

## The Effect of Precipitation Intensification on Salt Marsh Ecosystems and Their Services

### Introduction

The IPCC predicts that by the end of the century annual precipitation in Eastern North America will have increased by 5-10% (Christensen et al., 2007). Notably, the IPCC has predicted not only an overall increase in annual precipitation, but also an increase in the *intensity* of precipitation events (Meehl et al., 2007). Rainfall will be concentrated into fewer, larger storms punctuating longer periods of drought. The effects of this intensification may be especially important in ecosystems that are already under water stress – whether from too little water, or from an over-abundance that leads to waterlogging and anoxic conditions (Knapp et al., 2008). Ecosystem impacts could manifest as changes in the rate of plant growth and carbon uptake, the rates and relative ratios of the microbial processes driving nutrient cycling and decomposition, and the structure of plant and microbial communities. The objective of this research is to quantify the effects of precipitation intensification on the biogeochemistry and ecology of an important marine ecosystem: the salt marsh.

Salt marshes and other marine vegetated ecosystems are important providers of ecosystem services including habitat provision for fisheries, nitrogen removal, and carbon sequestration (Costanza et al., 1997). Indeed, salt marshes - along with seagrass meadows and mangrove forests - have some of the highest rates of soil carbon burial (Chmura, 2003; Mcleod et al., 2011). Per unit area, the “blue carbon” sequestered by marine vegetated ecosystems even exceeds the carbon sequestered in terrestrial forest soils in the same latitudes (Mcleod et al., 2011). Precipitation changes could impact multiple carbon cycling processes with consequences for global carbon storage and feedbacks to climate change. However, to my knowledge, there are no direct measurements of greenhouse gas fluxes in salt marsh precipitation experiments in the scientific literature, and data on other carbon cycling pools and processes are limited. The motivation for my current research is to fill in these knowledge gaps. I am doing this by addressing the following research questions:

### Research questions

1) *How do changes in precipitation affect macrophyte communities?*

Many salt marsh ecosystem services are the result of the high productivity of marsh grasses such as *Spartina patens*. These grasses are ecosystem engineers (Gedan and Bertness, 2009) that build marshland and stabilize the shore with large root systems. They provide materials, food, and habitat for economically important species (Costanza et al., 1997). Without the productivity of salt marsh grasses, shorelines would be more prone to damage from storm surges and erosion, and habitat for economically and culturally important species would decline (Gedan et al., 2010).

2) *How do changes in precipitation affect litter decomposition?*

Carbon is sequestered through the burial of carbon-rich sediment and biomass. Marshes are sequestration hotspots because their anoxic sediments promote very slow decay, allowing carbon

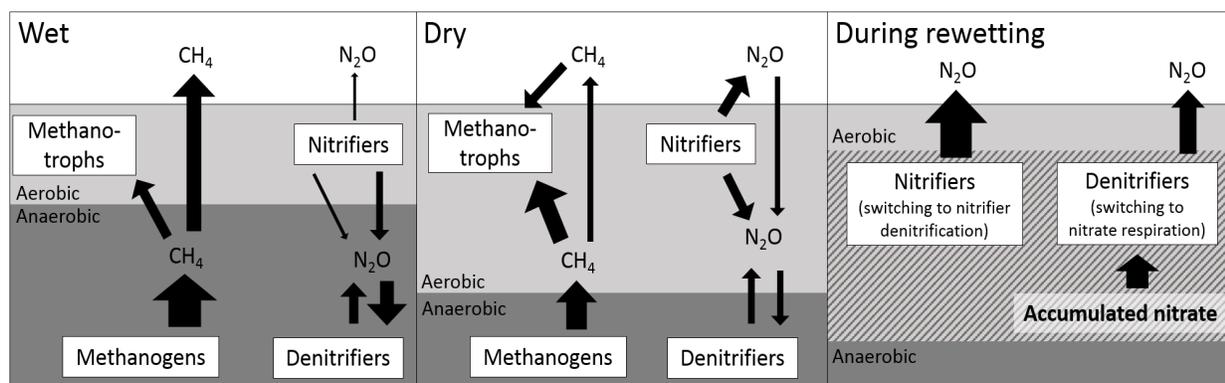
to stay trapped in senesced biomass. Compared to other types of wetlands where decay is also slow, salt marshes produce very little methane (CH<sub>4</sub>) (Poffenbarger et al., 2011). This is significant because CH<sub>4</sub> has a global warming potential (GWP) of 23, meaning it is a greenhouse gas 23 times more powerful than CO<sub>2</sub> (Barker, 2007). An acceleration of biomass decomposition would decrease the strength of the salt marsh carbon sink, compromising this important ecosystem service. A decline in carbon sequestration rates could serve as a positive feedback to climate change, increasing and reinforcing the social and environmental effects of climate change.

### 3) How do changes in precipitation affect greenhouse gas emissions and uptake?

Carbon sequestration estimates based solely on carbon mass balance overlook the difference in GWP between CO<sub>2</sub> and CH<sub>4</sub>, as well as the contribution of non-carbon GHGs like N<sub>2</sub>O (GWP of 298), to a system’s overall GWP. All three of these gases can be both produced and consumed by various microbes in the sediment (and plants, in the case of CO<sub>2</sub>). A shift from aerobic (CO<sub>2</sub>-generating) to anoxic (CH<sub>4</sub>-generating) decomposition would increase the GWP potential of a marsh, as would an increase in net production or decrease in net consumption.

## Scientific Background

The effects of precipitation intensification may be especially complex in salt marshes: larger storms could exacerbate waterlogging and stress from anoxia, but also alleviate the usual salinity stress. Likewise, longer droughts could alleviate chronic anoxia, but also concentrate the minerals and other substances dissolved in porewater, thus increasing salinity and sulfide stress. The results from salt marsh precipitation experiments to date have been mixed, reflecting this complexity. In a field experiment, salt marsh hay (*Spartina patens*) productivity increased under drought (Charles and Dukes, 2009), but in experimental mesocosms, plant productivity *decreased* under drought (Watson et al., 2014). In this latter experiment, large storms punctuating the drought apparently did not alleviate the effects of drought, as plant productivity was decreased in this case as well. In these experiments, decomposition of above-ground litter



**Figure 1:** Conceptual diagram of expected microbial responses to changes in precipitation. When the water table is high (“Wet”), anaerobic processes dominate, when the water table is lower (“Dry”), aerobic ones take over. As the water table moves up (“During rewetting”), a pulse of N<sub>2</sub>O is produced.

accelerated under doubled precipitation and slowed under drought (Charles and Dukes, 2009), whereas decomposition of belowground biomass did not respond to decreased or intensified precipitation (Watson et al., 2014).

The microbial processes that produce and consume trace greenhouse gases such as CH<sub>4</sub> and N<sub>2</sub>O in salt marshes are likely to be sensitive to precipitation intensification via several mechanisms. For example, precipitation increases could dilute or flush sulfate-rich seawater from marsh sediment pores, reducing the available substrate for sulfate-reducing bacteria. Sulfate reducers typically outcompete methanogens (CH<sub>4</sub> producers) in salt marshes, so a decrease in sulfate may lead to an increase in methanogenesis. Precipitation impacts may also occur indirectly via plant roots. Methanogenesis is tightly linked to primary productivity because fresh photosynthate exuded from plant roots is an excellent carbon source (Bridgham et al., 2013), and salt marsh plant productivity both above and belowground is likely to respond to precipitation intensification (Charles and Dukes, 2009; Watson et al., 2014).

Changes in the water table that result from precipitation change may alter the thickness of the surface aerobic sediment layer, and therefore the ratio of aerobic processes to anaerobic ones, with consequences for GHG production (Figure 1). Methanogenesis is performed by various archaea in anaerobic sediments, while CH<sub>4</sub> oxidation can be accomplished by a number of mostly aerobic bacteria (Bridgham et al., 2013). Increased precipitation may lead to waterlogging, allowing CH<sub>4</sub> produced in anaerobic layers to escape CH<sub>4</sub> oxidation and enter the atmosphere. N<sub>2</sub>O is produced as an intermediate or end product in several nitrogen cycle processes including denitrification and nitrification. Under low oxygen conditions, nitrifiers that typically make only small amounts of N<sub>2</sub>O can switch to the alternative nitrifier denitrification pathway with N<sub>2</sub>O as the main end product (Wrage et al., 2001). Thus, an increase in waterlogging could lead to greater N<sub>2</sub>O production by nitrifiers.

In addition, the cycle of drying and subsequent re-wetting of sediments itself has consequences for microbial metabolism. Upon drying, oxygen and many alternative terminal electrons acceptors in the soil column (e.g. nitrate, iron, magnesium) are replenished. Upon rewetting, the availability of these more energetically-favorable terminal electron acceptors will delay methanogenesis until they are depleted again (Laanbroek, 2010). Therefore, drying and rewetting cycles that penetrate more deeply and affect a greater sediment volume may suppress methanogenesis. On the other hand, a pulse of N<sub>2</sub>O production may be observed shortly after rewetting as denitrifiers rapidly consume the nitrate that accumulated while the sediment was aerobic, and nitrifiers simultaneously switch to nitrifier denitrification (N<sub>2</sub>O production). Therefore, if precipitation intensification increases the volume of sediment that experiences a drying/rewetting cycle, it may lead to larger pulses of N<sub>2</sub>O even if precipitation totals remain constant.

## Methods

**Treatments:** In April 2014, I established the Precipitation Intensification in Salt Marshes Experiment (PrISME) at the West End salt marsh in Provincetown, MA (Figure 2). In this



**Figure 2:** Location of experimental structures at the West End marsh in Provincetown, MA. Three sets of 4 structures are faintly visible in satellite imagery, indicated by white arrows. Imagery courtesy of Google Earth. Imagery dated 6/15/2014.

experiment, 1.5 m<sup>2</sup> plots in the *Spartina patens* (high marsh) zone were subjected to one of 5 precipitation treatments. Ambient plots received ambient rainfall, wet plots received double ambient rainfall, and dry plots received no precipitation. Plots in an additional treatment (“extreme”) first received ambient precipitation, then drought conditions during the summer dry season, and finally doubled precipitation beginning in the fall. The extreme treatment is designed to simulate the intensification of precipitation patterns expected with global climate change. Rainout shelters built over the plots of these 4 treatments (Figure 3) collected all incoming precipitation, and distributed it to plots by irrigation tubing according to treatment. Plots of the fifth treatment were infrastructure controls with no shelter mediating rain delivery.



**Figure 3:** Rainout shelter constructed to deliver precipitation treatments to 1.5 m<sup>2</sup> plots at PrISME.

**Macrophyte Communities:** Peak season aboveground and belowground biomass samples were harvested October 1, 2014. The aboveground biomass rooted within a 25 x 25 cm quadrat was clipped 1 cm above the sediment surface. The biomass was rinsed, sorted to species, and dried to constant mass in a 65°C oven. Community composition parameters (richness, evenness) were calculated based on the mass per unit area of the species found. To estimate belowground biomass, a 5cm diameter x 30 cm deep sediment core (Figure 4) was collected from each plot in June 2014. A bag made of ¼” mesh was installed in the hole left by coring, and this was filled with root-free sediment collected nearby. These root ingrowth cores were collected from the plots on October 20, 2014. The contents of the original sediment cores were divided into three horizons: 0-5 cm, 5-15 cm, 15-30 cm, but this was not possible with the root ingrowth cores. The roots and rhizomes in each horizon or ingrowth core were removed from the sediment by sifting, rinsed, and dried to constant mass.



Figure 4: PrISME sediment core.



Figure 5: PrISME litter bag.

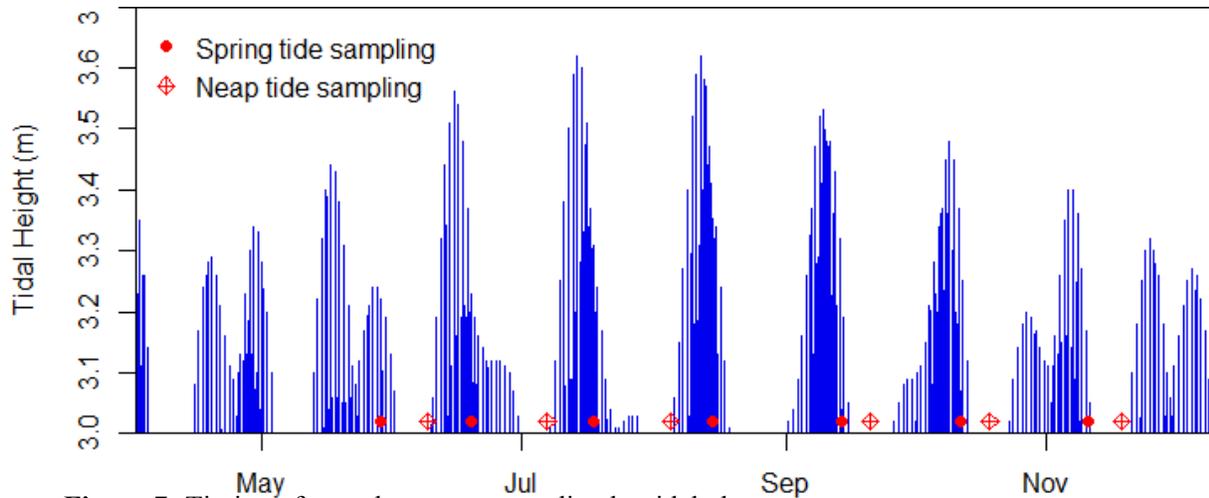
**Litter decomposition:** Senesced *Spartina patens* and *Spartina alterniflora* aboveground biomass (a low marsh species) was harvested, rinsed, and dried in January 2014. Litter bags (10 cm x 10 cm) of 2 mm mesh (Figure 5) containing a known mass (approximately 1 g) of this senesced biomass were installed in each plot in May 2014. Two litter bags of each species were collected from each plot in July and again in September 2014. The litterbags were gently rinsed with deionized water, and the contents dried to constant mass. Undeployed litter bags were used to control for the effects of rinsing. Decay rates were inferred from the mass lost

during incubation in the plots. Analyses of the chemical composition of the litter, including C:N ratio and silica contents, are currently underway.

**Greenhouse gas fluxes:** Greenhouse gas fluxes (Figure 6) were measured twice a month at distinct points in the lunar cycle (Figure 7). Each month, measurements were made at the end of a ~7-day period of twice-daily tidal inundation (end of spring tide), and at the end of a 1-2 week period of no tidal inundation (end of neap tide). Soil respiration was measured with a LiCor 6400-09 (Figure 8) soil chamber (LiCor, NE) at triplicate permanently installed soil collars in each plot as described in (Suseela



Figure 6: Static chamber system for measuring greenhouse gas fluxes.



**Figure 7:** Timing of greenhouse gas sampling by tidal phase.

et al., 2012). Fluxes of CH<sub>4</sub> and N<sub>2</sub>O, and net ecosystem exchange of CO<sub>2</sub> (ecosystem respiration – photosynthesis) were measured with transparent static chambers (Figure 6) at one permanently installed collar in each plot as described in (Emery and Fulweiler, 2014). Briefly, the airtight chambers were placed on the collars, and over a period of approximately 30 minutes, six 25-mL gas samples were extracted by inserting a syringe through a rubber septum. Each sample was transferred to a pre-evacuated Exetainer vial for later analysis. A battery operated fan inside the chamber mixed the air during the 30 minute flux period. Temperature and humidity during the flux were monitored via a digital display inside the chamber. CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O concentrations inside each Exetainer vial were determined within 30 days with a Shimadzu GC-2014 gas chromatograph (Shimadzu, Japan). This instrument uses a flame ionization detector (FID) to measure CH<sub>4</sub> and CO<sub>2</sub> (after nickel catalyst reduction) and electron capture detector (ECD) to measure N<sub>2</sub>O. Gas fluxes were calculated based on the linear change in concentration of each gas over the 30-minute period, normalized to the footprint area of the chamber.

**Other response variables:** Sediment cores were taken at the start and near the end of the experiment to assess sediment characteristics including organic content, C:N ratio, and sediment grain size. Porewater is sampled from PVC wells installed in each plot to a depth of 50 cm for salinity, pH, and inorganic nutrient concentrations (NO<sub>3</sub><sup>-</sup>, NO<sub>2</sub><sup>-</sup>, NH<sub>4</sub><sup>+</sup>, PO<sub>4</sub><sup>3-</sup>, Si).

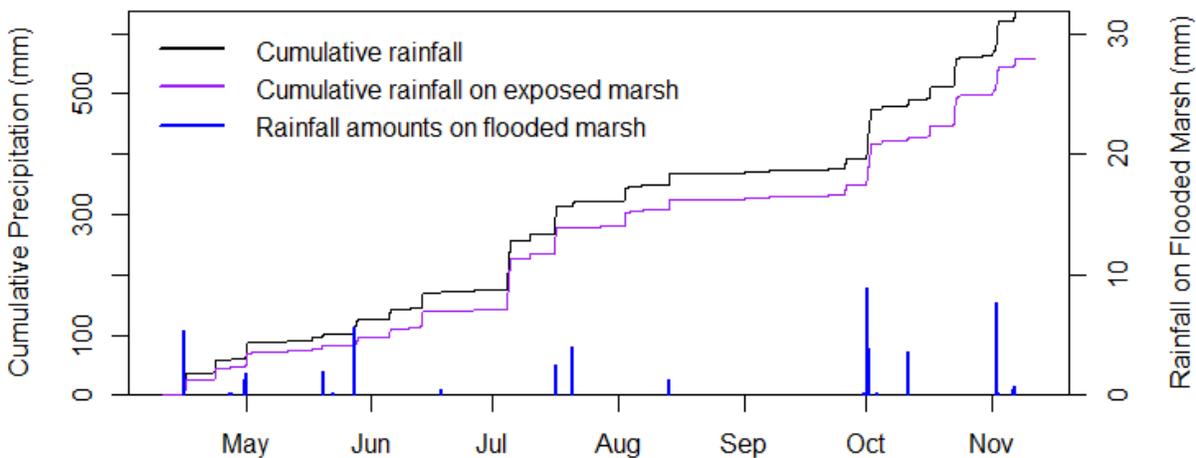


**Figure 8:** LiCor 6400 soil chamber system for measuring soil respiration.

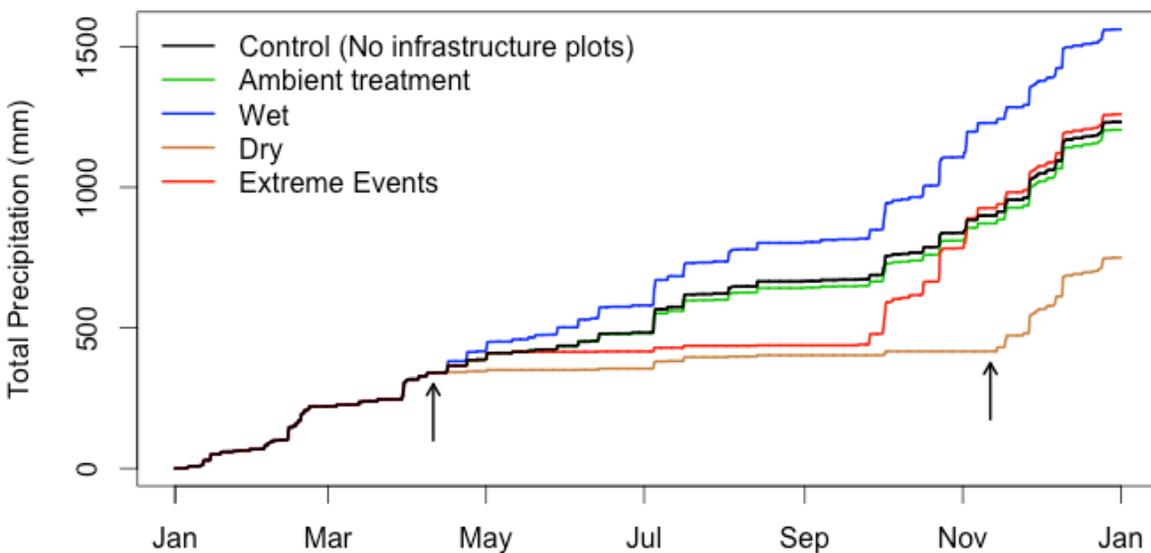
## Results

### *Treatment implementation*

Hourly precipitation data collected by the RAWS station in Truro (<http://www.raws.dri.edu/cgi-bin/rawMAIN.pl?txMCAP>) were used to estimate incoming precipitation at the Provincetown site. Based on estimates of tidal inundation derived from NOAA tide gauge data, the majority (~90%) of the rain that fell during the experiment fell on the marsh surface itself, and only a small proportion of the total was intercepted by seawater flooding the marsh (Figure 9).



**Figure 9:** Cumulative incoming rainfall as recorded at the weather station (black line), and cumulative incoming rainfall to the marsh surface (purple line). Rainfall events intercepted by tidal flooding are indicated by blue bars (note difference in scale).

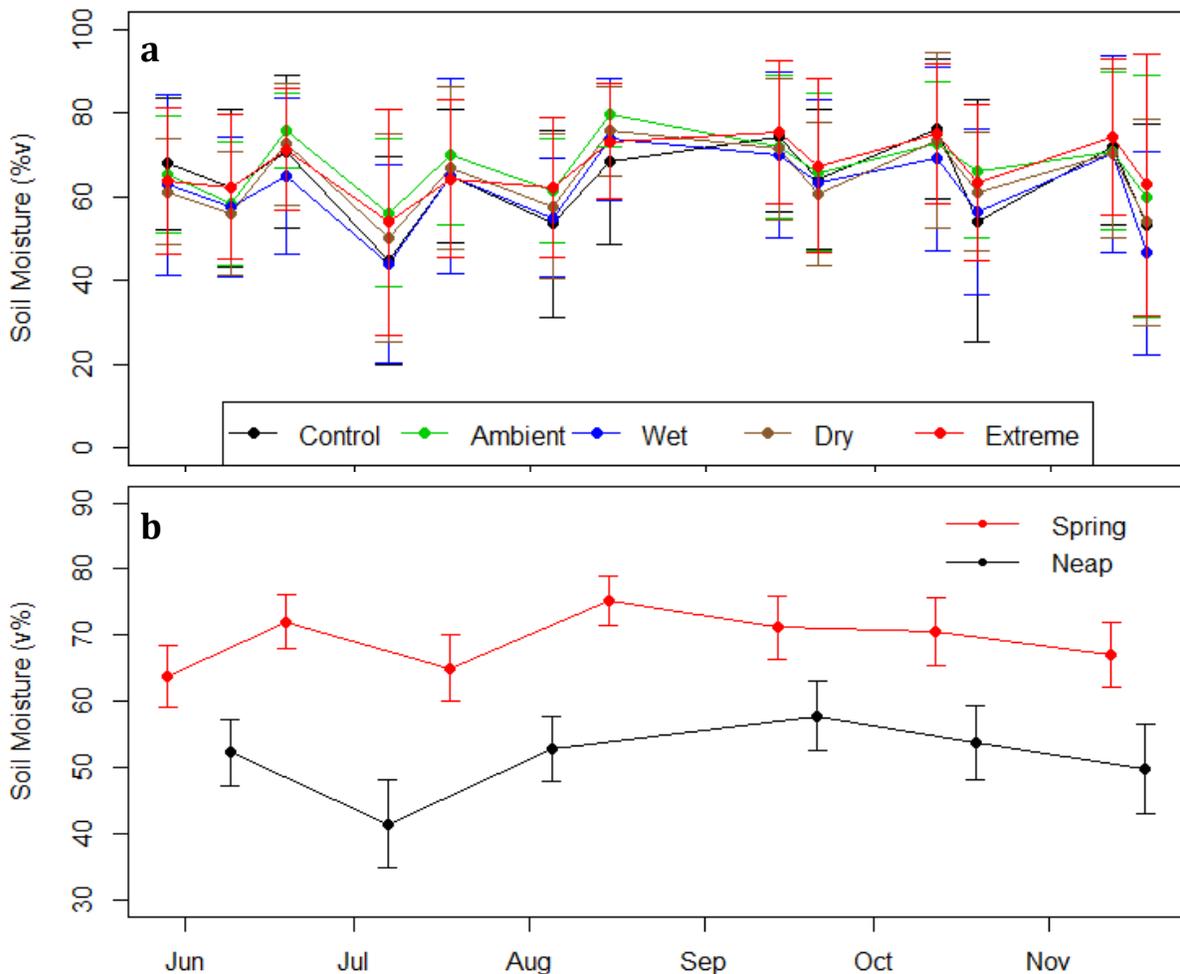


**Figure 10:** Cumulative incoming rainfall as recorded at the weather station (black line), and as estimated for each precipitation treatment (colored lines). Arrows indicate the beginning and end of experimental manipulations.

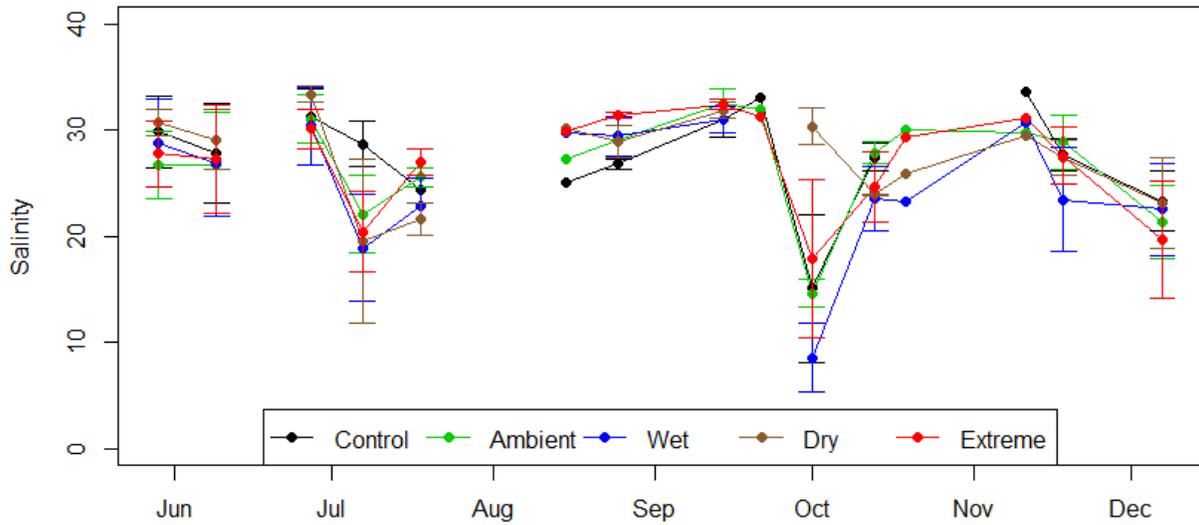
Precipitation treatments succeeded in changing the rain delivered to PrISME plots. On a few occasions the volume of incoming rain exceeded the limits of the irrigation system, and as a result dry plots received some rain via spillover and wet plots likewise did not receive a full doubling of rain (Figure 10). Extreme plots initially experienced ambient precipitation, were subjected to the dry treatment beginning a few weeks into the experiment, and finally received greater than double the incoming precipitation during the fall.

***Treatment performance***

To assess the efficacy of the precipitation treatments, soil moisture was monitored nondestructively via a dielectric probe (conductivity probes, while typically more accurate, cannot be used in saline environments). No differences in moisture between the treatments were detected (Figure 11a). However, as expected it was significantly drier in all treatments at the “neap” sampling dates compared to the “spring” sampling dates (Figure 11b).

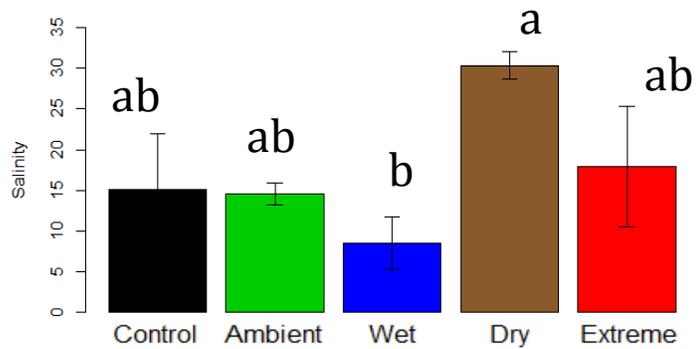


**Figure 11:** Soil moisture in PrISME plots through the 2014 growing season by treatment (a) and by tidal phase (b). Error bars indicate standard error of the mean (n=3 in a and n=15 in b).



**Figure 12:** Porewater salinity in PrISME plots. Gaps in the data occurred on dry days when there was insufficient water in the wells to obtain a sample. Error bars indicate standard error of the mean ( $n \leq 3$ , some data are missing).

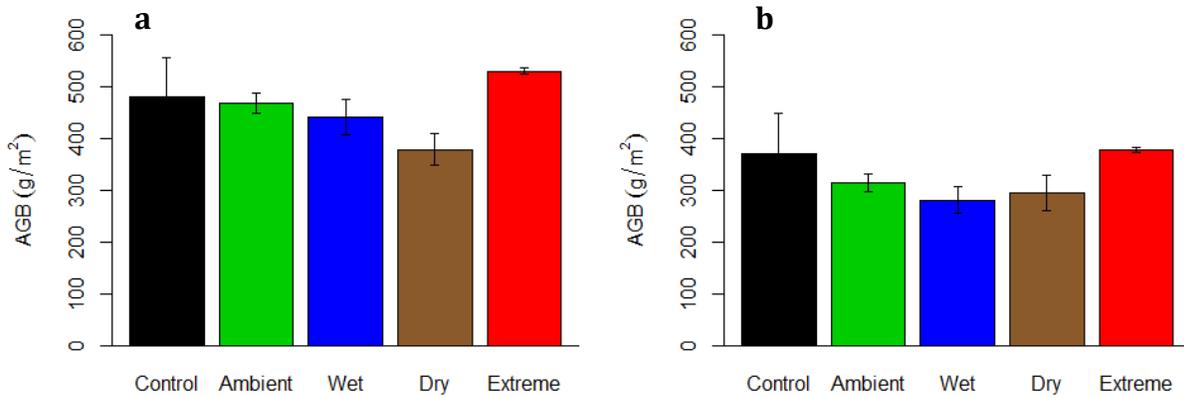
Although no differences were detected in soil moisture between treatments, differences in incoming freshwater may nevertheless affect salinity by treatment. Although salinity was similar in all plots on most sampling days, on two occasions – the first a few days after a large storm and the other during a large storm – there was an observable precipitation effect on salinity (Figure 12). During the October 1, 2014 sampling, which took place during heavy rain, porewater in the dry treatment plots maintained a salinity above 30 (PSU), while the wet plots averaged below 10 due to the incoming freshwater. Plots in the control, ambient, and extreme (at that time 10 days past conversion from dry to wet) treatments were intermediate (Figure 13).



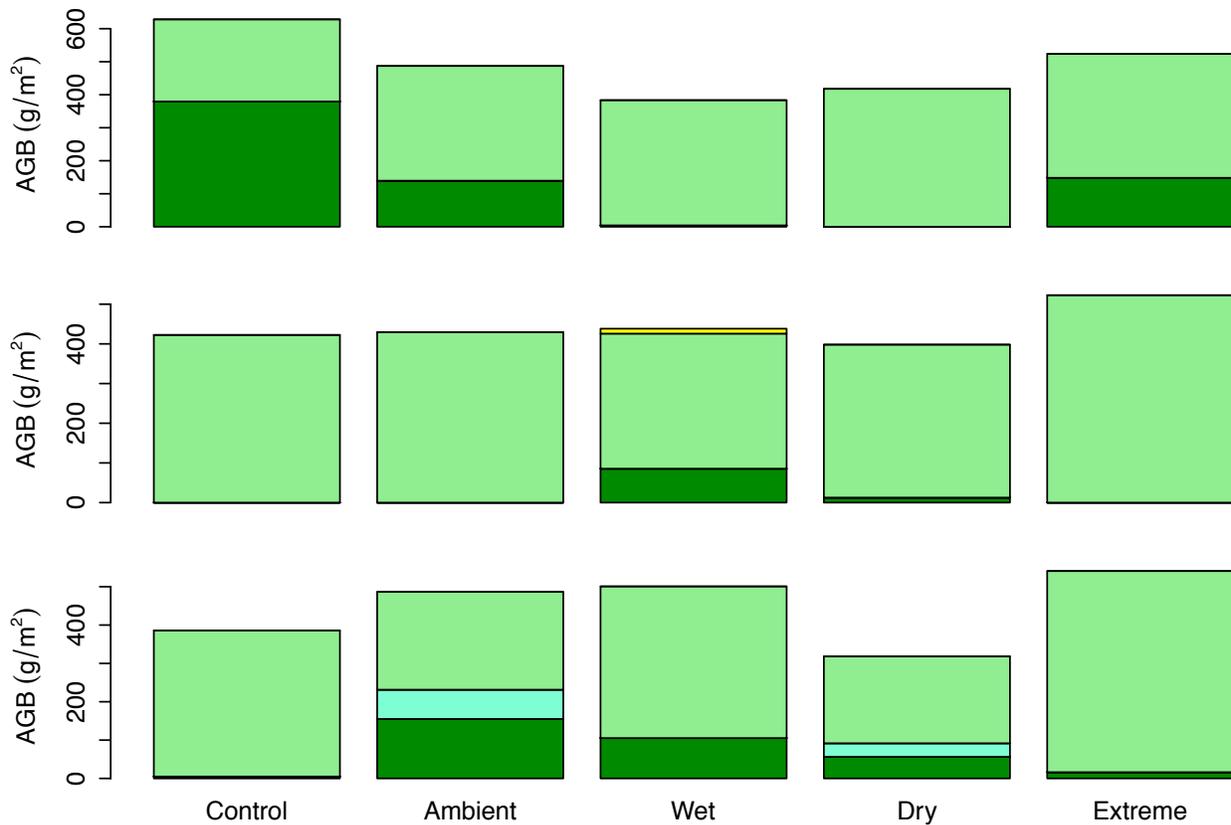
**Figure 13:** Porewater salinity in PrISME plots during the October 1, 2014 rainstorm. Error bars indicate standard error of the mean ( $n=3$ ). Lowercase letters indicate significant differences: treatments that share a letter are not different.

**Macrophyte communities**

There were no significant differences in live and dead biomass by treatment (Figure 14), and no apparent differences in the community structure (Figure 15).



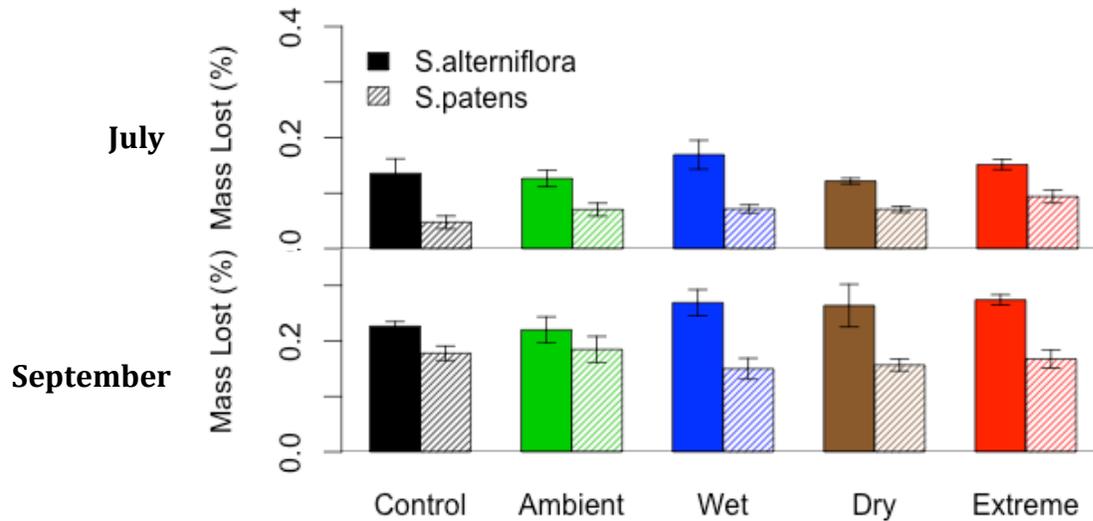
**Figure 14:** Peak season live (left) and dead (right) biomass in PrISME plots. Error bars indicate standard error of the mean (n=3).



**Figure 15:** Plant community composition in all 15 PrISME plots. Dark green (*Puccinella* spp.) and light green (*Spartina patens*) blocks indicate the majority high marsh grasses. Light blue indicates sparse patches of *Spartina alterniflora*. *Distichlis spicata*, *Salicornia* sp, *Sueda linearis*, and *Limonium* sp. were also identified, but in much smaller amounts.

### Litter decomposition

*Spartina alterniflora* litter lost significantly more mass than that of *S. patens*, but no differences were detected between treatments for either species at either harvest.



**Figure 16:** Mass lost from litter bags incubated in PrISME plots and harvested in July (top) or September (bottom).

### Greenhouse gas fluxes

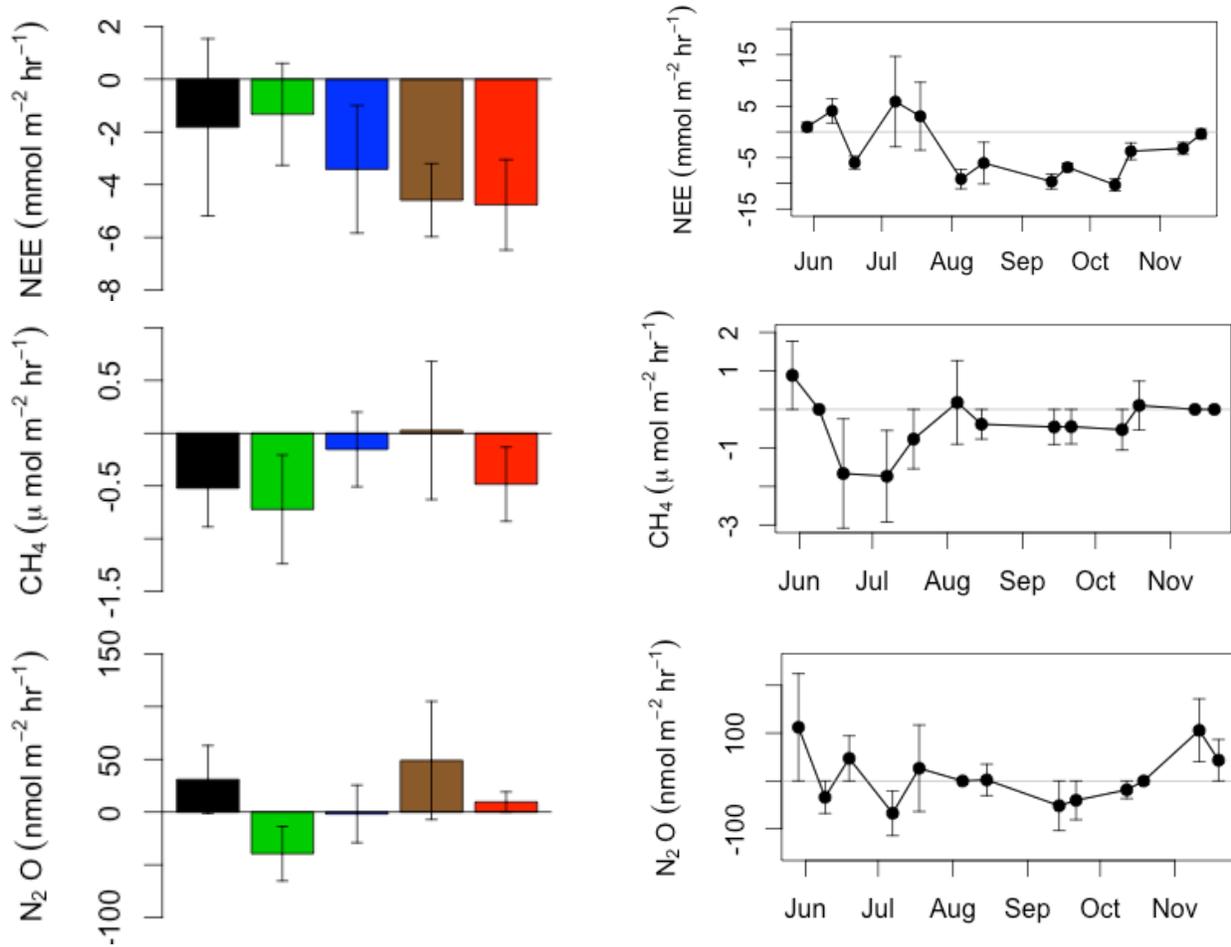
CH<sub>4</sub> fluxes were generally negative, which is unusual in salt marshes (Figure 17 b). The biggest uptake of CH<sub>4</sub> occurred in the early to mid-summer (Figure 17 e). N<sub>2</sub>O fluxes were low, were variously both positive and negative, and in general were not significantly different from zero (Figure 17 c). Tentatively, there was some tendency for N<sub>2</sub>O fluxes to be negative when the marsh was drier and positive when it was wetter (Figure 17 f), but this needs further exploration.

No differences in CO<sub>2</sub>, CH<sub>4</sub>, or N<sub>2</sub>O fluxes were observed between treatments during the 2014 season at PrISME (Figure 17 a-c). Some seasonal patterns and differences between tidal phase (neap vs. spring tide) were suggested by the data when averaged across treatments (Figure 17, d-f). The net ecosystem exchange (NEE), which is the CO<sub>2</sub> flux that includes both photosynthesis and ecosystem respiration, was overall negative during the summer months, indicating that photosynthesis exceeded respiration during these mid-day, non-light-limited, measurements. Photosynthesis was greatest during the late summer and early fall when the plants were largest (Figure 17 d).

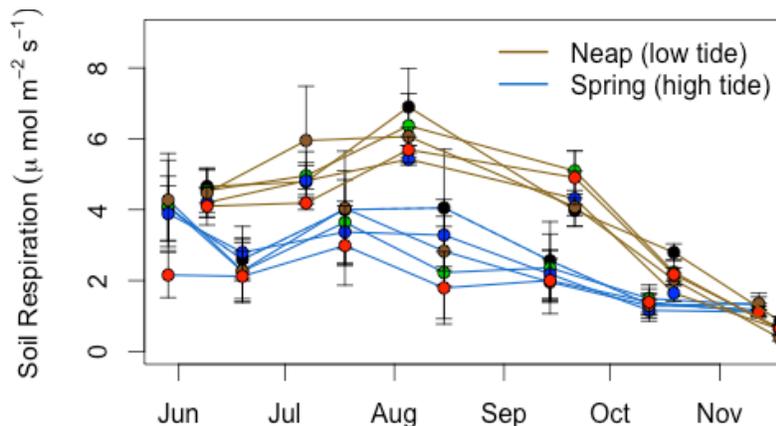
Soil respiration fluxes (made in opaque chambers to exclude photosynthesis) were also not significantly different between treatments, but varied predictably with season according to soil temperature. The warmer months featured the highest effluxes of CO<sub>2</sub> from soil respiration (Figure 18). Soil respiration was also tightly related to soil moisture, as illustrated by the differences in respiration observed between periods of spring tide and neap tide (Figure 18).

Soil respiration is driven by both moisture and temperature in this system, with each variable being more important under different conditions. When the marsh was warmest (May-

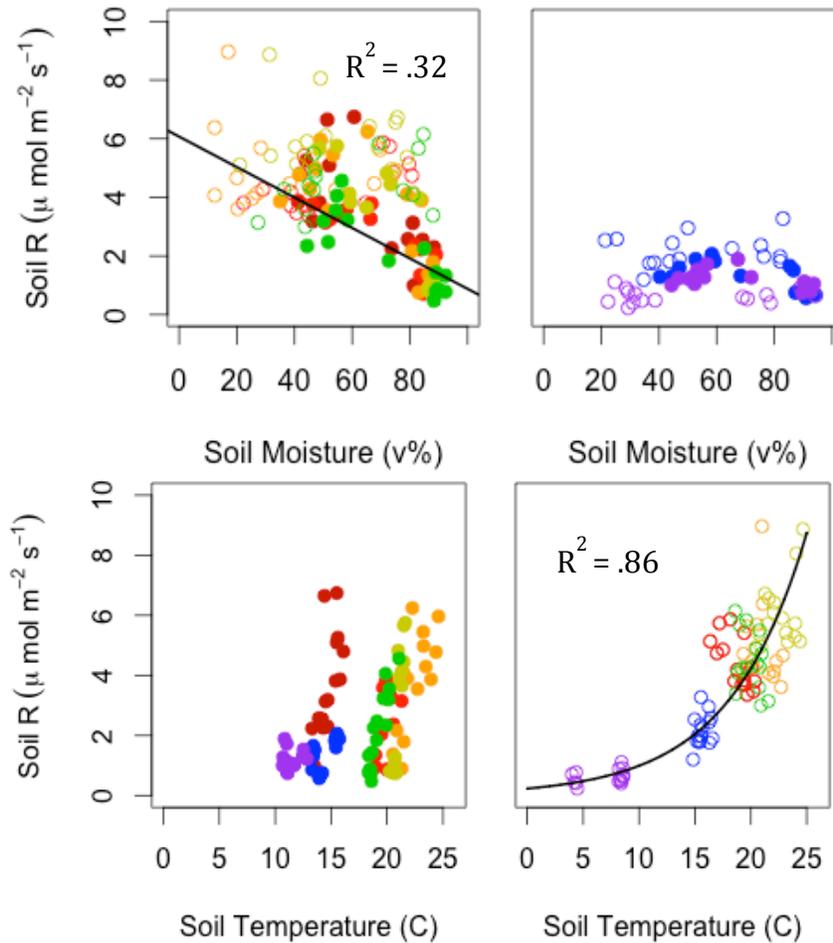
September), there was a significant linear relationship between moisture and soil respiration ( $R^2=0.32$ ,  $p<.001$ ), but that relationship did not exist during the cooler months of October and November (Figure 19). Conversely, when the marsh was driest (during neap tide phases), there was a significant exponential relationship between temperature and soil respiration ( $R^2=.86$ ) that did not exist during spring tidal phases (Figure 19).



**Figure 17:** Greenhouse gas fluxes from PrISME plots by treatment (a, b, and c) and over time (d, e, and f). Colors follow Figure 16. Error bars represent standard error of the mean.



**Figure 18:** Soil Respiration from PrISME plots. Precipitation treatments are indicated by symbol color: black = no infrastructure, green = ambient rainfall, blue = doubled rainfall, brown = no rainfall, red = drought followed by more than doubled rainfall. Tidal phase is indicated by line color. Error bars indicate standard deviation of the mean.



**Figure 19:** Relationship between soil respiration from PrISME plots and soil moisture (top row) or soil temperature (bottom row). Circle color indicates measurement month: May = brick red, June = red, July = orange, August = yellow, September = green, October = blue, November = purple. Filled circles indicate measurements made during spring tidal phases, and open circles indicate measurements made during neap tides.

### Conclusions and Future Directions

According to my preliminary analyses, I am confident that the precipitation treatments I imposed in the PrISME plots worked, since I saw differences in salinity and observed the infrastructure delivering rain in real time. However, the effect of tidal inundation on moisture seemed to overwhelm any effects that may have been caused by precipitation change, and the only significant relationship I found with moisture – the negative relationship with soil respiration - was associated with moisture due to tides not rain.

During the 2015 growing season, I have extended this project by repeating the precipitation experiment in a contrasting marsh. The new marsh, in Rowley MA, has peaty sediments and likely a greater connection to freshwater groundwater input from upland areas, while the West End marsh is extremely sandy with salinities rarely below that of the ocean. This new phase of the experiment also includes new analyses coupling observed fluxes of greenhouse gases with microbial expression of functional genes related to greenhouse gas consumption and production.

Because this project is still ongoing, as of October 2015 many laboratory and statistical analyses have not yet been performed. Therefore, the findings and conclusions presented here are preliminary and only a subset of what will be contained in the final analysis.

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