1 **Title:** Effects of transient *Phragmites australis* removal on brackish marsh greenhouse gas fluxes

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Abstract

Phragmites australis is a common invasive reed of North American coastal marshes, and efforts to control or eradicate it often are included in coastal marsh restoration efforts. While much research has tested impacts of *P. australis* removal on plant and faunal communities, less is known about biogeochemical responses to *P. australis* removal. Since coastal marshes are valued for their robust carbon sequestration, understanding the effect of *P. australis* removal on marsh carbon cycling dynamics is important. Temporary *P. australis* aboveground biomass clearing conducted as part of a restoration effort provided an opportunity to evaluate changes in fluxes of the greenhouse gases (GHGs) carbon dioxide (CO₂) and methane (CH₄) during *P. australis* removal and recovery. In Experiment 1 (2014 growing season), GHG fluxes were compared between a *P. australis* stand cleared mechanically and recovered within months of initial removal and an uncleared stand in the same marsh system. CO₂ uptake increased dramatically in the cleared stand as *P. australis* regrew, but CH₄ emissions remained unchanged, demonstrating that *P. australis* did not directly contribute to CH₄ emission. In Experiment 2 (2015 manipulations), to test mechanisms of *P. australis*' impact on GHG fluxes, fluxes (light and dark) were compared between unimpacted *P. australis* plots, cut *P. australis* plots with litter, and cleared *P. australis* plots without litter. *P. australis* cutting (independent of litter removal) resulted in increased CO₂ and CH₄ emissions. Recovery of *P. australis* directly drove the rapid recovery of CO₂ uptake, and did not increase (and possibly attenuated) CH₄ emissions. Results of this study suggest that at this site, *P. australis* removal, in the absence of native vegetation recovery, may exacerbate GHG emission of coastal marshes in the short term, and that longer-term impacts warrant investigation.

44 **Keywords:** carbon dioxide, methane, ecosystem services, invasive species, restoration

1. Introduction

Phragmites australis (Cav.) Trin. ex Steud. is a well-documented invader of coastal wetlands in North America. Since the plant is more sensitive than native species to high soil salinity and sulfide concentrations, it does not typically encroach into regularly-inundated lower marsh elevations. However, it may establish itself under conditions of minimal seawater influence (Bart and Hartman, 2003) such as lowered soil salinity and sulfide concentrations associated with restricted tidal flow (Chambers et al., 2012). As a result, tidally restricted marshes often become dominated by *P. australis* as it outcompetes native species, and are transformed into potentially highly productive (Windham, 2001) but low-diversity (Silliman and Bertness, 2004) systems.

Coastal salt marshes store C at rates greater even than terrestrial forests (Mcleod et al., 2011) due to their high productivity (Mcleod et al., 2011) and low decomposition rates (Mitsch and Gosselink, 2000). In addition, carbon dioxide (CO₂) uptake is substantial during the growing season due to high plant productivity and photosynthetic uptake, while methane (CH₄) emissions are small if seawater influence is sufficient (Poffenbarger et al., 2011). *P. australis* invasion may alter coastal marsh C cycling, and therefore the ecosystem service of GHG uptake and C sequestration. *P. australis* is highly productive (Windham, 2001) and is associated with greater CO₂ uptake relative to native coastal marsh vegetation (Martin and Moseman-Valtierra, 2015). *P. australis* may alter rhizosphere conditions in ways that enhance (provision of C substrates) soil CO₂ (Mueller et al., 2016b) and CH₄ emission. Conversely, *P. australis* may inhibit methane emission by the mechanism of root zone oxygenation (Armstrong et al., 2006; Colmer, 2003; Lovell, 2005). Due to its large internal ventilation system, the plant is known to

conduct products of root zone microbial metabolism (CO_2 , CH_4) into the atmosphere via humidity- and Venturi-induced convection (Armstrong et al., 1996; Colmer, 2003). Therefore, *P. australis* invasion likely increases wetland CH_4 emission, as has been demonstrated by recent work in coastal systems (Martin and Moseman-Valtierra, 2015; Mueller et al., 2016a). This may be viewed as motivation for controlling it in coastal marsh ecosystems.

A variety of control measures are used to reduce *P. australis* cover as part of restoration, and some may affect coastal marsh GHG fluxes. In some instances, tidal flow restoration is used to render soil conditions unfavorable for *P. australis* and therefore shift species assemblages to native marsh perennials (Chambers et al., 2012). Tidal flow restoration is likely to have the secondary effect of decreasing CH_4 emissions from wetlands, but may substantially diminish CO_2 uptake if *P. australis* cover is reduced and native vegetation fails to recolonize. Methods (sometimes used in combination with tidal flow restoration) for *P. australis* removal commonly include herbicide application and less effective mechanical methods such as mowing.

Mechanical methods may stimulate an increase in *P. australis* shoot density (Hazelton et al., 2014), a phenomenon which has potential to alter plant-mediated impacts to GHG fluxes. *P. australis* clearing results in the presence of abundant litter on the marsh surface. Detrital leaf litter plays an important role in coastal marsh food webs as a substrate for decomposers (Teal, 1962). Along with edaphic conditions including soil moisture, pH, and redox potential, organic C availability is a control on soil microbial processes that drive CO_2 and CH_4 production. A study of effects of organic amendments (leaf litter and compost) on CO_2 and CH_4 production potential found significant increases in both gases with both amendments (Morrissey et al., 2014). Organic C inputs such as plant root exudates and litter may provide C sources that are

more labile than organic matter available in soil, or may “prime” soil for enhanced decomposition rates (Kuzakov, 2002; Mueller et al., 2016b). Litter may also alter abiotic conditions, such as lowering soil temperature by shading and increasing soil moisture by attenuating evaporation effects.

Research testing effects of *P. australis* control and eradication on coastal marsh ecosystem functions has included monitoring vegetation (Buchsbaum et al., 2006; Chambers et al., 2012; Smith and Warren, 2012) and faunal (Dibble et al., 2013; Gratton and Denno, 2005; Raposa and Roman, 2003, 2001; Roman et al., 2002) responses. However, fewer studies have tested effects of *P. australis* removal on coastal marsh biogeochemistry (Aldred et al., 2016).

A temporary clearing of *P. australis* aboveground biomass conducted as part of a restoration effort provided an opportunity to evaluate changes in GHG fluxes during *P. australis* removal and recovery and to test impacts of plot-scale manipulations of aboveground biomass and/or plant litter on GHG fluxes. Specifically, objectives were as follows: (1) to compare GHG fluxes over the course of a growing season between a *P. australis* stand recently subjected to mechanical clearing and an unimpacted stand within the same marsh system and (2) to test effects of *P. australis* removal and litter clearing on GHG fluxes (measured in light and dark).

It was hypothesized that *P. australis* removal would cause a shift from photosynthetic CO₂ uptake to emission and that clearing litter would decrease decomposition and therefore CO₂ emission relative to uncleared emissions. *P. australis* regrowth was expected to increase CH₄ emission, and clearing to decrease CH₄ emission, given known gas transport via plant tissues from soils to the atmosphere. Clearing leaf litter was hypothesized to decrease emission of CH₄ due to removal of a C substrate for methanogenesis.

2. Methods

2.1 Study Site

Round Marsh (Figure 1), a 27.1 ha marsh complex owned by the town of Jamestown, Rhode Island and the Rhode Island Audubon Society, was the site of a restoration project and this study. Vegetation at the site is characteristic of New England salt marshes; the high marsh is dominated by *Spartina patens* and *Distichlis spicata*, and low marsh vegetation consists primarily of *Spartina alterniflora*. Tidal flow is restricted to the eastern part of Round Marsh by a road with a small culvert bisecting the marsh, and historic manmade channels connecting the marsh's eastern reaches to the main creek have become clogged. These conditions have impeded tidal inundation and freshwater drainage from the marsh surface. Increased surface freshwater pooling and vegetation dieback in the high marsh zone, and progressive invasion of *P. australis* in recent years, have been attributed to these hydrologic conditions (Anne Kuhn and Wenley Ferguson, personal communication). Based on surveys performed by Save The Bay in their summer 2012 and 2013 statewide salt marsh assessment, the eastern portion of Round Marsh was targeted for restoration. Restoration work at the site included dredging the clogged channel that runs through the eastern *P. australis* stand, digging network of ditches to promote drainage and tidal exchange, and mulching *P. australis* using low-impact equipment with the aim of decreasing its extent and density and allowing native vegetation to recolonize. No herbicides were used as part of this *P. australis* management.

Figure 1. Study site (Round Marsh) with *P. australis* reference and restored stands.

Two *P. australis* stands, the stand on the far eastern side of the marsh where mulching was performed (hereafter “restored stand”) and a smaller, unimpacted stand on the northern edge of the marsh (hereafter “reference stand”), were examined (Figure 1). The restored stand was approximately 0.66 ha in extent, and the reference stand was about 0.05 ha. The restored stand abutted a forested freshwater swamp to the southeast and the reference stand was situated on the north edge of the marsh south of agricultural fields and a band of woody shrubs. Efforts to

promote hydrologic reconnection, including channel excavation in the restored stand and ditch excavation (close to both stands) were performed with the aim of promoting freshwater drainage and tidal inundation. Soils in both stands consist of mucky peat. Over the course of the experiment, the two stands were observed to flood only during one exceptionally high tide in August 2014 (Martin, personal observation).

2.2 Experimental Setup

A mensurative comparison of GHG fluxes and edaphic conditions between the restored (n=6) and reference (n=6) stands (Experiment 1) was conducted at Round Marsh during summer 2014. The first cutting of the restored *P. australis* stand, as well as excavation of the main channel running through it (Figure 1) and ditching, took place in late March and early April 2014. Within a week of mulching, the reference stand was selected based on similarity in edaphic conditions (soil temperature, moisture, surface salinity) (Table 1) and hydrology to the restored stand. In each stand, PVC collars to support chambers for GHG flux measurements were installed at least 2 weeks prior to the first set of measurements and were left intact for the duration of each experiment to avoid soil disturbance. Six collars were installed at least 15 m apart within each of the reference and restored stands. Collars were treated as experimental units for edaphic conditions, pore water and vegetation measurements. On a monthly basis beginning in May and ending in late August 2014, GHG fluxes (CO₂ and CH₄) and soil conditions (moisture, temperature, oxidation-reduction (redox) potential and surface salinity) were measured. Pore water sulfide concentration was determined for May, July and August. Vegetation characteristics (stem density and average height) were measured during the active growing season (June and July).

During winter 2014-2015, the restored stand was mulched for a second time, and more extensive ditching was added to the existing network based on observed surface water pooling in the high marsh adjacent to the *P. australis* stand. A second experiment (Experiment 2), performed during summer 2015 in the restored stand, tested responses of GHG fluxes to two treatments: *P. australis* cutting alone and *P. australis* cutting with litter cleared. In May 2015, 3 treatments (each 20 m²) were established in the restored stand. *P. australis* was left unimpacted in one plot and cut by hand at the soil surface in the two others. In one of the cut plots, *P. australis* litter was removed by thorough raking, and the other had litter left in place after cutting. New shoots were clipped if needed in cut and cleared plots on a biweekly basis for the duration of the experiment. Treatment plots will be referred to hereafter as “control”, “cut”, and “cleared”. Four PVC collars to support chambers for GHG flux measurements were placed at random and installed in each plot at least 2 weeks prior to May measurements and were left intact for the duration of the experiment. Collars were treated as experimental units and were used as locations for edaphic condition measurements, pore water collection and vegetation measurements. Measurements of GHG fluxes (CO₂ and CH₄), edaphic conditions (soil temperature, moisture, redox potential, surface salinity, pore water salinity), pore water chemistry (sulfide and ammonium concentrations), and vegetation characteristics were performed on 4 occasions: once in May as a pre-treatment baseline to test for uniform conditions between the plots prior to application of treatments, and on 3 occasions beginning about 1 month after treatment application (1 in June, 2 in July). On the final measurement date, light and dark GHG flux measurements were performed on the control and cut plots to separate plant (photosynthetic) and soil microbial respiration effects on CO₂ fluxes. To test for effects of *P.*

australis and litter clearing on decomposition, litterbags containing *P. australis* litter (n=4 per treatment, paired with flux chamber collars) were deployed for 1 month to test for differences in decomposition rates between the 3 treatments.

2.3 Soil and vegetation characteristics and pore water chemistry measurements

The following methods describe data collection for both Experiments 1 and 2. Soil variable data and pore water collection was conducted just outside chamber collars at the time of GHG flux measurements. Soil redox potential (ORP) was measured using an ORP probe and pH/ORP meter (Mettler Toledo, Greifensee, Switzerland). Temperature was measured with a digital thermometer inserted 10 cm into soil, and moisture content was measured using a volumetric water content sensor (Decagon Devices, Pullman, WA) inserted 5 cm into soil. Soil surface (top 2 cm) pore water for salinity measurements was extracted by pressing soil against paper filters using a syringe, and salinity was measured using a handheld refractometer. For average stem height, 10 stems per plot were selected for measurement at random and their heights were averaged. All stems in the collars were included in density measures. Pore water (15 cm depth) for salinity and sulfide and ammonium concentration analysis was collected during pre-treatment measurements and on 2 post-treatment dates using 15 cm Rhizon Soil Moisture Samplers (Ben Meadows, Janesville, WI), preserved using 1 M zinc acetate, and frozen at -20 C until analysis. Sulfide and ammonium concentrations were analyzed using standard colorimetric techniques (Cline, 1969; Solorzano, 1969).

For Experiment 2, litterbags to estimate decomposition rates in the 3 treatments contained weighed, oven-dried *P. australis* leaf and stem litter collected from the site. Litterbags were

buried 15 cm beneath the soil surface and were deployed for approximately 1.5 months. Post-deployment litter was dried and weighed. Mass lost during deployment was used as a proxy for decomposition.

2.4 GHG Flux Measurements

All GHG flux measurements were performed between 9:00 and 16:00 to avoid confounding effects of diurnal variability and were conducted for 5-10 minutes per plot, based on observed periods for linear rates of change. A cavity ring down spectroscopy (CRDS) analyzer (Picarro G2508) and a 0.3 m in diameter x 2 m tall cylindrical transparent static flux chamber, tall enough to encompass *P. australis* plants without damage, were used to measure CO₂ and CH₄ concentrations in real-time (as described in Martin and Moseman-Valtierra, 2015)). Hobo[®] data loggers (Onset, Bourne, MA) were suspended within chambers during all flux measurements to record air temperature and light intensity at 30 s intervals. On the last measurement date for the 2015 experiment, both light and dark measurements were performed. Dark measurements were conducted by placing a light-blocking, light-colored cloth sheath over the capped chamber for the duration of measurements. The Ideal Gas Law was used to calculate changes in gas concentrations over time using within-chamber air temperatures and ambient atmospheric pressure and accounting for chamber volume and footprint area. When slopes had an R² value of less than 0.85, data were not included in the analysis (4 instances for CO₂ and 3 for CH₄ during 2014 and 1 instance each for CO₂ and CH₄ during the 2015 experiments). Positive gas flux values indicate emission, while negative values denote gas uptake.

2.5 Statistical Analysis

2.5.1 2014 Stand Comparison (Experiment 1)

For the 2014 stand comparison experiment, early-season (April) edaphic conditions were compared between restored and reference stands using Wilcoxon Signed-Rank Tests to account for non-normality and heteroscedasticity. To compare GHG fluxes and soil conditions between the 2 stands and among the 4 months of measurement (May-August), 2-factor repeated measures ANOVA tests were used. Stand and month were treated as fixed effects, and plot was treated as a random effect. CH₄ fluxes were log-transformed prior to analysis due to skewness. Pairwise t-tests were used for post-hoc pairwise comparisons when appropriate, and p values were corrected using the Holm-Bonferroni method. Plant characteristics (density and average stem height) were compared between restored and reference stands using 1-factor ANOVAs. Relationships between GHG fluxes and soil, pore water, and plant variables were tested for in each stand using Spearman's correlation analysis.

2.5.2 2015 Vegetation and Litter Removal Experiment (Experiment 2)

To test for uniform plot conditions prior to treatments, GHG fluxes, edaphic conditions, pore water sulfide and ammonium concentrations and vegetation characteristics were compared between the three treatments (control, cut and cleared) using Kruskal-Wallis tests to account for non-normality and heteroscedasticity.

To compare GHG fluxes (excluding dark chamber fluxes) and soil and pore water conditions between the three treatments (control, cut and cleared) from three measurement dates, repeated-measures ANOVA tests were performed as described previously. Treatment was set as

249 a fixed effect, and measurement date was treated as a random effect. CH₄ fluxes were log-
250 transformed prior to analysis due to skewness. Pairwise t-tests were used for post-hoc pairwise
251 comparisons when appropriate, and p values were corrected using the Holm-Bonferroni method.
252 Light vs. dark GHG fluxes from the control and cut treatments were compared within each
253 treatment using paired Student's t-tests. To test for differences in CO₂ emission not driven by
254 photosynthetic effects, dark CO₂ fluxes from control plots were compared with light CO₂ fluxes
255 from cleared and cut plots (from the same measurement date) using a 1 factor ANOVA. Effects
256 of treatment on litterbag decomposition rates were tested using a 1-factor ANOVA. All
257 statistical analyses were performed in R (R Core Team, 2012). Statistics were interpreted at a
258 significance level of 0.05.

3. Results

3.1 Comparison of restored and reference *Phragmites australis* stands (2014)

Over the course of the growing season, *P. australis* quickly re-vegetated the mulched (restored) stand and (averaged over June and July measurements) was shorter ($F_{1,16}=221.50$, $p<0.001$) and denser ($F_{1,22}=4.28$, $p=0.05$) than in the reference stand. In the reference stand, *P. australis* sprouts around 10 cm in height were observed in May, and sprouts were observed in the restored stand 1 month later (about 2 months after mulching). In June, *P. australis* plants in the reference stand were taller (at 157.82 ± 14.23 cm) than plants in the restored stand (at 43.77 ± 8.31 cm), and restored stand *P. australis* plants were twice as dense as those in the reference stand (95.28 ± 20.71 stems m^{-2} vs. 52.43 ± 19.71 stems m^{-2}). By July, *P. australis* in the restored stand was 3 times as dense (with 164.28 ± 24.71 stems m^{-2} relative to 59.57 ± 22 stems m^{-2} in the reference stand), but reference plants were still taller (173.23 ± 4.83 cm vs. 65.81 ± 4.41 cm).

In the earliest comparison (April 2014) of soil conditions in the restored and reference *P. australis* stands (during the week following first mulching), soil salinity, moisture, and temperature were similar between stands ($W=16.5$, $p=0.87$; $W=13$, $p=0.48$; $W=7$, $p=0.89$, respectively). These similarities supported our choice of reference stand.

Beginning in May, several soil variables differed between reference and restored *P. australis* stands (Tables 1 and 2). For the duration of the growing season, soil moisture was consistently slightly higher in the reference stand. Redox potential (Eh) (measured only in July and August) was substantially greater in the restored stand (310.67 ± 39.56 mV in July and 128.33 ± 66.51 mV in August) than in the reference stand (20.33 ± 72.12 mV in July and 17.5 ± 17.43 mV in August). Soil temperature was greater in the restored stand during May, but did not

differ between stands during later months. Neither surface soil salinity nor pore water sulfide concentrations differed between stands.

Most soil variables varied over the course of the growing season (Tables 1 and 2). Soil temperature increased as the growing season progressed in both stands. Salinity measured during August was significantly higher in both stands than salinity measured during other months due to an unusually high tide on that date causing seawater inundation prior to measurements. In both stands, pore water sulfide concentrations were significantly higher in May (reference: $106.97 \pm 71.03 \mu\text{M}$, restored: $95.52 \pm 38.52 \mu\text{M}$) than in July (when concentrations were $0 \mu\text{M}$ in both stands) or August (reference: $17.51 \pm 15.21 \mu\text{M}$, restored: $5.33 \pm 6.53 \mu\text{M}$).

CO_2 fluxes, which did not differ significantly between stands (Figure 2A), ranged from slight emission in May (around $3 \mu\text{mol m}^{-2} \text{s}^{-1}$ from both stands) to uptake of greater than $15 \mu\text{mol m}^{-2} \text{s}^{-1}$ in July from both stands. CO_2 fluxes in May (when emission occurred) differed significantly from fluxes measured in July (when the most uptake occurred) (Table 2).

During May, CH_4 fluxes ranged from just over $0 \mu\text{mol m}^{-1} \text{h}^{-1}$ in the restored stand to nearly $4,000 \mu\text{mol m}^{-2} \text{h}^{-1}$ in the reference stand. CH_4 fluxes decreased substantially in the reference stand but increased slightly in the restored stand as the growing season progressed (Figure 2B). CH_4 fluxes were significantly greater from the reference stand only during May, and were similar between the two stands for the remainder of the growing season (Table 2). In general, CH_4 fluxes were characterized by high spatial variability, as has been observed in other coastal wetland studies (Emery and Fulweiler, 2014; Martin and Moseman-Valtierra, 2016).

302 GHG fluxes did not significantly correlate with soil, pore water or plant variables in either
303 reference or restored stands.

Figure 2. Daytime average CO₂ (A) and CH₄ (B) fluxes ± SE from reference (n=6) and restored (n=6) *P. australis* stands measured monthly from May-August.

3.2 Effect of *Phragmites australis* and litter removal on GHG fluxes (2015)

Pre-treatment measurements indicated that plots did not differ significantly in any of the variables measured prior to initiation of the experimental treatments, except for a 1°C higher average soil temperature in the control plots. This trend did not persist in subsequent measurements, and so was not thought to bias results.

CO₂ and CH₄ fluxes were both significantly affected by treatment (Table 4). CO₂ fluxes during pre-treatment measurements were small (between -3 and 3 µmol m⁻² s⁻¹) (Figure 3A). After treatment, fluxes increased in magnitude to between -18 and 8 µmol m⁻² s⁻¹. CO₂ fluxes differed significantly between cut and cleared plots and the control plot (p<0.001 in both cases). CO₂ emission of similar magnitude was observed from cut and cleared plots and net uptake due to photosynthesis was observed in the control plot. Although CH₄ fluxes displayed great spatial variability, treatment effects were discerned. While CH₄ fluxes from the control plot (less than 200 µmol m⁻² h⁻¹) did not increase on average between pre- and post-treatment measurements, fluxes from the cut and cleared plots more than doubled (from less than 150 µmol m⁻² h⁻¹ to over 300 µmol m⁻² h⁻¹) (Figure 3B). CH₄ emissions were significantly greater from the cleared than unimpacted plot (p=0.05), and that there was a trend of greater emission from the cut relative to unimpacted plot (p=0.09). Emissions did not differ between cut and cleared plots (p=0.65).

Figure 3. Average CO₂ (A) and CH₄ (B) fluxes $\pm$ SE measured in control, cut, and cleared plots on pre-treatment (May) and each of the 3 post-treatment measurement dates in 2015.

Light and dark CO₂ fluxes from control plots differed significantly ($t_2=2.85$, $p=0.04$), with uptake observed during light measurements and emission observed during dark measurements as expected. Cutting did not alter emissions ($10.52 \pm 1.55 \mu\text{mol m}^{-2} \text{s}^{-1} \text{CO}_2$) relative to control plots ($11.44 \pm 2.51 \mu\text{mol m}^{-2} \text{s}^{-1} \text{CO}_2$), but there was a strong trend ($F_{2,9}=3.78$,

p=0.06) of smaller emissions when litter was cleared ($5.80 \pm 0.98 \mu\text{mol m}^{-2} \text{s}^{-1} \text{CO}_2$). CO_2 emissions did not differ between light and dark measurements in the cut/cleared treatments ($t_2=2.85$, $p=0.10$), and CH_4 emissions did not differ between light and dark measurements for control ($t_3=1.71$, $p=0.18$) or cut/cleared treatments ($t_2=-0.10$, $p=0.93$).

Soil conditions varied among sampling visits, but none differed among treatments (Table 3, Table 4). Litterbag mass loss generally was greater in cut and cleared than in control plots (Table 3), although not statistically significant ($F_{2,8}=2.06$, $p=0.19$).

4. Discussion

4.1 Effects of control efforts on *Phragmites australis*

Over the course of this short-term study, rapid recovery of *P. australis* to clearing efforts was observed. Although excavation of ditches (< 0.3 m in diameter) to promote hydrological connectivity was performed throughout the eastern portion of Round Marsh, the bulk of excavation (dredging of an existing manmade channel > 1m in diameter) took place immediately north of the restored stand. Resulting increased drainage in the restored stand is reflected decreased moisture and increased redox potential both relative to the reference stand (Table 1) and between 2014 and 2015 (Table 3). While excavation of channels and ditches appeared to result in drier restored stand peat by allowing freshwater drainage, it does not appear to have promoted increased tidal inundation. Pore water salinity and sulfide concentrations did not differ between reference and restored stands in 2014, and in the restored stand salinities remained low and pore water sulfide concentrations were nearly 0 μM by 2015 (Table 3).

The rapid regrowth of the restored *P. australis* stand during the 2014 growing season was likely stimulated by drying soil conditions, since anoxic conditions and high sulfide concentrations restrict *P. australis* spread (Chambers et al., 2012; Bart and Hartman, 2003). Greater stem densities in the restored than reference *P. australis* stand support the finding that cutting, in the absence of treatment with herbicides or other control measures, increases *P. australis* stem density (Hazelton et al., 2014).

4.2 *Phragmites australis* presence may enhance marsh net GHG uptake

In contrast to the hypothesized increase in CH₄ emission with *P. australis* presence, results of Experiment 1 indicated that the plant did not exacerbate and possibly even decreased CH₄ emissions. Emissions in the restored stand were very low relative to the reference stand in the spring, and remained constant throughout the growing season as *P. australis* regrew. The pattern in the reference stand of decreasing emissions as vegetation matured (Figure 2B) may indicate plant-driven promotion of CH₄ oxidation (and therefore decreased CH₄ emission). *P. australis* can ameliorate anoxic soil conditions that support methanogenesis by oxygenating and drying its root zone. When compared to adjacent marsh vegetated with native high marsh species, redox potentials in a *P. australis* stand in a brackish New Jersey tidal marsh were found to be higher (Windham and Lathrop, 1999), and increases of +400 mV have been reported (Armstrong et al., 2006). *P. australis* takes up abundant water via evapotranspiration, and can locally lower water tables (Windham and Lathrop, 1999), and resulting aerobic soil conditions could impede methanogenesis.

While *P. australis* recovery in the restored stand was not associated with an increase in CH₄ emission as hypothesized, it was accompanied by an increase in CO₂ uptake, as expected. Restored stand CO₂ uptake trended toward outpacing that observed in the reference stand by August (Figure 2). Greater restored stand CO₂ uptake can be attributed to greater *P. australis* stem density in the restored stand (although biomass was not measured directly).

4.3 Effects of *Phragmites australis* clipping and litter on CO₂ and CH₄ fluxes

Contrary to hypothesized reduction of CH₄ emissions with *P. australis* removal, results of the 2015 experiments support the potential, also suggested by Experiment 1, for *P. australis* presence to attenuate CH₄ emissions (as in Grünfeld and Brix, 1999). Greater CH₄ emissions from cut and cleared treatment plots than in the control plot support the notion that for intact plants, oxygenation of its root zone (Colmer, 2003) limits anaerobic methanogenesis, and may perhaps couple methanogenesis and methanotrophy (Lovell, 2005), decreasing net emissions where plants remain intact. Results of the 2015 experiments contradict the hypothesized decrease in CH₄ emission with *P. australis* removal. Further, they suggest that leaf litter does not seem a likely driver of CH₄ emissions, given the comparable emissions between cut and cleared plots on the short timescale of this study.

CO₂ uptake in the control (unimpacted *P. australis*) plot demonstrates photosynthetic uptake greater in magnitude than CO₂ emission from plant and heterotrophic respiration, and, like Experiment 1, demonstrates the positive effect if *P. australis* presence on GHG uptake at this site. The trend of smaller CO₂ emissions from cleared than from cut or reference plots may support the hypothesis of a stimulative effect of *P. australis* litter on soil microbial respiration. However, the modest increase in CO₂ emission (about 4 μmol m⁻²s⁻¹) is small relative to net CO₂ uptake where plants were unimpacted.

4.4 Implications for management: Decreased GHG emissions as a restoration goal

The findings of these short-term experiments suggest a potential role for *P. australis* in maintaining or enhancing the coastal marsh ecosystem service of C sequestration by decreasing

GHG emissions at one coastal marsh site. Coupled with rapid declines in CO₂ uptake and potential increases in CH₄ in response to *P. australis* clearing, removal of the plant could negatively affect marsh ecosystem GHG emissions. Using a conservative global warming potential of 21 (IPCC 2007) to compute net daytime, growing season GHG fluxes in CO₂ equivalent units, cleared and cut plots were net emitters of GHGs (956 and 1,230 mg m⁻² h⁻¹, respectively) during the study, while the control plot had a net GHG uptake rate twice as large (-2,707 mg m⁻² h⁻¹) due to substantial CO₂ uptake and smaller CH₄ emissions. To determine longer-term effects of *P. australis* control on GHG fluxes, future investigations encompassing the full duration of restoration activities and subsequent years are needed. In addition, future investigations should test applicability of these findings over varying spatial scales and across gradients of environmental conditions. Introduced *P. australis* is exceptionally genetically diverse (Saltonstall, 2003), and regional and environment-specific differences in ecology and physiology could affect its responses to removal as well as its impacts on C cycling and GHG flux dynamics.

While the two experiments presented here tested effects of *P. australis* recovery and compared *P. australis*-vegetated and bare marsh, it must be considered that the aim of *P. australis* removal is to facilitate re-colonization of native marsh vegetation. Therefore, in theory, the marsh from which *P. australis* was eradicated would be colonized by native species, which has been shown to generally occur within three or more years following restoration activities (Konisky et al., 2006). Nevertheless, as reviewed in Chambers et al. 2012, restoration of tidal flow may not achieve a return to the desired native species assemblage. Rather, the invasive plant may recolonize, or native species may fail to establish in the cleared area. In the case of

the mechanically-cleared *P. australis* stand in this experiment, revegetation was rapid and, in keeping with results of previous investigations (see Hazelton et al., 2014), *P. australis* in the stand that had been cleared grew back at densities substantially greater than in the reference stand. Other, reportedly more effective methods of *P. australis* removal such herbicide use and burning (Hazelton, 2014), though, are likely to sufficiently damage plants such that regrowth is minimized and native plants may colonize if conditions are favorable. Depending on methods and frequency of *P. australis* removal and on known controls on CH₄ fluxes including hydrology and salinity, unvegetated patches of marsh may persist for months or years, potentially resulting in increased emission of CH₄ with no compensatory CO₂ uptake.

In conclusion, results of these experiments suggest that at this restoration site, *P. australis* removal may exacerbate marsh GHG emissions, at least over short terms. It is important to note that limitations of a single study site, compounded by the exceptional genetic diversity of *P. australis*, precludes generalization of these results to other restoration scenarios. In addition, effects of *P. australis* on aspects of ecosystem function including wildlife habitat provision and species diversity must also be accounted for in management contexts. Nevertheless, these findings demonstrate the potential for *P. australis* removal to impact coastal marsh carbon sequestration, and suggest that future studies of longer-term effects of *P. australis* removal under varying restoration circumstances are warranted.

Table 1. Average edaphic characteristics $\pm$ SE for reference and restored *P. australis* stands

	April	May	June	July	August
Soil Temperature (C)					
Reference Stand	9.27 $\pm$ 0.16	13.42 $\pm$ 0.41	16.30 $\pm$ 0.25	19.08 $\pm$ 0.18	20.42 $\pm$ 0.24
Restored Stand	8.92 $\pm$ 0.11	11.95 $\pm$ 0.26	16.63 $\pm$ 0.20	19.00 $\pm$ 0.09	19.85 $\pm$ 0.03
Soil Moisture (%)					
Reference Stand	58.60 $\pm$ 1.49	54.39 $\pm$ 0.91	51.42 $\pm$ 1.93	57.47 $\pm$ 1.58	--
Restored Stand	56.57 $\pm$ 1.21	49.35 $\pm$ 1.29	46.43 $\pm$ 1.39	50.27 $\pm$ 1.26	--
Soil Salinity (ppt)					
Reference Stand	4.58 $\pm$ 1.45	1.33 $\pm$ 0.49	4.33 $\pm$ 0.71	4.50 $\pm$ 1.48	28.00 $\pm$ 2.08
Restored Stand	4.42 $\pm$ 0.74	3.67 $\pm$ 0.33	2.33 $\pm$ 0.21	4.20 $\pm$ 1.24	18.00 $\pm$ 1.74

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Table 2. Results of statistical tests of effects of stand and month on GHG fluxes and edaphic variables from comparisons of erence and restored *P. australis* stands

	Results 2-factor (Stand x Month) ANOVAs			Results of post-hoc pairwise t-tests for month
	Stand	Month	Stand x Month	
Soil redox (mV)	$F_{1,18}=5.26$, p=0.03*	$F_{2,18}=0.04$, p=0.96	--**	--
Soil moisture (%)	$F_{1,33}=5.00$, p=0.03*	$F_{3,33}=14.18$, p,0.001*	$F_{2,33}=0.45$, p=0.64	May ^{ab} , June ^a , July ^b , Aug ^{bc}
Soil temp.(°C)	$F_{1,36}=0.52$, p=0.48	$F_{3,36}=411.64$ p<0.001*	$F_{3,36}=5.82$, p=0.002*	May ^a , June ^b , July ^c , Aug ^d
Surface salinity (psu)	$F_{1,32}=0.35$, p=0.56	$F_{3,32}=135.74$, p<0.001*	$F_{1,33}=10.54$, p<0.001*	May ^a , June ^a , July ^a , Aug ^b
Pore water sulfide (umol)	$F_{1,10}=1.39$, p=0.27	$F_{2,10}=5.52$, p=0.02*	$F_{2,10}=0.02$, p=0.98	May ^a , July ^b , Aug ^b
CH ₄ flux (umol m ⁻² h ⁻¹)	$F_{1,32}=1.19$, p=0.28	$F_{3,32}=0.92$, p=0.44	$F_{3,32}=4.30$, p=0.01*	--
CO ₂ flux (umol m ⁻² s ⁻¹)	$F_{1,31}=0.00$, p=0.99	$F_{3,31}=4.66$, p=0.008*	$F_{3,31}=1.81$, p=0.17	May ^a , June ^{ab} , July ^b , Aug ^{ab}

F statistics, degrees of freedom, and p-values are reported for 2-factor (*Phragmites* stand x Month) ANOVA tests

In post-hoc comparison column, months not connected by the same letter are significantly different

* = Significant at $\alpha = 0.05$

**Insufficient month data for test of interaction (only July and August measured)

Table 3. Pre- and post-treatment average edaphic and vegetation characteristics $\pm$ SE from the summer 2015 vegetation clearing experiment

	<i>Moisture</i> (%)	<i>Temp.(°C)</i>	<i>Redox (Eh)</i>	<i>Salinity</i> (psu)	<i>Sulfide</i> (μ M)	<i>Ammonium</i> (μ M)	<i>Stem</i> <i>Density</i>	<i>Avg. Height</i> (cm)	<i>%Litterbag</i> <i>mass lost</i>
Pre-Treatment									
<i>Control</i>	25.03 $\pm$ 6.45	14.98 $\pm$ 0.18	511.75 $\pm$ 15.16	2.67 $\pm$ 1.63	4.14 $\pm$ 4.78	9.27 $\pm$ 4.92	6.00 $\pm$ 2.83	58.85 $\pm$ 7.45	--
<i>Cut</i>	29.73 $\pm$ 1.59	13.98 $\pm$ 0.20	507.00 $\pm$ 24.72	16.75 $\pm$ 10.97	0.00 $\pm$ 0.00	13.37 $\pm$ 4.26	5.25 $\pm$ 1.66	51.30 $\pm$ 3.25	--
<i>Cleared</i>	23.25 $\pm$ 4.17	13.88 $\pm$ 0.32	460.00 $\pm$ 23.41	20.25 $\pm$ 3.69	0.00 $\pm$ 0.00	33.35 $\pm$ 5.74	6.25 $\pm$ 2.23	59.44 $\pm$ 2.44	--
Post-Treatment*									
<i>Control</i>	36.58 $\pm$ 1.84	17.95 $\pm$ 0.74	444.64 $\pm$ 16.42	3.33 $\pm$ 0.93	2.29 $\pm$ 1.96	11.95 $\pm$ 2.78	10.38 $\pm$ 0.94	75.09 $\pm$ 6.85	14.67 $\pm$ 3.71
<i>Cut</i>	30.13 $\pm$ 2.46	17.52 $\pm$ 0.81	443.83 $\pm$ 15.89	3.00 $\pm$ 1.08	0.00 $\pm$ 0.00	7.33 $\pm$ 1.85	--	--	21.10 $\pm$ 4.87
<i>Cleared</i>	35.83 $\pm$ 3.57	17.73 $\pm$ 0.75	470.00 $\pm$ 13.96	3.92 $\pm$ 1.11	0.00 $\pm$ 0.00	7.38 $\pm$ 1.64	--	--	24.47 $\pm$ 4.75

n=4 per treatment

*Averaged over 3 post-treatment measurement dates in June and July, with the exception of litterbag mass lost (quantified between early June and late July)

Table 4. Results of statistical tests of effect of treatment (Intact, Cut, and Cleared) and sampling date on GHG fluxes and edaphic variables from the summer 2015 experiment

	Results 2-factor (Treatment x Date) ANOVAs			Results of post-hoc pairwise t-tests for dates 1-3
	<i>Treatment</i>	<i>Date</i>	<i>Treatment x Date</i>	
<i>Soil redox</i>	$F_{2,23}=1.08$, p=0.36	$F_{2,23}=4.53$, p=0.02*	$F_{4,23}=0.64$, p=0.64	1 ^a 2 ^b 3 ^{ab}
<i>Soil moisture</i>	$F_{2,24}=0.45$, p=0.64	$F_{2,24}=21.72$, p<0.001*	$F_{4,24}=1.58$, p=0.21	1 ^a 2 ^a 3 ^c
<i>Soil temp</i>	$F_{1,36}=0.57$, p=0.57	$F_{3,36}=528.07$ p<0.001*	$F_{3,36}=1.05$, p=0.40	1 ^a 2 ^b 3 ^c
<i>Surface salinity</i>	$F_{2,24}=0.75$, p=0.48	$F_{3,24}=137.58$, p<0.001*	$F_{1,24}=4.47$, p=0.008*	1 ^a 2 ^b 3 ^c
<i>Pore water ammonium</i>	$F_{2,15}=1.33$, p=0.29	$F_{1,15}=8.00$, p=0.01*	$F_{2,15}=1.10$, p=0.36	1 ^a 2 ^b 3 ^c
<i>CH₄ flux</i>	$F_{2,24}=3.27$, p=0.05*	$F_{2,24}=1.24$, p=0.31	$F_{2,24}=0.56$, p=0.69	--
<i>CO₂ flux</i>	$F_{2,24}=5.50$, p=0.01*	$F_{2,24}=0.41$, p=0.67	$F_{2,24}=0.95$, p=0.45	--

n=4 per treatment

F statistics, degrees of freedom, and p-values are reported for 2-factor (treatment x sampling date) ANOVA tests

In post-hoc comparison column, dates (1, 2, 3) not connected by the same letter are significantly different

* = Significant at $\alpha = 0.05$

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