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Plant manipulations and diel cycle measurements test drivers of carbon dioxide and methane fluxes in a *Phragmites australis*-invaded coastal marsh

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ABSTRACT

Invasion of coastal marshes by *Phragmites australis* may alter carbon cycling, including fluxes of the greenhouse gases (GHGs) carbon dioxide (CO_2) and methane (CH_4). Understanding patterns and drivers of these GHG fluxes in *P. australis*-invaded coastal marshes is critical to predicting how this widespread biological invasion may impact carbon (C) sequestration in coastal marshes. The objectives of this study were (1) to test effects of *P. australis* aboveground vegetation removal on GHG fluxes over short timescales (up to 4 months) and (2) to contrast diel patterns of GHG fluxes in *P. australis*-vegetated and cleared plots. First, effects of mechanical aboveground *P. australis* biomass removal on GHG fluxes and soil variables were tested over a series of short-term durations (from min to months). Next, on 3 dates, GHG fluxes were measured every 3 h over complete diel cycles. Net daytime CO_2 uptake (-60 to -100 mmol m^{-2} s^{-1}) was observed where *P. australis* was left intact. All durations of vegetation removal produced similar CO_2 emissions to those measured from intact *P. australis* plots during evening hours. CH_4 fluxes did not differ where *P. australis* was removed or left intact. Greater daytime CH_4 emissions (75–100 μmol m^{-2} h^{-1}) were found than at night (20–40 μmol m^{-2} h^{-1}) from both cleared and vegetated plots. Results of this study suggest that CO_2 fluxes in this system vary primarily due to substantial photosynthetic uptake by *P. australis*, and that CH_4 emissions are likely driven by abiotic factors, such as temperature, that vary on diel cycles. Calculation of net GHG fluxes in this *P. australis*-invaded coastal marsh indicates that it is a GHG sink during the growing season.

1. Introduction

Characterizing carbon dioxide (CO_2) and methane (CH_4) fluxes from coastal marshes is critical to understanding the role these marshes play in global climate. In wetlands, fluxes of CO_2 and CH_4 may vary spatially with vegetation communities (Mozdzer and Megonigal, 2013) and abiotic conditions (Bartlett et al., 1987; Ma et al., 2012; Poffenbarger et al., 2011) and across a range of temporal scales from diel (Tong et al., 2013) to annual (Segarra et al., 2013).

Shifts in vegetation community structure may drive changes in GHG flux patterns as plant communities are characterized by distinct physiological traits and impacts on environmental conditions. Recent studies demonstrate the potential for *Phragmites australis*, a common invader of North American wetlands (Chambers et al., 1999), to alter coastal marsh CO_2 and CH_4 fluxes. Martin and Moseman-Valtierra (2015) measured GHG fluxes from *P. australis* and native species (*Spartina patens* and *Distichlis spicata*) zones monthly during a growing season in three New England marshes along a salinity gradient and found greater CH_4 emission (by up to 3 orders of magnitude) and substantially greater CO_2 uptake (up to 30× greater) in the *P. australis* zones, making *P. australis* zones greater net daytime GHG sinks. Recent work by Mueller et al., 2015 demonstrates increasing CH_4 emission from a coastal marsh along transects of *P. australis* invasion into native high marsh vegetation, supporting the idea that increased CH_4 emissions are exacerbated by *P. australis* invasion. Improved understanding of the balance of CO_2 and CH_4 fluxes in *P. australis*-dominated coastal marshes is needed to predict whether such wetlands will function as net GHG sinks or sources.

Drivers and patterns of CH_4 fluxes in *P. australis*-dominated freshwater wetlands have been well-characterized. *P. australis* mediates diel patterns of CH_4 emission due to light-driven pat-

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terns of convective gas transport (which carries rhizosphere gases through plant culms and into the atmosphere) (Brix et al., 1996; Grünfeld and Brix, 1999; Van Der Nat et al., 1998). However, less is known about CH_4 flux dynamics in *P. australis*-invaded coastal brackish and salt marshes. There are several key differences between freshwater and coastal wetlands in environmental conditions that influence both plant processes and abiotic controls on GHG fluxes, with seawater inundation resulting in distinct soil biogeochemistry and microbial communities relative to freshwater wetlands (Poffenbarger et al., 2011) as well as differences in *P. australis* growth (Burdick et al., 2001a,b; Chambers et al., 1998). The need to characterize patterns and drivers of CH_4 fluxes in *P. australis* invaded coastal marshes is particularly pressing in light of these marshes' potential role in sequestering C.

P. australis invasion may alter coastal marsh GHG fluxes either by direct mechanisms including photosynthetic uptake and gas transport or indirectly by modifications to the environment. *P. australis* is more productive than native high marsh grasses (Windham and Lathrop, 1999) and so its invasion may result in an increase in net marsh CO_2 uptake. *P. australis* has also been shown to conduct rhizosphere-derived gases, especially CH_4, into the atmosphere through its massive internal gas transport system (Armstrong et al., 1992). In mesocosm experiments, this direct influence of aboveground *P. australis* biomass on CH_4 emission has been illustrated by positive correlation of CH_4 emission with *P. australis* root mass, ramet density, and leaf area (Mozdzer and Megonigal, 2013). However, root zone oxygenation (Armstrong et al., 1992; Colmer, 2003) and locally lowered water tables (Windham and Lathrop, 1999) can promote CH_4 oxidation and thus lower net CH_4 emissions (Madigan, 2012). Provision of organic C exudates (Lovell, 2005) may sustain methanogens or CO_2 producing communities of different abundance or structure relative to those supported by native plant communities (Ravit et al., 2003).

Measuring GHG fluxes before and immediately after removing aboveground biomass tests direct effects (i.e., convective transport) on fluxes, while vegetation removal over longer durations tests for potential indirect effects, such as rhizosphere oxygenation and exudate provision, on GHG fluxes. In this study, we performed two experiments to improve understanding of drivers of GHG fluxes in a *P. australis*-invaded coastal salt marsh. Experiment 1, conducted during the 2014 growing season, tested effects of mechanical aboveground *P. australis* biomass removal on GHG fluxes and surface soil variables over a series of short-term durations (from several minutes following the manipulation and 1–4 months). Aboveground biomass removal was hypothesized to reverse CO_2 fluxes from photosynthetic uptake (negative fluxes) to emission (positive fluxes) and to rapidly decrease CH_4 emission as plant-mediated transport was possibly curtailed. In the months following *P. australis* removal, a decline in root zone oxygenation and/or increase in organic substrates from senescing roots was expected to result in increased CH_4 emission relative to vegetated plots.

Experiment 2, conducted during June 2015, tested effects of diel period on GHG fluxes from cleared and vegetated areas in a *P. australis* marsh. Soil, pore water and plant variables were also measured and tested for relationships to GHG fluxes across diel cycles. Methane emissions were expected to be greater during daytime in both vegetated and cleared areas due to increases in methanogenesis rates as soil temperatures warmed. However, vegetated plots were expected to emit more daytime CH_4 due to plant-mediated transport. In vegetated plots, CO_2 uptake by plants during the day and emission at night (due to diel photosynthetic patterns) was expected, while CO_2 emissions from cleared plots were hypothesized to vary to a lesser extent on diel cycles due to removal of intact plants and loss of their photosynthetic activity.

2. Methods

2.1. Study site

Fox Hill Marsh is located on the west coast of Conanicus Island in the town of Jamestown, Rhode Island. The approximately 0.34-acre invasive *Phragmites australis* stand used for this study is positioned at the western edge of the marsh system. Downslope of the *P. australis* stand, marsh vegetation is dominated by *S. patens*. Soil type in the *P. australis* stand consists of Ipswich Peat and Succotash Sand (Rector, 1981). Groundwater levels in the *P. australis* stand (determined with water loggers at 3 points throughout the stand during the 2015 growing season) were approximately 35–40 cm from the soil surface, and the stand rarely experienced tidal inundation. The marsh has been estimated to received small inputs of anthropogenic N (at approximately 10 kg N ha^{-1} yr^{-1}) relative to marshes further north in Narragansett Bay (Wigand et al., 2003), and previous measurements at the site revealed an absence of detectable nitrous oxide (N_2O) fluxes (Martin and Moseman-Valtierra, 2015) with a 30-s averaging period and minimal detection limit of approximately 1.4 μmol m^{-2} h^{-1} (Brannon et al., 2016).

2.2. Experimental designs

For experiments performed as part of this study, round PVC collars (24 cm tall × 30 cm diameter) to support static flux chambers for GHG flux measurements were used as units of replication. On each collar, six evenly spaced, approximately 2 cm diameter drainage holes were positioned beneath the soil surface to avoid pooling of tidal or rainwater.

2.2.1. Experiment 1: testing effects of P. australis clearing on GHG fluxes

Collars for GHG flux measurements were installed during spring 2014 in the *P. australis* stand and left in place for the duration of the growing season (May–August 2014). There were 3 plots containing 3 collars each. In early spring, one collar per plot was cleared of aboveground vegetation (by clipping at the soil surface) and roots and rhizomes around the plot were severed to depths of 0.2 m. Vegetation was allowed to persist in the other two collars.

To test for effects of vegetation removal on GHG fluxes over the course of the growing season, fluxes were measured on a monthly basis from May to August from each of the 9 collars. Within each collar, soil surface salinity, pH, moisture, temperature, and oxidation-reduction potential (redox) data were also collected at the time of GHG flux measurements.

In August 2014, an additional experiment tested near-immediate effects of vegetation removal on GHG fluxes by measuring them before and within 2 min of clipping aboveground vegetation from one intact vegetation collar per plot. To ensure that clipped stems (<2 cm tall) were not facilitating gas transport in the cleared collars, clipped stem bases were plugged with petroleum jelly and a third gas flux measurement was performed within 12 min of vegetation clipping.

All GHG flux measurements for Experiment 1 were conducted between 9:00 AM and 3:00 PM and within 3 h of low tide.

2.2.2. Experiment 2: testing effects of diel cycles on GHG fluxes under cleared and vegetated conditions

Three plots were established within the same portion of the *P. australis* stand used for the 2014 clearing experiment, but plot locations were changed to avoid effects of the previous year's vegetation clearing. Within each of three plots, two paired (vegetation intact and cleared) collars were installed 1 week prior to measurements. Vegetation was cleared following the same methods as Experiment 1. GHG fluxes were measured approximately every