SPATIOTEMPORAL VARIABILITY IN GREENHOUSE GAS FLUX WITHIN A TEMPERATE SALT MARSH ECOSYSTEM

by

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(Under the Direction of Ford Ballantyne and Elizabeth King)

ABSTRACT

The salt marsh ecosystem plays an integral role in the global carbon budget and can act as a significant carbon sink. However, emissions of carbon dioxide (CO_2), nitrous oxide (N_2O) and methane (CH_4) have the potential to reduce their sink capacity. This study examines Georgia salt marshes on Jekyll and Sapelo Islands to understand zonation patterns and seasonal variability on greenhouse gas (GHG) flux and to put these in the context of the total carbon budget. I found that CO_2 and CH_4 flux rates vary significantly by vegetation type and season, with the highest rates in tall *Spartina* areas during June. N_2O emissions were negligible from the marsh. Even considering these GHG fluxes, salt marshes behave as strong sinks of carbon. My research suggests that vegetation type can be used as a proxy for scaling GHG emissions to larger spatial scales, which can inform the creation of blue carbon markets that shift economic favor toward conservation of coastal wetlands.

INDEX WORDS: greenhouse gas flux, blue carbon, salt marsh, coastal wetlands, *Spartina alterniflora, Juncus roemerianus*

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CHAPTER 1

AN OVERVIEW OF TEMPORAL AND SPATIAL VARIABILITY IN THE CARBON BUDGET OF GEORGIA SALT MARSHES

Salt marshes are among the most productive ecosystems in the world but face unprecedented rates of loss as coastal development continues to rise worldwide (Martinez et al. 2007, Mcleod et al. 2011). If development does not slow, further losses are to be expected along with the reduction or alteration of salt marsh ecosystem services. In particular, as coastal ecosystems are cleared or degraded, the carbon stored in them is released, contributing significantly to global climate change (Pendleton et al. 2012, Macreadie et al. 2013). Here, I briefly outline the components of the globally-important salt marsh carbon budget and highlight the spatial and temporal variability that impacts the marsh's ability to store carbon.

Salt Marshes are Globally Important

Carbon is sequestered in vegetated coastal ecosystems across the globe in coastal stocks, often referred to as "blue carbon". Generally, the net primary productivity of coastal wetland areas is higher than that of terrestrial areas per unit area, and often their relative importance to the global cycle exceeds their land area (Reddy and DeLaune 2008, Mcleod et al. 2011). High levels of root production and low decomposition rates in salt marsh sediments can result in substantial carbon sequestration (Chmura et al. 2003, Mcleod et al. 2011). Tidal salt marshes sequester an estimated

4.8 to 87.2 Tg C each year, more per unit area than any other habitat worldwide (Mcleod et al 2011). The long-term sequestration of carbon in wetland soils has created stocks of blue carbon that can endure for up to a millennium in salt marsh ecosystems (Mcleod et al. 2011, Pendleton et al. 2012). These characteristics suggest that salt marsh management may play an important role in mitigating climate change.

Salt Marsh Carbon Budget

The annual carbon budget of a salt marsh depends on the total carbon losses subtracted from carbon inputs, and this balance determines whether the marsh acts as a sink or source of carbon to the atmosphere (Theuerkauf et al 2015). A marsh's carbon storage components are composed of aboveground biomass (ie. grasses), belowground biomass (ie. roots and rhizomes), and soils (Figure 1.1). Accumulation of carbon in the underlying soil is a function of the balance between net primary productivity and decomposition. Most annual productivity occurs belowground, with root to shoot ratios ranging anywhere from 1.4 to 50 in salt marsh plants (Howard et al. 2014), similar to other grasslands, but an order of magnitude greater than ratios observed in forest ecosystems (Jackson et al 1996). Primary productivity in salt marshes/coastal ecosystems is highly variable, often depending on vegetation type, edaphic conditions, and nutrient availability (Mitsch and Gosselink 2007).

Throughout the season, as salt marsh plants senesce, the majority of aboveground biomass is converted to the detrital pool (Reddy and DeLaune 2008). Detrital plant tissue is deposited on the soil surface, where it is decomposed (Reddy and DeLaune 2008), often under anaerobic conditions. Because of highly anoxic conditions, plant litter is often buried under newer material leading to high accumulation rates of organic material (Reddy and DeLaune 2008, Elsey-Quirk et al. 2011, Howard et al. 2014). Decomposing roots add additional carbon to the soil (Drake et al. 2015). Louisiana salt marshes demonstrate organic matter accumulation rates of 200-300 g/m^2 yr (Hatton et al 1983). Thus, within salt marsh systems the belowground carbon pool is considered to be from 66% to 98% of the total, long term carbon stock in the marsh (Batjes 1996, Howard et al 2014) making it one of the most important components of the salt marsh carbon budget. The salt marsh's carbon sequestration abilities are also based on soil accretion and tidal patterns. Daily tides typically bring in sediment at a rate that exceeds sea level rise and leads to the accumulation of sediment stores, aided by marsh vegetation (Morris 2002).

Within the salt marsh, gaseous end products produced during the decomposition of organic matter can be released into the atmosphere (Reddy and DeLaune 2008), and represent a key output within the salt marsh carbon budget. However, the number of studies on carbon sequestration, storage and emissions in coastal ecosystems remains limited (Grimsditch et al 2013). Several knowledge gaps persist including adequate accounting for other potent greenhouse gases besides CO_2 and accurate estimates of all greenhouse gas (GHG) emissions at the landscape level (Howard et al. 2014). Excessive release of N_2O and CH_4 into the atmosphere can negate the benefits of carbon accumulation in the marsh; they have 25 and 298 times the global warming potential as CO_2, respectively (Craft et al. 2008).

Typically understudied in coastal areas, methane release is assumed to be limited due to a high concentration of sulfate in the incoming seawater, which suppresses methane production (Poffenbarger et al. 2011). Salinity must reach 18 psu to suppress methanogenesis (Poffenbarger et al 2011), and southeastern salt marshes experience salinities ranging from 0.5 to 30 psu (Wiegert and Freeman 1990). Nitrous oxide emissions are considered a negligible byproduct of denitrification in the salt marsh sediment (Seitzinger and Kroeze 1998). However, studies show that anthropogenic nitrogen inputs from rivers and groundwater can lead to the release of nitrous oxide to the atmosphere from salt marsh ecosystems (Liu and Greaver 2009, Moseman-Valtierra 2011). Deegan et al. 2012 found significantly higher fluxes of N_2O in marshes with nutrient enrichments 15-times higher than ambient conditions as compared to reference marshes, despite evidence that 30-40% of the added nutrient were removed by the marsh during tidal cycles.

Spatial variability in the salt marsh

The salt marsh is a spatially heterogeneous landscape marked by distinctive plant zonation (Schalles 2013) that is associated with differences in soil carbon content along the successional zonation of marsh habitat (Choi 2001). The marsh's distinctive zonation pattern may present the possibility of using easily measured environmental characteristics, such as plant community, as a proxy for GHG flux. In fact, one study in brackish marshes assessed the extent to which primary producers, based on NDVI measurements using remote sensing, could be used to quantify CH_4 (Gross et al 1993).In general, elevation and related factors like salinity and inundation determine the spatial distribution of salt marsh vegetation communities (Pennings and Callaway 1992, Morris et al. 2002, Mudd et al. 2004). Within the state of Georgia, the lower elevations are characterized by tall, monospecific stands of *Spartina alterniflora* with the highest tolerance to tidal inundation (Figure 1.2). As elevation increases, short *Spartina alterniflora* becomes dominant, followed by patches of dieback and patches of *Juncus roemerianus* (Alber et al. 2008, Figure 1.2). Extensive dieback occurred in Georgia in the early 2000's leading to the conversion of widespread areas of *Spartina alterniflora* to bare marsh (Alber et al 2008). The edaphic conditions that influence the distribution of vegetation also directly influence GHG flux, like salinity and distance to tidal channel (Hladik and Alber 2014).

The conditions that drive salt marsh vegetation are the result of both abiotic and biotic factors that can in turn also affect greenhouse gas flux (Figure 1.3). Due to elevational differences, each of the vegetation types experiences a different daily tidal range. Tidal range determines sediment aeration and porewater flow, which in turn impacts belowground carbon dynamics by influencing root production and carbon burial rates (Ouyang and Lee 2014). For example, root zone depth decreases with distance from the tidal channel, impacting oxygenation and plant productivity (Ellison et al. 1986). Tall *Spartina*, which occurs adjacent to the tidal channel, has the most extensive root zone, and increased drainage due to its porous root zone allows for higher oxygenation belowground and likely more aerobic respiration (Howes et al. 1985, Howes and Teal 1994, Pennings and Bertness 2001). Tall *Spartina* has a more developed aerenchyma system, leading to rhizosphere oxidation and increased utilization of marsh nutrients (Bertness 1991, Howes and Teal 1994). Redox potential, referring to the availability of electrons in the soil, generally decreases with distance from the tidal channel, but then increases moderately in areas vegetated with *Juncus* (Howes et al. 1981, Woerner and Hackney 1997). The tides also impact the distribution of soil nutrients and levels of anoxia within the sediment (Kulawardhana et al 2015). Along the channel, tides deliver nutrients and high sediment loads (Kulawardhana 2015); this daily influx of nutrients likely support higher GHG activity in tall *Spartina* areas compared to other zones with greater distance from the tidal channel.

Tides also deliver sulfates to the salt marsh, resulting in further zonal distinctions. While sulfate reduction occurs along the entire zonation gradient, a lack of water movement in short *Spartina* and *Juncus* dominated areas, at higher elevation, results in high accumulation of sulfides (Gribsholt 2003, Mileu and Kiene 2004, Koretsky et al 2008). Generally, sulfate-reducing bacteria limit methanogenesis by outcompeting methanogens (Reddy and Delaune 2008), and sulfides, a by-product of sulfate reduction, further limit both aerobic respiration and methanogenesis (Koretsky et al. 2008), likely leading to decreased emissions in these areas. Salinity levels also reach a maximum in mid-marsh, short *Spartina* zones, followed by a slight decrease in *Juncus* zones (Packham and Willis 1997, Pennings and Bertness 2001, Chmura et al 2016). In addition to inhibiting methanogenesis, high salinity can suppress plant growth and photosynthetic rates (Sheng et al 2015).

Biological differences also follow the zonation gradient. *Spartina* is a C4 plant, and both growth forms have an increased water use efficiency compared to *Juncus*, a C3 plant. *Spartina* plants have a high tolerance for the seasonal high temperatures experienced in the Georgia salt marsh (31-32°C), while *Juncus* has an optimum temperature range that peaks at 25°C (Giurgevich and Dunn 1978). *Spartina* thus has higher net photosynthesis (Giurgevich and Dunn 1982) and likely higher GHG flux due to an increase in labile carbon in its root zone compared to *Juncus*. Patches of dieback also differ biologically as they have notably less labile root material, compared to other zones (Marsh 2007).

Temporal variability in the salt marsh

Along with spatial variability, the marsh exhibits temporal variability in environmental conditions. Previous studies demonstrate highest CO_2 production in summer months and lowest flux rates in winter months (Chen et al 2012, Wang 2016). Factors like soil temperature and moisture influence

GHG emissions and tend to vary seasonally (Chen et al 2012, Tong 2014, Wang 2016). Seasonal changes in flooding may impact surface soil temperature and redox potential, driving variation in emissions throughout the year (Neubauer 2005). Rates of microbial processes increase with temperature and higher organic matter availability during summer months (Weston 2014), and microbial pathways may also shift throughout the year (Neubauer 2005, Moseman-Valtierra et al 2011, Weston 2014). For example, lower temperatures favor the reduction of sulfate, while higher temperatures favor methanogenesis (Gauci et al. 2004, Hu et al. 2017), which may subsequently influence CO_2 and CH_4 emissions. Seasonal changes in production affect the release of labile carbon in root exudates, impacting microbial processes like denitrification (Picek et al. 2007, Moseman-Valtierra et al 2011).

Georgia's salt marshes mark the southern extent of marsh habitat in the U.S., and display seasonal patterns distinct from marshes found at more northern latitudes (Wieski and Pennings 2013). The Georgia coast experiences a sub-tropical climate with long, hot summers and short, mild winters (O'Donnell and Schalles 2016). Temperatures and precipitation are typically greatest during the summer months, resulting in higher productivity and more aboveground biomass (Wieski and Pennings 2013, O'Donnell and Schalles 2016). Salinity is lower at the beginning of summer, due to high Altamaha River discharges during the spring months (Wieski et al. 2010). Higher temperatures and precipitation along with lower relative salinities likely coalesce to cause peak GHG fluxes during the summer months. *Spartina* productivity can increase with flooding (Kirwan and Blum 2011), and in years with high discharge, tall *Spartina* biomass can be three times higher than in years of low discharge (Weston et al 2003, Wieski and Pennings 2014).

Plant zonation along with seasonal drivers impact how certain parts of the salt marsh store or emit carbon and other GHGs to the atmosphere. Understanding these relationships presents the possibility of using a combination of season and plant zone as a reliable predictor for greenhouse gas flux at different spatial extents, and ultimately to predict the ability of a marsh area to act as a carbon source or sink. Considering the importance of the salt marsh in the global carbon budget, there is a strong need to pursue research on the spatial and temporal variability in GHG fluxes to understand how salt marshes contribute to climate change mitigation. As scientists and managers look to conserve these important coastal areas, there remain crucial knowledge gaps, including a better understanding on the way variability shapes the salt marsh's global role as a source or sink.

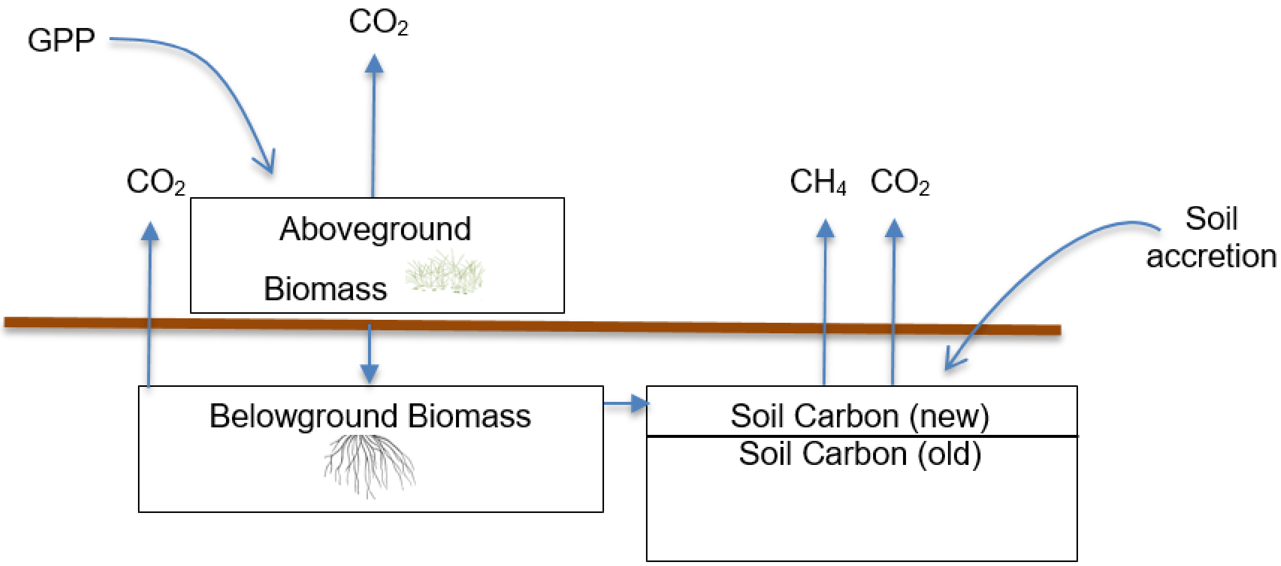


Figure 1.1. Diagram of the salt marsh carbon budget. GPP is a representation of carbon produced from photosynthesis which enters the above and belowground biomass pools. Each of these pools in turn respire CO_2 to the atmosphere. A portion of the carbon from the belowground biomass also enters the soil carbon pool, which refers to the marsh's long term soil carbon store. It is composed of new carbon, which includes a microbial pool, and old, recalcitrant carbon that can be stored in the marsh for up to a millennium. CH_4 and CO_2 are emitted from both soil carbon pools, though a majority of emissions are associated with the new carbon pool. Carbon also enters the soil carbon pool via soil accretion, as the salt marsh accretes sediment to keep pace with sea level rise.

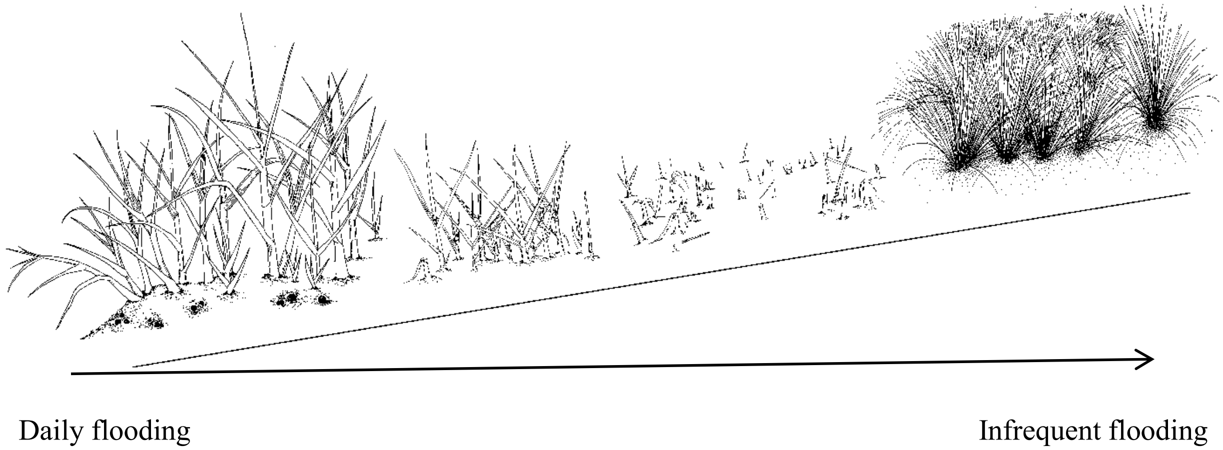


Figure 1.2 Georgia salt marsh zonation pattern, illustrated by Rebecca Atkins

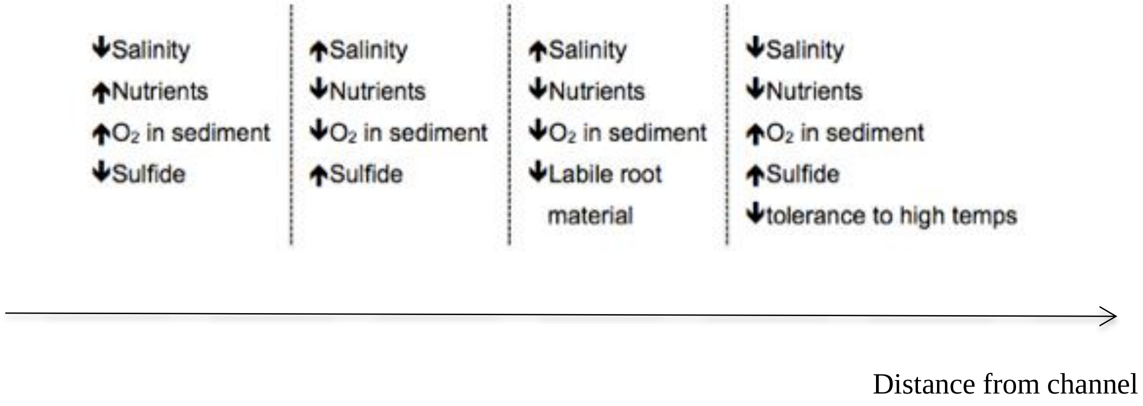


Figure 1.3 Changes in environmental condition with distance from tidal channel

CHAPTER 2

SPATIOTEMPORAL VARIABIITY IN GREENHOUSE GAS FLUX WITHIN A TEMPERATE SALT MARSH ECOSYSTEM

Introduction

Salt marshes are among the most productive ecosystems globally per unit area and sequester large quantities of carbon (Chmura et al. 2003, Mcleod et al. 2011). Carbon is stored in vegetated coastal ecosystems across the globe in coastal stocks, often referred to as “blue carbon”. Despite their value as a potential carbon sink, salt marshes have undergone rapid global decline, with losses expected to continue (Bridgham 2006, Duarte 2008). Consequently, climate finance mechanisms have been considered to prevent these projected losses based on the role of the salt marsh in climate change mitigation (Nelleman et al 2009, Mcleod et al 2011, Pendleton et al. 2012, Grimsditch et al. 2013, Ullman et al 2013, Thomas 2014). The proposed mechanisms use funds mobilized by governments, NGOs, and the private sector, to conserve or restore coastal wetland areas, often involving the use of voluntary or regulatory carbon markets (Ullman 2013, Thomas 2014). These mechanisms further highlight the importance of coastal habitats and their carbon services, which are not broadly recognized by managers and policymakers (Ullman 2013).

To date, pilot blue carbon projects tend to focus on mangrove ecosystems (Wylie et al. 2016), due to the relative ease of including these systems in already existing policies on terrestrial forests.

Furthermore, regional estimates for carbon sequestration, storage and emissions for salt marshes and other coastal areas are needed to inform policy creation and implementation (Grimsditch et al. 2013, Sutton Grier et al 2016). Most studies to date on blue carbon have focused on sequestration, neglecting greenhouse gas (GHG) emissions which are vital in determining overall climate mitigation impacts (Ullman et al 2013). Several knowledge gaps persist including adequate accounting for greenhouse gases other than CO_2, and accurate estimates of all GHG emissions at the landscape level (Howard et al. 2014). Excessive release of N_2O and CH_4 into the atmosphere can negate the benefits of carbon accumulation in the marsh; they have 25 and 298 times the global warming potential as CO_2, respectively (Craft et al. 2008).

The salt marsh is a spatially heterogeneous landscape, exhibiting low plant diversity with predictable patterns of zonation (Schalles 2013). Within the state of Georgia, the lower elevations closest to tidal channels are dominated by monospecific stands of *Spartina alterniflora*'s tall growth form (reaching heights of 100-250 cm), which exhibits the highest tolerance to tidal inundation (Anderson and Treshow 1980). As elevation increases, *Spartina alterniflora*'s short growth form dominates, reaching heights of 50-80 cm, followed by patches of dieback and patches of *Juncus roemerianus* (Alber et al. 2008). Extensive dieback occurred in Georgia in the early 2000's with the conversion of widespread areas of *Spartina alterniflora* to bare marsh (Alber et al 2008).

The zonation occurs along a gradient of changing in nutrient availability, oxygenation, salinity, and sulfide concentration. Nutrient availability, especially in the nitrogen-limited salt marsh (Delaune 1984) is an important consideration for GHG flux; in areas with low nutrients, lower emissions can be expected. Inundation from the tidal channel impacts plants and resultant GHG flux by impacting oxygen availability but also by acting as a source of freshwater and nutrient-rich flow (Mitsch and Gosselink 2007). Oxygenation of the soil determines whether aerobic or anaerobic respiration takes place, which influences which GHGs will be emitted and in what quantities (Howes et al. 1985, Korestsky et al. 2004). Salinity can impact the microbial processes that drive CH_4 emissions (Poffenbarger et al 2011), in some instances making these emissions negligible. Lastly, the presence of sulfides can inhibit anaerobic respiration and nutrient uptake (Howes et al. 1981).

Beyond this spatial variability, the marsh exhibits temporal variability with seasonal changes throughout the year. Georgia salt marshes are characterized by long, wet, and hot summers and short, dry winters (Wieski and Pennings 2013) that cause changes in abiotic and biotic conditions that drive GHG flux. Elevated temperatures during the extended summer may imply a greater possibility of southern marshes acting as a seasonal source (Cao et al 1996). Aerobes are particularly dominant during the summer months, contributing to the higher summer CO_2 emissions, while the ratio of aerobes to anaerobes is closer to one during the winter (Keith-Roach et al 2002). Seasonal changes in salinity and precipitation can further coalesce to influence changes in GHG flux throughout the year (Megonigal et al. 2005, Neubauer 2005), with lower relative salinity and higher precipitation likely leading to higher GHG flux.

Quantifying spatial and temporal variability in GHG flux will improve our ability to scale up greenhouse gas emissions to the extent needed to develop more comprehensive climate mitigation budgets. Here, we aimed to quantify the flux of CO_2, N_2O, and CH_4 from salt marsh sediment to understand first how greenhouse gas flux varies across the primary Georgia salt marsh vegetation zones and across season. The marsh's distinctive zonation pattern may present the possibility of using easily measured environmental characteristics, such as plant community, as a proxy for GHG flux, in part because the same factors that influence vegetation will also influence GHG production. These data will help fill in a crucial, though frequently overlooked aspect of the salt marsh ecosystem. We hypothesized that the marsh zones would exhibit significant differences in gas flux due to differences in nutrients, oxygenation, salinity, and presence of sulfides and that seasonal trends would also be significant with higher GHG flux during summer months with elevated temperatures and precipitation.

Methodology

Study Site

We conducted the first phase of the study examining plant zonation in salt marshes on Jekyll Island (31.1° N, 81.4° W), a barrier island on the southeastern coast of Georgia (Figure 2.1). Jekyll Island is part of the Georgia State Parks system, with salt marsh habitat comprising 30% of its cover (Jekyll Island Master Plan). Three salt marsh sites were selected for study on the western side of the island based on the presence of the four main salt marsh communities: tall *Spartina alterniflora*, short *Spartina alterniflora*, *Juncus roemerianus*, and dieback.

We conducted the second phase of the study examining seasonal patterns on Sapelo Island (31.4° N, 81.3° W), also located on the Georgia coast (Figure 2.1). The studied marshes are located within the Georgia Coastal Ecosystems Long Term Ecological Research site (GCE LTER) that was established in 2000. The three study sites are located at the southern end of the island, within the boundaries of the UGA Marine Institute. These sites are characterized by tall *Spartina alterniflora*, short *Spartina* *alterniflora* and *Juncus roemerianus* communities. Both study sites, Jekyll and Sapelo Islands, experience semidiurnal tides with amplitudes between 2 and 3 meters. Along the Georgia coast, maximum temperatures range from 15° C to 33° C with the lowest generally observed in January and February and the highest during June and July (NOAA National Centers for Environmental Information 2017).

Field sampling and analysis

Plant zonation

We conducted the first phase of study in July of 2014 on Jekyll Island to coincide with peak growing season of *Spartina*. Within each sampling site, we placed 30 m transects through areas of tall *Spartina,* short *Spartina*, dieback, and *Juncus* for a total of 12 transects among all sites. We used gas flux chambers made of white, non-reactive PVC pipe for sampling. We inserted chamber anchors 3 cm into the ground at the study sites, and established chambers at ten randomly selected points along each transect. The chambers had a diameter of 15.24 cm and a height of 12.8 cm covering a surface area of 182.41 cm^2, exceeding the minimum recommended area suggested by other similar studies (Parkin 2010). We outfitted the chambers with rubber septa to enable the removal of gas samples via syringe.

At the time of sampling, always within a four-hour window around low tide, we inserted a syringe into the chamber septa to remove 12 mL gas samples at four time intervals over the course of an hour (0 min, 15 min, 30 min, 45 min). We inserted the samples into sealed, evacuated Labco Limited Exetainer vials with grey butyl rubber septa for transport. After transporting back to the lab, we analyzed the gas samples on a SRI Greenhouse Gas Chromatograph equipped with a flame ionization detector (FID) for measuring concentrations of CO_2, CH_4, and an electron capture detector (ECD) for N_2O within one week of collection. We established a standard curve daily prior to running samples using an Airliquide Specialty Greenhouse Gas Blend, and we ran samples from individual chambers in the order of collection.

In addition to the gas samples, we measured percent cover, plant height and number of stems within a 0.5 m x 0.5 m quadrat at the site of each chamber. We measured soil temperature at the time of sampling and climate data was taken from publicly accessible sources (National Weather Service). To estimate total aboveground biomass, we used allometric equations established by Wieski and Pennings 2014 and Oliveras et al. 2013 based on the height of shoots, number of shoots per quadrat, and presence of inflorescence.

Seasonal study

The second phase of study was carried out over four seasons on Sapelo Island spanning from 2015 to 2016 (June 2015, August 2015, October 2015, and February 2016). Sampling coincided with important phases of the growing season in the salt marsh. Using the same methodology employed on Jekyll Island, we sampled gases in tall *Spartina*, short *Spartina*, and *Juncus* areas. Dieback areas did not exist on Sapelo Island at the time of the study. We collected biomass measurements using the same methodology as Jekyll Island.

Data Analysis

Plant zonation and seasonal study

To estimate rates of flux for CO_2, CH_4 and N_2O we fit linear models with concentration as the response, time, site, biomass, and vegetation type as fixed effects, with random intercepts for chamber and an error term for time. We included these random effects to account for potential differences in the chambers used and for non-independence of the time measurements for each chamber. The analysis was performed using R (R Core Team 2013) and the *nlme* package (Pinheiro et al. 2013). We created a separate model for each gas and the best-fit models were selected based on a combination of Akaike's Information Criteria (AIC) and Bayesian Information Criterion (BIC). Using this approach, the gas flux rate for each salt marsh zone was represented by the interaction between time, and vegetation type. We compared model coefficients using *multcomp* in R to test our hypothesis that gas flux rate would differ by vegetation type. The Ideal Gas Law was used to convert gas concentration (ppm) per minute into flux rate (μmol/m^2 min). For the seasonal study, we fit models using the *nlme* package and selected the best-fit model based on a combination of AIC and BIC Criterion with the addition of season as a fixed effect.

Results

Effects of Plant Zonation on Gas Fluxes

Vegetation type exerted significant influence on CH_4 flux across site (Table 2.1). The tall *Spartina* zone had the highest average CH_4 flux (0.267 μmol/m^2 min), followed by short *Spartina*, dieback and *Juncus* (Figure 2.2). The tall *Spartina* flux rate differed significantly from short *Spartina* ($p<0.001$), dieback ($p=0.00165$), and *Juncus* ($p<0.001$). The random effects of chamber and time accounted for substantial variation in CH_4 flux particularly in the tall *Spartina,* short *Spartina* and dieback areas. Biomass measurements were not good predictors for gas flux rate.

Similar to CH_4, vegetation significantly influenced CO_2 flux (Table 2.1). The tall *Spartina* zone had the highest average CO_2 flux (78.257 μmol/m^2 min), followed by short *Spartina*, *Juncus*, and dieback (Figure 2.2). Again, biomass measurements were not good predictors for gas flux rate. The tall *Spartina* flux rate differed significantly from *Juncus* ($p=0.028$) and from dieback areas ($p=0.005$); no other flux rates differed.

Seasonal Changes in Gas Fluxes

Following the examination of GHG flux variation among plant communities, seasonal fluctuations in CH_4 and CO_2 flux were assessed in tall *Spartina*, short *Spartina*, and *Juncus* zones. The best-fit model for CH_4 included time, vegetation type, and season as fixed effects (Table 2.1). In the tall *Spartina* community, peak mean CH_4 flux was found to occur in June (0.239 +/- 0.0204 μmol CH_4/m^2 min) (Figure 2.3). Short *Spartina* also had peak CH_4 flux during June (0.102 +/- 0.0142 μmol CH_4/m^2 min), while *Juncus* had the highest CH_4 flux during October (0.0786 +/- 0.008 μmol CH_4/m^2 min). The CH_4 flux was negative in both *Juncus* and short *Spartina* areas during February, however all other plant and season combinations had a positive flux. The best model fit indicates that vegetation type is a more important driver of flux compared to season. Across the seasons, the tall *Spartina* CH_4 rate was significantly different from both *Juncus* ($p<0.001$) and short *Spartina* ($p<0.001$). Flux rates during February were significantly different from June, August, and October ($p<0.001$) and June rates were different from October ($p<0.001$). Biomass measurements were not good predictors for CH_4 gas flux rate, and site was also dropped from the best-fit model.

The best-fit model for CO_2 included time, vegetation type, and season as fixed effects in a three-way interaction (Table 2.1). Peak CO_2 flux was measured in the short and tall *Spartina* communities in June (84.515 +/- 6.82 and 84.266 +/- 5.96 µmol CO_2/m^2 min, respectively) followed by August and October (Figure 2.4). Fluxes were lowest for all plant communities in February, with *Juncus* having a comparatively higher flux rate at this time (17.083 +/- 2.49 µmol CO_2/m^2 min). CO_2 flux was positive at all sampling points throughout the study. The best-fit model had a three-way interaction between time, vegetation type and season. Importantly, this suggests that season differentially affects fluxes in different vegetation types. Tall *Spartina* differed significantly from *Juncus* ($p<0.001$) and from short *Spartina* ($p=0.0198$) across seasons. All of the seasons displayed significant differences from one another ($p<0.001$). Models using biomass measurements were not good predictors for flux rate, and site was dropped from the model of best fit.

N_2O Flux

N_2O concentrations did not display any pronounced flux. Furthermore, the observed concentration levels of N_2O fall in a range that is often considered below minimum detection levels by other studies, and thus the gas flux rates were considered negligible across the plant communities.

Biomass

Biomass estimates were not good predictors for GHG flux for the plant zonation or seasonal study, but did differ between the plant communities. For the plant zonation study, tall *Spartina* had the largest mean aboveground biomass (847 g dwt/m^2), followed by *Juncus* (486 g dwt /m^2) and short *Spartina* (394 g dwt /m^2) (Table 2.4). In the seasonal study, aboveground biomass for all three plant communities reached a peak during October. Tall *Spartina* had the highest biomass (993 g dwt /m^2), followed by *Juncus* (594 g dwt/m^2) and short *Spartina* (372 g dwt/m^2). The timing for peak aboveground biomass differed from peak GHG emissions, apart from *Juncus*.

Discussion

We observed gas flux rates that were comparable to those found using chamber based methods in other North American salt marsh ecosystems along the eastern coast (Table 2.6). Plant community was a significant predictor of CO_2 and CH_4 flux rates, with the highest rates observed in tall *Spartina* (.267 µmol CH_4/m^2 min, 84 µmol CO_2/m^2 min) and the lowest in *Juncus* areas (-0.143 µmol CH_4/m^2 min, 17 µmol CO_2/m^2 min). The decreasing flux from tall *Spartina* to short *Spartina* to *Juncus* parallels change in edaphic conditions, which suggests that patterns of GHG emissions are partly due to the conditions driving plant zonation; including distance from the tidal channel, nutrient availability, oxygenation, salinity, and sulfide concentration.

Tall form *Spartina* experiences exposure to nutrient-rich tidal and freshwater flow due to its position along the tidal creek bank (Mitsch and Gosselink 2007), supporting higher GHG emissions in this area compared to other vegetation types further from the channel. Salt marshes are nitrogen limited (Delaune 1984), but total nitrogen content is greatest in tall *Spartina* biomass (Wieski et al 2010). This may be due to the fact that nitrogen fixation rates are two to seven times more active in areas with tall form *Spartina* than those in short *Spartina* (Hanson 1977), and short *Spartina*'s shallower root zone may further limit nitrogen uptake capacity (Ellison et al. 1986). Nitrogen fertilization increases growth in short *Spartina* but not tall *Spartina* (Gallagher 1975, Broome et al. 1975), and thus, nitrogen availability is likely the factor driving the difference in growth between *Spartina* forms (Morris and Bradley 1990).

Areas adjacent to the tidal channel experience greater oxygenation in the underlying soil relative to areas further away from the channel. Tall *Spartina* has an extensive aerenchyma system and consequently oxidizes sediment around its roots more than does the short form and *Juncus* (Howes et al 1985, Howes and Teal 1994). Tall *Spartina* areas have a higher density and deeper penetration of macrofaunal burrows (typically *Uca spp*.), which promotes aerobic respiration due to enhanced O_2 transport during low tide (Koretsky et al. 2004). Net photosynthesis of tall form *Spartina* is higher than both *Juncus* and short form (Giurgevich and Dunn 1982), especially during the summer months. Further, *Juncus*, a C3 plant, has an optimum temperature range well below the daily summer highs on Jekyll and Sapelo Islands (Giurgevich and Dunn 1978). Higher photosynthesis rates in tall *Spartina* suggest that more photosynthesis products are allocated to roots, supporting autotrophic respiration (Bagwell et al 1998). Increased oxygenation leads to higher microbial activity in tall *Spartina* (Kostka 2002), and further microbial respiration is higher under exposure to *Spartina* litter as compared to *Juncus* litter (Elsey-Quirk 2011).

Tall *Spartina* grows in sediments with relatively low salinity due to greater tidal flushing (Packham and Willis 1997), such that salinity levels likely fall beneath the threshold required to suppress methane production. Salinity levels tend to peak in the short *Spartina* zone due to increased evaporation, which concentrates salt in the soil (Pennings and Bertness 2001, Chmura et al 2016). Highly saline conditions are associated with the suppression of methane emissions, thus the differences in CH_4 emissions between short and tall *Spartina* may be due to inherent variation in their position along the zonation gradient.

Tides deliver sulfates to the salt marsh, stimulating the activity of sulfate-reducing bacteria which suppress methanogenesis (Weston et al. 2010) due to a higher energy yield from sulfate reduction. Sulfate is rapidly depleted with depth in short *Spartina* areas, suggesting that organic matter degradation is dominated by sulfate reduction (Koretsky et al 2008), a probable cause for the relatively lower CH_4 emissions in this area. Furthermore, dissolved sulfide concentration has the greatest accumulation in short *Spartina* areas due to low tidal water movement, implying that nutrient uptake rates may become less efficient (Howes et al. 1981, King et al. 1982, Gribsholt 2003, Koretsky et al 2008). *Juncus* areas also experience relatively high sulfide accumulation; in high quantities sulfide is toxic and can limit both aerobic respiration and methanogenesis (Koretsky et al 2008).

Observed gas flux rate in dieback areas on Jekyll Island was generally low. Prior to the dieback phenomenon, these areas were vegetated by short *Spartina*. Salt marsh dieback may be related to periods of drought that cause soil desiccation, decreased pH, and increased availability of toxic metals (McKee et al. 2004). Toxic metals can cause oxidative stress including a decrease in chlorophyll levels and browning and blackening of roots (Rozema, Luppes, Broekman 1985, Connolly and Guerinot 2002, Dominguez et al 2009). Within the state of Georgia, drought-induced stress may have worked synergistically with snail grazers to further drive marsh vegetation into decline (Silliman et al 2005). Dieback patches still demonstrate reduced soil water retention and changes in sediment consistency (McFarlin et al 2015). While these parameters were not measured in this study, if these stressful conditions still exist, it is not surprising that gas flux rates remain low. Lacking aboveground biomass, these areas lack oxygen transport to the rhizosphere, and it is likely that the labile belowground substrates have declined considerably with time. Furthermore, the depth of the former belowground biomass was likely shallow because these areas were formerly colonized by short form (Ellison et al. 1986).

Throughout the year, seasonality influences GHG emissions (Howes et al 1985, Bartlett et al 1987, Bridgham et al 2006, Mueller 2016). Seasonal changes in temperature play a significant role in controlling rates of processes that regulate organic matter decomposition, impacting the production of both CO_2 and CH_4 (Reddy and DeLaune 2008). Wang et al. 2016 showed that GHG flux in Chinese salt marshes followed a pattern similar to that of air temperature, suggesting it as a key factor for emissions (Wang et al. 2016). Elevated summer temperatures combined with increases in labile organic carbon from plant growth accelerate the rates of sulfate reduction and other metabolic processes contributing to emissions of CH_4 and CO_2. (Neubauer 2005). While marsh microbial biomass responds to warm conditions in the spring and summer time, it tends to decline in colder temperatures (Keith-Roach et al 2002, Koretsky et al 2003, Neubauer 2005).

Seasonal changes in discharge also impact marsh vegetation and related processes. Periods of high river discharge can lead to low water column salinities, resulting in low porewater salinities, especially in the creekbank zone where tall *Spartina* is found (Wieski and Pennings 2014). Furthermore, increased summer precipitation provides an input of freshwater to the marsh and can increase both CO_2 production and methanogenesis (Megonigal et al 2005, Neubauer 2013) by lowering salinity, leading to lower plant stress and allowing methanogens to dominate decomposition. Within the context of this study, the June sampling period coincided with the highest monthly precipitation and relatively lower salinities because of high spring discharge. A synergism between higher temperatures, precipitation and relatively lower salinity can lead to accelerated autotrophic and heterotrophic respiration rates, like those seen during the June sampling period. The February sampling period experienced high discharge, but there is likely less available substrate for respiration due to lack of plant growth at this time of year. Both Juncus and short *Spartina* exhibited negative CH_4 flux in February, indicating the likely occurrence of methane consumption. There are three main pathways for the oxidation of methane, but considering the high discharge in February of year it seems likely that anaerobic methane oxidation using sulfate as a substrate is taking place, resulting in the production of sulfides and bicarbonate (King and Wiebe 1978).

Marsh productivity tends to peak during the summer months and decline through the winter (Blum et al 1978), though Georgia is less sensitive to seasonality than marshes at higher latitudes. GHG flux did not follow the same trend as biomass, with the exception of peak CH_4 flux coinciding with peak *Juncus* aboveground biomass during October. It is possible that this peak is due to the influence of the tidal channel on the high marsh area at this time of year due to king tides, or the highest high tides of the year (Patel 2006). This delivery of tidal flow to *Juncus* areas likely drives the increase in methane production observed in October. Typically, the high marsh experiences the least influence from the tidal channel, but resultant increased soil moisture from the tide likely promotes methanogenesis in this area.

On an annual basis, total carbon emissions vary between each of the vegetation types. These emissions were calculated by averaging seasonal measurements and converting from μmol/m^2 min to g C/m^2 yr. Mean CO_2 emissions are highest in tall *Spartina* (333 g C/m^2 yr), followed by short *Spartina* (270 g C/m^2 yr) and then *Juncus* (244 g C/m^2 yr). CH_4 emissions follow the same pattern with 2.99 g C/m^2 yr in tall *Spartina*, 0.102 g C/m^2 yr in short *Spartina* and 0.0158 g C/m^2 yr in *Juncus*. Based on these quantities, the vast majority of total carbon emissions are due to CO_2 (Table 2.7). However, it is important to note that CH_4 has 25 times the global warming potential of CO_2, and thus likely has a disproportionate influence on the atmosphere. With these values, we can consider the percent area of each vegetation type, and determine how carbon emissions scale up across the landscape. For example, within the Sapelo Island complex, a majority of cover is attributed to short *Spartina* (72.7%) (Table 2.7), implying that the level of emissions from this plant type carries the greatest importance at the landscape level. Furthermore, changes in percent cover can carry implications for emissions into the future. For instance, an increase in tall *Spartina* cover could indicate a subsequent increase in carbon emissions to the atmosphere. Understanding how emissions vary between the plant communities can provide essential information to planning for blue carbon markets, and these measurements will be addressed again as we estimate the Sapelo Island carbon budget in Chapter 3.

The salt marsh study sites do not appear to be a source of N_2O. This suggests that the marsh study areas have low nitrogen loading from adjacent developed areas, or that denitrification proceeds to completion. Typically, salt marshes with low nitrogen are not important contributors of N_2O, however with increasing coastal development this may change. It will be important to monitor N_2O alongside CO_2 and CH_4 to ensure that nitrogen loading has not increased, particularly since N_2O emissions have 298 times the global warming potential as CO_2 (Craft et al. 2008).

Model fitting indicated that the biomass measurements did not carry substantial predictive power for the observed gas flux patterns. It is likely that emissions are impacted more heavily by heterotrophic respiration as opposed to autotrophic respiration from the soils. Belowground plant pools represent a higher percent of organic soil carbon in *Spartina* compared to *Juncus* (Elsey-Quirk 2011), but these differences were not captured with the biomass metrics used in this study. Our biomass measurements are similar to studies demonstrating declines in *Spartina* biomass on the Georgia coast. O'Donnell and Schalles 2016 reported declines between 33-39% over the last 28 years, and our biomass measurements fall in a similar range. If this trend continues, there may be significant implications for the future of blue carbon market type projects, and for the impact of salt marshes on the global carbon cycle.

Conclusion

This study recorded CH_4 and CO_2 flux values similar to those reported in other North American salt marshes. The results demonstrate that vegetation type predicts greenhouse gas flux rates in the Georgia salt marsh. It further suggests that vegetation cover, an easily measured characteristic, can act as a proxy for determining flux from the local scale to the landscape level. Changes in species cover thus can have significant implications on whether a salt marsh is acting as a sink or source for carbon. Additionally, there is a significant seasonality component to GHG emissions in the salt marsh, with highest flux rates during the summer months. This information can provide regional estimates and fill in significant knowledge gaps for blue carbon policymaking. As research continues on coastal blue carbon, it will be necessary to understand the entire carbon budget of the salt marsh. A full assessment will require accounting for components like carbon sedimentation rate and belowground biomass production. Understanding the full carbon budget will better inform coastal management decisions and help lend support towards bringing coastal wetlands to market.

Figure 2.1. Maps of study sites on Georgia coast a) Location of Jekyll and Sapelo Islands on the Georgia coast b) Salt marsh study sites on Sapelo Island, GA c) Salt marsh study sites on Jekyll Island, GA

Table 2.1. Best-fit models for plant zonation and seasonal study

Gas	*Study*	*Fixed Effects*	*Random Effects*
CH_4	Plant zonation	Time*Vegetation type + Site	~Time|Chamber
CO_2	Plant zonation	Time* Vegetation type + Site	~Time|Chamber
CH_4	Seasonal	Time*Vegetation type*Season-Time:Vegetation type:Site	~Time|Chamber
CO_2	Seasonal	Time*Vegetation type*Season	~Time|Chamber

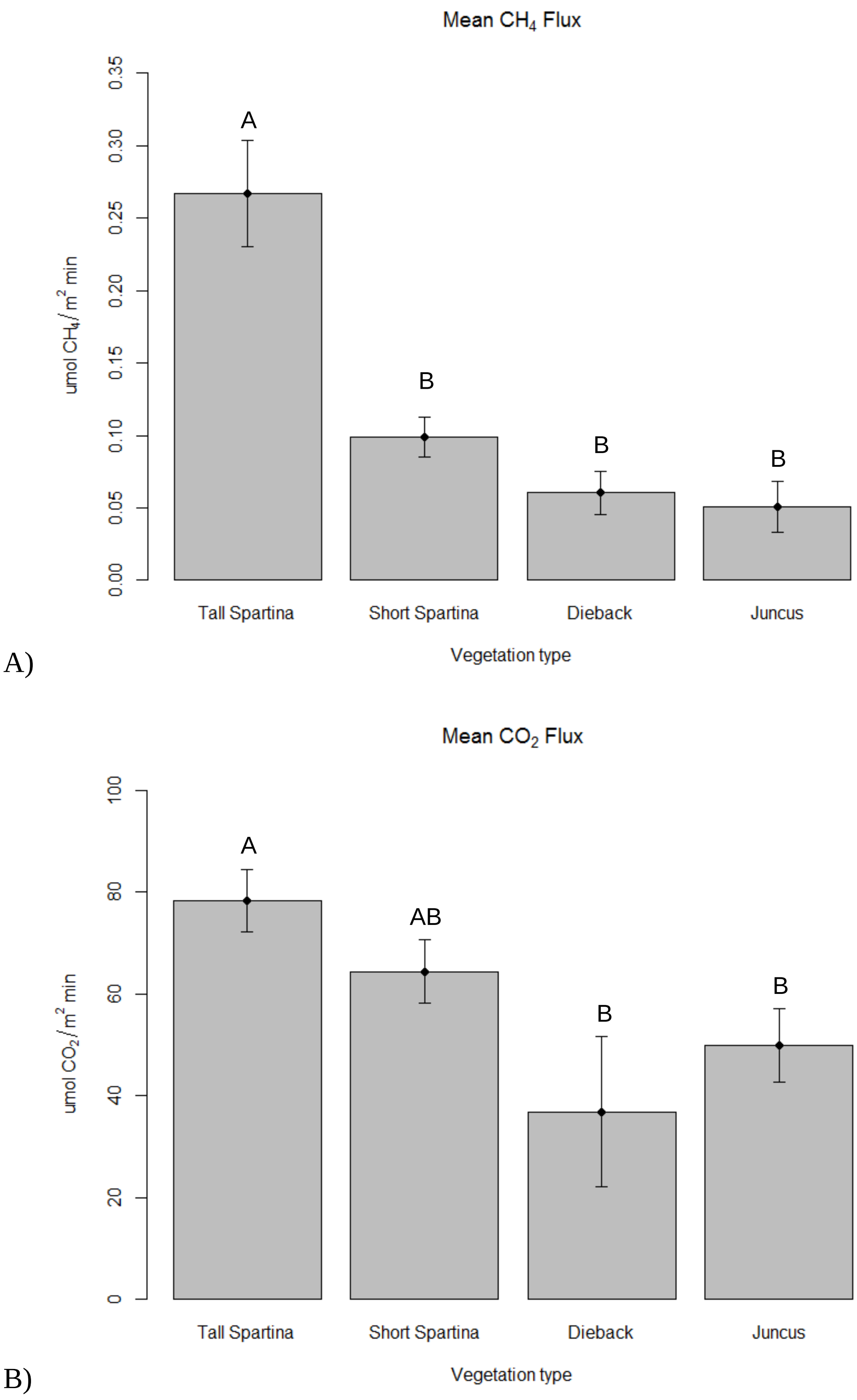
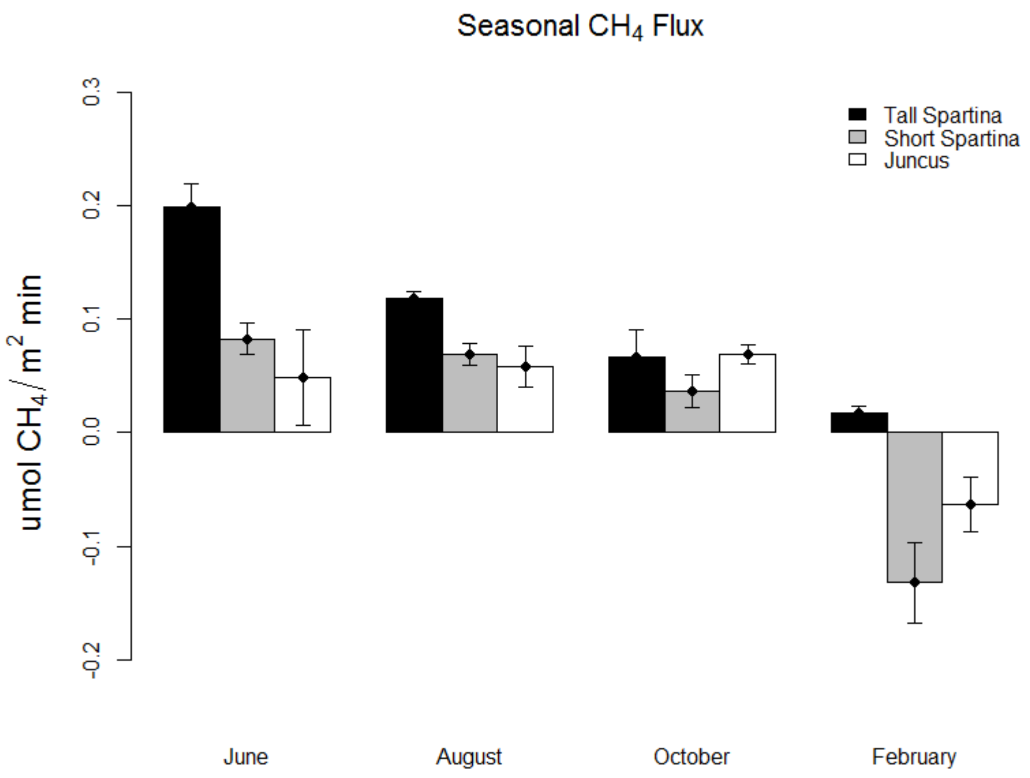


Figure 2.2 Gas flux rates for plant zonation study A) CH_4 flux rates by vegetation type, B) CO_2 flux rates by vegetation type. Error bars reflect standard error.

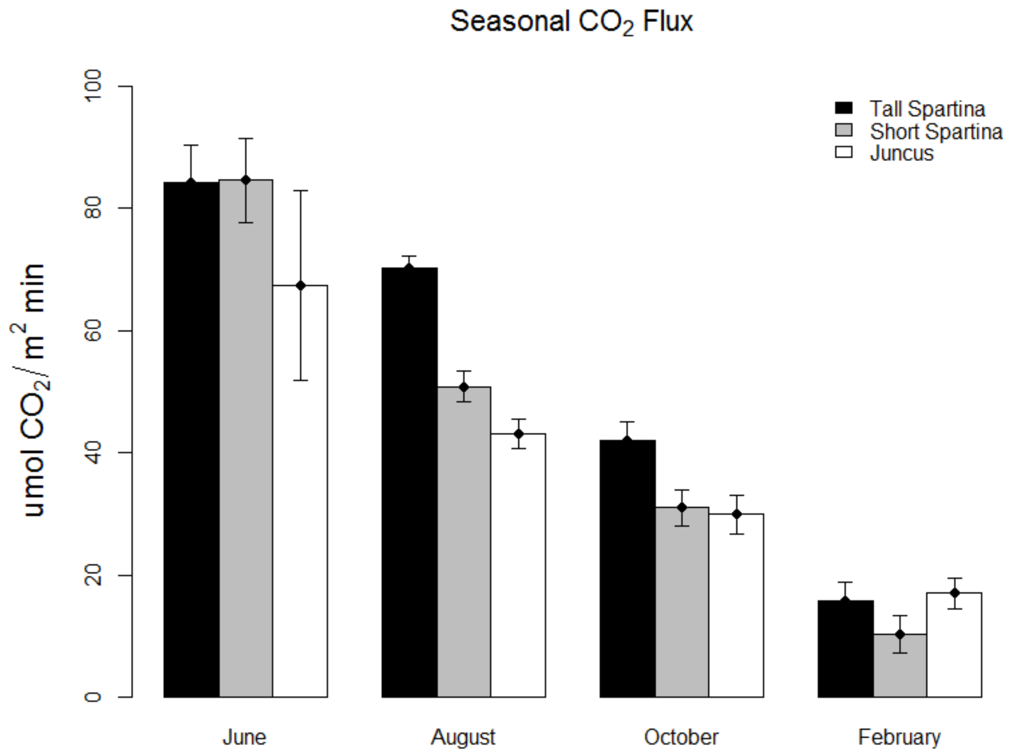
Table 2.2 Mean values of gas flux rate across all sites with standard error for plant zonation study

Plant Community	**Mean CH_4 Flux (μmol/min m^2)**	**Mean CO_2 Flux (μmol/min m^2)**	**Mean N_2O Flux (nmol/min m^2)**
Tall *Spartina*	0.2671 +/- 0.0366	78.258 +/- 6.189	Negligible
Short *Spartina*	0.0989 +/- 0.0136	64.407 +/- 6.261	Negligible
Dieback	0.0604 +/- 0.0152	36.841 +/- 14.780	Negligible
Juncus	0.0509 +/- 0.0178	49.838 +/- 7.260	Negligible



Significant comparisons	**p-values**
Tall Spartina-Short Spartina	$p<0.001$
Tall Spartina-Juncus	$p<0.001$
February-June	$p<0.001$
February-August	$p<0.001$
February-October	$p<0.001$
June-October	$p<0.001$

Figure 2.3 CH_4 flux rates for seasonal study by month with p-values for significant comparisons. Error bars reflect standard error.



Significant comparisons	**p-values**
Tall Spartina-Short Spartina	$p=0.038$
Tall Spartina-Juncus	$p<0.001$
February-June	$p<0.001$
February-August	$p<0.001$
February-October	$p<0.001$
June-August	$p<0.001$
June-October	$p<0.001$
August-October	$p<0.001$

Figure 2.4. CO_2 flux rates for seasonal study with p-values for significant comparisons. Error bars reflect standard error.

Table 2.3 Mean gas flux rates for seasonal changes study in either µmol CH_4/m^2 min or µmol CO_2/m^2 min with standard error

Season	**Plant community**	**CH_4 flux (µmol CH_4/m^2 min)**	**CO_2 flux (µmol CO_2/m^2 min)**	**N_2O flux**
June	Tall *Spartina*	0.239 +/- 0.0204	84.266 +/- 5.96	Negligible
	Short *Spartina*	0.102 +/- 0.0142	84.515 +/- 6.82	Negligible
	Juncus	0.0595 +/- 0.042	67.343 +/- 15.4	Negligible
August	Tall *Spartina*	0.138 +/- 0.006	70.249 +/- 1.88	Negligible
	Short *Spartina*	0.0786 +/- 0.009	50.833 +/- 2.54	Negligible
	Juncus	0.0681 +/- 0.0180	43.176 +/- 2.39	Negligible
October	Tall *Spartina*	0.0841 +/- 0.0236	42.108 +/- 2.97	Negligible
	Short *Spartina*	0.0464 +/- 0.0141	31.025 +/- 2.90	Negligible
	Juncus	0.0786 +/- 0.008	29.948 +/- 3.17	Negligible
February	Tall *Spartina*	0.0167 +/- 0.0063	15.889 +/- 3.01	Negligible
	Short *Spartina*	-0.162 +/- 0.0351	10.393 +/- 3.10	Negligible
	Juncus	-0.143 +/- 0.0241	17.083 +/- 2.49	Negligible

Table 2.4. Mean aboveground biomass on Jekyll Island during July 2014

Plant community	**Mean biomass (g dwt /m^2)**
Tall *Spartina*	847 +/- 77
Short *Spartina*	394 +/- 36
Juncus	486 +/- 47

Table 2.5. Mean aboveground biomass with standard error in (g dwt/m^2) for seasonal study on Sapelo Island

Mean aboveground biomass (g dwt/m^2)	**June**	**August**	**October**	**February**
Tall *Spartina*	686 +/- 72	858 +/- 99	993 +/- 101	400 +/- 34
Short *Spartina*	280 +/- 64	342 +/- 32	372 +/- 42	258 +/- 23
Juncus	454 +/- 43	490 +/- 39	594 +/- 84	372 +/- 31

Table 2.6. Greenhouse gas flux using chamber based methods across geographical areas

Study	Time of year	Latitude	CO_2 flux	CH_4 flux	N_2O flux
Chmura et al 2011	End of growing season	Bay of Fundy, Canada (45˚ 9' N, 64˚ 18' W)	150-183 µmol CO_2 /m^2 min	0.020-0.036 µmol CH_4 / m^2 min	1.757-4.9 nmol N_2O / m^2 min
Moseman Valtierra 2011	July, April, June	Plum Island Estuary, MA (42°44.782′N, 70°50.966′W)	258 µmol CO2/m2 min	0.097-0.581 µmol CH_4 / m^2 min	29 nmol N_2O / m^2 min
Bartlett et al 1987	Annual	Queens Creek, Williamsburg VA (37.27N, 76.71W)	Not measured	0-2.01 µmol CH_4/m^2 min	Not measured
Wigand et al 2015	Summer	North Inlet, SC (33°19'39" N, 079°09'58" W)	100.2 µmol CO_2/m^2 min	Not measured	Not measured
This study	Seasonal	Coastal GA (31.1° N, 81.3° W and 31.1° N, 81.4° W)	10.393 – 84.515 µmol CO_2/ m^2 min	-.143-.2671 µmol CH_4 / m^2 min	Negligible

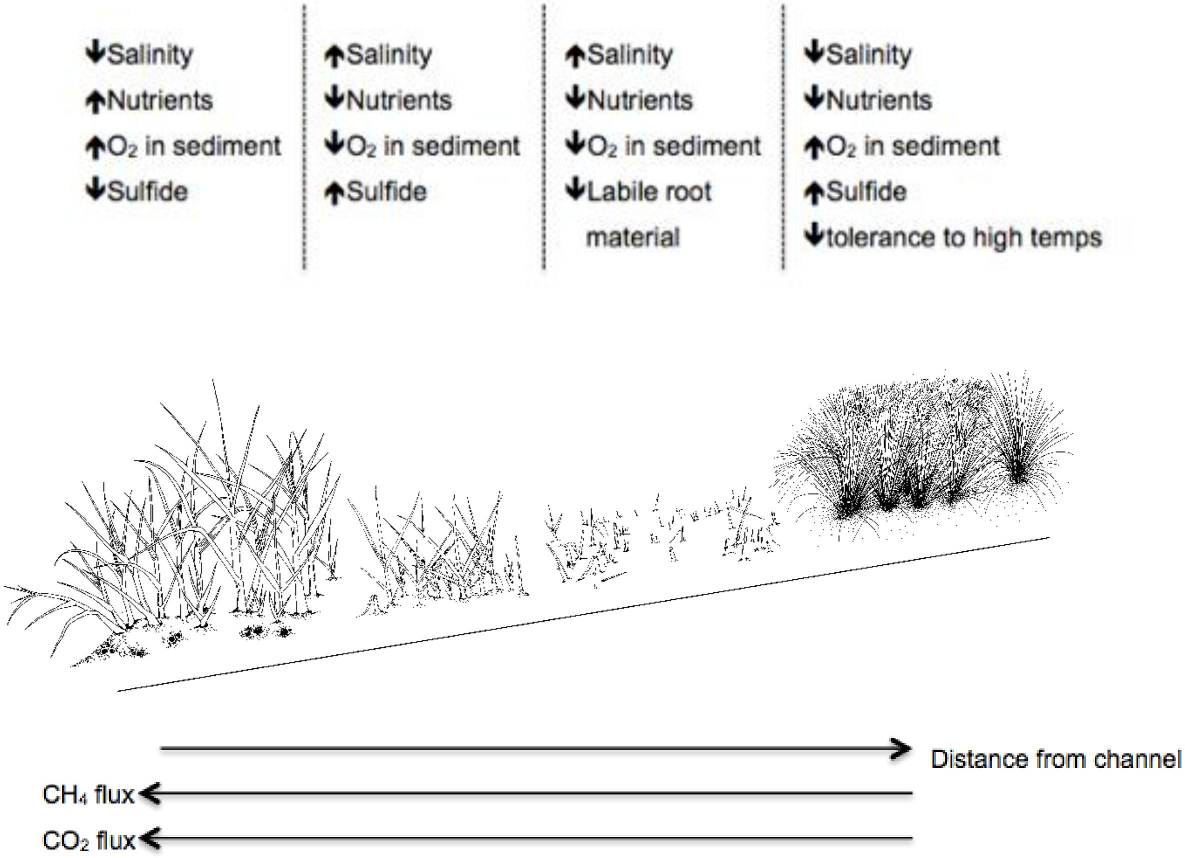


Figure 2.6. Biotic and abiotic characteristics with distance from tidal channel. Illustrated provided by Rebecca Atkins.

Table 2.7. Mean annual emissions by plant species on Sapelo Island. Percent cover values (80% accuracy) from Schalles et al. 2013

	Tall *Spartina*	**Short *Spartina***	***Juncus***
Mean CO_2 emissions	333 g C/m^2 yr	270 g C/m^2 yr	244 g C/m^2 yr
Mean CH_4 emissions	2.99 g C/m^2 yr	.102 g C/m^2 yr	.0158 g C/m^2 yr
Total carbon emissions	335.99 g C/m^2 yr	270.102 g C/m^2 yr	244.0158 g C/m^2 yr
% emissions from CH_4	.8%	.03%	.006%
% Cover on Sapelo*	16.2%	72.7%	3.6%

CHAPTER 3

CONCLUSION: POSSIBILITIES FOR SCALING UP USING SAPELO ISLAND AS A CASE STUDY

The potential for coastal ecosystems to act as carbon sinks has presented the opportunity to use climate finance as motivation for restoration and conservation activities (Nelleman et al 2009, Mcleod et al 2011, Pendleton et al. 2012, Grimsditch et al. 2013, Ullman et al 2013, Thomas 2014). Not all of the proposed mechanisms operate in a market context, but carbon markets that operate across different scales present one viable option to provide incentives for climate mitigation (Thomas 2014). Currently, there are two major types of carbon markets, compliance and voluntary. While still ineligible for a compliance market as of 2012, coastal wetland conservation and restoration activities are eligible for carbon offset generation on the voluntary market (Emmer et al. 2015). Carbon markets are based on the concept that carbon stored can be quantified and sold as credits to buyers who wish to offset emissions (Wylie et al. 2016). This can be achieved by either conserving historically-sequestered carbon pools or by restoring degraded areas (Crooks et al. 2011).

Scaling up GHG measurements to the landscape level is necessary for bringing coastal wetlands to market. Issues with relating phenomena across scales have emerged as a central problem in ecology (Levin 1992). While static chambers like those used in this study may not be an ideal method to quantify the greenhouse gas budget at large scales (Denman et al 2007), they demonstrate differences in flux rate across plant communities. In particular, these differences would be hard to detect using techniques like eddy covariance towers. The results presented here indicate that vegetation type can be used as a relative proxy for greenhouse gas flux rate to give broad scale estimates using other methods, like remote sensing. Methods exist to perform vegetation classifications within salt marshes with an overall accuracy as high as 90% (Hladik, Schalles and Alber 2013). These methods involve the use of hyperspectral remote sensing imagery in conjunction with LiDAR-derived Digital Elevation Models, all of which are publicly and freely available for most geographical areas within North America.

In order to assess the climate mitigation role of the salt marsh, various inputs and outputs need to be considered. Using Sapelo Island as a case study, we compare the inputs, consisting of annual net primary productivity and annual sediment carbon accumulation, to the outputs, consisting of carbon emissions, to determine whether the salt marshes there are acting as a sink or source of carbon to the atmosphere. Salt marshes in southern latitudes have peak biomass during the fall, and biomass measurements from this time represent an estimate for annual net aboveground primary productivity (O'Donnell and Schalles 2016). With root to shoot ratios established by previous work on Sapelo Island (Schubauer et al 1984, Pennings 2016), we can use October aboveground biomass measurements to estimate approximate belowground biomass for each plant species at this same time (Appendix I). While aboveground biomass has an annual turnover rate of 1, we multiply the belowground biomass by 0.7 based on belowground turnover rates in salt marshes in South Carolina (Dame and Kenny 1986).

These above and belowground biomass measurements can be converted to g C/m^2 yr using carbon conversions established in the Blue Carbon literature for salt marshes (0.45 for aboveground, 0.34 for belowground, Howard et al. 2014) (Table 3.1). This approximate measure for annual net primary productivity, along with estimates for annual carbon accumulation in the soil, represent the biotic inputs to the system (Table 3.2). For the salt marshes in the Altamaha River watershed, like those on Sapelo Island, abiotic carbon accumulation rate is estimated to be approximately 26.5 g C/m^2 yr (Loomis and Craft 2010, Ouyang and Lee 2014).

Using the values we determined for annual emissions, or outputs, in Chapter 2 (335.99 g C/m^2 yr, 270.10 g C/m^2 yr, 244.02 g C/m^2 yr), we can determine the marsh's role as a source or sink. When the inputs are compared to the outputs, we find that the Sapelo Island salt marshes behave as a sink, with the greatest annual carbon sequestration occurring in tall *Spartina* areas, followed by short *Spartina* and then *Juncus* (302 g C/m^2 yr, 141 g C/m^2 yr, 120 g C/m^2 yr, Figure 3.1). It appears the values for annual carbon sequestration rate follow the same zonation gradient as the vegetation types; with increasing distance from the tidal channel, sequestration values decrease. Despite having the highest emissions out, the inputs to the areas closest to the tidal channel appear to offset these losses, leading to overall high sequestration in this area. If we only used the aboveground biomass component without the belowground values, the marsh would be acting as a sink in tall *Spartina* and *Juncus*, but as a source in the short *Spartina* areas. This is significant as estimates show that the short *Spartina* areas compose nearly 73% of the salt marsh cover on Sapelo Island (Table 3.3).

Based on these estimates for annual carbon sequestration, we can use values from the voluntary carbon market along with estimates for spatial coverage of each vegetation type to put a price on the annual provision of this ecosystem service on Sapelo Island. Using a market value of $21/ton C yr (Schmidt et al. 2014) and a map of land cover with 80% accuracy (Schalles et al. 2013), the annual value of carbon sequestration on Sapelo Island is approximately $36,124.20 based on a total of 1720.2 tons C sequestered annually (Appendix II). Further exploration on how the uncertainty of the various budget components affect this value could provide information on the accuracy of these estimates; for example, a Monte Carlo approach could be used to estimate confidence intervals (Buckland 2006) allowing these values to be compared more directly to other global studies. This value for annual carbon sequestration services falls on the lower end of the range of values found at other salt marshes (Beaumont et al. 2013, Drake et al. 2015, Macreadie et al. 2017). Variation in value may be due to differences in estimates used for value per ton of carbon (Beaumont et al. 2014, Turner and Schaafsma 2015). Furthermore, prices for carbon are generally higher on the regulatory market (Emmer et al. 2015), lending support to continued research on blue carbon in order to open up this more profitable market to coastal wetlands.

With this level of detail on carbon sequestration rates by vegetation type, we can make predictions for how marshes may behave into the future with changes in vegetation cover. If we shift the percent cover so that tall *Spartina* covers all the salt marshes of Sapelo Island, we find that 3085 tons of C are stored annually for a total value of $64,785 on the voluntary carbon market. This shift nearly doubles the annual value for carbon sequestration, demonstrating the importance of understanding carbon sequestration rate by vegetation type. It is particularly relevant as tall *Spartina* cover is expected to increase into the next century with sea level rise (Watson et al. 2014), and ecosystem managers concerned with blue carbon will need to be able to make informed projections into the future.

Generally, estimates for carbon offsets tend to also include the avoided carbon emissions caused by the destruction of habitat in addition to the value of carbon sequestered (Ullman et al 2013). While not considered in this study, values taken from the literature suggest that Sapelo Island's avoided emissions value may be as high as \$5.4 million annually (Appendix III, Pendleton et al. 2012). However, it should be noted that subsequent publications have suggested that Pendleton's work overestimates these values (Macreadie et al. 2013). Some policymakers have explored the idea of including co-benefits into voluntary carbon markets (Hejnowicz 2015) which could provide an opportunity to include other valuable ecosystem services from the salt marsh into accounting and increase potential profits from the market. For example, the coastal protection services provided by the marsh have been valued from \$250 to 51,000 ha^{-1} yr^{-1}(Costanza et al 2008).

In order for a blue carbon project of this nature to be feasible the benefits will have to outweigh the costs. The potential costs include accounting for the carbon in the ecosystem, monitoring and verification, and oftentimes legal fees (AGEDI 2014, Emmer 2015). If remote sensing can be used, some of the costs for the initial carbon accounting can be greatly reduced. Projects of this nature operate on an economy of scale as well, where working in larger areas tends to be more cost-effective (AGEDI 2014). Thus, when considering the Georgia coast, it could be wise to include a larger area than Sapelo Island into a blue carbon project. Furthermore, an area like Sapelo Island may not even be considered for a project of this nature. To be eligible for carbon offsets, an area needs to either be at risk for development or be a degraded area that needs rehabilitation; that is to say, a project must demonstrate additionality, or that it would not occur without the financial benefits from the offsets (Emmer et al. 2015). Considering Sapelo's status as a LTER site, it likely would not meet this additionality requirement. However, if these carbon sequestration estimates can be generalized across the region, then there are certainly other at-risk areas along the Georgia coast where these estimates will be useful.

Overall, this study's work can lend support to regional estimates of GHG fluxes and to future carbon project planning, particularly since a lack of regional estimates is a key knowledge gap for blue carbon (Emmer et al. 2015). While methods used to calculate annual carbon sequestration values for Sapelo Island were not direct measurements, they can provide a broad estimate for the role of each vegetation type and its climate mitigation potential. Future projects will need to consider potential changes to the salt marsh into the future, and how those changes may impact carbon sequestration abilities. In particular, with reports predicting higher rates of sea level rise into the future, those factors associated with distance to channel and elevation, such as salinity, will be important to explore further (Hansen et al 2016). Furthermore, sustained declines in salt marsh biomass, like those observed in Georgia (O'Donnell and Schalles 2016), could impact blue carbon accounting into the future and impact long-term projections. Future investigation in this area can provide support for the conservation and restoration of coastal wetlands worldwide – support that is much needed considering current rates of habitat loss.

Table 3.1. Mean aboveground, belowground and total (above + below) biomass in (g C/m^2) by plant species. Conversions to g C/m^2 were done using estimates from Blue Carbon literature (0.45, 0.35, Howard et al. 2014)

	Mean ABG biomass (g C/m^2)	**Mean BG g C/m^2**	**Total (above + below) in g C/m^2**
Tall *Spartina*	446	165	611
Short *Spartina*	167	218	385
Juncus	267	71	338

Table 3.2. Sapelo Island carbon budget inputs, including average total carbon content (above and belowground) for each plant species and annual carbon accumulation rate for salt marshes in the Altamaha watershed (*Ouyang and Lee 2014)

	Inputs (g C/m^2 yr)
Tall *Spartina* mean total carbon content	611
Short *Spartina* mean total carbon content	385
***Juncus* mean total carbon content**	338
Annual C accumulation rate*	26.5

Table 3.3. Carbon budget outputs, or annual carbon emissions by vegetation type (*Values provided by Schalles et al. 2013)

	Outputs (g C/m^2 yr)
Tall *Spartina*	335.99
Short *Spartina*	270.102
Juncus	244.0158

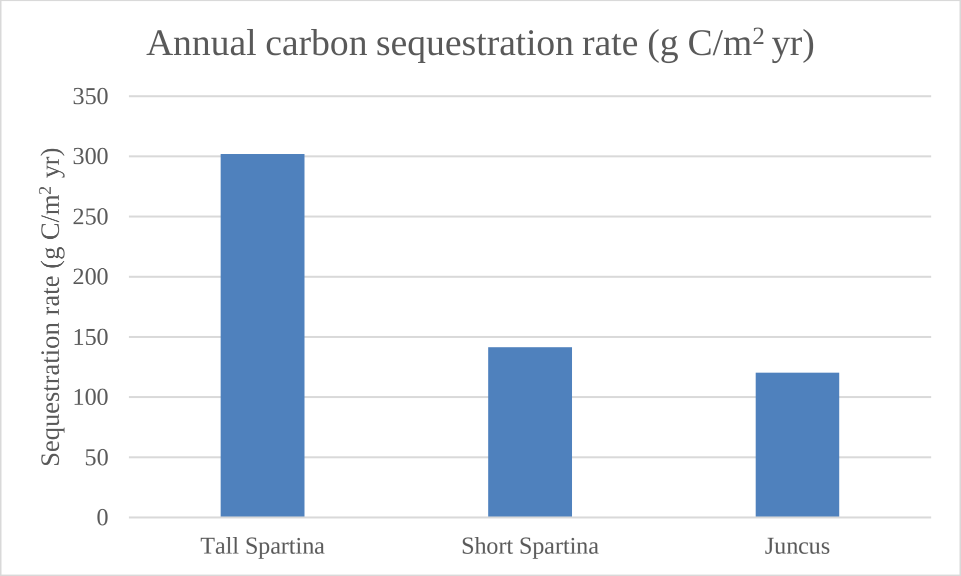


Figure 3.1. Estimate for annual carbon sequestration rate on Sapelo Island by vegetation type based on balance between annual inputs and outputs

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APPENDIX I
ROOT TO SHOOT RATIOS

Vegetation type	**June**	**August**	**October**	**February**
Tall	.96	.855	.70	1.3
Short	1.86	2.2	2.4	2.47
Juncus	.5	.5	.5	.5

(Schubauer 1984, Pennings 2016)

APPENDIX II
CALCULATIONS FOR VALUATION OF CARBON SEQUESTRATION ON SAPELO ISLAND

	C sequestered in g C/m^2 yr	**Area on Sapelo in m^2**
Tall *Spartina*	302	1,623,200
Short *Spartina*	141	7,284,500
Juncus	120	360,000

	C sequestered in g C/yr
Tall *Spartina*	490,206,400
Short *Spartina*	1,027,114,000
Juncus	43,200,000

Using conversion rate of 1 gram = 1.10231e-6 tons

	Tons C/yr
Tall *Spartina*	540.4
Short *Spartina*	1132.2
Juncus	47.6
TOTAL	1720.2

1720.2 tons C X $21/t C * (*Value for ton C based on the voluntary carbon market, Schmidt et al. 2014)

= $36,124.20 for the annual carbon sequestration services on Sapelo Island

APPENDIX III
AVOIDED CARBON EMISSIONS CALCULATION FOR SAPELO ISLAND

.55PgC/2.2Mha (Represents potential avoided annual emissions from salt marshes based on Pendleton et al 2012)

=276 tons C/ha

276 tons C/ha * 926 ha of salt marsh (on Sapelo Island) = 255,576 tons C of avoided emissions

255,576 tons C * $21 (value on the voluntary carbón market)

= ~$5.4 million for annual avoided carbon emissions on Sapelo Island