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Carbon Dioxide Fluxes and Plants Interactions across the Succession of a Created Brackish Marsh in Southwestern Louisiana

Andy T. Muench
Louisiana State University and Agricultural and Mechanical College

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CARBON DIOXIDE FLUXES AND PLANT INTERACTIONS ACROSS THE SUCCESSION OF A CREATED BRACKISH MARSH IN SOUTHWESTERN LOUISIANA

A Thesis

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Master of Science

in

The Department of Oceanography and Coastal Sciences

Andy T. Muench
B.S., University of Wisconsin-Madison, 2015
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ABSTRACT

The purpose of this study was to examine: 1) carbon dioxide (CO$_2$) fluxes in different plant communities in a created and natural brackish marsh and 2) the role of an early colonizing species, *Spartina alterniflora*, in facilitating or suppressing a later colonizer and higher marsh species, *Spartina patens*. CO$_2$ fluxes were measured in four key successional stages: 1) non-vegetated sediment of a newly created marsh; 2) *Spartina alterniflora*-dominated areas of a newly created marsh; 3) *S. alterniflora*-dominated natural marsh; and 4) *Spartina patens*-dominated natural marsh. *Spartina alterniflora*-dominated areas were sinks for CO$_2$ in both created and natural marsh with an average CO$_2$ uptake rate of 7.0 ($\pm$ 1.0) $\mu$mol m$^{-2}$s$^{-1}$. Bare sediment in the created marsh and *S. patens* in the natural marsh had approximately net neutral CO$_2$ fluxes with bare sediment averaging 0.2 ($\pm$ 1.0) $\mu$mol m$^{-2}$s$^{-1}$ of CO$_2$ efflux and *S. patens* areas averaging 0.2 ($\pm$ 1.0) $\mu$mol m$^{-2}$s$^{-1}$ of CO$_2$ uptake. CO$_2$ fluxes were found to be mainly determined by plant community type and significantly related to aboveground biomass. Because vegetation develops much faster than soil properties in created marshes, these findings indicate that CO$_2$ fluxes can reach similar levels to that of natural marshes relatively quickly following marsh creation. To determine *S. alterniflora* interactions with *S. patens* in developing created marshes, *S. patens* were transplanted into either bare sediment or within *S. alterniflora* clones. *Spartina patens* transplanted into the bare sediment expanded at a rate of 33.0 ($\pm$ 9.0) cm$^2$month$^{-1}$, and had a stem density of 2115 ($\pm$180) stems m$^{-2}$. *Spartina patens* transplanted within *S. alterniflora* contracted in area at a rate of -3.0 ($\pm$ 3.0) cm$^2$month$^{-1}$, and had a stem density of 1362.5 ($\pm$164) stems m$^{-2}$. These results indicate that *S. alterniflora* presence impedes *S. patens* establishment in a created marsh. The created marsh was found to have a large reserve of available nitrogen in the bare sediment possibly favoring *S. alterniflora*. Together these studies
illustrate that created marsh plant community development is important for CO$_2$ fluxes but plant iterations may differ in a young created marsh from a natural marsh.
INTRODUCTION

Coastal wetlands are being lost at high rates worldwide due to sea level rise, human development, and land subsidence. The coasts of Louisiana are experiencing some of the largest coastal wetland losses in the world. To help mitigate some of these coastal wetland losses marshes are being created in coastal regions. This thesis focused on a marsh created from dredged material in the southwestern Louisiana coast, and how its functions and attributes compared to a natural marsh.

When creating and restoring ecosystems it is important to evaluate if it either has similar functions and characteristics of a natural ecosystem or can develop to be similar to natural marshes. This thesis looked to analyze two aspects of a newly created marsh function and characteristics. The first chapter compared CO₂ fluxes in both a newly created marsh and a natural marsh in varying plant communities. Natural coastal marshes function as carbon sinks so it is important to understand how CO₂ fluxes compare in a created marsh with different soil and plant community characteristics. The second chapter of this thesis looked at an early colonizing plant interactions with a later successional plant species. This is to help determine how plant communities develop in created marshes. Overall both these chapters will increase the understanding of created marshes functions and development in southwestern Louisiana.
CHAPTER 1. CARBON DIOXIDE EXCHANGE ACROSS SUCCESSIONAL BRACKISH PLANT COMMUNITIES IN SOUTHWESTERN LOUISIANA

1.1. Introduction

Coastal saline marshes are important global carbon sinks as these ecosystems have been found to be extremely productive (Odum, 1988), can sequester large amounts of carbon per area relative to terrestrial ecosystems (Mcleod et al. 2011; Chmura et al. 2003) and, unlike freshwater wetlands, have relatively low emissions of methane gas (Brevik and Homburg, 2004). Carbon dioxide (CO₂) fluxes play a large role in saline marsh carbon sequestration as the carbon fixed from primary productivity can be potentially stored in the soil for long periods of time. Despite being important carbon sinks, coastal marshes are being lost at an alarming rate (Dunbar et al. 1992; Sanzone and McElroy 1998). To mitigate wetland loss, coastal marshes are being created to restore important services like carbon sequestration. The development time of structural properties in created marshes can vary with vegetation developing much quicker (5-10 years) than soil characteristics (30-50 years, Craft et al. 2003). Few studies, however, have focused on ecological processes (Cornell et al. 2007; Poach and Faulkner 1998) of created marshes.

As the initial colonizer of newly created or developing marshes, benthic algae, including macroalgae and microphytobenthos, may be the first to contribute to carbon cycling (Craft et al. 2003; Zheng et al. 2004). Benthic algae can be highly productive, in some cases accounting for 25 – 70% of marsh primary productivity (Zedler et al. 1978, Adamus 1988). In the bare sediment of newly created marshes, benthic algae are able to colonize within weeks (Levin and Talley, 2002; Underwood, 1997), providing a number of important functions including C-fixation, food for microorganisms, sediment organic matter, and sediment stabilization (Levin and Talley, 2002; Craft et al. 2003; Zheng et al 2004; Graham et al. 2009). Algal communities can become representative of natural marshes with respect to biomass, chlorophyll a, and species...
composition within two years of creation (Janousek et al. 2007). As created bare soil marshes transition to vegetated ecosystems, algal primary productivity may become limited by thick plant canopies, which reduce light penetration to the sediment (Zedler, 1980). With the transition from algal- to plant-dominated ecosystems, carbon fluxes are predicted to increase associated with higher net primary productivity of vascular plants (Sheng, 2015; Picek et al., 2007).

In the northern Gulf of Mexico, created marshes undergo a successional transition from non-vegetated sediment to full coverage by Spartina alterniflora within 5 to 10 years (Proffitt et al. 1999; Proffitt et al. 2005). Microbial respiration increased following plant colonization of bare sediments, associated with greater sediment organic carbon inputs by the plants (Yang et al. 2016; Picek et al. 2007). Sediment organic matter content has been found to increase with marsh age as plants introduce organic material to the sediment, potentially causing a shift in the relative magnitude of ecosystem productivity and respiration (Craft et al. 2003). Thus, the early stages of plant colonization are predicted to be characterized by larger carbon dioxide (CO₂) exchanges than bare sediments, associated with higher rates of C-fixation and higher rates of both plant and sediment respiration. What is not known is how gross ecosystem production (GEP) and ecosystem respiration (ER) evolve over time as both the plant community and ecosystem develops. As a whole, carbon fluxes represent the difference between gross CO₂-fixation (GEP) and CO₂ lost through respiration (ER), as net ecosystem CO₂ exchange (NEE). When GEP exceeds ER, there is a net C uptake by the marsh. Conversely, when ER exceeds GEP, there is a net release of CO₂. These CO₂ fluxes are determined by photosynthetic uptake and fixation of CO₂ by plants and algae, and by cellular respiration of CO₂ by plants, algae, and respiration by microorganisms decomposing organic matter.
The rapid expansion and growth of *S. alterniflora* in a developing marsh (Proffitt et al. 1999, Proffitt et al. 2005) may cause a spike in marsh productivity which could shift NEE of the marsh. Net primary productivity of *S. alterniflora* in created marshes can exceed that within natural marshes with the youngest created marshes having the highest productivity, which decline as marshes age (Edwards and Mills, 2005). Greater productivity of *S. alterniflora* in created salt marshes relative to natural marshes may allow for higher rates of NEE, indicating that created marshes have a greater carbon sink potential than natural marshes. However, Cornell et al. (2007) found no significant difference in NEE between a *S. alterniflora* dominated natural marsh and a newly created marsh with significantly less plant biomass. *Spartina alterniflora* in the created marsh had greater leaf nitrogen content which can be indicative of greater photosynthetic rates, which was hypothesized to contribute to greater productivity per unit biomass (Cornell et al. 2007). This suggests that differences in nitrogen availability and/or nitrogen uptake efficiency influence CO₂ fluxes. The expansion of *S. alterniflora* in a newly created marsh will eventually become limited by intra- and/or inter-specific competition for space, light and nutrients. A shift in plant community can occur in the higher elevations of marshes as *S. alterniflora* is outcompeted by less flood tolerant species such as *Spartina patens* (Bertness, 1991). A change in dominant species may also result in a shift in CO₂ exchange. For example, higher NEE was measured in a high marsh restoration site dominated by *S. patens* than in low marsh restoration sites dominated by *S. alterniflora* (Artigas et al. 2015). A higher NEE in *S. patens* areas may have been related to a higher above and belowground NPP than *S. alterniflora* (Hopkinson et al., 1978, 1980). Higher marsh elevations also experience less tidal inundation, which can result in greater sediment microbial activity and respiration (Miller et al. 2001) possibly increasing ER.
As marshes age and experience vegetation shifts, nitrogen availability may play a large role in influencing CO$_2$ fluxes. Nitrogen additions have been found to significantly increase the photosynthetic rates of $S.$ alterniflora (Dai and Wiegert, 1997). Photosynthetic rates of primary producers have been found to be positively related with NEE (Strachan, 2016; Nobrega, 2008; Yurova, 2007). It was hypnotized that $S.$ alterniflora had a larger NEE per biomass in the newly created marsh because leaf nitrogen content was higher relative to a natural marsh indicating greater photosynthetic rates (Cornell et al. 2007). The high leaf nitrogen content in the created marsh was unexpected as created marshes tend to have less sediment nitrogen than natural marshes (Craft et al. 1999; Zedler and Callaway, 1999). This may be indicative that $S.$ alterniflora growing in the created marsh are either more efficient at nitrogen uptake, have a more extensive belowground biomass for greater nutrient uptake, have less competition for nitrogen, or have less nutrient uptake limitations due to higher redox potential from less sediment organic material in the created marsh. This study will aim to add greater understanding on how nitrogen differences between natural and created marshes effect plant communities NEE.

For this study, CO$_2$ fluxes (GEP, ER, NEE) were measured bi-monthly in static chambers from May to September in four successional stages of marsh development, two in a newly created marsh: (1) non-vegetated sediments and; (2) rapidly expanding $S.$ alterniflora clones; and two in a natural marsh: (3) $S.$ alterniflora; and (4) $S.$ patens. NEE was expected to be greater in vegetated as compared to bare sediments, primarily associated with a greater GEP from higher rates of carbon-fixation (Sheng, 2015). Rapidly expanding $S.$ alterniflora in the newly created marsh was predicted to have higher overall NEE than that in a natural marsh due to a lack of competition, increased photosynthetic rates, greater utilization of nutrients resulting in greater productivity, and reduced ER from less sediment organic matter and lower microbial respiration.
rates (Cornell et al. 2007; Edwards and Mills, 2005; Craft et al. 1999; Craft et al. 2003). Based on previous findings, NEE was hypothesized to be greater in *S. patens* than *S. alterniflora* in the natural marsh (Artigas, 2015). Overall, it was hypothesized that NEE increases with plant colonization in created marshes, decreases as a low elevation marsh develops, and increases with successional shifts in the plant community of the mid-high elevated marshes.

1.2. Methods

1.2.1. Site Study

This research was conducted in Sabine National Wildlife Refuge (SNWR) between the Sabine and Calcasieu rivers on the Gulf coast in southwestern Louisiana. Salt water intrusion has resulted in marsh loss at SNWR due to its close proximity to the Calcasieu River ship channel (U.S. Fish and Wildlife, 2013). Dredging of the Calcasieu channel in the 1930s has led to salt water intrusion into SNWR causing vegetation death and conversion to open water in previously oligohaline marshes (DeLaune et al., 1983). Due to the loss of wetland area, six marshes have been created over the last 34 years using sediments from the maintenance dredging of the Calcasieu ship channel (Inman, 2014). All marshes were created by pumping a slurry of dredge sediments into open water until elevated enough to support a salt marsh ecosystem. All marshes were naturally colonized by vegetation. The average elevation of the studied created marsh was 20.0 ± 2.8 cm, while the average height of the natural marshes was 10.2 ± 1.7 cm (NAVD88, Abbott and Quirk, 2017). Hydrology in this system was affected by tides, tidal gate openings, wind, and precipitation, making the water levels difficult to predict and control for based on tidal predictions (Bernier et al., 2011). Study locations for the present study were a newly created marsh constructed in 2015 and a nearby natural marsh (Figure 1.1). At the time of the study (2017), the young created marsh had sparse clones of *S. alterniflora*, which expanded over the
course of the study period. The natural marsh was dominated by a mix of species with stands of *S. alterniflora* at lower elevations and *S. patens* at higher elevations.

![Figure 1.1](image-url) Study locations in Sabine National Wildlife Refuge in Louisiana, USA including the Natural and 2015 Created marshes.

1.2.2. Stages of Succession

Four stages of marsh succession were the focus of this study, two in the created marsh:

1. non-vegetated sediments where the dominant primary producers were likely algae and microphytobenthos; and
2. newly colonized *S. alterniflora* clones; and two in the natural marsh:

3. *S. alterniflora*; and
4. *S. patens*.

1.2.3. Carbon flux

Carbon dioxide fluxes were measured in five replicate plots at each successional stage (n=5). Carbon dioxide flux was measured using the static chamber method (Rolston, 1986; Lindau and DeLaune, 1991; Yu et al. 2013). Gas chambers for the vegetated treatments consisted of a 30 cm³ acrylic base unit placed to a depth 10 cm below the surface approximately one month prior to measurements. The chamber also consisted of 1 to 3 stackable 30 cm³ acrylic chambers, which were stacked to the height of the plant during measurement. In the non-vegetated
treatment, a base and one top unit were placed on the day of the measurement and allowed to sit for 20 minutes prior to measurement. Chambers were enclosed with the upper-most unit having a rubber stopper with plastic tubing connecting the inside of the chamber to an EGM-4 (PP Systems©, Amesbury, MA), which measured CO2 concentration in the chamber to the nearest part per million by infra-red gas analysis techniques. To prevent altering CO2 concentrations in the chambers during measurement, air was recycled from the EGM-4 back to the chamber via tubing. To ensure an air tight seal, the top of all the stacked chambers had a water-filled collar to limit external gas diffusion into the chamber. Carbon dioxide concentration in the chamber was measured at 1 minute intervals for a total of 20 minutes (10 to 15 minutes in September due to time constraint of shorter days) or until the CO2 concentration was below detection limits (~250 ppm). Net ecosystem exchange (NEE) was measured using transparent chambers while ecosystem respiration (ER) was measured using opaque chamber units to prevent photosynthetic processes. For the ER measurements, 20 minutes were allowed following placement of opaque chamber for equilibration before measuring CO2 concentrations. Carbon dioxide flux data was collected three times over the growing period in May, July, and September of 2017.

Net ecosystem exchange and ER have been found to vary with temperature and levels of photosynthetically active radiation (PAR) (Neubauer et al., 2000; Baldocchi et al., 2001; Larcher, 2003). Therefore temperature and PAR were measured along with CO2 using a probe attached to the EGM-4 (PP Systems©, Amesbury, MA).

1.2.4. CO2 Calculations

NEE and ER were determined by linear regression of CO2 change during the sampling interval where a strong linear slope was present. The slope of that regression was used as either the NEE (clear chamber) or ER (opaque chamber). The slope for NEE was only taken when full
sunlight occurred in the sampling interval which is generally 1000 µmol m\(^{-2}\)s\(^{-1}\) or greater (Cornell, 2007). Examples of the raw CO\(_2\) ppm data are presented in Figure 1.2.

Figure 1.2. Raw CO\(_2\) concentrations in representative plots for each plant community in May, July, and September under light and dark conditions in a newly created (CM) and natural marsh (NM) in Sabine National Wildlife Refuge, Calcasieu, Louisiana.
The amount of CO$_2$ in the chamber at a given time was calculated as:

\[ CO_2 \mu\text{mol} = \frac{CO_2 \text{ ppm}}{(22.4 \times (273+C)/273)} \times 27X \]

The coefficient X is the number of chamber units stacked at each plot. Each chamber unit contains 27 liters of air, and therefore X was multiplied by 27. The coefficient C is the temperature (°C) at the time of measurement. It should be noted that 22.4 is the molar volume of CO$_2$ at the pressure 1 ATM and 0°C. Since our sites are at sea level they are generally at 1 ATM but the temperatures within the chambers were between 25°C and 40°C so temperature was corrected for in the above equation.

The GEP was calculated as:

\[ GEP = -(\text{NEE}) + ER \]

A negative NEE indicates carbon uptake. To determine GEP, NEE is multiplied by negative 1 and added to ER. It was assumed that respiration rate during the dark incubations was equal to the respiration rate during daylight conditions, but this may not be the case as leaf respiration tends to increase under dark conditions (Brooks and Farquhar, 1985; Kromer, 1995; Atkin et al. 1997; Schulz, 2003).

1.2.5. Elevation

Elevation (NAVD88) was measured at each plot using Leica Real Time Kinematic GS14. Three elevations were taken at each plot and then averaged to estimate the elevation. Horizontal and vertical accuracies of the measurements were 1 and 2 cm, respectively.

1.2.6. Sediment Chlorophyll $a$

To examine variation in algal biomass across treatments, sediment was collected adjacent to each gas exchange plot for chlorophyll $a$ analysis during May, July, and September. Chlorophyll $a$ content was determined from the top 2 cm of sediment by using sonication and 90% acetone (modified from Welschmeyer, 1994). Approximately 0.2 g of the sampled sediment
was placed in 90% acetone, centrifuged at 5000 X g for 5 minutes, and then sonicated. Following sonication for 30 seconds, the samples were placed in a freezer for one day and then centrifuged again at 5000 X g for 5 minutes again the next day. Chl a content was then measured using a fluorometer (Turner Designs TD-700) after the last centrifuging.

1.2.7. Extractable Ammonium and Potentially Mineralizable Nitrogen

Extractable ammonium (NH$_4^+$) is used to indicate the availability of nitrogen for primary producers in marsh sediment measured as mg of nitrogen per kg dry sediment. Potentially mineralizable nitrogen (PMN) is the measure of the rate at which extractable ammonium increases with time in the sediment and indicates the rate at which nitrogen becomes available in the sediment via the microbial community (White and Reddy, 2000).

Sediment cores (7 cm diameter by 20 cm depth) were collected in May 2017 at transplant plots using a plastic core. A 20 cm depth was selected because $S$. *patens* and $S$. *alterniflora* typically have the majority of belowground biomass in the upper 20 cm (Windham, 2000; Gross et al. 1991). Two depth intervals of 0-10 and 10-20 cm were sectioned and analyzed to determine whether there was a difference in nutrient availability with depth and with the presence of plants.

For extractable NH$_4^+$, 5 g of homogenized sediment sample from each depth section of each core was placed into a 50-ml centrifuge tube with 20 ml of 2 mol L$^{-1}$ KCL. Tubes were placed into a horizontal shaker for one hour and then centrifuged at 5000 g for 10 minutes. The samples were filtered through 0.45 um glass fiber filters into 20 ml disposable scintillation vials where one drop of concentrated H$_2$SO$_4$ was added. Samples were refrigerated at 4°C until analysis. Extractable NH$_4^+$ was determined using an AQ2 Automated Discrete Analyzer (Seal Analytical Inc.) via colorimetric analysis (USEPA, 1993).
The PMN was determined by measuring extractable NH$_4^+$ at days 0, 2, 5, and 10 of incubation. Day 0 was determined from initial extractable NH$_4^+$ concentrations from the soil samples. Three subsamples of each core were homogenized and placed into three serum bottles with rubber caps and aluminum seals. To produce an anaerobic environment, the gas in each bottle was evacuated and replaced with 99.99% N$_2$. The bottles were then injected with water at a salinity of 10 psu, approximately the average salinity at the study sites. The serum bottles were then placed into an incubator (IS-971R, Jeio Tech) at 40°C and continually oscillating at 100 rpm. The replicate serum bottles were removed at day 2, 5, and 10 and extracted with 25 ml of 2 mol L$^{-1}$ KCl. Vials were placed into a horizontal shaker for one hour and then centrifuged at 5000 g for 10 minutes. The samples were filtered with 0.45-um filter into 20 ml disposable scintillation vials where one drop of H$_2$SO$_4$ was added. The vials of sample were refrigerated at 4°C until analysis. Extractable ammonia was determined using an AQ2 Automated Discrete Analyzer (Seal Analytical Inc.) for colorimetric analysis of the samples (USEPA, 1993). PMN was determined for each sample using linear regression of extractable NH$_4^+$ vs time.

1.2.8. Sediment bulk density and organic matter content

Homogenized subsamples of sediment cores used for extractable NH$_4^+$ and PMN were also used to determine bulk density and organic matter content at 0-10 and 10-20 cm depths. Subsamples were weighed and dried to a constant weight at 60°C. The dry fraction of the soil was then estimated by dividing the dry weight of the sample by the wet weight. Bulk density was calculated as the wet mass of the sediment of the whole core multiplied by the dry fraction and divided by the volume of the core section. A 1 g portion of the dried subsample was then combusted in a muffle furnace at 550°C for four hours. Soil organic matter content (SOM) was calculated by the proportion of sample lost on ignition (LOI).
1.2.9. Biomass estimation

Aboveground biomass was estimated using stem height and density measurements taken within the study plots in July and September 2017. The height of up to 15 stems were taken in each plot. Stems density was determined by counting the number of stems within 0.09 m$^2$ for $S. alterniflora$, 0.01 m$^2$ for $S. patens$. To estimate the biomass of $S. alterniflora$ in the natural marsh the following equation was used (Quirk, unpublished data):

$$AB = -2032 + 521(\log \text{height}) + 136(\log \text{density})$$

The equation used for $S. alterniflora$ in the natural marsh was not used for $S. alterniflora$ in the created marsh because the relationships between stem height, density and biomass may differ due to the different soil conditions of the created marsh. For $S. alterniflora$ in the created marsh and $S. patens$ in the natural marsh a coefficient relating height and density was derived from data in a previous study in the same marshes that measured stem height, stem density, and biomass (Abbott and Quirk, 2017). The coefficient was determined from the average biomass divided by the product of stem density and average stem height.

The equation used for $S. alterniflora$ in the created marsh was:

$$AB = 0.0755(\text{height})(\text{density})$$

The equation used for $S. patens$ in the natural marsh was:

$$AB = 0.0058(\text{height})(\text{density})$$

For all equations, height was measured in cm, density in stems m$^{-2}$, and biomass in g m$^{-2}$.

1.2.10. Data Analysis

One-way analysis of variance was used to test whether CO$_2$ fluxes (GEP, ER, and NEE) differed among successional stages within and across sampling dates. Interactions between succession stage and date sampled were not tested in a two-way analysis because marsh flooding
was not controlled between dates as precipitation and not tides played a large role in marsh water level. A separate one-way analysis of variance was used to test differences in Chlorophyll a, extractable NH$_4^+$, PMN, bulk density and sediment organic matter content between successional stages. Regression analysis was used to examine the influence of Chlorophyll a, extractable NH$_4^+$, PMN, bulk density and sediment organic matter content on CO$_2$ flux rates. All data were tested for normality, and log transformed as necessary. Data were analyzed using JMP SAS 13. For all of the statistical analysis significance was determined by $\alpha = 0.05$.

1.3. Results

1.3.1. Environmental Conditions

Elevation. Marsh plot elevations ranged from 0.08 to 0.20 m (NADV88). *Spartina patens* in the natural marsh was an average of 6 cm higher in elevation than the bare sediment plots in the created marsh (0.16 ± 0.01 and 0.10 ± 0.01 m, NAVD88, respectively; $F_{3, 19} = 5.52$, $p = 0.009$). *Spartina alterniflora* plots in the created and natural marshes did not statistically differ from the other sites and averaged 0.13 ± 0.01 m, NAVD88.

Chl a. Chlorophyll a concentrations were greater in the *S. alterniflora* natural marsh community (3970 ± 660 mg Chl a kg$^{-1}$ sediment) than all other communities (972 ± 660 mg Chl a kg$^{-1}$ sediment; $F_{3, 59} = 9.40$, $p < 0.001$).

Biomass. There was no significant difference among the estimated biomass of *S. alterniflora* in the natural and created marsh (1054 g ± 83, 1026 g ± 83, respectively), and *S. patens* (941 g ± 83) in the natural marsh.

Sediment Nitrogen. The amount of extractable NH$_4^+$ in the created marsh bare sediment at a depth of 10 to 20 cm was significantly greater than that of all the vegetated plant communities ($F_{3, 19} = 12.6$, $p < 0.001$; Table 1.1). This indicates that there is a large reservoir of available
nitrogen in May at the non-vegetated created marsh. Despite high amounts of extractable NH$_4^+$ at
the lower depth, the bare sediment had the lowest amount of extractable NH$_4^+$ in the upper 10 cm
as compared to all other community types. The communities with plants did not significantly
differ in extractable NH$_4^+$ content at either depth interval (Table 1.1).

Table 1.1. Sediment bulk density, loss on ignition, extractable NH$_4^+$, and PMN (± SE) for depths
of 0-10 cm and 10-20 cm taken in May 2017 at Sabine National Wildlife Refuge, Calcasieu,
Louisiana for four community types. A one way analysis of variance and post hoc Tukey test
was conducted for each sediment measurement for both depths to find significant differences
between community types, different letters indicate significant differences between communities.
B = created marsh bare sediment, SC = *Spartina alterniflora* in the created marsh, SN = *Spartina
alterniflora* in the natural marsh, and SPN = *Spartina patens* in the natural marsh.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Depth (cm)</th>
<th>Vegetation Type</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>B</td>
<td>SC</td>
</tr>
<tr>
<td><strong>Bulk Density (g/m$^2$)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0-10</td>
<td>0.81 ± 0.04$^a$</td>
<td>0.77 ± 0.04$^a$</td>
</tr>
<tr>
<td>10-20</td>
<td>0.68 ± 0.05$^{ab}$</td>
<td>0.74 ± 0.05$^a$</td>
</tr>
<tr>
<td><strong>SOM (organic soil mass g / total soil mass g)</strong></td>
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<td></td>
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<tr>
<td>0-10</td>
<td>0.10 ± 0.03$^a$</td>
<td>0.11 ± 0.03$^a$</td>
</tr>
<tr>
<td>10-20</td>
<td>0.10 ± 0.02$^a$</td>
<td>0.11 ± 0.02$^a$</td>
</tr>
<tr>
<td><strong>Extractable NH$_4^+$ (mg N kg$^{-1}$ sediment)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0-10</td>
<td>2.0 ± 8.0$^a$</td>
<td>4.3 ± 8.0$^{ab}$</td>
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<tr>
<td>10-20</td>
<td>45.6 ± 3.0$^a$</td>
<td>1.2 ± 3.0$^b$</td>
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<tr>
<td><strong>PMN (mg N kg$^{-1}$ sediment d$^{-1}$)</strong></td>
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<td></td>
</tr>
<tr>
<td>0-10</td>
<td>2.7 ± 2.0$^a$</td>
<td>3.7 ± 2.0$^a$</td>
</tr>
<tr>
<td>10-20</td>
<td>4.0 ± 3.0$^a$</td>
<td>4.3 ± 3.0$^{ab}$</td>
</tr>
</tbody>
</table>
PMN rates were generally higher in the natural marsh communities than in the created marsh communities (p < 0.001) indicating the rate that nitrogen becomes available to plants is higher in natural marshes. One exception was a similar PMN in *S. patens* in the natural marsh and *S. alterniflora* in the created marsh at 10-20 cm depth (Table 1.1).

Sediment bulk density and organic matter content. Sediment bulk density at 0-10 cm depth was approximately three times greater in the created marsh than in the natural marsh (F<sub>3,19</sub> = 63.6, P < 0.001; Table 1.1). Bulk density at the 10–20 cm depth in *S. alterniflora* in the natural marsh was lower than in the created marsh (F<sub>3,19</sub> = 10.1, p = 0.001; Table 1.1). Bulk density was generally consistent with depth within the same community.

Soil organic matter was significantly greater in the natural marsh than in the created marsh at both 0-10 (F<sub>3,19</sub> = 15.7, P < 0.001) and 10–20 cm depths (F<sub>3,19</sub> = 13.3, P < 0.001). There were no significant differences in SOM between plant community types within the same marsh (Table 1.1).

1.3.2. CO₂ fluxes

The bare sediment had approximately 13 µmol m⁻² s⁻¹ less GEP and 8 µmol m⁻² s⁻¹ less ER than the vegetated plots (all p values ≤ 0.003, Figure 1.3). *S. patens* had a similar average NEE to the bare sediment despite having significantly higher rates of ER and GEP throughout the experiment (all p values ≤ 0.003, Figure 1.3). *S. patens* community was a source for CO₂ in May, a sink in July, and then as a relatively small sink in September (Table 1.2). This change from a source to a sink in *S. patens* was likely due to an increase in productivity after May.

Overall, average GEP was significantly lower in *S. patens* than in *S. alterniflora* (p = 0.001) due to *S. patens*’ low May GEP (Figure 1.3). There was no significant difference in ER among the vegetation communities with all of them generally having significantly higher rates of ER than
the bare sediment. *Spartina alterniflora* in the natural and created marsh had similar rates of GEP and ER throughout the experiment, resulting in a similar NEE. *Spartina alterniflora* was a consistent sink for CO$_2$ in both the natural and created marsh during the three sampling dates.

Table 1.2. Gross ecosystem production, ecosystem respiration, and net ecosystem exchange of CO$_2$ (± standard error) in May, July, and September 2017, in a created and natural marsh in Sabine National Wildlife Refuge, Calcasieu, Louisiana. B = created marsh bare sediment, SC = *Spartina alterniflora* in the created marsh, SN = *Spartina alterniflora* in the natural marsh, and SPN = *Spartina patens* in the natural marsh

<table>
<thead>
<tr>
<th>Vegetation Type</th>
<th>B</th>
<th>SC</th>
<th>SN</th>
<th>SPN</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>GEP (µmol m$^{-2}$s$^{-1}$)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>0.0 ± 2.8</td>
<td>15.0 ± 2.2</td>
<td>16.7 ± 2.2</td>
<td>5.4 ± 2.2</td>
</tr>
<tr>
<td>July</td>
<td>0.0 ± 2.2</td>
<td>17.3 ± 2.2</td>
<td>17.8 ± 2.2</td>
<td>9.8 ± 2.2</td>
</tr>
<tr>
<td>Sept</td>
<td>0.1 ± 2.4</td>
<td>9.9 ± 2.4</td>
<td>17.5 ± 2.4</td>
<td>10.8 ± 2.4</td>
</tr>
<tr>
<td>Avg.</td>
<td>0.1 ± 1.4</td>
<td>14.1 ± 1.3</td>
<td>17.3 ± 1.3</td>
<td>8.7 ± 1.3</td>
</tr>
<tr>
<td><strong>ER (µmol m$^{-2}$s$^{-1}$)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>0.0 ± 1.8</td>
<td>9.9 ± 1.4</td>
<td>9.7 ± 1.4</td>
<td>8.4 ± 1.4</td>
</tr>
<tr>
<td>July</td>
<td>0.2 ± 1.5</td>
<td>6.9 ± 1.5</td>
<td>10.8 ± 1.5</td>
<td>6.7 ± 1.5</td>
</tr>
<tr>
<td>Sept</td>
<td>0.2 ± 1.4</td>
<td>5.7 ± 1.4</td>
<td>7.9 ± 1.4</td>
<td>10.4 ± 1.4</td>
</tr>
<tr>
<td>Avg.</td>
<td>0.2 ± 0.9</td>
<td>7.5 ± 0.8</td>
<td>9.5 ± 0.8</td>
<td>8.5 ± 0.8</td>
</tr>
<tr>
<td><strong>NEE (µmol m$^{-2}$s$^{-1}$)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>0.0 ± 2.0</td>
<td>-5.1 ± 1.8</td>
<td>-7.0 ± 1.8</td>
<td>3.1 ± 1.8</td>
</tr>
<tr>
<td>July</td>
<td>0.5 ± 1.5</td>
<td>-10.3 ± 1.5</td>
<td>-6.9 ± 1.5</td>
<td>-3.1 ± 1.5</td>
</tr>
<tr>
<td>Sept</td>
<td>0.3 ± 1.4</td>
<td>-4.3 ± 1.4</td>
<td>-9.7 ± 1.4</td>
<td>-0.5 ± 1.4</td>
</tr>
<tr>
<td>Avg.</td>
<td>0.2 ± 1.0</td>
<td>-6.6 ± 1.0</td>
<td>-7.7 ± 1.0</td>
<td>-0.2 ± 1.0</td>
</tr>
</tbody>
</table>
Figure 1.3. Gross ecosystem production, ecosystem respiration, and net ecosystem exchange of CO₂ in May, July, September, and the average across sampling dates in 2017 for four marsh community types within Sabine National Wildlife Refuge, Calcasieu, Louisiana. Different letters indicate significant differences within the same month sampled (p < 0.05).
1.3.3. Relationship between CO$_2$ fluxes and environmental conditions

Elevation. In July ER was positively related to plot elevation across all plant communities (Figure 1.4). For May, GEP significantly increased with elevation only within the *S. patens* community (Figure 1.5). During both May and July in the *S. alterniflora* natural marsh community, elevation and NEE were significantly related (Figure 1.6).

![Figure 1.4](image)

Figure 1.4. Relationship between elevation and ecosystem respiration in July for all of the four marsh communities within Sabine National Wildlife Refuge, Calcasieu, Louisiana. B = created marsh bare sediment, SC = *Spartina alterniflora* in the created marsh, SN = *Spartina alterniflora* in the natural marsh, and SPN = *Spartina patens* in the natural marsh.

![Figure 1.5](image)

Figure 1.5. Relationship between elevation and the gross ecosystem production in *S. patens* in Sabine National Wildlife Refuge, Calcasieu, Louisiana. The regression line denotes a significant relationship found only in May.
Figure 1.6. Relationship between elevation and net ecosystem CO₂ exchange in *S. alterniflora* in a natural marsh at Sabine National Wildlife Refuge, Calcasieu, Louisiana. The regression line denotes a significant relationship found in May and July.

Sediment Chl a. Sediment chlorophyll *a* content was significantly related to NEE, ER, and GEP (Figure 1.7). Sediment chlorophyll *a* content was positively related to both ER and GEP which indicated that more algae in the sediment increases respiration and productivity of the marsh. Sediment chlorophyll *a* content was negatively related to NEE suggesting that sediment with greater benthic algae act as greater sinks of CO₂. While regressions between chlorophyll *a* and CO₂ flux were significant, the relationship was relatively weak with low R² values.

Figure 1.7. Relationship between the sediment chlorophyll *a* with net ecosystem CO₂ exchange, ecosystem respiration, and gross ecosystem production sampled from a created and natural marsh in May, July, and September at Sabine National Wildlife Refuge, Calcasieu, Louisiana.
Biomass. Biomass across all vegetated plots was positively related to ER and GEP (Figure 1.8) while there was no significant relationship with NEE. This may suggest that increasing biomass in the vegetated marsh may not increase its ability to act as a carbon sink due to increasing both the productivity and respiration of the marsh at similar rates.

Figure 1.8. Relationships between the estimated plant biomass and ecosystem respiration, and gross ecosystem production over three vegetated marsh communities in Sabine National Wildlife Refuge, Calcasieu, Louisiana. SC = *Spartina alterniflora* in the created marsh, SN = *Spartina alterniflora* in the natural marsh, and SPN = *Spartina patens* in the natural marsh.

NEE per gram of plant biomass was significantly higher in the *S. alterniflora* created and natural marsh communities than the *S. patens* community (-0.0068 μmol CO₂ sec⁻¹ g⁻¹, -0.0077 μmol CO₂ sec⁻¹ g⁻¹, -0.0021 μmol CO₂ sec⁻¹ g⁻¹, respectively; F₂,29 = 6.1, p =0.007). While for GEP per gram of biomass, only *S. alterniflora* in the natural marsh was significantly greater than *S. patens* (0.0167 μmol CO₂ sec⁻¹ g⁻¹, 0.0109 μmol CO₂ sec⁻¹ g⁻¹, respectively; F₂,29 = 3.7, p =0.037). There was no significant difference in ER per gram of plant biomass between the vegetated communities.
Sediment Nitrogen. Extractable NH$_4^+$ of 0-10 cm depth interval was found to be significantly related to ER and GEP positively in the month of September (Figure 1.9). Extractable NH$_4^+$ at the 10-20 cm depth interval was significantly related to NEE in May and July, ER in May and July, and GEP during all three months (Figure 1.10). At sediment 10-20 cm depth interval, generally as extractable NH$_4^+$ increased so did NEE, while ER and GEP decreased. This relationship between extractable NH$_4^+$ at the 10-20 cm depth interval and CO$_2$ fluxes was likely caused by the bare sediment community having a very high extractable NH$_4^+$ content and low CO$_2$ fluxes. If the bare sediment communities were removed for the data set there was no significant relationship seen between extractable NH$_4^+$ and the carbon fluxes. This indicates that the relationship between extractable NH$_4^+$ and CO$_2$ fluxes is likely due to the presence of plants increasing GEP and ER, while decreasing NEE and extractable NH$_4^+$ rather than extractable NH$_4^+$ directly effecting CO$_2$ fluxes.

Figure 1.9. The relationship between the sediment extractable ammonium in May from a depth interval of 0-10 cm with ecosystem respiration, and gross ecosystem production in September over four marsh communities in Sabine National Wildlife Refuge, Calcasieu, Louisiana. B = bare created marsh sediment, SC = Spartina alterniflora in the created marsh, SN = Spartina alterniflora in the natural marsh, and SPN = Spartina patens in the natural marsh. Extractable ammonium data was found to not have a normal distribution so data was log transformed.
Figure 1.10. The relationship between the sediment extractable ammonium in May from a depth range of 10 to 20 cm with net ecosystem exchange of CO$_2$, ecosystem respiration, and gross ecosystem production over three different months sampled and across four marsh communities in Sabine National Wildlife Refuge, Calcasieu, Louisiana. The regression lines denote a significant relationship found. The extractable ammonium data was found to not have a normal distribution so data was log transformed.

Figure 1.11. The relationship between the potentially mineralizable nitrogen in May from a depth interval of 0-10 cm with ecosystem respiration in July and September, and gross ecosystem production in September over four vegetated marsh communities in Sabine National Wildlife Refuge, Calcasieu, Louisiana. B = bare created marsh sediment, SC = Spartina alterniflora in the created marsh, SN = Spartina alterniflora in the natural marsh, and SPN = Spartina patens in the natural marsh. The potential mineralizable nitrogen data was found to not have a normal distribution so data was log transformed.
The PMN at 0-10 cm depth interval in May was positively related to ER in July and September, and to GEP (Figure 1.11) in September. It should be noted that if the bare sediment plots were removed from the data set that no significant relationships were found between PMN with ER and GEP. This may indicate that the low levels of carbon flux and PMN in the bare sediment are driving this relationship and that PMN is not directly effecting carbon fluxes. There was no significant relationship between PMN at the depths of 10-20cm and CO₂ fluxes. Sediment bulk density and organic matter content. Bulk density of 0-10 cm depth interval was negatively related to the ER in July and GEP (Figure 1.12) in September. Soil organic matter content at 0-10 cm depth interval was negatively related to the September ER (Figure 1.13). For both bulk density and SOM no significant relationship was found with GEP and ER when the bare sediment community was removed. This may indicate that the low levels of carbon flux with low SOM and high bulk density in the bare sediment are the main force of this relationship and that bulk density and SOM are not directly impacting carbon fluxes.

Figure 1.12. The relationship between the bulk density from a depth range of 0 to 10 cm with ecosystem respiration in July, and gross ecosystem production in September over four vegetated marsh communities in Sabine National Wildlife Refuge, Calcasieu, Louisiana. B = bare created marsh sediment, SC = Spartina alterniflora in the created marsh, SN = Spartina alterniflora in the natural marsh, and SPN = Spartina patens in the natural marsh.
Figure 1.13. The relationship between the sediment loss on ignition from a depth range of 0 to 10 cm with ecosystem respiration in September over four vegetated marsh communities in Sabine National Wildlife Refuge, Calcasieu, Louisiana. B = bare created marsh sediment, SC = *Spartina alterniflora* in the created marsh, SN = *Spartina alterniflora* in the natural marsh, and SPN = *Spartina patens* in the natural marsh.

1.4. Discussion

Plant community composition had a major impact on CO$_2$ fluxes in the created and natural brackish marshes. Differences between non-vegetated and vegetated areas and between plant species impacted CO$_2$ fluxes and influenced whether the marshes were net autotrophic or heterotrophic during the time of measurement. In contrast, marsh type (created vs. natural) had little influence on CO$_2$ fluxes when the plant community remained constant, with *S. alterniflora* communities having similar CO$_2$ fluxes regardless if in the natural or newly created marsh. Soil organic matter was low and nitrogen availability for plants was high in the created marsh in comparison to the natural marsh. The difference in soil characteristics between the created marsh and natural marsh but similarity of CO$_2$ fluxes when dominated by the same plant species
suggests that the development of plant communities is more directly connected to CO₂ fluxes than soil characteristics.

Rates of NEE in the present study fall within the range of those measured in coastal marshes. NEE ranged in the present study (-10 to 3 μmol s⁻¹ m⁻¹) was similar to those in a restored marsh in New Jersey (-12 to 6 μmol s⁻¹ m⁻¹; Artigas et al. 2015), a created marsh in North Carolina (-3 to -12 μmol s⁻¹ m⁻¹; Cornell et al., 2007), and natural marshes in Massachusetts (-15 to 0 μmol s⁻¹ m⁻¹; Moseman-Valtierra, 2016), and Texas (-10 to 12 μmol s⁻¹ m⁻¹; Heinsch et al. 2004). These studies demonstrated that marshes NEE are variable between sampling date and time, marsh environmental conditions, and marsh community type.

Few studies, however, have evaluated marsh CO₂ fluxes during the successional development of a created marsh. Cornell et al. (2007) did a comprehensive study in North Carolina evaluating how CO₂ fluxes change with created marsh age, and compared CO₂ fluxes of created marshes to natural marshes dominated by *S. alterniflora*. Cornell et al. (2007) came to the conclusion that C fluxes in created marshes can reach levels similar to natural marshes in less than 5 years, at a pace similar to plant community development. Our study supported their findings that plant community influenced CO₂ more than soil development as *S. alterniflora* in a young created marsh had similar CO₂ fluxes to *S. alterniflora* in the natural marsh. But where our study found that biomass tracked with GEP and ER, Cornell et al. (2007) did not find that biomass was related to CO₂ fluxes in created marshes due to young marshes having a higher rate of CO₂ fluxes per biomass. *Spartina alterniflora*’s leafs in the created marsh had high nitrogen content possibly indicating high photosynthetic rates. The high amount of CO₂ fluxes per biomass allowed the young marsh, with low biomass in relation with natural marshes, to have similar NEE, ER, and GEP to natural marshes. Since newly created marshes are typically on
nutrient poor substrates it was hypothesized that *S. alterniflora* allocated more resources to root production for nutrient mining, allowing them to have higher leaf nitrogen contents and photosynthetic rates. Cornell et al. (2007) predicted that CO$_2$ fluxes may be able to reach natural levels faster than plant biomass as plants on young marshes can have high rates of CO$_2$ exchange. Our study showed no significant differences in *S. alterniflora* biomass or CO$_2$ fluxes per gram of biomass between the created and natural marsh, our soil nitrogen results may give some insight as to why leaf nitrogen content could be higher in a young created marsh. PMN was generally lower in the created marsh than in the natural marsh, indicating greater availability of N with a stable SOM source. However, the non-vegetated sediment at 10-20 cm depth interval in the young created marsh had higher amounts of extractable NH$_4^+$ than the vegetated sites, potentially associated with lower plant uptake (Hurst et al. 2016). Therefore, high leaf nitrogen content in a young created marsh may be due to greater N availability which can allow for greater photosynthetic rates in comparison to natural marshes (Cornell et al. 2007). Though it should be noted that leaf nitrogen in the marsh can also be impacted by flooding and salinity concentrations, where leaf nitrogen is typically greater in high flooding and salinity environments (Tobias et al. 2010). Overall, these studies indicate that CO$_2$ fluxes in created marshes can rapidly reach natural marsh levels likely due to the relatively quick pace of vegetation colonization.

Plant species significantly impacted CO$_2$ fluxes. *Spartina alterniflora* dominated areas were a consistent CO$_2$ sink and were net autotrophic in both the natural and created marsh. NEE of *Spartina patens* dominated areas in the natural marsh, however, changed over time. *Spartina patens* areas were source for CO$_2$ in May, a sink in July, and neutral in September. Averaged over the whole study, NEE was neutral in *S. patens*. Differences in NEE between *S. alterniflora*
and *S. patens* communities was due GEP with *S. patens* areas having lower CO$_2$ uptake (by 7 μmol m$^{-2}$s$^{-1}$) than *S. alterniflora*. Another study using continuous measurements from eddy covariance towers over the course of a year, however, showed *S. patens* with greater CO$_2$ uptake (8 μmol m$^{-2}$s$^{-1}$ greater) than the low marsh dominated by *S. alterniflora* (Artigas et al., 2015). It may be possible that *S. alterniflora* is more of a carbon sink in the summer, while *S. patens* can be more of a sink year round. *S. patens* has been observed to maintain green stems for longer periods over the year than *S. alterniflora* (Artigas et al. 2015). Similar to our findings, another study found a low marsh dominated by *S. alterniflora* was a significant CO$_2$ sink while the high marsh plant community consisting of mostly *Juncus gerardii* and *Distichlis spicata* had a neutral NEE, associated with higher biomass in the low marsh (Moseman-Valtierra et al. 2016). However, in the present study, aboveground biomass did not significantly differ between *S. alterniflora* and *S. patens*, yet NEE and GEP per gram of biomass was significantly higher in *S. alterniflora* than *S. patens*. This could indicate that *S. alterniflora* had greater photosynthetic capabilities than *S. patens*, though photosynthetic rates have been found to be similar between these two species (Maricle et al. 2007).

GEP of *S. patens* in May increased with increasing elevation. *Spartina patens* is a mid to high marsh species and is more susceptible to anaerobic soils than *S. alterniflora* (Bertness, 1991; Lonard, 2010). Therefore, *S. patens* typically have greater below ground and above ground biomasses at higher elevations (Snedden et al. 2015; Konisky & Burdik, 2004). In May *S. patens* acted as a greater CO$_2$ source at lower elevations possibly due to lower productivity. However, GEP in *S. patens* was not related to elevation in July and September when the community was a CO$_2$ sink and NEE neutral, respectively.
NEE of *S. alterniflora* in May and July was also greater at higher elevations. At lower elevations in the natural marsh, *S. alterniflora* acted as a greater CO$_2$ sink. *Spartina alterniflora* tends to be more productive at lower elevations (Edwards and Mills, 2005; Morris et al. 2002). *Spartina alterniflora* may be more productive at lower elevations with less competition from mid to high marsh species (Edwards and Mills, 2005; Edwards and Proffitt, 2003). Elevation did not relate with NEE in the newly created marsh possibly due to little competition for *S. alterniflora* from other plant species. In September, no relationship between NEE and elevation was found in the *S. alterniflora* natural marsh community, potentially due to extensive and prolonged flooding as a result of Hurricane Harvey.

Flooding varied among months and likely affected CO$_2$ fluxes. The marshes were drained in May, moderately flooded (~10cm) in July, and flooded completely to an approximate depth of 35 cm in September. Flooding can reduce NEE in salt marshes by decreasing plant and soil CO$_2$ fluxes (Moffet et al. 2010; Kathilankal et al. 2008). Photosynthesis of *S. alterniflora* can decline 66% under flooded conditions, causing a 46% reduction in NEE (Kathilankal et al. 2008). Flooded conditions can also suppress benthic algal photosynthesis by 48-66% (Holmes and Mahall). Soil CO$_2$ flux was depressed under flooding as anaerobic conditions become more prominent reducing microbial activity (Nyman & Delaune, 1991, Magenheimer et al. 1996). The differences in flooding between sampling dates likely caused the CO$_2$ fluxes to be reduced in July and September relative to May when the marsh was dry.

Regardless of date sampled or marsh environmental condition, the bare created marsh sediment consistently had a negligible GEP and ER when compared to vegetated marsh communities. The lack of plants is the likely cause of low NEE, GEP and ER as there was a significant increase in CO$_2$ fluxes in the created marsh when *S. alterniflora* was present. Non-
vegetated marsh sediments have relatively little CO$_2$ fluxes compared to vegetated marshes (Sheng et al. 2015) where the plant production increases GEP (Weston et al. 2014; Sheng et al. 2015) and plants increase ER through multiple processes (Mueller et al. 2016; Yang et al. 2016). Plants contribute to ER directly through metabolism, and indirectly by increasing the decomposition of SOM. There are two processes by which SOM decomposition is enhanced by plants. One is by providing more electron acceptors for microbes via root oxygen loss (Wolf et al., 2007) and the second, by contributing labile organic compounds to the rhizosphere which are then decomposed by microbes (Blagodatskaya & Kuzyakov, 2008). Plants can increase SOM-derived respiration by up to 267% as compared to non-vegetated soils (Mueller et al. 2016). *Spartina alterniflora* invasion onto bare mud flats significantly increased the soil microbial biomass and respiration by providing greater belowground carbon substrate for decomposition (Yang et al. 2016). Increases in rhizome biomass and diameter caused a greater soil CO$_2$ emission likely due to an increase in rhizome oxygen loss, and addition of labile organic compounds (Wigand et al. 2015). In addition to increasing SOM decomposition, plants also add to ER through their own metabolism. In terrestrial systems, root metabolism can contribute to 45 to 60% of total soil respiration (Andrew et al. 1999; Hanson et al. 2000). Root respiration from *S. alterniflora* can account for more soil respiration than microbial activity in a salt marshes (Magenheimer, 1996). Within a 24 hour period *S. alterniflora* typically respires 30 to 55% of the carbon it has fixed back to the atmosphere (Spivak and Reeve, 2015). The difference in respiration between non-vegetated and vegetated marsh communities in this study can likely be attributed to the presence of plants due to metabolic respiration and enhancement of soil microbial respiration.
Plant community significantly influenced CO$_2$ fluxes, with ER also related to soil carbon and nitrogen content. The relationship between ER with soil nitrogen and carbon were likely caused by created marsh bare sediment communities having extremely low CO$_2$ fluxes coupled with low SOM, low PMN, and high subsurface extractable NH$_4^+$. No relationship was found between ER and SOM, PMN, or extractable NH$_4^+$ when the bare sediment community was removed from the data set. Though as a created marsh ages SOM tends to increase which can enhance the potential for soil microbial respiration (Craft et al. 2003). No difference was found in soil microbial respiration between a natural tidal flat with high SOM than a constructed tidal flat with low SOM (Lee et al. 1998). Past research has shown that large increases of nitrogen in wetlands can increase soil respiration (Song et al. 2013; Morris & Bradley, 1999; Caffrey et al. 2007; Darby & Turner, 2008), but small to moderate additions of nitrogen have a limited impact on soil respiration (Song et al. 2013; Keller et al. 2005). Higher nutrients may increase soil respiration through greater belowground biomass, which then can increase soil microbial activity and respiration (Wigand et al. 2015). Increases in belowground biomass from greater nitrogen availability can also lead to greater plant metabolic respiration (Morris & Bradley, 1999). Under high nutrient conditions more electron acceptors are available allowing microbes a greater respiration potential (Caffrey et al. 2007, Morris & Bradley, 1999). Despite the natural marsh generally having higher SOM and soil nitrogen than the created marsh, ER was similar in S. alterniflora stands in both marsh types illustrating that the plants were more impactful on CO$_2$ emissions than sediment characteristics.

While sediment carbon and nutrients seemed to have relatively limited influence on CO$_2$ gas exchange, greater soil algal content was positively related to ER and GEP, and negatively related to NEE indicating benthic algae had a net CO$_2$ intake. Benthic algae contribute to GEP
and can act as a CO$_2$ sink in marshes (Neubauer et al. 2000). Benthic algal biomass was highest in the natural marsh $S$. *alterniflora* community. While there was not significant relationship with surface soil nitrogen and Chl $a$ content in this study, greater nitrogen input has been found to increase algal biomass (Bucolo et al. 2008). In the natural marsh, Chl $a$ content in the $S$. *patens* community was lower than the $S$. *alterniflora* community likely due to a reduction in light availability. Benthic algae is greatly reduced in marshes with thick plant canopies that shade the soil (Zedler, 1980). *Spartina patens* grows at much higher densities than $S$. *alterniflora* and its dead stem material decomposes at a slower rate which may decrease light availability for benthic algae (Hopkins et al. 1980). Even though $S$. *alterniflora* in the natural marsh had a significantly higher amount of benthic algae than $S$. *alterniflora* in the created marsh they did not differ in carbon fluxes. This was likely due to benthic algae having low CO$_2$ fluxes overall in comparison to vegetation.

In conclusion, vegetation was the main determinant of marsh CO$_2$ fluxes, while sediment characteristics seemed to have relatively limited effects on CO$_2$ fluxes. Vegetation rapidly develops in created marshes with plant biomass quickly reaching that of natural marshes but sediment characteristics take much longer to develop (Craft et al., 2003; Edwards & Proffitt, 2003). This suggests that CO$_2$ fluxes in created coastal marshes can reach natural levels in a relatively short amount of time, potentially allowing created marshes to sequester CO$_2$ at similar rates to natural marshes. *Spartina alterniflora* communities were also net autotrophic while bare sediments and *S. patens* had a neutral net CO$_2$ flux.
CHAPTER 2. *SPARTINA ALTERNIFLORA* IS A DOMINANT COMPETITOR OF *SPARTINA PATENS* IN A HIGH ELEVATION CREATED MARSH

2.1. Introduction

Plant interactions such as competition and facilitation have been shown to be important in saline marshes, where plant species distribution is determined by tolerance to stressful conditions and biotic interactions (Bertness, 1991; Bertness and Ellison, 1987; Bertness and Hacker, 1994). Competition for resources such as nutrients and light has been shown to be more important in the high marsh where flooding and salinity stresses are lower than in the low marsh (Bertness, 1991; Levien et al. 1998; Bertness et al. 2002). In addition, species interactions are more likely in the high marsh, as species diversity also tends to increase away from the marsh edge with more benign conditions (Proffitt et al. 2003; Brewer et al. 1997). Facilitation is also an important biological interaction where one species benefits from the presence of another. Facilitation typically occurs when a stress-tolerant plant species modifies harsh environmental conditions such as creating or increasing shade, increasing sediment organic matter and nutrient concentrations, stabilizing the sediment, and increasing sediment moisture such that a less-stress-tolerant species can colonize, survive, and grow (Walker and del Moral, 2003; Bertness and Hacker, 1994; Moro et al. 1997; Underwood; 1997). Positive interactions among species tend to be more prevalent and amplified in ecosystems with harsh environmental conditions such as deserts and saline wetlands where stress-tolerant species can ameliorate harsh abiotic conditions for less-tolerant, potentially more competitive species (Callaway and Walker, 1997; Bertness and Callaway, 1994). The harsh conditions of salt marshes due to frequent flooding and high salinities increase the potential for facultative interacts which could play a role in the plant community development of these ecosystems.
In saline marshes along the Atlantic and Gulf coasts of the United States, *Spartina alterniflora* is a dominant grass species at frequently flooded lower intertidal elevations due to both morphological and physiological adaptations to low sediment oxygen and high salinities. *Spartina patens* along with *Distichlis spicata*, are dominant species of mid-high intertidal elevations with the highest marsh elevations occupied by shrubs such as *Baccharis halimifolia* and *Iva frutescens* (Bertness, 1991; Chapman, 1974). In the higher elevations of the marsh, competitive interactions tend to determine plant species occurrence. For example, *S. alterniflora* transplanted into a high marsh in New England, USA was found to be able to persist when competition pressure from neighboring plants was removed. However, when planted amongst higher marsh species, *S. alterniflora*’s biomass in the high marsh was greatly reduced and was almost eradicated from the high marsh (Bertness, 1991). Conversely, transplants of the high marsh species, *S. patens*, were unaffected by neighboring competitors in the high marsh, but could not establish in the lower marsh zone likely due to its inability to withstand increased flooding and anaerobic sediment conditions (Bertness, 1991; Burdick and Mendelssohn, 1990).

Anaerobic conditions, prevalent in marsh sediments are stressful to plant establishment and growth, but plants adapted to these conditions may facilitate the colonization of less flood-tolerant species by reducing the anaerobic sediment conditions. *Spartina alterniflora* possesses large rhizomes with abundant aerenchyma tissue (Teal and Kanwisher, 1966), which allow the transport of oxygen to submerged rhizomes and roots for respiration (Gleason, 1980). Wetland plants with well-developed aerenchyma can have radial oxygen loss into the rhizosphere introducing microsites of oxygenated sediments near the root surface (Koretsky, 2008). High marsh species such as *S. patens* tend to have smaller rhizomes with limited aerenchyma tissue which does not support aerobic respiration in completely flooded conditions (Burdick and
Mendelssohn, 1990; Watson, 2015). While an increase in oxygen concentration in the rhizosphere from plants with well-developed aerenchyma may allow for the facilitation of species that cannot tolerate anaerobic conditions in the created marsh, *S. patens* was not able to establish in the lower elevations of a natural marsh with *S. alterniflora* present (Bertness, 1991). Therefore, radial oxygen loss in low marsh environments does not likely increase rhizosphere oxygen concentrations sufficient enough to allow aerobic root respiration. In addition to a lack of oxygen, anaerobic sediments can have high concentrations of phototoxins such as reduced manganese and sulfides (Reddy and Delaune, 2008). *Spartina patens* has shown to be sensitive to these phototoxins, and radial oxygen loss has been shown to oxidize elements such as iron only in the immediate vicinity of a root (Pezeshki, 2001; Pezeshki et al. 1991, 1993). Thus, in the low marsh sediment oxygen influx through rhizomes was found to be insignificant in facilitating plant establishment and growth of *S. patens* (Bertness, 1991).

Sediment salinity is another stress that can limit species distribution and productivity of marsh plants. Plants in natural marshes under high salinity stress have been shown to benefit from neighboring plants due to greater shading, reduced evaporation, and lower sediment salt concentrations (Bertness and Ewanchuk, 2002; Penning et al. 2003; Bertness and Hacker, 1994). Specifically, along the United States Atlantic coast, marsh communities dominated by salt tolerant plant species had more competitive interactions while marshes dominated by more salt intolerant plants had more facilitative interactions, indicating that plant interactions are influenced by both species-specific tolerance and environmental conditions (Pennings et al. 2003). Facilitation was also found to be more prevalent in salt marshes with harsher temperature and salinity conditions as neighbors provided shade and reduced evaporation-induced sediment salinity increases (Bertness and Ewanchuk, 2002). Overall, marsh plants more susceptible to salt
stress increasingly rely on neighboring plants to reduce salinity as ecosystems become more saline, while more salt tolerant plants can be negatively impacted by competition.

Anaerobic sediment and high salinity are regulators of plant productivity creating potentially stressful environments which can promote facultative interactions, resources, such as light availability and nutrients, may also influence plant species interactions. Changes in resource availability can lead to changes in the outcome of competitive interactions. For example, the competitive ability of the stress-tolerant low elevation species, *S. alterniflora*, increased under high nitrogen conditions such that *S. patens* was out-competed in its higher marsh habitat (Levien et al. 1998, Bertness et al. 2002). Greater sediment nutrient availability made light the next most limiting resource, for which *S. alterniflora* grew taller and shaded out *S. patens* (Levien et al. 1998, Bertness et al. 2002; Watson et al., 2015). This suggests that nutrient availability can alter facilitative/competitive interactions among species and that *S. alterniflora* may be a better facilitator under low nitrogen conditions.

Ecosystems undergoing primary succession tend to have obligatory facilitators with pioneer species establishing on bare substrate and altering the environment such that other less tolerant species can establish resulting in a succession of plant species and communities over time (Connell and Slatyner, 1977; Gaynor and Wallace, 1998). Created ecosystems, which function as primary successional habitats, are environments in which facilitation may play an important role in ecosystem development. Newly created saline marshes are an ideal ecosystem to examine the influence of facilitation on succession because vegetation development can occur relatively quickly (within 5-10 years, Craft et al 2003; Proffitt et al. 1999) and environmental conditions can be harsh (e.g., high sediment salinity, low oxygen, high sulfide concentration) yet spatially and temporally variable (Bertness, 1991; Bertness and Hacker, 1994).
Facilitation can be particularly important in newly created marshes where stress-tolerant plant species such as *S. alterniflora* are the typical dominant initial colonizers in the first 5 to 10 years (Proffitt and Young, 1999; Proffitt et al. 2005). In high elevations of created marshes, *Spartina alterniflora* can have widespread coverage initially, but eventually is outcompeted by high marsh species (Proffitt and Young, 1999; Proffitt et al. 2005). *Spartina alterniflora* has been considered a foundation species (Pennings and Bertness, 2001), a keystone modifier (Seliskar et al. 2002), and an ecosystem engineer (Bruno, 2000). Because of its ability to colonize newly created marshes and modify the substrate and light conditions, it may facilitate the colonization of less stress-tolerant species (Egerova et al. 2003; Proffitt, 2005). The presence of *S. alterniflora* in mid-to-high elevations has been shown to positively influence the establishment of high marsh forbs and shrubs in a newly created marsh having twice as many new species establish in two years within *S. alterniflora* clones than bare substrate (Proffitt et al., 2005).

*Spartina alterniflora* functioned as a nurse plant for the shrub, *B. halimifolia*, in higher elevation areas of created marshes, increasing survivorship and height (Egerova et al. 2003). However, the facilitation effects seem to be species-specific as *S. alterniflora* suppressed the growth of a highly salt tolerant and early successional species, *Salicornia bigelovii*. The shift from a facilitator to a competitor may depend on the relative stress tolerance of the species.

*S. alterniflora* has been shown to facilitate establishment and growth of mid-to-high forb and shrub species onto the created marsh, though the mechanism of facilitation is not clear (Egerova et al. 2003; Proffitt et al. 2005). *Spartina alterniflora* in the created marsh tend to grow in clonal clumps that have bare senescent centers, when a common marsh shrub, *B. halimifolia*, was transplanted within the senescent center it grew to greater heights than if it were in the bare sediment. It was observed that sediment temperatures inside *S. alterniflora* clones where
significantly lower than the bare sediment, which may have reduced evaporation (Egerova et al. 2003), potentially reducing sediment salinity. Plants at higher marsh elevations experience less flooding and a reduction in sediment anaerobic conditions. However, created salt marsh sediments tend to have significantly less nitrogen than natural marsh sediments (Langis et al., 1991; Craft et al., 1999; Zedler and Callaway, 1999), which may reduce competitive interactions between S. alterniflora and other marsh species.

Generally, the presence of S. alterniflora in mid-to-high elevations positively influences the establishment of high marsh forbs and shrubs, but its effect on other grass species’ establishment, such as S. patens, is relatively unknown (Proffitt et al., 2005). Spartina alterniflora and S. patens were found to be competitors in a natural marsh limiting each other to around 80% of their average growth when they were transplanted over a gradient of salinity and elevations (Konisky and Burdick, 2004). Spartina patens is typically the dominant grass species in high elevation saline and in brackish marshes of the U.S. Atlantic coast and Gulf coasts, accounting for up to 97% of total biomass in some brackish marshes (White and Simmons, 1988; Lonard et al. 2010). Due to the abundance of both S. alterniflora and S. patens in brackish marshes it will be important to understand how they interact in a newly created brackish marsh.

This study aimed to test the ability of a pioneer species, S. alterniflora, to facilitate the establishment of a later successional, high marsh grass, S. patens, in a created brackish marsh and to examine the mechanisms influencing potential plant interactions. In the mid-to-high elevations of a created marsh, anaerobic conditions and competition for sediment nutrients were not predicted to be a limiting factor for establishment and growth of high marsh plants, while salinity may limit high marsh plant establishment. We tested the hypothesis that S. patens would
benefit by being in close proximity to *S. alterniflora* due to a reduction in salinity within *S. alterniflora* rather than non-vegetated sediment.

2.2. Methods

2.2.1. Site Study

This research was conducted along the Gulf coast in Sabine National Wildlife Refuge (SNWR) in southwestern Louisiana between the Sabine and Calcasieu rivers (Figure 2.1). Dredging of the Calcasieu channel in the 1930s led to salt water intrusion into SNWR causing vegetation death and conversion to open water in previously oligohaline marshes (Delaune et al., 1983). Subsequent dredging and subsurface fluid withdrawal has led to additional land subsidence in SNWR (Bernier et al., 2011). The substantial marsh loss primarily due to the creation of the channel (U.S. Fish and Wildlife, 2013) prompted the implementation of marsh creation projects using dredged sediment from the Calcasieu ship channel (Inman, 2014). Six marshes where created over the course of 34 years by pumping a slurry of dredged material into open water cells bounded by containment levees until elevated enough to support marsh vegetation communities. The study site for this research was a marsh recently created in 2015 (Figure 2.1). Marsh elevations varied within and among marshes as the created marshes ranged from -2.8 ± 2.5 cm to 35 ± 2.2 cm with the 2015 created marsh having an average elevation of 20.8 ± 2.8 cm while nearby natural marshes had an average elevation of 10.2 ± 1.7 cm (NADV 88; Abbott and Quirk, 2017). Flooding of the marshes at SNWR were greatly influenced by precipitation though tides and wind also impacted water levels (Bernier et al., 2011). The marsh in this study was not flooded during the measurements taken in March but was flooded during the measurements in August. The created marsh was being naturally colonized by *S. alterniflora*, which was growing as sparse clones across the dredge sediment.
2.2.2. Experimental Design

Twenty-two plugs (15 cm diameter by 15 cm depth) of marsh substrate with *S. patens* were collected from a nearby natural marsh using a plastic core barrel. In February 2017 individual plugs were transplanted into one of two paired plots, with 12 plots inside of *S. alterniflora* clones and 10 plots outside of *S. alterniflora* clones in non-vegetated sediment. Paired plots occurred from the marsh edge to the marsh interior to include variation in elevations. *Spartina patens* were transplanted either to bare sediment plots or to plots within senescent centers of *S. alterniflora* clones. Bare sediment plots were 10 meters from the outside of the *S. alterniflora* clone and at least 10 m from any other plants. *Spartina alterniflora* clones expanded outward at an average rate of 3.1 m/yr (Proffitt et al. 2003), and therefore, transplanting *S. patens* 10 m from any *S. alterniflora* ensured that vegetation would not be likely to grow into the plot during the duration of this study.
2.2.3. Vegetation Measurements

*Spartina patens* Transplants.

Morphometric Characteristics. Aboveground measurements including stem height, percent cover, area covered, and stem density of *S. patens* in transplanted plots were collected twice, in late March and late August. Plant height was estimated by measuring the height of 15 random individual stems within the 0.01 m² quadrat and calculating the average per plot. Stem density was also determined in the 0.01 m² quadrat. To estimate *S. patens* transplant expansion rate, vegetative area was measured by taking the length and width of the sediment covered by *S. patens* and solving for the area twice over the study period.

Specific Leaf Area. As an estimate of relative growth rate, specific leaf area (SLA), as leaf area per unit of dry mass, was measured for the transplanted *S. patens* (Perez-Hanguindey et al., 2013). For each plot, two stems were cut at the top of the sediment and placed into a zip lock bag and kept under cool conditions. In the lab, leaf blades were removed from each stem and digitally scanned (Xerox Workcenter 7845) to determine leaf area. Image processing was done in ImageJ to determine the leaf area of each leaf (Perez-Hanguindey et al. 2013). The leaves were placed in a 60°C drying oven for one week and were then measured to the nearest mg. SLA was measured in August 2017.

Leaf Nitrogen Content. Leaf nitrogen content is typically correlated with maximum photosynthetic rates which can also be an indicator of growth rates (Perez-Hanguindey et al., 2013). Nitrogen concentration in leaf tissue was determined by using the dried leaves collected for the SLA measurement which after the area and dry weight were recorded (Perez-Hanguindey et al., 2013). The dried samples were ground and dried at 60°C for 12 hours. Total nitrogen concentration was determined using a Costech 1040 CHNOS Elemental Combustion system.
Spartina alterniflora Clones.

Spartina alterniflora clone characteristics were predicted to be important in influencing survivorship and growth of S. patens transplants into clone centers. Spartina alterniflora clone area was measured by taking perpendicular diameter of each clone and calculating the area of an ellipse. Characteristics of the growing portion of each S. alterniflora clone were measured within a randomly placed 0.25 m² quadrat. Percent cover was determined by using a modified Daubenmire method using 10 predetermined cover classes. Plant height was estimated by measuring the height of 15 random individual stems within the 0.25 m² quadrat and calculating the average per plot. Stem density was also determined in the 0.25 m² quadrat. Vegetation measurements were collected two times over the study period, in late March and late August.

2.2.4. Environmental Conditions

Elevation. Elevation of each plot was measured in March 2017 using a GS-14 (LEICA Geosystems). Within each plot, elevation was taken at three locations within 0.25 m of each other and then averaged.

Sediment Salinity. To determine differences in sediment salinity between the bare sediment and sediment within S. alterniflora clones, salinity was recorded within 1 m of each transplanted S. patens in March and August 2017. Sediment salinity was tested in the field by squeezing porewater from a 2-cm deep sediment sample using a filter and syringe onto a refractometer (modified from Bertness, 2002).

Redox potential. Sediment redox potential was used as an indicator of sediment oxygen availability. Sediment redox potential was measured in August 2017 at each S. patens transplant plot, with measurements made at depths of 5 cm, 10 cm, and 20 cm. Electrodes were made of a Pt electrode attached to a positive end of a high resistance meter and a reference Ag-AgCl
electrode attached to the negative end of the meter (Megonigal and Rabenhorst, 2013). The electrodes were placed into the sediment in the center of *S. alterniflora* clone or in the bare sediment. The electrodes were allowed to equilibrate for at least 15 minutes before the redox potential was recorded.

Extractable Ammonium and Potentially Mineralizable Nitrogen. Extractable ammonium (NH$_4^+$) is used to indicate the availability of nitrogen for primary producers in marsh sediment measured as mg of nitrogen per kg dry sediment. Ammonium is used rather than nitrate because organic nitrogen converted to inorganic nitrogen which can be used by plants, accumulates as NH$_4^+$ rather than nitrate in the anoxic wetland sediments (Reddy and Patrick, 1984). Potentially mineralizable nitrogen (PMN) is the measure of the rate at which extractable ammonium increases with time in the sediment and indicates the rate at which plant-available nitrogen becomes freed in the sediment via the microbial community (White and Reddy, 2000).

Sediment cores (7 cm diameter by 20 cm depth) were collected in May 2017 at transplant plots using a plastic core. A 20 cm depth was selected since *S. patens* typically has most belowground biomass in the first 20 cm (Windham, 2000). Two depth intervals of 0-10 and 10-20 cm were sectioned and analyzed to determine whether there is a difference in nutrient availability with sediment near the surface and deeper sediment and to examine whether this depends on the presence of plants.

For extractable NH$_4^+$, 5 g of homogenized sediment sample from each depth section of each core was placed into 50-ml centrifuge tubes with 20ml of 2mol L$^{-1}$ KCL. Tubes were placed into a horizontal shaker for one hour and then centrifuged at 5000 X g for 10 minutes. The samples were filtered with 0.45-um glass fiber filter into 20 ml disposable scintillation vials where one drop of H$_2$SO$_4$ was added. The vials of sample were refrigerated at 4°C until analysis.
Extractable \( \text{NH}_4^+ \) was determined using an AQ2 Automated Discrete Analyzer (Seal Analytical Inc.) via colorimetric analysis (USEPA, 1993).

The rates of PMN were determined by measuring extractable \( \text{NH}_4^+ \) at days 0, 2, 5, and 10 of incubation. Day 0 was already determined from preforming extractable \( \text{NH}_4^+ \) from the cores. Three subsamples of each core were homogenized and placed into three serum bottles to be measured at day 2, 5, and 10 with rubber caps and aluminum seals. To produce an anaerobic environment, the gas in each bottle was purged and replaced with pure \( \text{N}_2 \). The bottles were then injected with water with a salinity of 10 psu, which was the average salinity at the study sites. The serum bottles were then placed into an incubator (IS-971R, Jeio Tech) at 40°C and oscillating at 100 rpm. The replicate serum bottles were removed at day 2, 5, and 10 and extracted with 25 ml of 2 mol L\(^{-1}\) KCl. The vials were placed into a horizontal shaker for one hour and then centrifuged at 5000 X g for 10 minutes. The samples were filtered with 0.45-um filter into 20 ml disposable scintillation vials where one drop of \( \text{H}_2\text{SO}_4 \) was added. The vials of sample were refrigerated at 4°C until analysis. Extractable ammonia was determined using an AQ2 Automated Discrete Analyzer (Seal Analytical Inc.) for colorimetric analysis of the samples (USEPA, 1993). Potentially mineralizable nitrogen was determined for each sample using linear regression of extractable \( \text{NH}_4^+ \) vs day of incubation.

2.2.5. Statistical Analysis

To test whether \( S. \text{patens} \) transplants differed when planted in bare sediment or within \( S. \text{alterniflora} \) clones between March and August, a two-way analysis of variance was used. The student’s t test was used to test the difference in sediment conditions (salinity, redox potential, and nitrogen), stem density, plant height, leaf percent nitrogen, and SLA between bare sediment and sediment within \( S. \text{alterniflora} \). Regression analysis was used to examine the influence
elevation, salinity, extractable NH$_4^+$, and PMN have on transplant height, density, vegetation cover, and percent cover. The data from this experiment were tested for normality, log (x) as necessary, and analyzed in JMP SAS 13. For all of the statistical analysis significance was determined by $\alpha=0.05$.

2.3. Results

2.3.1. Environmental Conditions

Sediment Salinity. The marsh was not flooded in March, but had ~20 cm surface water in August, which likely reduced sediment salinity (Figure 2.2). Salinity was an average of 2 psu lower inside S. alterniflora clones as compared to bare sediment in March, but was similar among habitats, and over 10 psu lower in August than in March (Figure 2.2).

Figure 2.2. The average sediment salinity ($\pm$ standard error) for bare sediment and sediment inside of S. alterniflora during sampling in March and August that took place in a created brackish marsh within Sabine National Wildlife Refuge, Calcasieu, Louisiana. The marsh was flooded in August but not flooded in March. A student’s t-test was conducted to determine the difference between sediment types in each month sampled.
Redox potential. Sediment redox potential was similar among depths (5 cm, 10 cm, and 20 cm) between the bare sediment and within *S. alterniflora* (Table 2.1).

Sediment Nitrogen. Bare sediment had a significantly greater extractable NH$_4^+$ content at depth interval 10-20 cm than sediment within *S. alterniflora* clones ($t = 2.306, p < 0.001$). But the extractable NH$_4^+$ content for the sediment depths interval 0-10 cm was similar. PMN at both the depth ranges of 0-10 and 10-20 cm did not significantly differ between the two habitats (Table 2.1).

Table 2.1. Sediment salinity, redox potential, extractable ammonium, and potentially mineralizable nitrogen (means ± standard error) at various depths in the bare sediment and sediment in senescent centers of *S. alterniflora* clones in a created marsh at Sabine National Wildlife Refuge, Calcasieu, Louisiana.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Depth (cm)</th>
<th>Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0-2</td>
<td>10-20</td>
</tr>
<tr>
<td>Salinity (ppt)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>March</td>
<td>Bare Sediment</td>
<td>16.3 ± 0.5</td>
</tr>
<tr>
<td></td>
<td>Sediment within <em>S. alterniflora</em></td>
<td>14.7 ± 0.5*</td>
</tr>
<tr>
<td>August</td>
<td>4.4 ± 0.5</td>
<td>4.3 ± 0.5</td>
</tr>
<tr>
<td>Redox potential (mV)</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-28.2 ± 16.4</td>
<td>-18.1 ± 16.4</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>-24.0 ± 10.6</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>-107.6 ± 28.2</td>
</tr>
<tr>
<td>Extractable NH$_4^+$ (mg N kg$^{-1}$ sediment)</td>
<td>0-10</td>
<td>1.9 ± 1.0</td>
</tr>
<tr>
<td></td>
<td>10-20</td>
<td>4.27 ± 1.0</td>
</tr>
<tr>
<td></td>
<td>0-10</td>
<td>45.5 ± 2.5</td>
</tr>
<tr>
<td></td>
<td>10-20</td>
<td>1.2 ± 2.5*</td>
</tr>
<tr>
<td>PMN (mg N kg$^{-1}$sediment d$^{-1}$)</td>
<td>0-10</td>
<td>2.7 ± 0.5</td>
</tr>
<tr>
<td></td>
<td>10-20</td>
<td>3.7 ± 0.5</td>
</tr>
<tr>
<td></td>
<td>4.0 ± 0.8</td>
<td>4.3 ± 0.5</td>
</tr>
</tbody>
</table>

* Significant ($p < 0.05$) between bare sediment and sediment within *Spartina alterniflora* clone
2.3.2. *S. patens* survivorship and growth

All the *S. patens* transplants in the bare soil survived, but two of the transplants in the center of *S. alterniflora* clones between March and August. *Spartina patens* in the bare sediment expanded at a rate of $1.1 \pm 0.3 \text{ cm}^2\text{d}^{-1}$ from March to August. However, transplants in the center of *S. alterniflora* clones did not expand from March to August and actually decreased in area by $-0.1 \pm 0.1 \text{ cm}^2\text{d}^{-1}$. *Spartina patens* area was over five times larger in bare sediment with $230.2 \pm 33.1 \text{ cm}^2$ ($F_{3,40} = 13.2; p < 0.001$, Figure 2.3). Similarly, percent cover of *S. patens* increased by $29.8 \pm 7.7\%$ in the bare sediment from March to August, but remained similar in the *S. alterniflora* clones with a small decrease of $4.8 \pm 3.5\%$ area from March to August ($F_{3,40} = 15.0; p = 0.001$, Figure 2.3).

![Figure 2.3](image)

Figure 2.3. The average vegetated area and percent cover (± standard error) of *S. patens* transplants in March and August 2017, in the bare sediment and sediment within *S. alterniflora*. This study took place in a created brackish marsh within Sabine National Wildlife Refuge, Calcasieu, Louisiana. A two way analysis of variance and a Tukey post hoc test was conducted to analyze the interactions between the sampling date and sediment type. Different letters indicate significant differences within the same month sampled ($p < 0.05$).
Stem density of transplants in bare sediment was almost twice that within *S. alterniflora* clones (*t* = 2.0, *p* = 0.004; Figure 2.4). No significant interactions were found between the density of transplants and sampling date.

Figure 2.4. The average *S. patens* transplant stem density (± standard error) in bare sediment and sediment inside of *S. alterniflora* from measurements taken in March and August. Sampling took place in a created brackish marsh within Sabine National Wildlife Refuge, Calcasieu, Louisiana. A student’s t-test was conducted to determine the difference between transplants types.

Figure 2.5. The average *S. patens* height (± standard error) transplanted in the bare sediment and inside of *S. alterniflora* during March and August at a created brackish marsh within Sabine National Wildlife Refuge, Calcasieu, Louisiana. A student’s t-test was conducted to determine the difference between sediment types in each month sampled.
Although lateral expansion rate, % cover and stem density of *S. patens* were all greater in the bare sediment than in the *S. alterniflora* clones by the end of the study, plant height was similar. Height of the bare sediment transplants was significantly greater in August than in March (t= 2.94, p =0.008, Figure 2.5) illustrating an increase in height over the course of this study. This was not observed in the transplants within *S. alterniflora*.

Specific leaf area and leaf percent nitrogen are both used as proxies for growth rate (Perez-Hanguindegay et al., 2013) and in this study they were found to be strongly correlated with each other ($r^2 = 0.84$, $P < 0.0001$, Figure 2.6). However, there was no significant difference in the SLA and leaf percent nitrogen between *S. patens* transplants in the bare sediment and those within *S. alterniflora* clones.

Figure 2.6. The relationship between leaf percent nitrogen and average SLA in *S. patens* transplants. Leaves were collected in August 2017 at Sabine National Wildlife Refuge, Calcasieu, Louisiana.
3.3.3. Relationships between environmental and transplant data

Elevation. The elevation ranged approximately 12 cm across the study plots. There was no significant difference between the elevation of transplants within *S. alterniflora* and transplants in the bare sediment. In bare sediment, there was no significant relationship between stem density of *S. patens* and elevation, which in the center of *S. alterniflora* clones, elevation explained approximately 53% of the variation in stem density at the end of the study (Figure 2.7). Similarly, elevation explained 67% of the variation in lateral expansion within *S. alterniflora* clones (Figure 2.7) but no significant relationship was found in the bare sediments. These data imply that the *S. patens* growing in close proximity with *S. alterniflora* have greater densities and area at higher elevations. Elevation positively related to salinity in August when the marsh was flooded (Figure 2.8), but did not relate to salinity in March when the marsh was dry. Elevation was not significantly related to PMN, Extractable NH$_4^+$, SOM, or bulk density.

Salinity. Sediment salinity when the marsh was not flooded in March ranged from 12 to 19 psu. In bare sediment, there was no significant relationship between height, stem density and vegetated area of *S. patens* and salinity, but in the center of *S. alterniflora* clones, salinity explained approximately 85% of the variation in stem height, 80% of the variation in stem density and 77% of the variation in vegetated area at the end of the study (Figure 2.9). This indicates that *S. patens* growing within *S. alterniflora* tends to grow to taller heights, greater densities, and larger areas in higher salinities at this brackish marsh. Salinity stress was likely not limiting in this brackish marsh as well.
Figure 2.7. Relationship between elevation and August stem density (upper) and August vegetation area (lower) of *S. patens* transplanted in bare sediment and *S. alterniflora* clone centers in a created marsh in Sabine National Wildlife Refuge, Calcasieu, Louisiana.

Figure 2.8. Relationship between elevation and August salinity in a created brackish marsh in Sabine National Wildlife Refuge, Calcasieu, Louisiana.
Figure 2.9. Relationship between March sediment salinity and August transplant height (upper), density (middle), and vegetative area (bottom) of *S. patens* transplanted in bare sediment and *S. alterniflora* clonal centers in a created marsh in Sabine National Wildlife Refuge, Calcasieu, Louisiana.
Sediment Nitrogen. Vegetation area was significantly but somewhat weakly related to the availability of NH$_4^+$ at 10–20 cm depth interval; (Figure 2.10). This relationship was influenced by greater NH$_4^+$ concentrations and high S. patens vegetation areas cover in bare sediments than in S. alterniflora clones. No other relationships were found between the sediment nitrogen properties measured and transplant measurements.

Figure 2.10. Relationship between extractable ammonium and S. patens transplant area covered at Sabine National Wildlife Refuge, Calcasieu, Louisiana.

Redox potential. No significant relationship was found between redox potential at any depth (5 cm, 10 cm, and 20 cm) and the transplant measurements.

2.4. Discussion

The results of this study illustrate that early successional plant species can limit the expansion and growth of later successional species in newly created ecosystems. In the present study, growth of Spartina patens, a late successional perennial grass, was greatly suppressed in a created marsh when in competition with the pioneer species, S. alterniflora. Spartina patens had a lower lateral expansion rate, percent cover, and stem density when transplanted into S.
*Spartina alterniflora* clones than when transplanted to bare sediment. *Spartina alterniflora* can establish within five years in newly created marshes in Louisiana (Proffitt & Young 1999; Proffitt et al. 2003) and has the potential to expand at all elevations in absence of interspecific competition (Bertness 1991; Proffitt & Young 1999; Proffitt et al. 2003; Travis et al. 2004). This study demonstrated that, while not typically found at early stages of marsh development, *S. patens* can also grow and expand when introduced to the mid and high elevations of a newly created brackish marsh without competition by other species. Together, these results suggest that dispersal and/or initial establishment of *S. patens* in bare substrates of newly created marshes may be limited, and growth and expansion may be further inhibited once the marsh is colonized by *S. alterniflora*.

*Spartina patens* transplanted in the bare sediment had a greater growth than transplants within *S. alterniflora*. *Spartina patens* expanded at a larger rate in bare sediment (1.1 ± 0.3 cm$^{-2}$d$^{-1}$) than *S. patens* transplanted within *S. alterniflora* (-0.1 ± 0.1 cm$^{-2}$d$^{-1}$). Transplant stem density was significantly higher in bare sediment (2115 ±180 stems m$^{-2}$) than within *S. alterniflora* (1362.5 ±164 stems m$^{-2}$). While plant height did not differ between the two transplant types, the *S. patens* in the bare soil had a significant increase in height from May to August while *S. patens* within *S. alterniflora* had no significant change in height. These results show that *S. patens* can establish and grow in the created marsh when not in competition with *S. alterniflora* and that *S. alterniflora* had more impact as a competitor than as a facilitator on *S. patens*.

*Spartina alterniflora* facilitates mid to high marsh forbs and shrubs (Egerova et al., 2003; Proffitt et al. 2005), but competes with *S. patens* in created marshes. Salinity reduction was hypothesized as the mechanism for *S. alterniflora* facilitative interactions with shrubs and forbs.
(Egerova et al. 2003). In the present study, sediment within *S. alterniflora* had roughly 2 psu lower salinity than the bare sediment indicating some potential for facilitative interactions. However, slight reduction in salinity likely was only a minor benefit for *S. patens* and was vastly outweighed by the competitive interactions *S. alterniflora* had on *S. patens*.

Plant interactions in created marshes differ than those in natural marshes. In low elevations of natural marshes, *S. patens* is limited by abiotic stressors, where the more stress tolerant *S. alterniflora* is the dominant species (Bertness, 1991). In the higher elevations *S. patens* can grow extensive roots which can outcompete *S. alterniflora* for nutrients, competitively excluding *S. alterniflora* from mid to high marsh elevations (Emery et al. 2001; Bertness, 1991). Our study shows *S. alterniflora* is outcompeting *S. patens* in the mid to high elevations of the created marsh which is not typical in a natural marsh. High elevations of natural salt marshes can have lower nitrogen and higher organic matter both of which stunt *S. alterniflora* growth (Bertness 1988; Bertness, 1991; Bertness et al. 2002). Sediment nitrogen and organic matter content was not related to elevation in the created marsh in this study due to the low development of sediment nitrogen and organic matter pools overall. Newly created marshes can have lower sediment organic matter (10 – 30 % lower, Craft et al. 1999; 2003) which could be advantageous for the establishment and growth of *S. alterniflora*. In the present study, extractable NH$_4^+$ at a sediment depth between 10 and 20 cm was almost 40 times that of sediment within *S. alterniflora* and sediment from a nearby natural marsh. The high amount of extractable ammonium was likely due to accumulation in subsurface sediment with limited plant uptake. Newly created marshes are largely non-vegetated initially as plants colonize, leaving a large reserve of plant available nitrogen. With high nitrogen availability, *S. alterniflora* can outcompete mid-to-high marsh species in natural marshes as belowground competition for
nutrients is reduced and aboveground competition for light is more prominent (Bertness et al., 2002; Emery et al., 2001). *Spartina alterniflora* has the potential to grow taller and shade high marsh species like *S. patens* in high nutrient environments (Emery et al., 2001). This large initial reserve of nitrogen in a newly created marsh may allow *S. alterniflora* to outcompete *S. patens* species trying to establish as high nutrient marshes typically favor *S. alterniflora* growth.

Edwards and Mills (2005) conducted a comprehensive study comparing the net primary productivity of *S. alterniflora* across a chronosequence of created marshes, and between natural and created marshes in SNWR. Net aboveground productivity was found to be highest in the younger created marshes and decreased with marsh age (Edwards and Mills, 2005). The aboveground productivity still remained higher in created marshes than natural marshes even after 20 years after marsh creation (Edwards and Mills, 2005). The net belowground productivity of *S. alterniflora* was less in young created marshes than in natural marshes, but increased as created marshes aged reaching levels similar to natural marshes after 6 to 8 years (Edwards & Mills, 2005). The young created marsh in our study had high amounts of extractable NH$_4^+$ which could explain why Edwards and Mills (2005) found *S. alterniflora* to have a relatively high aboveground productivity and low belowground productivity in comparison to the natural marsh as there was less need for roots to uptake nutrients in the created marsh. Vegetated created marsh sediment had a significantly lower extractable NH$_4^+$ content nearly 25 times less when compared to the non-vegetated sediment showing plant-available nutrients decline with vegetation expansion and growth. Depletion of this reservoir of available nitrogen and more competition for nutrients in aging created marshes likely causes *S. alterniflora* to invest greater resources in belowground productivity reducing aboveground productivity. This shift to greater emphasis on belowground biomass development may make *S. alterniflora* less competitive with *S. patens* as a
marsh ages since *S. patens* is a greater belowground competitor. However, it may take over 20 years for *S. alterniflora* aboveground productivity in the created marsh to decline to levels similar in the natural marsh which could negatively impact *S. patens* colonization, growth, and expansion in created marshes.

The high amount of extractable $\text{NH}_4^+$ in the bare sediment may have also benefited *S. patens* transplants in the bare sediment. Extractable $\text{NH}_4^+$ between the 10-20 cm depth interval was positively related to vegetative area of *S. patens* transplants. An increase in nitrogen availability enhances biomass of *S. patens* when not in completion with *S. alterniflora* (Watson et al., 2015; Merino et al., 2010; Meert and Hester; 2009). The bare sediment had a much greater extractable $\text{NH}_4^+$ than the sediment colonized by *S. alterniflora*, which also likely influenced the better growth of *S. patens* in bare sediment than within *S. alterniflora* clones. When not in competition with *S. alterniflora*, *S. patens* likely benefits from greater availability of nitrogen.

Growth rate, stem density and height of *S. patens* transplanted into *S. alterniflora* clones increased with increasing salinity (salinity range: 2 - 19 psu). Salinity can limit growth of many salt marsh species (Bradley and Morris, 1992; Broome et al., 1995). Therefore, a higher salinity may reduce competition from neighboring plants (Bertness and Ewanchuk, 2002; Konisky & Burdick, 2004; Crain et al. 2004). *Spartina patens* have greater biomass at lower salinities in absence of competition from other species (Merino et al. 2010; Crain et al., 2004). However, in the presence of other species, *S. patens* transplants had greater biomass at higher salinity, possibly due to reduced competition for light with neighboring plants having less aboveground biomass at higher salinity (Salinity range: 14-24 psu, Konisky & Burdick, 2004). We found no relationship between salinity and *S. patens* transplanted in the bare sediment indicating that higher salinities only benefited *S. patens* in competition with *S. alterniflora*. No correlation
between sediment salinity and the height or density of *S. alterniflora* was found suggesting there was no negative effect of salinity on *S. patens*’ competitor. However, in previous studies *S. alterniflora* productivity has been found to decrease with increasing salinity (Salinity range: 5-50 psu Bradley and Morris, 1991). So while sediment salinity seems to benefit *S. patens* when in competition with *S. alterniflora*, the mechanism was not determined from this study, but could be due to a reduction in *S. alterniflora* productivity.

Elevation was also positively related to density and vegetative area of *S. patens* transplanted within *S. alterniflora* clones. Salinity and elevation were not correlated when the marsh was dry in March but were correlated in August when the marsh was flooded. Flood events, which are more prominent at lower elevations, dilute accumulated salts (Gosselink, 1984, Mitsch and Gooselink, 2000). Flooding may lead to a reduction in salinity, particularly at lower elevations with less of an effect at higher elevations. Ultimately, higher elevations with higher salinity tended to benefit *S. patens* growing within *S. alterniflora* clones. Higher elevations experience less flooding and anaerobic soil conditions than the low marsh. *Spartina patens* has physiological limitations in oxygenating roots when soils are reduced making it susceptible to anaerobic conditions and regular flooding restricting it to higher marsh elevations (Gleason, 1980; Bertness, 1991). When transplanted to low, mid, and high elevations of a New England salt marsh, *S. patens* had the best growth in the mid to high elevations with a reduction in biomass at low elevations (Konisky & Burdick, 2004). Both above-and belowground biomass of *S. patens* is positively related to marsh elevation (Snedden et al. 2015). Interestingly the height, density, and vegetation area of the *S. patens* transplants in the bare sediment was not related to elevation. This indicates that the increase in *S. patens* growth at higher elevations was likely due to a reduction in competition with *S. alterniflora*. While our study found no relationship between
S. alterniflora height or stem density and elevation, another study found that S. alterniflora net primary productivity was negatively impacted at higher elevations in created marshes (Edwards & Mills, 2005). With S. alterniflora productivity reduced at higher elevations this may allow for S. patens to better establish and grow in the mid to high created marsh.

Spartina patens is considered the most prevalent emergent plant in Louisiana’s coastal wetlands (Chabreck, 1970) and its ability to establish in the mid-to-high elevations of created marshes is important for development of plant communities that resemble natural marshes. Spartina alterniflora was found to be a major competitor with S. patens, and severely limited its growth in a brackish created marsh. Since S. alterniflora is typically the dominant species in young created marshes (Proffitt and Young, 1999; Proffitt et al. 2003), it may prevent S. patens from colonizing. At higher salinities and elevations, S. alterniflora was a less effective competitor with S. patens indicating S. patens may better establish under these conditions. As a marsh ages and vegetation establishes, nutrients become more limited making S. alterniflora less competitive with S. patens. Further research could examine S. patens growth across a range of created marsh ages to see whether S. alterniflora is less competitive in older created marshes. This would increase understanding of created marsh development and how long it will take to reach favorable conditions for S. patens to colonize and compete in created brackish marshes.
CONCLUSION

Chapter 1 of this thesis found that marsh vegetation community significantly more so impacts CO₂ fluxes rather than the soil characteristics. When the plant community was dominated by *S. alterniflora* in both the newly created marsh and in the natural marsh CO₂ fluxes were similar, even though soil properties were different. The shift from bare sediment to vegetated communities and shift from plant species significantly changed CO₂ fluxes. Elevation also significantly related to CO₂ fluxes in the natural vegetated communities at certain months over the study. This chapter indicates that CO₂ can develop quickly in created marshes as the plant communities have been found to rapidly develop in these ecosystems, and that elevation may also impact CO₂ fluxes.

Chapter 2 found that *S. patens* when transplanted into the created marshes grew better when not in competition with *S. alterniflora*. This indicates that *S. alterniflora* does not facilitate *S. patens* growth in the created marsh like it does for other marsh shrubs and forbs. *Spartina patens* when in competition with *S. alterniflora* grew better at high elevations and salinities, but this trend was not seen with transplants in the bare soil. In the natural marsh *S. patens* typically outcompetes *S. alterniflora* in the mid to high elevations of the marsh, but in high nitrogen environments *S. alterniflora* can outcompete *S. patens*. The newly created marsh has high nitrogen reserves in the bare sediment which *S. alterniflora* can access possibly giving it the advantage over *S. patens*.

Overall these chapters deal with aspects of created marsh succession and development. Chapter 1 indicates that CO₂ fluxes in the created marsh can become similar to the natural marshes as plant communities develop. Chapter 2 shows that plant interactions in a developing created marsh may differ from that of a natural marsh.
REFERENCES


VITA

Andrew Muench was born and raised in Wisconsin getting his Bachelor of Science degree at the University of Wisconsin-Madison in 2015. Andrew then worked as a restoration technician in Wisconsin before going to graduate school at Louisiana State University. The author plans to graduate in May 2018 with a Master of Science in Oceanography and Coastal Sciences. Andrew will be working on coastal restoration policy as a Knauss fellow after graduation.