. 2012a; Vaccaro et al. 2009). After eight years of litter additions, mesocosm litter densities were similar to those observed in a coastal marsh invaded for more than 30 years with *Typha* (Lishawa, Unpublished results); however, mesocosm soil C values were lower than two of the three field soils we sampled (~5% vs. 10-15%). While increased C sequestration in wetland soils may be desirable to mitigate climate change, a full greenhouse gas analysis is required to determine how invasion by *Typha* and other productive macrophytes influences net radiative balance. Currently, it is unclear what proportion of methane emissions are derived from labile C released from decomposing litter vs. root exudates. If methane emissions are driven predominantly by labile C from decomposing litter, it is possible that aboveground harvesting of *Typha* and its litter for restoration and biofuel production (Lishawa et al. 2015) could reduce methane emissions from invaded wetlands, though field tests are warranted.

Similar to several field investigations of *Typha* invasion (Farrer and Goldberg 2009; Lishawa et al. 2010; Tuchman et al. 2009), we observed elevated soil N in *Typha*-invaded mesocosms, which was positively correlated with methane emissions. While in the current study we only measured soil N and not plant available inorganic N, a companion study conducted by Lishawa et al. (2014)

measured greater NH_4^+ in our *Typha*-invaded than native mesocosms, and observed greater NH_4^+ and NO_3^- in *Typha*-invaded than native-dominated areas of a local marsh. Plant invasion tends to increase soil N availability (Liao et al. 2008), which may indirectly promote methane emissions by increasing plant productivity. Comparison of our findings with fertilization studies should be done cautiously, but opportunistic wetland invaders often have stimulated growth responses to nutrient enrichment that could further enhance methane emissions. For example, Zhang et al. (2010) observed a 70% increase in methane emissions with N fertilization from the invading *Spartina alterniflora* relative to native *S. sueda* due to increased belowground biomass production and exudation of labile C substrates to the rhizosphere. *Typha* is competitively superior to native wetland species in the presence of excess nutrients (Woo and Zedler 2002), due to higher N uptake capacity and retention (Larkin et al. 2012b), suggesting that nutrient-rich runoff in agricultural and urban watersheds could further increase methane emissions by stimulating *Typha* productivity, though experimental tests are necessary to confirm this.

We used an experiment to test the effect of *Typha* invasion on soil methane flux by manipulating water levels and plant community composition using mesocoms that had soil conditions that were initially identical. Differences in hydrology and/or soil type are often confounded between vegetative communities (Lishawa et al. 2010), making it challenging to isolate the effect of *Typha* invasion on soil methane emissions *in situ*. Despite this, we attempted to quantify field estimates of methane emissions from *Typha*-invaded and native stands to complement our incubation and mesocosm data, but due to low water levels throughout the region in 2012 and 2013, we did not measure any detectable methane fluxes during three sampling campaigns. In the mesocosms, we quantified soil methane flux from plant-free chambers, so our estimates do not account for plant transport of methane through aerenchyma, which may account for a large proportion of the

methane emitted from wetlands (Chanton et al. 2002, Charmichael et al. 2014). Plant stems can enhance methane transport via aerenchyma by creating a conduit from anoxic soils to the atmosphere, allowing methane to avoid oxidated surface soils (Strom et al. 2005). For example, McInerney and Helton (2016) observed that the presence of *Typha* species increased CH_4 flux relative to unvegetated plots. However, our median estimates of methane flux from inundated *Typha*-invaded soils were higher than those reported by Yavitt (1997; 26.8 vs. 14.3 mg m^{-2} h^{-1}), who also examined soil-atmospheric (i.e., excluded plant stems) methane emissions from *T. latifolia* stands with mineral soil, and higher than mean methane emissions from several constructed wetlands dominated by *Typha* (0.15 – 3.4 mg m^{-2} h^{-1}; reviewed by McInerney and Helton 2016). Large inputs of litter associated with our *Typha* treatment may have resulted in rapid decomposition and CO_2 production, which in conjunction with stably flooded conditions could have resulted in selection for and enrichment of methanogens beyond what might be expected in the field.

Plant invasion can significantly alter soil microbial community structure and function (Angeloni et al. 2006; Kao-Kniffin and Balser 2007; Kourtev et al. 2002); in wetlands, plant invasion may modify the activity of methanogen and methanotroph communities by altering the availability of C and N sources, modifying the concentration of oxygen in the rhizosphere, or altering soil pH. In our incubation study, we found greater methane production potential from *Typha*-invaded soils, possibly due to differences in microbial communities. Neither soil C or N were correlated with methane production potential, though soil C and N are not necessarily representative of the labile pools of C and N; parameters such as acetate or H_2 (limiting methanogenic substrates) would likely better predict methane production. Despite our efforts to minimize the confounding effects of hydrology during field sampling, it is possible that *Typha* soils were more frequently inundated than native soils, and thus harbored more methanogens. Quantifying methanogenic and

methanotrophic communities and isotopic fluxes ($^{13}CH_4$ vs $^{12}CH_4$) could elucidate the mechanisms underlying increased methane production with *Typha* invasion.

Typha is rapidly displacing native wetland communities in the Great Lakes region (Freeland et al. 2013; Frieswyk and Zedler 2007; Lishawa et al. 2010; Tuchman et al. 2009; Tulbure et al. 2007; Vaccaro et al. 2009), as it is able to spread rapidly (4-5 m/year; Boers et al. 2007; McDonald 1955) via rhizomatous growth and quickly dominate a wetland (Smith 1967; Tulbure et al. 2007). Our data suggest that the replacement of large tracts of diverse wetlands with monocultures of this highly productive macrophyte could alter the net radiative forcing of wetlands at a regional scale, given that soil methane emissions were at least three-times greater from *Typha*-invaded than native plant-dominated mesocosms. Atmospheric enrichment of CO_2 (Kao-Kniffin et al. 2011) and N-rich runoff (Mozdzer and Megonigal 2013) may further increase methane emissions from *Typha*-invaded wetlands, though experimental tests are necessary.

Acknowledgments

We thank Mike Grant (University of Michigan Biological Station) and Margaret Workman (DePaul University) for assistance with chemical analysis, and Kim Greene, Emily Tuchman, and Jesse Albert for assistance with watering and data collection. This research was supported in part by a National Science Foundation award (AGS-1262634) to M. Carroll and D. Karowe which provided an REU to N. Hurst and B. Castillo, and a Great Lakes Restoration Initiative grant from the US Environmental Protection Agency (GL-00E00545) awarded to S. Lishawa, D. Albert, and N. Tuchman.

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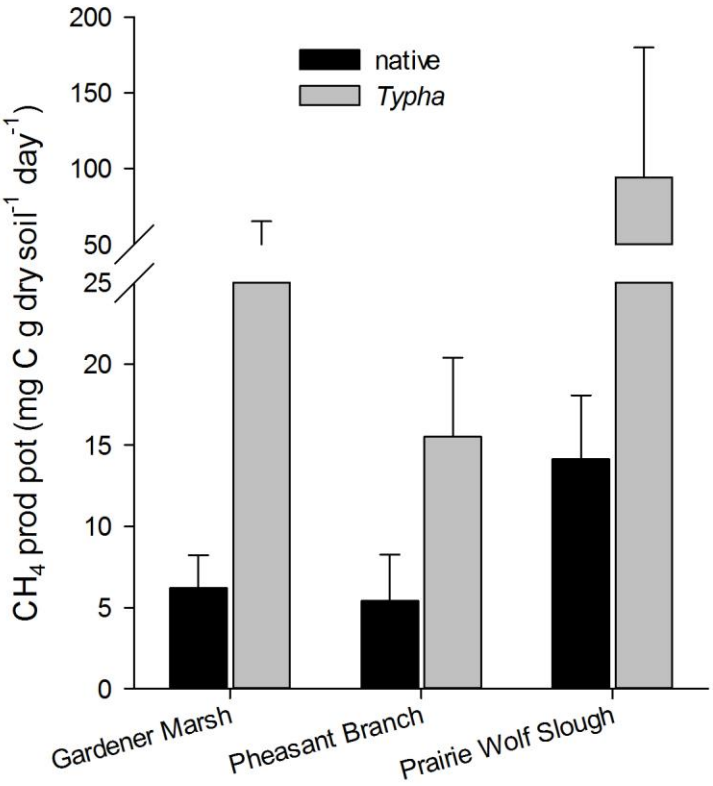
Figure Captions

Fig. 1 Soils collected from *Typha*-invaded stands had greather methane production potential than native wet meadows in three Midwestern wetlands (mean ± 1 SE; n = 5). Note: break and change in y-axis scale, and units differ from mesocosm emissions rates



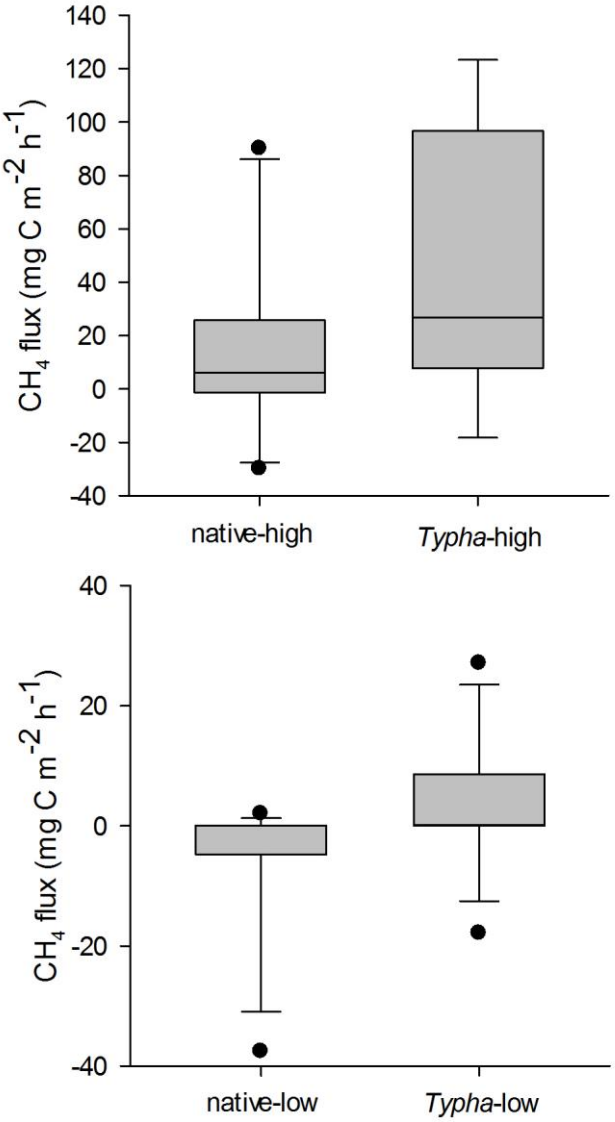


Fig. 2 Methane emissions between *Typha* and native treatments subjected to A) high water (+10cm) and B) low water levels (-10cm). Boxes show median and interquartile range. Data points outside the 10^{th} and 90^{th} percentile whiskers are identified.

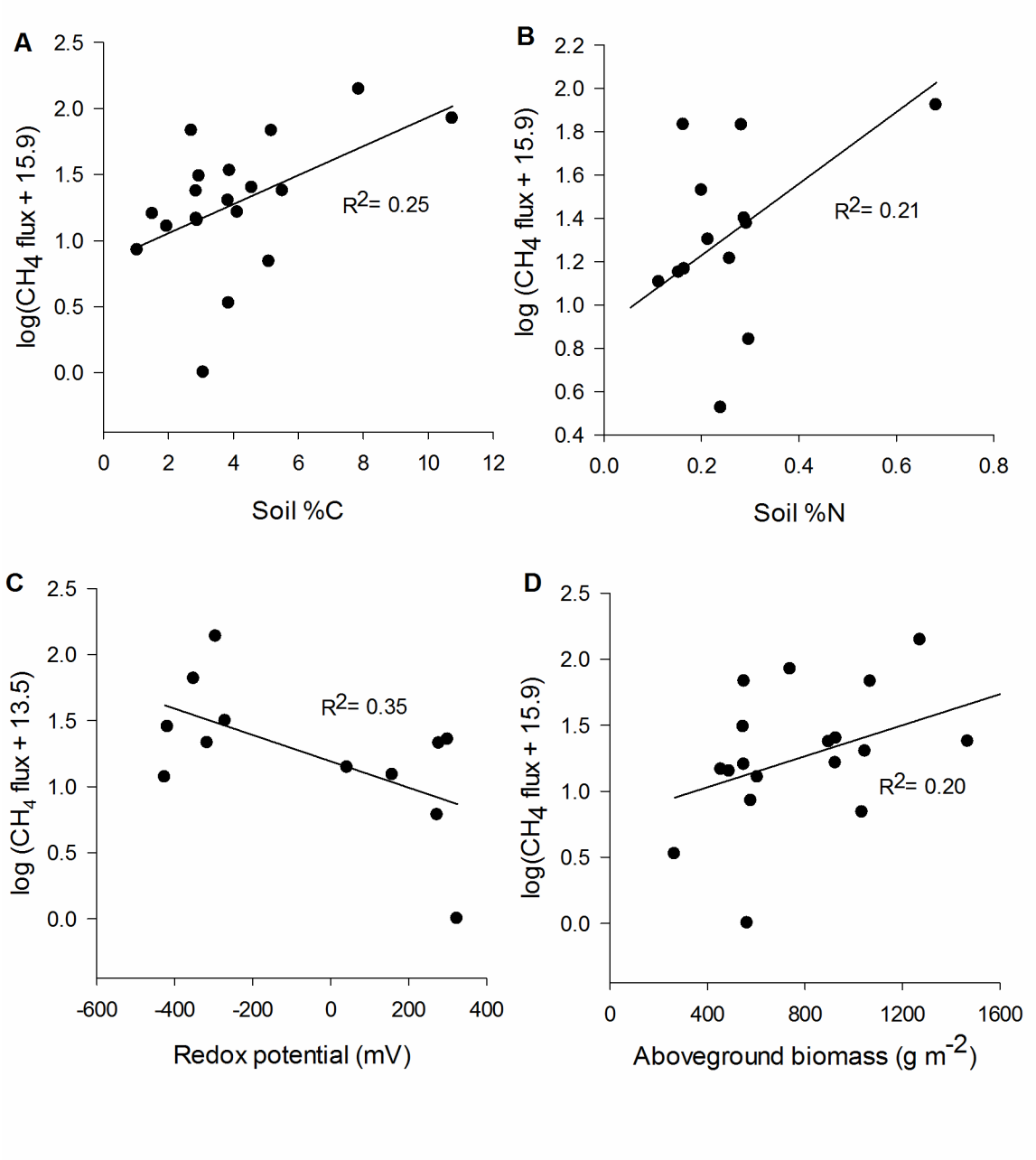


Fig. 3 Correlations between average mesocosm methane flux rates (mg CH_4-C m^{-2} h^{-1}; data were transformed by adding 1 + minimum flux value observed and then log-transformed) and A) soil % carbon, B) soil % nitrogen, C) redox potential (mV), and D) aboveground biomass (g m^{-2})

Tables

Table 1 Average (± 1 S.E.) soil parameters from the 2012 mesocosm experiment. For each parameter (%C, %N, C:N, pH, redox), treatments with non-overlapping letters differed significantly from each other after Tukey HSD post-hoc comparisons ($\alpha = 0.05$)

		%C	%N	C:N	pH	Redox (mV)
Vegetation						
	native	$2.65^{a} \pm 0.28$	$0.15^{a} \pm 0.02$	$17.85^{a} \pm 0.32$	$6.94^{a} \pm 0.10$	$-73^{a} \pm 148$
	Typha	$5.37^{b} \pm 0.73$	$0.31^{b} \pm 0.45$	$17.67^{a} \pm 0.45$	$6.91^{a} \pm 0.11$	$-43^{a} \pm 118$
Water level						
	high	$4.84^{A} \pm 0.83$	$0.27^{A} \pm 0.05$	$18.20^{A} \pm 0.38$	$6.74^{A} \pm 0.09$	$-346^{A} \pm 26$
	low	$3.18^{B} \pm 0.43$	$0.19^{A} \pm 0.03$	$17.31^{A} \pm 0.35$	$7.11^{B} \pm 0.09$	$230^{B} \pm 44$

Table 2 Average soil parameters from the three sites tested for methane production potential. Soils did not differ between *Typha* and native vegetation zones, but differed across sites. Sites that do not share a common letter differed significantly from each other after Tukey HSD post-hoc comparisons ($\alpha = 0.05$)

	% C	% N	C:N
Gardner Marsh	$14.92^{a} \pm 0.25$	$0.69^{a} \pm 0.02$	$21.71^{a} \pm 0.44$
Pheasant Branch	$10.13^{b} \pm 0.03$	$0.96^{b} \pm 0.03$	$10.56^{b} \pm 0.27$
Prairie Wolf Slough	$3.43^{c} \pm 0.23$	$0.67^{a} \pm 0.05$	$5.32^{c} \pm 0.41$