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Oligohaline wetland response and recovery following storm-driven saltwater intrusion in coastal Louisiana

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OLIGOHALINE WETLAND RESPONSE AND RECOVERY FOLLOWING STORM-
DRIVEN SALTWATER INTRUSION IN COASTAL LOUISIANA

A Dissertation

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
Doctor of Philosophy

in

The Department of Oceanography and Coastal Sciences

by
Whitney Marie Kiehn
B.S. University of Georgia, 2005
M.S. University of South Carolina, 2008
August 2013

To Adam and Carter.

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ABSTRACT

Coastal ecosystems occupy an interface between land and ocean, making them vulnerable to a variety of natural and anthropogenic disturbances. Large, episodic disturbances (mega-disturbances) cause immediate and long-lasting changes to coastal wetland plant communities and soils by changing the environmental conditions in which they exist. Here I examined the impacts of storm-induced saltwater intrusion and post-intrusion conditions on the structure and growth of an oligohaline wetland plant community, and on wetland soil biogeochemistry and conditions during and after saltwater intrusion. In the greenhouse, a six-week saltwater intrusion reduced canopy cover and species richness. Once intrusion stress was alleviated, plant community structure and growth were heavily influenced by water level during the 20-month recovery period. Plant resilience after subsequent but non-lethal disturbance (clipping) was dependent on the interaction of flooding and salinity, such that canopy cover recovered to pre-clipping condition more slowly under salty, drained conditions. I also found that sustained high water level favored belowground biomass accumulation, high shear strength, and a relatively low decomposition rate in oligohaline wetland soils in the greenhouse. In the field, plant community structure and growth following saltwater intrusion were heavily influenced by the degree of flooding during the recovery period. High flooding depressed canopy cover and species richness, and influenced species dominance. High flooding also resulted in reduced soil conditions in which sulfide accumulated, and in depressed belowground biomass accumulation. Conversely, sediment inputs enhanced wetland recovery from saltwater intrusion by increasing end-of-season aboveground biomass, providing nutrients, and lowering sulfide concentration

when flooding was high. Post-intrusion grazing intensity had few impacts on wetland plants and soils during the recovery phase. Soil response variables measured in intrusion-impacted and reference soils before, during, and after a 6-week saltwater intrusion event indicated that although some significant changes in microbial activity, abundance, and nutrient availability occurred due to saltwater intrusion, these impacts were generally transient, with post-intrusion conditions resembling pre-intrusion conditions.

In conclusion, storm-induced saltwater intrusion has some long-lasting impacts on oligohaline wetland plant communities, but mostly transient impacts on oligohaline wetland soils. Possibly more importantly, I found that the oligohaline wetland plant community and soil structure and function was determined by post-intrusion environmental conditions. Because oligohaline wetlands provide vital ecological services in many coastal regions, great effort should be put forth to understand both natural and human impacts to these systems. Information gained through research should be applied in a way that encourages the maintenance of healthy, productive, and diverse wetland communities.

CHAPTER 1

INTRODUCTION

Because coastal ecosystems occupy an interface between land and sea, they are vulnerable to a number of natural and anthropogenic disturbances of terrestrial and marine origin. For example, earthquakes uplift coastal wetlands, changing flooding duration and frequency, permanently changing the ecological landscape (Thilenius 1990). Severe drought alters normal coastal ecosystem functioning by causing die-offs of coastal wetland plants (McKee et al. 2004, Alber et al. 2008). Eustatic and local sea level rise drown once-healthy marshes where sediment and organic matter do not accumulate at a fast enough pace (Day and Templet 1989, Penland and Ramsey 1990, Day et al. 1999, Reed 2006). Grazing by herbivores causes physical disturbance of wetland soils due to grubbing of plant roots and rhizomes, as well as impacts to plant community structure and function and soil stability (Ford and Grace 1998, Randall and Foote 2005). Petroleum spills and releases of dam water cause long-term changes to coastal ecosystem functioning (Kershaw and Kershaw 1986, Baruah and Sarma 1996, Stevens et al. 2001). Large storms such as hurricanes and typhoons scour marshes, wash away beaches, and redistribute dune sands (Morton and Barras 2001, Park and Edge 2011, Udo 2012). Such mega-disturbances transform the coastal vegetative landscape, and alter the goods and services that the plant communities provide.

Hurricanes, or tropical cyclones, are ubiquitous, episodic mega-disturbances that impact coastal systems in multiple ways including delivering torrential rains, damaging winds, and storm surges to low-lying areas. Storm surges push ocean water into coastal shores, resulting in elevations in porewater salinity for weeks or months (Blood et al. 1991, Michener et al. 1997, Dix et al. 2008). These pulses of high salinity are detrimental

to plant health and alter soil chemistry (Blood et al. 1991, Neyland 2007). When wetland plants that are adapted to low salinity environments are exposed to ocean water, they experience osmotic stress, ion toxicity, and reduced nutrient uptake (Mitsch and Gosselink 2000). Salinity exposure may therefore lead to reduced growth, necrosis, or even plant death (Guntenspergen et al. 1995, Martin and Shaffer 2005). Loss of plant canopy leaves soils bare, allowing for an increase in evaporation rates, changes in wetland soil chemistry, and permanently altered wetland landscape (Henry and Jeffries 2009 and refs therein)

Excessive rainfall associated with hurricanes may increase nutrient loads to coastal areas from soil leaching, erosion, leakage from wastewater treatment facilities, and runoff from landfill and animal feeding operations (Mallin and Corbett 2006). Added nutrients can accelerate organic matter mineralization, weaken soils, and result in loss of soil strength, making wetland soils more susceptible to erosion during future storms (Turner 2011). Hurricanes also alter the geomorphology of the wetland landscape, causing changes in hydrological connectivity and affecting longer-term salinity and flooding patterns (Morton and Barras 2011). Extended periods of flooding cause wetland soils to become greatly biochemically reduced and have deleterious impacts to plant health, thereby reducing accumulation of belowground plant structures. Moreover, hurricane-associated wave and surge energy cause mats of wetland soil and plants to become detached from the underlying mud (Morton and Barras 2001, Turner 2011). Soil mats are folded, rolled into balls, and relocated, leaving bare soil and ponds behind. Beyond initial impacts of flooding and salinity intrusion, reworking of creek channels

and the wetland platform landscape by storm forces may result in long-term changes to flooding regimes.

The wetlands of coastal Louisiana are important habitat for birds, fishes, and other wildlife that depend on the survival of these marshes that face a variety of natural and anthropogenic threats. Additionally, coastal marshes provide goods and services, including coastal protection for near-shore residents by serving as a “horizontal levee” and absorbing storm energy, thereby reducing the probability and severity of damage to human welfare (Costanza et al. 2008). Among the threats to coastal wetland protection is local soil subsidence due to faulting and geological compaction, resulting in lower wetland platform elevation. By accelerating soil subsidence, these actions effectively raise the rate of relative sea level rise in affected areas (Morton et al. 2002, Morton et al. 2006). Past canal construction fragments wetlands, increasing hydrological connectivity to salty ocean water and enhancing saltwater encroachment inland (Boesch et al. 1994). Where saltwater encroaches into fresher marshes, marsh plants become stressed, resulting in a loss of aboveground vegetation that is crucial to maintaining wetland health (Bass and Turner 1997, Turner 1997, Day et al. 2000). Another type of disturbance facing Louisiana marshes is herbivory. Large rodents native to South America called nutria (*Myocaster coypus*) were introduced to coastal Louisiana in 1939 after a series of unintentional releases (Evans 1970). Because they are highly successful breeders and have few natural predators, nutria populations grew rapidly in Louisiana wetlands and quickly became a nuisance species. Previous studies of nutria impacts to coastal marshes have documented that intense grazing by the rodent results in a variety of adverse impacts. Wetland plant biomass, community structure, and soil integrity all suffer when

nutria graze (Johnson and Foote 1997, Ford and Grace 1998, Randall and Foote 2005). By eliminating healthy, vegetated marsh, and by lowering soil elevation, grazing by nutria has been implicated as an important contributor to the loss of coastal wetland area in Louisiana marshes (Ford and Grace 1998).

As human populations continue to grow and Earth's climate continues to change, impacts to coastal areas are likely to strengthen (Michener et al. 1997). For this reason, it is crucial that we gain a better understanding of how climactic and anthropogenic factors interact to affect the well-being of wetland systems. Although impacts of hurricane-induced saltwater intrusion have been well documented, less is understood concerning wetland recovery after saltwater intrusion and the factors controlling recovery (Flynn et al. 1995, Baldwin and Mendelssohn 1998). Because storm events can have such significant impacts on the physical structure and hydrology of coastal wetlands, recovery conditions are often different from pre-storm conditions; however, much uncertainty exists about how and to what extent wetland plants and soils recover following such events. Critical to the recovery of these wetlands is their ability to quickly regrow plants which contribute to the maintenance of healthy soil and platform-elevation by trapping sediment, accumulating organic matter, and building soil strength. Because environmental conditions such as post-intrusion nutrient status, salinity, water level, and herbivore pressure often work in concert with one another to shape wetland plant and soil function and structure, it is important to consider their interactions in a post-saltwater intrusion setting.

The goals of this dissertation were to:

- Reduce the scientific uncertainty associated with predicting recovery rates of wetland vegetation after short-term saltwater intrusion, similar to what may occur with the passing of a hurricane.
- Assess the effect of post-hurricane condition on the ability of these communities to recover from a subsequent disturbance, thus providing a measure of how ecosystem resilience was modified by the post-salt intrusion environment.
- Determine how and to what extent post-storm conditions affect oligohaline wetland soils following hurricane-induced salinity intrusion.
- Determine how and to what extent a storm-associated saltwater pulse affects oligohaline soil biogeochemistry and how soil biogeochemistry changes once intrusion pressure was relieved.

Chapters 2 through 5 of this dissertation examine the effects of storm-associated saltwater intrusion on coastal oligohaline wetland plants and soils, and the environmental drivers of wetland form and function during recovery from intrusion.

In Chapter 2, I examined the impacts of storm-induced saltwater intrusion and post-intrusion conditions, including water level, nutrient status, and salinity, on the structure and growth of an herbaceous oligohaline plant community in a greenhouse mesocosm experiment. Additionally, I assessed resilience of the plant community to subsequent disturbance. In Chapter 3, I describe the interactive impacts of these post-intrusion conditions on oligohaline wetland soil form and function following saltwater intrusion in the same mesocosm experiment described in Chapter 2. Particularly, I

examine the effects of these environmental drivers on belowground biomass accumulation, soil shear strength, decomposition rate, and other important soil physico-chemical responses. In Chapter 4, I describe a 26-month field study aimed at determining how sediment addition, water level, and herbivory interact to shape the recovering of plant community structure and growth. In Chapter 5, I describe how oligohaline wetland soils respond to a single pulse saltwater intrusion, similar to what may occur during a hurricane-associated storm surge, by measuring soil response variables before, during, and after a 6-week saltwater intrusion. This chapter focuses on impacts to microbial activity and abundance, and nutrient dynamics. Finally, Chapter 6 summarizes my findings and describes the implications and potential applications of information described within the dissertation.

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CHAPTER 2

WATER LEVEL CONTROLS POST-INTRUSION RECOVERY OF OLIGOHALINE WETLAND PLANT COMMUNITY STRUCTURE AND GROWTH

INTRODUCTION

Episodic natural and anthropogenic disturbances of herbaceous plant communities have profound immediate and long-lasting impacts that alter community structure and function. For example, herbaceous plant communities disturbed by wildfire experience an increase in canopy cover and plant abundance for years after the initial disturbance (Swan Jr. 1970, McGee et al. 1995, Hutchinson 2005). Similarly, herbaceous understory in hardwood forests impacted by catastrophic wind events, such as tornadoes, becomes more abundant after disturbance (Peterson and Pickett 1995), and abundance and cover may remain high for years, even after the overstory canopy has begun to recover (Nelson et al. 2008). Episodic anthropogenically-driven disturbances, such as petroleum spills and dam water releases, may also result in immediate and extended shifts in plant community dynamics (Kershaw and Kershaw 1986, Baruah and Sarma 1996, Stevens et al. 2001). For example, decade-old crude oil spill sites had greater plant diversity and lower canopy cover than did unoiled reference sites (Kershaw and Kershaw 1986). By affecting plant community structural and growth traits, such as biodiversity, species composition, and productivity, large episodic disturbances result in overall shifts in ecosystem functioning, potentially destabilizing ecosystem processes for extended periods (Lavorel and Garnier 2002, Kim and Holt 2012, Rzyanny and Voigt 2012).

Because coastal ecosystems occupy an interface, they are especially susceptible to large episodic disturbances (mega-disturbances) originating from both ocean and land. Enormous amounts of energy derived from hurricanes and tsunamis scour marshes, wash

away beaches, and redistribute dune sands (Morton and Barras 2001, Park and Edge 2011, Udo 2012). Earthquakes uplift coastal wetlands, changing flooding duration and frequency, and permanently shift plant zonation patterns (Thilenius 1990). Extreme weather events, such as extended and severe drought, alter normal coastal ecosystem functioning and cause die-offs of coastal wetland plants (McKee et al. 2004, Alber et al. 2008). Mega-disturbances transform the coastal vegetative landscape, and alter the goods and services that the plant communities provide.

Hurricanes, or tropical cyclones, are ubiquitous, episodic mega-disturbances that impact coastal systems in multiple ways including delivering torrential rains, damaging winds, and storm surges to low-lying areas. Storm-associated surge pushes salty ocean water into coastal regions for brief or extended periods of time. In areas where plants are not well adapted to elevated salinities, such as fresh or oligohaline wetlands, vegetation becomes stressed and necrotic due to high salinity and water level. Hurricane impacts on coastal plant communities are well-documented. After Hurricane Andrew in 1992, salt burn was reported for *Panicum virgatum* and *Sagittaria lancifolia* species in oligohaline and freshwater coastal marshes in Louisiana (Guttenspergen et al. 1995). The effects of salt water intrusion were also documented after Hurricane Hugo, which made landfall at Charleston, South Carolina in 1989. Hook et al. (1991) reported that major damage was done to the coastal forests by salt, both wind-blown (salt spray) and salt transported by the storm surge. They estimated that tree mortality due to saltwater infiltration amounted to 38,850 m³ of timber. Similar patterns of salt stress were also reported after Hugo by Gardner et al. (1991). Storm surge associated with Hurricane Katrina, which struck the United States' central Gulf of Mexico coast in August of 2005, salt burned pine trees

along the Mississippi coast (Fritz et al. 2007). During the same year, Hurricane Rita severely damaged freshwater marshes in the southwestern portion of Mississippi River Delta Complex in Louisiana with wind and salt burn (Neyland 2007). More recently, storm surge associated with Hurricanes Gustav and Ike, which struck the central Gulf of Mexico coast in 2008, resulted in the browning and loss of herbaceous marsh plants along a large portion of the LA coastline, creating extensive swaths of necrotic marsh (Landreneau and Brazzell 2008).

Although impacts of hurricane-induced saltwater intrusion have been well documented, less is understood concerning wetland recovery after saltwater intrusion and the factors controlling recovery (Flynn et al. 1995, Baldwin and Mendelssohn 1998). Because storm events can have such significant impacts on the physical structure and hydrology of coastal wetlands, recovery conditions are often different from pre-storm conditions. When Hurricane Hugo struck South Carolina in 1989, soil salinity increased to 13 ppt and remained elevated for months. Available nitrogen concentration also increased and remained high mainly due to ammonium mobilization (Blood et al. 1991). After landfall of four tropical storms in the Guana Tolomato Matanzas National Estuarine Research Reserve in Florida in 2004, total nitrogen and total phosphorus concentrations increased in a Reserve creek due to high runoff from the surrounding watershed (Dix et al. 2008). Net increases or decreases in marsh-surface elevation due to sediment redistribution and/or erosion during storm events cause long-term changes in flooding regimes (Reed 1995, Turner et al. 2006). Because of the complexity of post-storm conditions, rates of habitat recovery are hard to predict.

The goal of this research was to reduce the scientific uncertainty associated with predicting recovery rates of wetland vegetation after short-term salt stress, similar to what may occur with the passing of a hurricane. To achieve this goal, I experimentally determined how and to what extent water-level, nutrient status and salinity influenced the capacity of coastal oligohaline wetlands to recover from short-term saltwater intrusion. I subjected oligohaline marsh sods to a simulated saltwater intrusion event, and then exposed the sods to varying combinations of flooding level, nutrient additions, and water salinities to examine how the interactions of post-intrusion conditions influence community structure and growth during recovery. Because oligohaline wetland plant communities are comprised of a diverse array of plant species with varying salt tolerances, I hypothesized that only a few species with high salt tolerances would dominate the plant community immediately following the removal of intrusion stress. However, I expected relatively low water, nutrient enrichment, and low salinity would favor a more diverse, productive plant community during the recovery phase of the experiment. Furthermore, I assessed the effect of post-hurricane condition on the ability of these communities to recover from a subsequent disturbance, thus providing a measure of how ecosystem resilience was modified by the post-salt intrusion environment. I hypothesized that low water level combined with low salinity and elevated nutrients would allow for a faster and greater degree of recovery of the plant community.

METHODOLOGY

Experimental Design

I evaluated in the greenhouse the influence of post-intrusion nutrient status, water-level, and salinity on the capacity of oligohaline marsh sods to recover from elevated

salinity impact, similar to what occurs during hurricane-induced salt water intrusion. The experimental design was a completely randomized factorial arrangement (2 x 2 x 2) with three post-intrusion dieback treatments: (1) nutrient status (ambient and enriched) (2) water-level (drained or flooded), and (3) recovery salinity (low and high). Each treatment level combination was replicated 5 times.

Sods of intact vegetation and soil were collected from an oligohaline marsh near Madisonville, LA located on the west bank of the Tchefuncte River (30° 23' 12.87" N, 90° 09' 34.38" W) during May 2009. The plant community is dominated by *Sagittaria lancifolia* L. (Alistmataceae) and the soil is classified as a Kenner series Histosol (Graham and Mendelssohn, 2010; Slocum and Mendelssohn, 2008). The average interstitial salinity is 0.96 ± 0.03 psu (Baldwin and Mendelssohn, 1998). The marsh sods, approximately 30 cm in diameter and 30 cm in depth, were placed in 7 gallon plastic buckets containing a 4-cm bottom layer of course gravel. The sods of vegetation were established as marsh mesocosms in a greenhouse on the campus of Louisiana State University. The mesocosms were maintained for five weeks in a moist, well-drained condition by watering and draining at least 3 times weekly. After the 5-week acclimation period, plant dominance was assessed during June 2009 (see Analytical Methods for details). The sods then received a salinity (20 ppt) application (as in Flynn et al. 1995). Synthetic sea water (Instant Ocean, Spectrum Brands, Inc. Atlanta, GA) was used as the salinity source. Sods were flushed with saltwater (20 ppt, as measured the greenhouse using a refractometer) for approximately 1 week by flooding the sods with saltwater, allowing them to rest overnight, and then draining the water from the sod. This process was repeated daily until interstitial salinities reached 20 ppt. Once the target interstitial

water salinity had been reached, saltwater-flooded sods were allowed to rest undisturbed for an additional five weeks. During this time, sods were flooded to a level of 12 cm above soil height. Five additional mesocosms served as undisturbed controls. The salinity of the undisturbed mesocosms was maintained at ambient (2.0 ± 0.5 ppt) and the flooding regime that of the completely drained treatment-level (details below). Water lost due to evapotranspiration was replaced with fresh tap water for all sods. A total of 45 marsh sods were used in the experiment.

Once the dieback of the original vegetation occurred (approximately 6 weeks after seawater application), all sods [treatment ($n = 40$) and control ($n = 5$)] were flushed with freshwater until interstitial salinities returned to their original (ambient) level during August 2009. Dead biomass was removed and plant dominance was reassessed. The mesocosms were then randomly assigned to a recovery phase nutrient/salinity/water-level treatment combination. The undisturbed controls were maintained as such throughout the experiment. Two recovery phase salinity levels [low (2.0 ± 0.5 ppt) and high (6.0 ± 0.5 ppt)] in combination with two different water level regimes [drained (-12 cm) and flooded (+12 cm)], in combination with two nutrient regimes (ambient and elevated [equivalent of $20 \text{ g N m}^{-2} \text{ y}^{-1}$ and $3 \text{ g P m}^{-2} \text{ y}^{-1}$]) were established during August 2009. Porewater salinities were monitored by measuring porewater conductivity, then converting measured values to salinity using standard methods. Ammonium nitrate and potassium phosphate were used as nutrient sources. Treatment and control mesocosms were maintained under these treatment conditions in the greenhouse for 20 months to assess both short and longer-term effects on plant structure (e.g., species composition, percent cover, dominance, importance, and richness), as well as growth attributes (e.g.,

aboveground biomass and productivity, photosynthesis, and net community CO₂ exchange; see Analytical Methods for details).

Analytical Methods

Plant cover and dominance

Vegetation structure, including composition, plant cover, and dominance, was sampled in each greenhouse sod seasonally (spring, summer, winter and fall). Percent cover was ocularly estimated for each species according to 8 cover classes; 0, 0 ≤ 1%, 1-5%, 5-25%, 25-50%, 50-75%, 75-95%, 95-100%. Mid-points of each cover were statistically analyzed. Average canopy height for each species present was determined by measuring the height from the soil surface to the canopy mid-point. Species dominance was calculated for each plant species by multiplying percent cover by its average canopy height.

Importance value

Importance value was determined seasonally as the sum of relative shoot density and relative dominance. Live shoot density was calculated as the number of shoots per species per unit area in each sod. Relative shoot density for each plant species present in an individual sod was determined by dividing the number of shoots for a given species by the total number of shoots for all species per sod. Relative dominance was calculated by dividing the dominance value for each plant species present in an individual sod by the total dominance calculated for all species within the sod.

Species richness

Species richness was determined seasonally by counting the number of species present in each sod.

Growth rate

I measured shoot elongation on as many as three *Sagittaria lancifolia* shoots as an index of growth rate (mm/day) seasonally for up to three *S. lancifolia* shoots, which were not yet fully expanded. The three elongation rates were averaged for each sod for each sampling for statistical analysis. This method has been used successfully for a variety of herbaceous plants and produced results that correlated closely with changes in aboveground biomass and photosynthesis (Hester and Mendelssohn, 1990).

Aboveground biomass and annual productivity

Plant aboveground (AG) biomass and annual productivity were also sampled. To determine AG biomass (g sod^{-1}), all vegetation within the sod was clipped at the ground surface at the end of the 2009 and 2010 growing seasons, divided according to species, dried to a constant weight at 60°C , and weighed. To determine AG productivity ($\text{g sod}^{-1}\text{ yr}^{-1}$), all dead vegetation from January to November 2010 was clipped, divided according to species, dried, and weighed. Dead vegetation weights were combined with the 2010 end-of-the-growing-season biomass data to determine annual productivity.

Net photosynthesis rate

Net photosynthetic rate (P_n , $\mu\text{mol CO}_2\text{ m}^{-2}\text{ s}^{-1}$) was recorded on up to three *S. lancifolia* leaves per sod, one measurement per leaf (Ewing et al. 1995). The photosynthetic rates for each sod were averaged for statistical analysis. Measurements were conducted on the middle portion of an expanding and visually healthy (green) leaf using a portable infrared gas analysis system (LI-6400R, LiCor, Lincoln, Nebraska, USA). Carbon dioxide concentration ($370\text{ }\mu\text{mol mol}^{-1}$), flow ($350\text{ }\mu\text{mol s}^{-1}$) and light intensity ($2000\text{ }\mu\text{mol s}^{-1}$) were controlled.

Resilience and stability

Non-lethal disturbance (clipping at ground surface) was applied to the experimental units at the termination of the experiment in May 2012, and resilience, i.e., the rate of reestablishment, was measured to estimate how the post-saltwater intrusion treatments affected marsh resilience and stability. Resilience and stability was assessed by evaluating the rate and degree, respectively, of vegetation recovery (Suding 2004). Total percent cover and species richness was assessed immediately before disturbance, and at 4, 8, 12, and 23 weeks after disturbance using methods described previously. Aboveground biomass was measured at the initiation of disturbance (week 0) and approximately 23 weeks post-disturbance using methods formerly defined.

Data Analysis

I used a multivariate analysis of variance (MANOVA; PROC GLM) to determine the overall and interactive effects of water-level, nutrient status, and salinity on dominance, biomass, and importance value of the four most commonly-occurring plant species during recovery from saltwater intrusion (SAS version 9.2, SAS Institute). Treatment effects were determined using the Wilks' lambda test statistic. Where significant effects were identified, an individual mixed model ANOVA (PROC MIXED) with repeated measures was used to identify the specific dependent variables (i.e., plant species) that contributed to the significant overall effect (Graham and Mendelssohn 2010). For example, because there was an overall impact of flooding on dominance for the three most commonly-occurring plant species (MANOVA), an ANOVA was performed to identify which of the four plant species were impacted by flooding.

For all other response variables measured during recovery from saltwater intrusion (e.g., total cover, species richness, total aboveground biomass, etc.), a mixed model ANOVA was used to determine significant overall effects. All measures of significance were identified at $p < 0.05$. Significant differences in treatment-level means were determined with the Tukey-Kramer adjustment for multiple comparisons.

Residuals were checked for normality using the Shapiro-Wilk test and for homogeneity of variance using the Levene's test. Where residuals were found not to be normally-distributed or residual variances were not homogeneous, I transformed the data. The following variables were log-transformed: aboveground biomass, production, photosynthesis rate, and growth rate. Total cover and importance values were square-root transformed. Residuals for species richness were normally-distributed, but residual variance was not homogenous. Because transformation did not improve variance homogeneity of variance, I did not transform these data (Levene's, $p < 0.05$). Although square-root transformation of species-specific dominance (MANOVA) improved the homogeneity of residual variance, residuals were not normally distributed. ANOVA is relatively robust concerning deviations in residual normality and homogeneity of residual variance, especially when sample sizes are equal (Eisenhart 1947, Box 1953).

To assess resilience, a simple linear regression fitted through the origin determined the rate of change in *S. lancifolia* dominance and total percent canopy cover between the time of clipping disturbance (i.e., time 0) and 12 weeks after clipping disturbance. Total aboveground biomass stability, *S. lancifolia* dominance stability, and total percent canopy cover stability were assessed by calculating the degree of recovery to pre-clipping conditions after 12 weeks of regrowth [stability = $(X_{\text{week 12}} \div X_{\text{pre-clipping}})$]

* 100, where X is the response variable]. Although I measured response variables for 23 weeks following clipping disturbance, these data were not included in resilience and stability calculations because they reflected end-of-season conditions when plants had begun to senesce and were therefore not indicative of recovery. Treatment effects on the rate of change (resilience) and the degree of recovery (stability) were determined using a mixed model ANOVA. Tests for residual normality and homogeneity of variance were performed using methods described in the previous paragraph.

RESULTS

Plant Community Response to Saltwater Intrusion

Saltwater intrusion resulted in a reduction of total cover from 67 ± 4 (mean \pm standard error [SE]) to 19 ± 1 percent, whereas cover for sods not receiving a saltwater intrusion (controls) remained constant (70 ± 5 pre-intrusion, 70 ± 5 post-intrusion). Species richness was reduced from 5.1 ± 0.2 to 3.1 ± 0.2 species per sod for those sods receiving a saltwater intrusion, whereas the number of species for control sods was 5.4 ± 0.2 and 5.2 ± 0.6 species sod⁻¹ pre- (June 2009) and post-intrusion (Aug. 2009), respectively. Between June and Aug. 2009, the control sods lost three species of plants whereas those sods receiving a saltwater intrusion lost four (Table 2.1); both gained *Cyperus sp.* during this time. For sods exposed to the saltwater intrusion, *Sagittaria lancifolia* was the only plant species that was not lost in at least one sod (Table 2.1). However, percent cover of *S. lancifolia* was reduced from 33.1 ± 1.9 pre-intrusion to 11.7 ± 0.7 post-intrusion for sods exposed to saltwater intrusion, but remained constant at 37.5 ± 0 for control sods pre- and post-intrusion.

Table 2.1 Plant species and frequency of occurrence (%) for those plants present immediately pre- and post-intrusion (June and August 2009, respectively) in control and intrusion-impacted sods, and species lost or gained during the saltwater intrusion period.

	June 2009	August 2009
Control	<i>Alternanthera philoxeroides</i> (60)	<i>Alternanthera philoxeroides</i> (60)
	<i>Eleocharis fallax</i> (80)	<i>Cyperus sp.</i> (20)
	<i>Galium sp.</i> (20)	<i>Eleocharis fallax</i> (100)
	<i>Ipomoea sagittata</i> (80)	<i>Ipomoea sagittata</i> (80)
	<i>Lythrum lineare</i> (20)	<i>Lythrum lineare</i> (20)
	<i>Polygonum punctatum</i> (80)	<i>Polygonum punctatum</i> (100)
	<i>Sagittaria lancifolia</i> (100)	<i>Sagittaria lancifolia</i> (100)
	<i>Spartina patens</i> (40)	<i>Spartina patens</i> (20)
	<i>Schoenoplectus robustus</i> (20)	<i>Symphotrichium subulatum</i> (20)
	<i>Symphotrichium subulatum</i> (20)	
Intrusion	<i>Vigna luteola</i> (20)	
	<i>Alternanthera philoxeroides</i> (52.5)	<i>Alternanthera philoxeroides</i> (37.5)
	<i>Eleocharis fallax</i> (87.5)	<i>Cyperus sp.</i> (5)
	<i>Galium sp.</i> (2.5)	<i>Eleocharis fallax</i> (70)
	<i>Iva frutescens</i> (30)	<i>Iva frutescens</i> (25)
	<i>Ipomoea sagittata</i> (52.5)	<i>Ipomoea sagittata</i> (17.5)
	<i>Lythrum lineare</i> (17.5)	<i>Lythrum lineare</i> (10)
	<i>Ptilimnium capillacium</i> (20)	<i>Polygonum punctatum</i> (5)
	<i>Polygonum punctatum</i> (97.5)	<i>Sagittaria lancifolia</i> (100)
	<i>Sesbania herbacea</i> (2.5)	<i>Spartina patens</i> (20)
	<i>Sagittaria lancifolia</i> (100)	<i>Schoenoplectus robustus</i> (7.5)
	<i>Spartina patens</i> (25)	<i>Symphotrichium subulatum</i> (2.5)
	<i>Schoenoplectus robustus</i> (5)	
	<i>Symphotrichium subulatum</i> (7.5)	
	<i>Vigna luteola</i> (22.5)	
	Species Lost	Species Gained
Control	<i>Galium sp.</i>	<i>Cyperus sp.</i>
	<i>Schoenoplectus robustus</i>	
	<i>Vigna luteola</i>	
Intrusion	<i>Galium sp.</i>	<i>Cyperus sp.</i>
	<i>Ptilimnium capillacium</i>	
	<i>Sesbania herbacea</i>	
	<i>Vigna luteola</i>	

Table 2.2 Plant species identified within study sods and their dominance values presented as the mean and maximum for sods which were exposed to saltwater intrusion and those which were not. Values listed were measured during recovery from saltwater intrusion (Oct. 2009 - April 2011).

Species	Family	Intrusion Exposed ^a		Control	
		Dominance	Maximum	Dominance	Maximum
<i>Sagittaria lancifolia</i>	Alismataceae	877	7,620	480	2,175
<i>Polypogon monspeliensis</i>	Poaceae	712	8,775	1,247	5,776
<i>Spartina patens</i>	Poaceae	452	11,050	609	6,250
<i>Eleocharis fallax</i>	Cyperaceae	379	9,672	252	2,250
<i>Alternanthera philoxeroides</i>	Ameranthaceae	369	10,200	96	1,350
<i>Iva frutescens</i>	Asteraceae	357	12,750	0	0
<i>Ipomoea sagittata</i>	Convolvulaceae	169	6,875	500	6,563
<i>Lythrum lineare</i>	Lythraceae	114	6,250	84	1,200
<i>Echinochloa crus-galli</i>	Poaceae	35	2,850	5	150
<i>Galium sp.</i>	Rubiaceae	32	2,813	5	75
<i>Schoenoplectus robustus</i>	Cyperaceae	12	1,500	0	0
<i>Polygonum punctatum</i>	Polygonaceae	9	840	281	2,063
<i>Baccharis halimifolia</i>	Asteraceae	8	990	0	0
<i>Ptilimnium capillaceum</i>	Apiaceae	1	159	14	495
<i>Cyperus sp.</i>	Cyperaceae	0	0	305	3,875
<i>Symphotrichium subulatum</i>	Asteraceae	5	900	193	3,938
<i>Vigna luteola</i>	Fabaceae	0	0	12	258
<i>Phalaris sp.</i>	Poaceae	0	31	2	20

^aMinimum dominance values for all species was zero.

Plant Community Structure during Recovery from Saltwater Intrusion

Within the plant community recovering from saltwater intrusion, I identified 15 species from 10 families (Table 2.2). Within the control community, I identified the same number of species from 11 families. In general, the most commonly occurring species throughout all flooding x nutrient x salinity treatment-combinations through time included *Alternanthera philoxeroides*, *Eleocharis fallax*, and *S. lancifolia*. These species were also commonly observed in the control treatment. *Polypogon monspeliensis* was commonly observed, but was not present in all treatment combinations early in the experiment. *Iva frutescens*, *Schoenoplectus robustus*, and *Baccharis halimifolia* were

present only in the intrusion-exposed treatment, whereas *Cyperus sp.*, *V. luteola*, and *Phalaris sp.* were present only in the control treatment. *B. halimifolia* was only ever present in one sod and persisted from Oct. 2009 until July 2010. *S. lancifolia* was the only plant species that persisted in all treatment combinations through time.

Percent cover

Total plant canopy cover was enhanced by post-intrusion low water levels and by nutrient enrichment, but salinity had no significant impact (Table 2.3; Fig. 2.1). Percent cover for drained sods was 71 ± 3 percent, while cover for flooded sods was 45 ± 2 percent. Nutrient enrichment resulted in a mean cover of 62 ± 3 percent, while ambient nutrients resulted in a mean percent cover of 53 ± 3 . Although salinity had no significant impact on cover, cover tended to be greater in low salinity treatments during several sampling dates including July 2010. Mean percent cover for low salinity treatments was 61 ± 3 and was 55 ± 3 for high salinity treatments. Time also had a significant impact on total cover. On average, cover was greatest during July 2010 (80 ± 7) and least during January 2010 (27 ± 3). Although the effect of flooding on cover varied significantly with time (Table 2.3), this was primarily due to the last sampling event when there was no difference in cover between these conditions (Fig. 2.1A).

Dominance

For intrusion-impacted sods, mean dominance was greater for *S. lancifolia* than for any other species (Table 2.2); *P. monspelinis* had the greatest dominance in the control sods. *I. frutescens* achieved the greatest dominance when compared to all other species in intrusion-impacted sods, however, *I. frutescens* was present in a maximum of 5 sods and the frequency of occurrence decreased to 2 sods by the end of the experiment.

Ipomoea sagittata achieved greatest dominance within the control treatment. Because no species was present in all sods at all times, minimum dominance for all species was zero. When dominance for the three most commonly-occurring plant species (*A. philoxeroides*, *E. fallax*, and *S. lancifolia*) was analyzed together, MANOVA results indicated an overall effect of flooding, time, and their interaction (Table 2.4A). Neither nutrient status nor any of its two- or three-way interactions had a significant impact on plant dominance when dominance of each of the three plant species was analyzed together. Although the salinity effect was not significant at the $\alpha = 0.05$ level, there was a significant effect at the $\alpha = 0.10$ level when plant species were analyzed together.

Table 2.3 Univariate analysis of variance results for the main and interactive effects on various plant community characteristics during recovery from saltwater intrusion. Aboveground (AG) biomass was measured as sum of all species present in a sod.

	Total Cover	Species Richness	AG ^a Biomass	AG Production	Shoot Elongation	Photo- synthesis	CO ₂ Exchange
Effect	p-value	p-value	p-value	p-value	p-value	p-value	p-value
Flooding (F)	< 0.0001	< 0.0001	0.0229	< 0.0001	0.0001	0.1304	0.0664
Nutrients (N)	0.0100	0.3195	0.1295	0.0035	0.6751	0.8710	0.3988
Salinity (S)	0.3443	0.6885	0.0041	0.1751	0.4510	0.0732	0.3407
F x N	0.2118	0.3195	0.0710 ^b	0.0934	0.5877	0.5708	0.9931
F x S	0.1814	0.0892	0.8860	0.8847	0.1321	0.4787	0.1871
N x S	0.3642	0.3873	0.9968	0.6530	0.1568	0.7750	0.8405
F x N x S	0.4562	0.9467	0.5183	0.7778	0.4778	0.6385	0.1871
Time (T)	< 0.0001	< 0.0001	< 0.0001	n.a. ^c	< 0.0001	< 0.0001	n.a.
F x T	< 0.0001	< 0.0001	0.2150	n.a.	0.5273	0.2722	n.a.
N x T	0.9991	0.3425	0.3080	n.a.	0.1236	0.6376	n.a.
S x T	0.2032	0.5626	0.0677	n.a.	0.1304	0.7957	n.a.
F x N x T	0.4930	0.3582	0.2570	n.a.	0.4525	0.4559	n.a.
F x S x T	0.4352	0.7869	0.1299	n.a.	0.3931	0.6393	n.a.
N x S x T	0.8912	0.0832	0.7252	n.a.	0.1555	0.1447	n.a.
F x N x S x T	0.2527	0.5837	0.7578	n.a.	0.2026	0.5256	n.a.

^a AG = aboveground

^b p-values < 0.1000 were explored further in the text

^c n.a. = not applicable

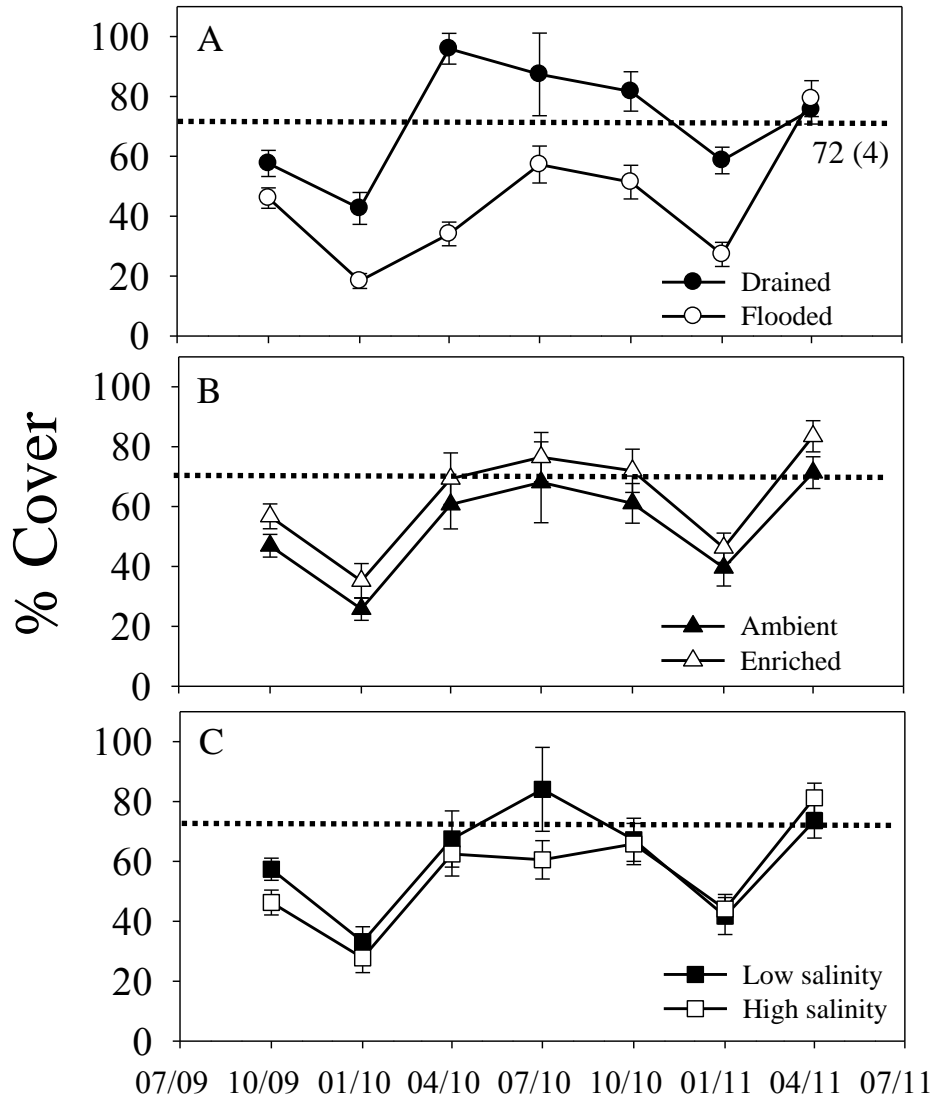


Figure 2.1 Total canopy cover by sampling date for (A) flooding, (B) nutrient, and (C) salinity treatments. Percent cover for the control treatment is represented by a dashed line (mean \pm 1 SE). Drained = water level maintained 12 cm below soil surface. Flooded = water level maintained 12 cm above soil surface. Ambient = no additional nutrients added. Enriched = 20 g N m⁻² yr⁻¹ and 3 g P m⁻² yr⁻¹ added. Low salinity = 2 \pm 0.5 ppt. High salinity = 6 \pm 0.5 ppt.

When these three species were analyzed individually (ANOVA), flooding had a significant stimulatory impact on *E. fallax* and *S. lancifolia* dominance (Table 2.4B; Fig. 2.2B, C). Mean dominance values for *E. fallax* and *S. lancifolia* were 216 \pm 75 and 510 \pm 72 for drained sods and 542 \pm 64 and 1243 \pm 107 for flooded sods, respectively. While

the main effect of flooding on *A. philoxeroides* dominance was not significant at the $\alpha = 0.05$ level, there was a significant flooding x time interaction for this species by which drained conditions tended to have a stimulatory impact on *A. philoxeroides* dominance at certain times (Fig. 2.2A). The difference between drained and flooded treatments for this species was greatest during October 2010. Mean *A. philoxeroides* dominance was 594 ± 133 for drained sods and 144 ± 31 for flooded sods. The interaction between flooding and time was also significant for *E. fallax* and *S. lancifolia*. For *E. fallax*, the difference between flooding treatments was greatest during the last three sampling periods compared to earlier samplings. For *S. lancifolia*, the difference between flooding treatments was greatest during the April to October 2010 growing season. Average dominance for the control treatment was 609 ± 268 during the recovery period.

Although the dominance of *S. lancifolia* was not significantly affected by salinity, low salinity tended to have a stimulatory impact on *S. lancifolia* dominance. Mean *S. lancifolia* dominance for the low salinity treatment was 1042 ± 115 and 711 ± 71 for the high salinity treatment. The difference in *S. lancifolia* dominance was greatest during Oct. 2009 and the difference was relatively small during the rest of the recovery period (Fig. 2.2D).

Importance value

The overall effects of flooding, time and their interaction were significant for the three most commonly-occurring plant species (MANOVA, Table 4A). There was no significant impact of nutrients, salinity, or any of their interactions. When species were analyzed individually (ANOVA), flooding had a significant stimulatory impact on

Table 2.4 (A) Multivariate and (B) univariate analysis of variance results for the main and interactive effects on plant community characteristics during recovery from saltwater intrusion.

A. MANOVA Effects						
	Dominance		Importance Value		AG Biomass ^a	
	d.f.	p-value	d.f.	p-value	d.f.	p-value
Flooding (F)	3,30	< 0.0001	3,30	< 0.0001	3,30	0.0013
Nutrients (N)	3,30	0.9485	3,30	0.6999	3,30	0.9927
Salinity (S)	3,30	0.0752 ^b	3,30	0.1327	3,30	0.0087
F x N	3,30	0.8750	3,30	0.5963	3,30	0.9557
F x S	3,30	0.6698	3,30	0.6924	3,30	0.1621
N x S	3,30	0.1427	3,30	0.4098	3,30	0.5101
F x N x S	3,30	0.5165	3,30	0.4092	3,30	0.5414
Time (T)	18,538	< 0.0001	18,538	< 0.0001	18,538	< 0.0001
F x T	18,538	< 0.0001	18,538	< 0.0001	18,538	< 0.0001
N x T	18,538	0.6879	18,538	0.7947	18,538	0.9909
S x T	18,538	0.2824	18,538	0.3336	18,538	0.0209
F x N x T	18,538	0.5734	18,538	0.6702	18,538	0.5432
F x S x T	18,538	0.4105	18,538	0.7676	18,538	0.8447
N x S x T	18,538	0.7224	18,538	0.5881	18,538	0.3909
F x N x S x T	18,538	0.3219	18,538	0.8084	18,538	0.8157
B. ANOVA Effects						
F						
<i>A. philoxeroides</i>	1,32	0.0518	1,32	0.1534	1,32	0.0852
<i>E. fallax</i>	1,32	0.0182	1,32	0.0210	1,32	0.1267
<i>S. lancifolia</i>	1,32	< 0.0001	1,32	< 0.0001	1,32	0.0009
S						
<i>A. philoxeroides</i>	1,32	0.4836	n.a. ^c	n.a.	1,32	0.4474
<i>E. fallax</i>	1,32	0.6879	n.a.	n.a.	1,32	0.7282
<i>S. lancifolia</i>	1,32	0.0106	n.a.	n.a.	1,32	0.0008
T						
<i>A. philoxeroides</i>	6,192	< 0.0001	6,192	< 0.0001	6,192	0.0007
<i>E. fallax</i>	6,192	< 0.0001	6,192	< 0.0001	6,192	< 0.0001
<i>S. lancifolia</i>	6,192	< 0.0001	6,192	< 0.0001	6,192	< 0.0001
F x T						
<i>A. philoxeroides</i>	6,192	0.0003	6,192	0.4297	6,192	0.0413
<i>E. fallax</i>	6,192	0.0097	6,192	< 0.0001	6,192	0.0002
<i>S. lancifolia</i>	6,192	< 0.0001	6,192	< 0.0001	6,192	< 0.0001
S x T						
<i>A. philoxeroides</i>	n.a.	n.a.	n.a.	n.a.	6,192	0.1967
<i>E. fallax</i>	n.a.	n.a.	n.a.	n.a.	6,192	0.3251
<i>S. lancifolia</i>	n.a.	n.a.	n.a.	n.a.	6,192	0.0022

^a AG = aboveground

^b p-values < 0.1000 were explored further in part B of the table

^c n.a. = not applicable

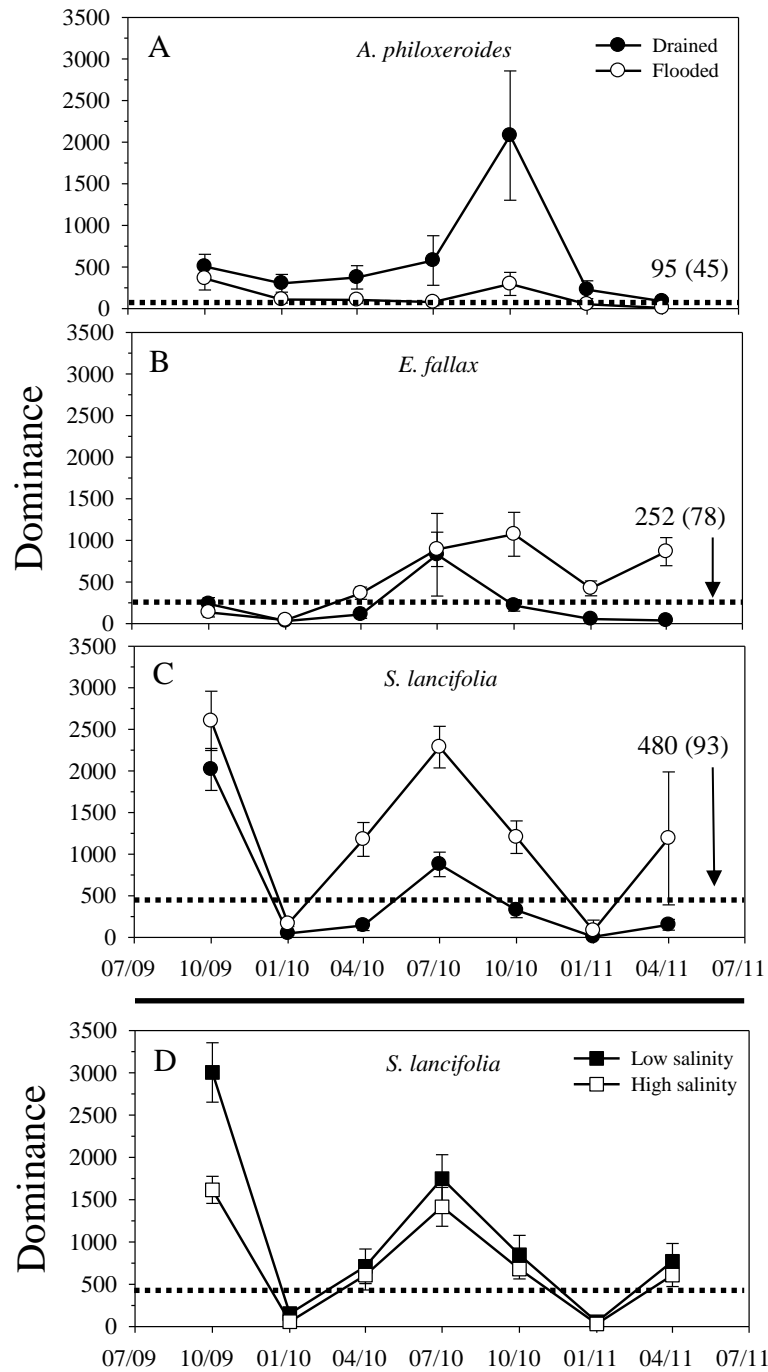


Figure 2.2 Plant dominance by sampling date for (A) *Alternanthera philoxeroides*, (B) *Eleocharis fallax*, (C) *Sagittaria lancifolia* by flooding treatment, and (D) *S. lancifolia* by salinity treatment. Dominance for the control treatment is represented by a dashed line (mean \pm 1 SE in parenthesis). Drained = water level maintained 12 cm below soil surface. Flooded = water level maintained 12 cm above soil surface. Low salinity = 2 ± 0.5 ppt. High salinity = 6 ± 0.5 ppt.

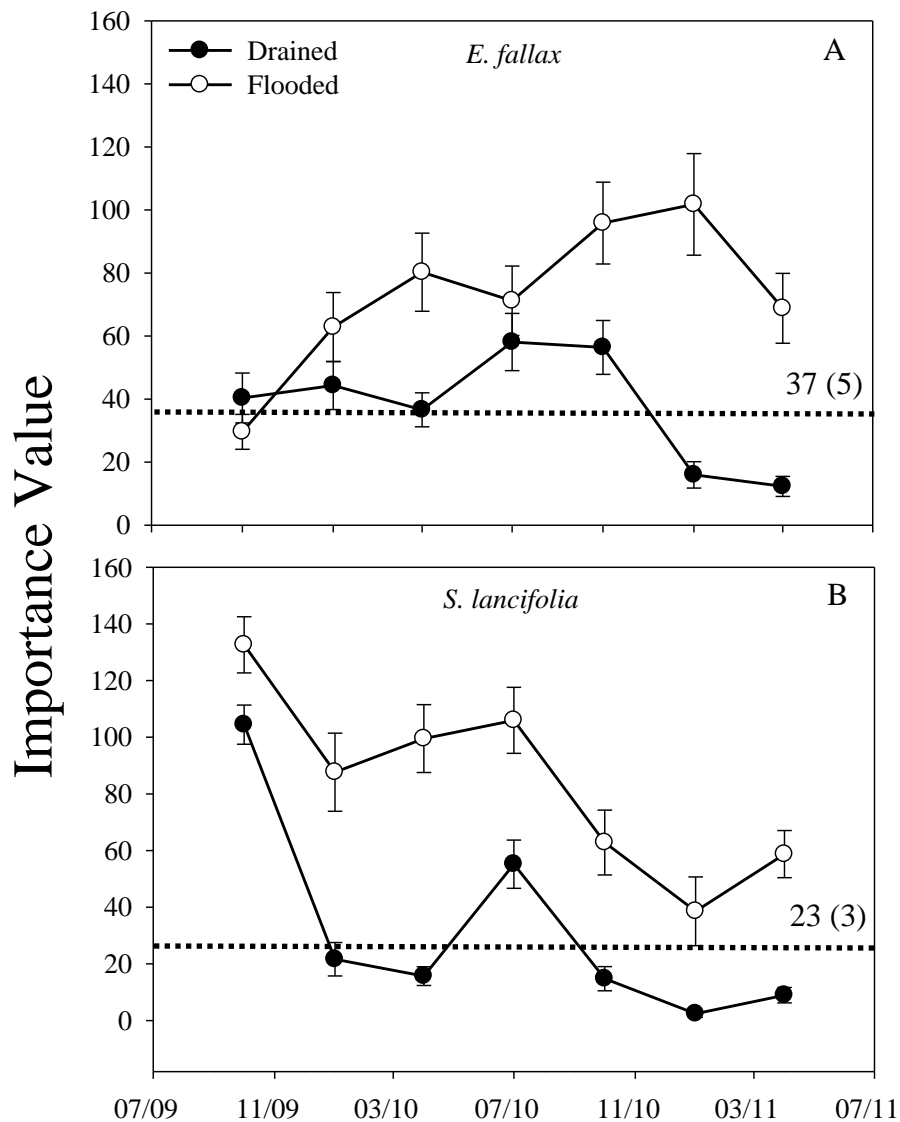


Figure 2.3 Importance value by flooding treatment by sampling date for (A) *Eleocharis fallax* and (B) *Sagittaria lancifolia*. Importance value for the control treatment is represented by a dashed line (mean \pm 1 SE in parenthesis). Drained = water level maintained 12 cm below soil surface. Flooded = water level maintained 12 cm above soil surface.

E. fallax and *S. lancifolia* importance values (Fig. 2.3). The mean importance values for *E. fallax* and *S. lancifolia* were 38 ± 3 and 32 ± 3 for drained treatments, respectively, and 73 ± 5 and 84 ± 5 for flooded treatments. The influence of time on *E. fallax* and *S. lancifolia* was different. The importance of *E. fallax* in flooded sods trended upward, but

importance trended downward for drained sods (Fig. 2.3). *S. lancifolia* importance trended downward for both drained and flooded treatment-levels over time. Mean importance of *A. philoxeroides* and *S. patens* was 4 ± 1 and 26 ± 9 for control treatments, respectively, and was 18 ± 2 and 17 ± 2 for intrusion-exposed sods.

Species richness

Flooding had a negative impact on species richness (Table 2.3; Fig. 2.4). Mean species richness for drained sods was 4.3 ± 0.11 , while richness for flooded sods was 3.1 ± 0.09 . There was also a significant flooding x time interaction by which richness was significantly different between flooding and drained conditions for the first five sampling periods but was similar for the last two samplings. Nutrients, salinity, nor any of their interactions had a significant effect on species richness ($p > 0.05$). However, species richness varied significantly with time. Richness was greatest during April 2010 and April 2011 (4.8 ± 0.24 and 4.4 ± 0.12 , respectively) and was lowest during January 2011 (2.9 ± 0.14 ; Fig. 2.4). Species richness for the control treatment followed a similar trend to those sods exposed to the intrusion salinity (data not shown). However, richness in the control treatment was consistently greater than richness in either flooding treatment-level of the intrusion-exposed sods.

Plant Community Growth during Recovery from Saltwater Intrusion

Biomass and production

End of season aboveground (AG) biomass summed for all species in a single sod was enhanced by drained water level and by low salinity (Table 2.3, Fig. 2.5). AG biomass was unaffected by nutrient status alone, but nutrient status interacted with flooding such that AG biomass was lowest when flooded with ambient nutrient levels

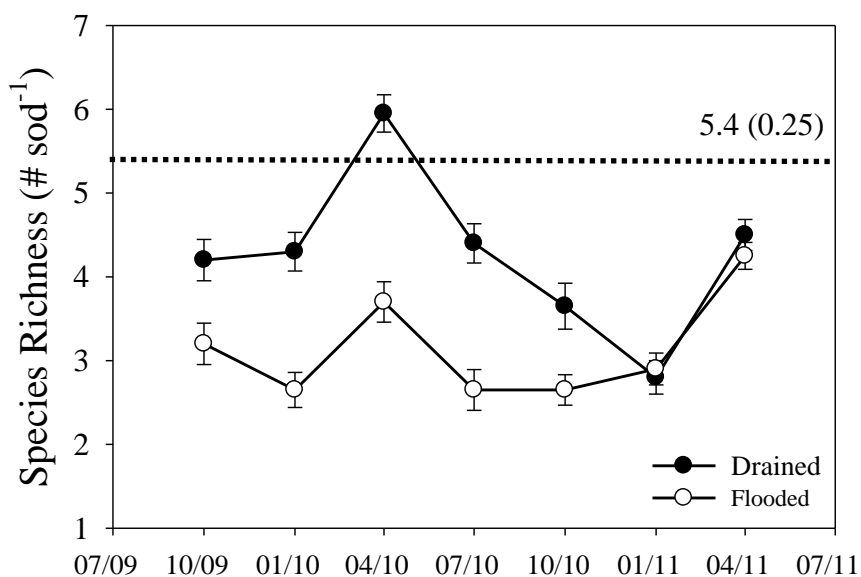


Figure 2.4 Species richness by sampling date. Richness for the control treatment is represented by a dashed line (mean \pm 1 SE in parenthesis). Drained = water level maintained 12 cm below soil surface. Flooded = water level maintained 12 cm above soil surface.

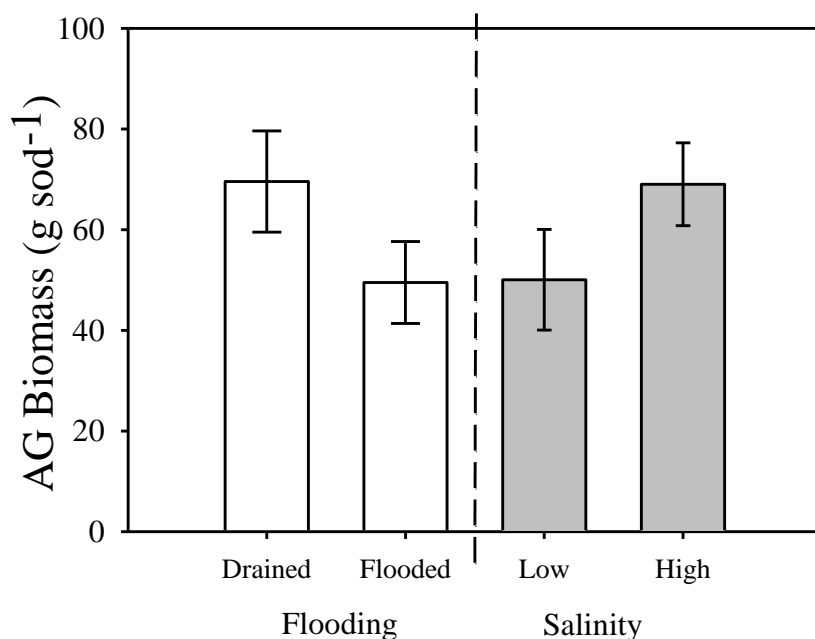


Figure 2.5 End of season aboveground biomass by flooding and salinity treatments (mean \pm 1 SE). Drained = water level maintained 12 cm below soil surface. Flooded = water level maintained 12 cm above soil surface. Low salinity = 2 ± 0.5 ppt. High salinity = 6 ± 0.5 ppt.

($33.5 \pm 4.4 \text{ g sod}^{-1}$), and was greatest when water level was drained, regardless of nutrient treatment (Fig. 2.5). Time had a significant impact on total biomass such that AG biomass was less in October 2009 ($29.5 \pm 2.1 \text{ g sod}^{-1}$) than in October 2010 ($89.5 \pm 11.1 \text{ g sod}^{-1}$).

Overall, the effects of flooding, time, and their interaction on AG biomass of the three most commonly-occurring plant species were significant (MANOVA, Table 2.4A). At the end of the 2009 growing season, there was no significant difference in aboveground biomass for flooding treatments for any of the four species (ANOVA and Tukey-Kramer method; Fig. 2.6A). However, flooding had a stimulatory impact on *E. fallax* and *S. lancifolia* biomass in 2010, but flooding negatively impacted *A. philoxeroides* biomass during this time (Fig. 2.6B). Salinity also interacted with time such that high salinity depressed *S. lancifolia* biomass during the 2009 growing season, but not during 2010 (Fig. 2.6C, D).

Total annual aboveground production during the 2010 growing season was negatively impacted by flooding and was stimulated by nutrient enrichment (Table 2.3). For drained and flooded treatments, mean annual production was $155 \pm 13 \text{ g sod}^{-1}$ and $85 \pm 15 \text{ g sod}^{-1}$, respectively. Nutrient enrichment increased mean production by approximately 50% from $98 \pm 14 \text{ g sod}^{-1}$ to that of $143 \pm 16 \text{ g sod}^{-1}$. There was no significant impact of salinity or any two- or three-way interaction. Mean annual production for control treatments was $110 \pm 25 \text{ g sod}^{-1}$.

Growth rate

Flooding had a stimulatory impact on *S. lancifolia* growth, measured as shoot elongation (Table 2.3); growth rate was $9.6 \pm 1.7 \text{ mm d}^{-1}$ for drained water levels and

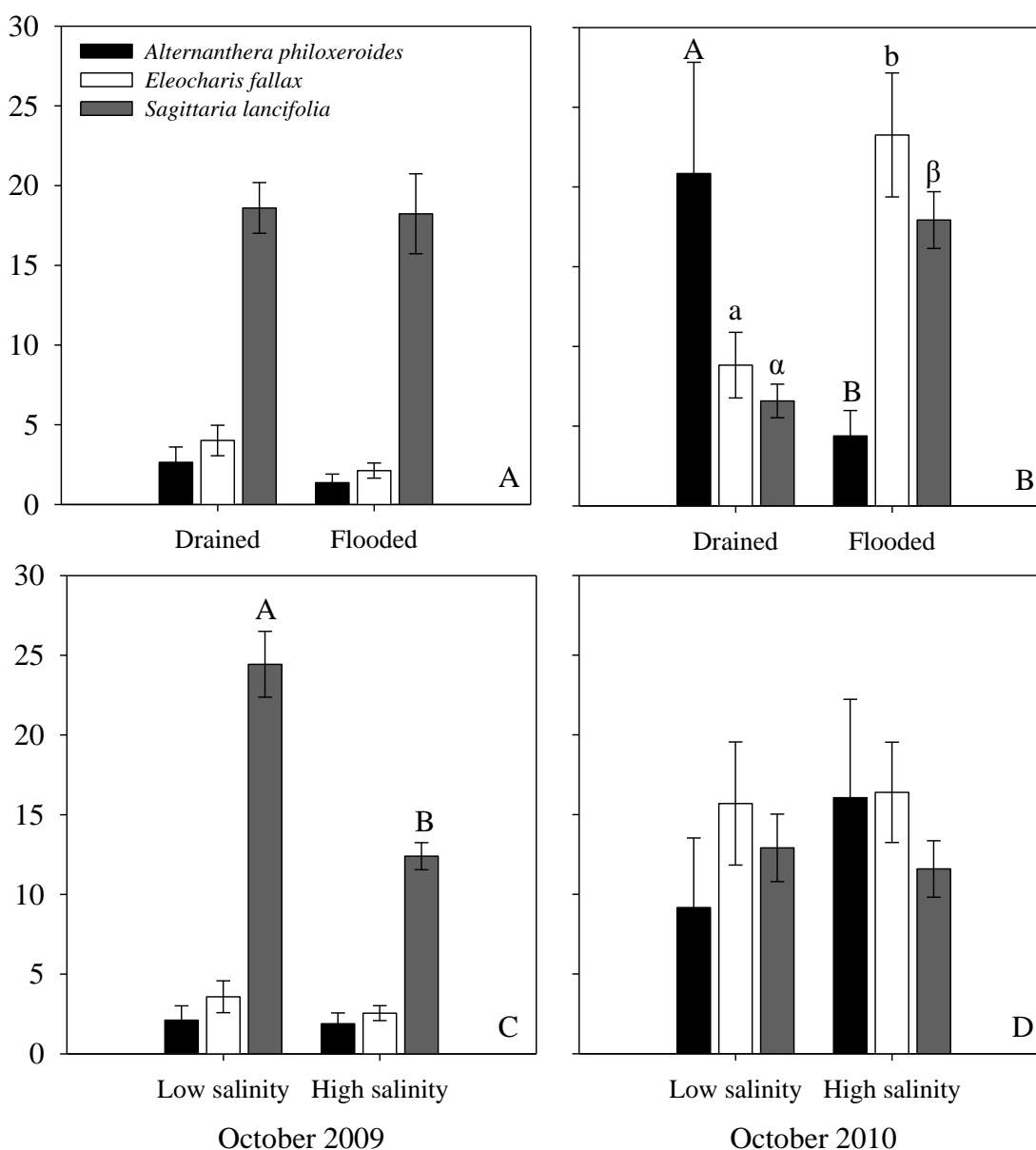


Figure 2.6 Aboveground end of season biomass (g sod⁻¹) (mean \pm 1 SE) by flooding (A and B) and salinity (C and D) treatments for 2009 and 2010. Different letters represent statistically significant differences ($p < 0.05$) between treatments when compared by plant species, during a given year. No letter indicates that there was no significant difference between treatments by plant species, during a given year. Drained = water level maintained 12 cm below soil surface. Flooded = water level maintained 12 cm above soil surface. Low salinity = 2 ± 0.5 ppt. High salinity = 6 ± 0.5 ppt.

Photosynthesis and net community CO₂ exchange rates

20.7 ± 2.2 mm d⁻¹ for flooded water levels. Also, *S. lancifolia* growth changed with time; stem elongation was greatest during April 2010 (31.5 ± 0.90 mm d⁻¹) and least during October 2009 (15.1 ± 0.52 mm d⁻¹). Nutrients, salinity, nor any of their interactions significantly impacted *S. lancifolia* growth rate (Table 2.3).

S. lancifolia photosynthetic rate was unaffected by nutrient status, flooding, and their two- and three-way their interactions (Table 2.3). While low salinity tended to favor higher rates of *S. lancifolia* photosynthesis, differences in photosynthetic rates were not ecologically significant (20.3 ± 0.8 and 21.3 ± 0.7 µmol CO₂ m⁻² s⁻¹). Time had a significant impact on photosynthetic rate. Generally, photosynthetic rates among salinity-exposed sods were similar for all sampling dates (20.9 ± 0.6 µmol CO₂ m⁻² s⁻¹) except for those measured in April 2010 (31.5 ± 0.9 µmol CO₂ m⁻² s⁻¹; Tukey-Kramer).

Nutrients, salinity, nor any of their interactions had a significant impact on community CO₂ exchange (Table 2.3). Flooding had a significant effect at the 0.0664 probability level (Table 2.3); elevated water level tended to decrease CO₂ uptake (-17.6 ± 1.6 µmol CO₂ m⁻² s⁻¹) when compared to those sods receiving the drained treatment (-22.1 ± 1.8 µmol CO₂ m⁻² s⁻¹). The overall average exchange rate for intrusion-exposed sods was -19.9 ± 1.2 µmol CO₂ m⁻² s⁻¹, while the exchange rate for control sods was -19.0 ± 2.6 µmol CO₂ m⁻² s⁻¹.

Plant Community Resilience and Stability

Overall, the effect of salinity on the resilience of total canopy cover after the nonlethal disturbance (clipping) was dependent on flooding (Table 2.5). High salinity reduced total cover resilience, and this effect was strongest under drained water level

conditions. Total cover resilience was similar for all other flooding x treatment combinations. Canopy cover stability was significantly affected by the interaction of flooding, salinity, and nutrient treatments (Table 2.5A); canopy cover stability was greatest when sods were flooded, experienced low salinity, and nutrient conditions were

Table 2.5 (A) Univariate analysis of variance results for the main and interactive effects on the stability of aboveground biomass, and the resilience and stability of *Sagittaria lancifolia* dominance and total canopy cover following clipping disturbance and (B) means of response variables by significant treatment effect. Low salinity = 2 ± 0.5 ppt. High salinity = 6 ± 0.5 ppt. Ambient = no additional nutrients added. Enriched = $20 \text{ g N m}^{-2} \text{ yr}^{-1}$ and $3 \text{ g P m}^{-2} \text{ yr}^{-1}$ added.

A. ANOVA	Total Cover Resilience	Total Cover Stability	<i>S. lancifolia</i> Dominance Resilience	<i>S. lancifolia</i> Dominance Stability	AG* Biomass Stability
Effect	p-value	p-value	p-value	p-value	p-value
Flooding (F)	0.1847	0.3993	<0.0001	0.5663	0.3265
Nutrient (N)	0.5230	0.5040	0.0723	0.1754	0.7170
Salinity (S)	0.0566	0.0054	0.0633	0.8276	0.4214
F x N	0.7423	0.0548	0.8822	0.9100	0.6569
F x S	0.0030	0.7870	0.0266	0.1582	0.1374
N x S	0.8919	0.8629	0.9693	0.8812	0.1593
F x N x S	0.4280	0.0310	0.6710	0.1667	0.9190
B. Means					
Drained, Low Salinity	8.6 \pm 0.82 (a)		51.3 \pm 22.1 (c) [†]		
Ambient Nutrients			102.0 \pm 21.7 (abc)		
Enriched Nutrients			158.3 \pm 30.2 (ab)		
Drained, High Salinity	4.9 \pm 0.87 (b)		61.6 \pm 20.6 (c)		
Ambient Nutrients			82.6 \pm 35.0 (c)		
Enriched Nutrients			70.0 \pm 20.2 (c)		
Flooded, Low Salinity	7.3 \pm 0.44 (ab)		281.1 \pm 29.0 (a)		
Ambient Nutrients			182.0 \pm 31.2 (a)		
Enriched Nutrients			97.6 \pm 9.6 (bc)		
Flooded, High Salinity	8.2 \pm 0.48 (a)		172.3 \pm 29.1 (b)		
Ambient Nutrients			96.9 \pm 12.5 (bc)		
Enriched Nutrients			93.0 \pm 11.5 (bc)		

* AG = aboveground

[†] different letters in parentheses indicate significant differences (Tukey's pair-wise)

^{††} p-values < 0.1000 were explored further in the text

ambient (Table 2.5B). Canopy cover was least stable when sods were drained and salinity was high, irrespective of nutrient condition. No high-salinity treatment-combination returned to pre-clipping cover values by week 12, whereas all low salinity treatment combinations returned to pre-clipping levels by week 12 except for those which were flooded with enriched nutrient levels (Table 2.5B). The interaction of flooding and low salinity resulted in a high rate of recovery of *S. lancifolia* dominance, whereas drained conditions lessened the resilience of *S. lancifolia* dominance, irrespective of salinity conditions (Table 2.5B). *S. lancifolia* dominance resilience also affected by nutrient and salinity main effects such that low salinity favored greater resilience (166 ± 31 vs. 117 ± 21) and ambient nutrient status favored greater resilience (165 ± 25 vs. 118 ± 29). In contrast to resilience, *S. lancifolia* dominance stability was unaffected by any treatment combination, as was the stability of total aboveground plant biomass (Table 2.5A).

DISCUSSION

Simulated hurricane-induced saltwater intrusion and post-intrusion conditions had immediate and lasting impacts on oligohaline wetland plant community structure and growth. Initial exposure to saltwater (20 ppt) caused the plant community to become visibly stressed and aboveground tissue quickly became necrotic. Plant cover was reduced by over 70% during this time, and species richness decreased. Once high salinity stress was alleviated and plant community regrowth began, post-intrusion conditions, such as recovery water level, controlled community structure and production during the months following initial disturbance. For example, drained conditions promoted greater plant richness for a duration of about 18 months after intrusion was alleviated, while high water level favored the dominance of *S. lancifolia* during this time. Post-intrusion

conditions were also important for determining plant community response to subsequent disturbance (clipping). During the assessment of plant community resilience and stability nearly three years after the initial saltwater intrusion disturbance, water level and salinity were still important determinants of community recovery.

Plant Community Structure during Recovery from Saltwater Intrusion

Flooding had a negative impact on several structural responses such as percent cover, dominance of *A. philoxeroides* with time, and species richness. The adverse impact of elevated water level and extended flooding on plant community structure has been well documented. Species richness and aboveground biomass is often low under highly flooded conditions (Flynn et al. 1995, Pollock et al. 1998, Casanova and Brock 2000). The reduction in percent cover, dominance of select species, and species richness due to flooding was likely a result of soil conditions resulting from long-term flooding. Although not presented here, soil Eh was significantly lower (more reducing) in flooded treatments than in drained (see Chapter 3). Soil waterlogging often results in reduced oxidation-reduction (redox) potential due to a decrease in oxygen diffusion rate. Reduced soil conditions can lead to stressful conditions for plants including root oxygen deficiency, decreased nutrient uptake, and build-up of toxic compounds such as reduced iron and manganese (Valiela and Teal 1974, Laanbroek 1990), as well sulfide, when some salt is present (Koch and Mendelssohn 1989, Krairapanond et al. 1992, Mendelssohn and Morris 2000).

Elevated water level had a positive impact on the dominance and importance values of different species such as *Eleocharis fallax* and *Sagittaria lancifolia*. The frequency of occurrence of both species was relatively unaffected by saltwater intrusion,

both persisting in many sods in which they were originally present (Table 1). However, unlike *S. lancifolia*, *E. fallax* has been shown to be relatively sensitive to flooding with biomass and seedling emergence being reduced by elevated water level (Baldwin et al. 1996, Baldwin and Mendelssohn 1998). While contrary to previous results, our observation that *E. fallax* dominance and importance value is greater under flooded conditions following salinity exposure suggests that *E. fallax* may gain an important competitive advantage over other oligohaline wetland species due to the combination of short-term salinity exposure followed by flooding because it was able to survive the initial disturbance better than many other plant species. Furthermore, the close association of *E. fallax* with *S. lancifolia* in flooded soils may have afforded *E. fallax* an advantage in that roots and rhizomes of *S. lancifolia* are often large and allow for ample oxygen diffusion to belowground organs. By oxidizing its rhizosphere, *S. lancifolia* may be able to promote plant growth (Howes et al. 1981) and allow *E. fallax* to survive under flooded conditions.

Nutrients and salinity were of secondary importance in their effects on plant community structure following intrusion, although nutrient enrichment did result in greater total cover than did ambient nutrient levels. In previous studies, nutrient addition in oligohaline wetlands had varying impacts on vegetation structure (Sundareshwar et al. 2003, Slocum and Mendelssohn 2008, Graham and Mendelssohn 2010). For example, in an investigation of nitrogen and phosphorus fertilization impacts on oligohaline wetland vegetation, only nitrogen addition resulted in a shift in relative abundance and this effect varied by species; relative abundance of *Polygonum punctatum* increased when nitrogen was added, whereas relative dominance of *E. fallax* decreased and *S. lancifolia* was

unaffected (Graham and Mendelssohn 2010). Because nutrients did not impact dominance or importance value of a specific species (among the three most commonly-occurring) in our study, but did impact overall cover, it is likely that nutrient addition stimulated the growth of a number of species, allowing for net increase in total cover despite no obvious impact of nutrients on percent cover of any individual species.

Post saltwater intrusion, salinity level had varying impacts on community structure depending on the species observed. For example, high salinity negatively impacted *S. lancifolia* dominance, but had no observable impacts on *Alternanthera philoxeroides* or *E. fallax* dominance. That higher salinity decreased *S. lancifolia* dominance is not surprising, as elevated salt content has been shown to have negative impacts on many *S. lancifolia* growth metrics (McKee and Mendelssohn 1989, Baldwin and Mendelssohn 1998, Howard and Mendelssohn 1999b, 2000). However, *A. philoxeroides* and *E. fallax* are also known to be relatively salt-sensitive (Baldwin and Mendelssohn 1998), but salinity status during the recovery period of our study had no observed impact on their dominance. These varied results suggest that some species such as *A. philoxeroides* and *E. fallax* may gain a competitive advantage in their ability to persist through a short-term salinity intrusion, but other species, such as *S. lancifolia* may be more sensitive to longer-term salinity conditions despite the species' ability to persist through a short-term period of elevated salinity.

Plant Community Growth during Recovery from Saltwater Intrusion

The effects of elevated water level on recovery from saltwater intrusion had varying impacts on plant community growth. While *A. philoxeroides* biomass and community-wide annual production were suppressed by flooding, greater inundation

facilitated an increase in *E. fallax* and *S. lancifolia* biomass and enhanced *S. lancifolia* growth rate. These results are consistent with the observations made about the impacts of flooding on community structure. Flooding tended to favor the persistence of *E. fallax* and *S. lancifolia* while suppressing *A. philoxeroides* and some less flooding-sensitive species. *S. lancifolia* is well adapted to flooding conditions; it exhibits rapid vegetative growth, is able to germinate under flooded conditions, has large belowground organs which are able to maintain a well-oxidized rhizosphere, and is relatively resilient in its ability to survive disturbance (Baldwin et al. 1996, Baldwin and Mendelssohn 1998). It is because of these physiological adaptations that *S. lancifolia* is dominant under flooded conditions. However, despite the ability of *S. lancifolia* to thrive under flooded conditions, the more diverse community that existed under less stressful conditions was more productive.

Nutrients status impacted only a single growth response: community-wide annual production. A previous study by Graham and Mendelssohn (2010) reported that nitrogen addition to the same wetland from which our sods were harvested resulted in an asymptotic increase in net above-ground primary productivity (NAPP). NAPP increased by about 36% from $1,243 \pm 75$ to $1,695 \pm 163 \text{ g m}^{-2} \text{ y}^{-1}$ when $20 \text{ g N m}^{-2} \text{ y}^{-1}$ was added to the marsh via slow-release fertilizer throughout the growing season. NAPP increased by about 46% when the same level of nitrogen was added in our study through monthly additions. Although I did not determine whether single-nutrient limitation or co-nutrient limitation occurred in our experiment, it is likely that nitrogen limited primary productivity and not phosphorus, given the results of Graham and Mendelssohn (2010).

Salinity had few impacts on plant community growth; however, high salinity depressed *S. lancifolia* biomass and stem elongation rate. Although *S. lancifolia* was able to survive a relatively short period of elevated salinity during our simulated intrusion event (20 ppt), standing aboveground biomass and growth suffered when exposed to long-term exposure at 6 ppt. The negative impacts of chronic salinity exposure have been demonstrated previously. McKee and Mendelssohn (1989) showed that *S. lancifolia* biomass and stem elongation rate were very sensitive to salinity exposure and that aboveground tissue showed evidence of damage at and above 4.8 ppt. I did not visually observe any apparent tissue damage at the 6 ppt salinity treatment level besides a decrease in stem elongation rate and reduced biomass.

Although flooding and salinity were important determinants of community-wide and species-specific AG biomass recovery, the impact of nutrient status on AG biomass recovery was not significant. That there was no observed impact of nutrient status on AG biomass was surprising, though this phenomenon has been previously documented. In a nutrient-addition experiment performed in an herbaceous oligohaline marsh near the Chesapeake Bay, Baldwin (2009) observed that aboveground biomass of *Acorus calamus* and *Typha* spp. was affected by nutrient addition, but total aboveground biomass remained consistent. Given the diverse array of plants that originally existed in our donor marsh, it is plausible that even if nutrient status affected individual species, compensation of loss by one species occurred through the enhancement of biomass by another. By these means, total aboveground biomass could remain similar whether or not nutrients were added.

Plant Community Resilience and Stability

The rate at which the wetland community recovered from subsequent clipping disturbance (resilience) and the degree of recovery (stability) was dependent on the combination of flooding and salinity conditions. Sods that recovered from clipping disturbance under high salinity and drained water level regained canopy cover slower than did communities recovering under other flooding x salinity treatment-combinations. Further, communities recovering under high salinity conditions regained cover to a lesser extent, i.e., lower stability, than did communities regrown under low salinity. These observation contrasts with observations made in earlier stages of this experiment; during the years in which plants were recovering from saltwater intrusion, recovery salinity did not have an observable impact on total percent canopy cover. Noble and Slayter (1980) explains that species subjected to recurrent disturbances must possess more than one set of vital attributes, each set allowing the species to survive different types of disturbances. With this idea in mind, it's possible that the community type that established in high-salinity mesocosms following lethal saltwater intrusion may not have contained the set of vital attributes that may have provided stability of canopy cover for subsequent disturbance.

Different combinations of flooding and salinity also impacted the rate of recovery of *S. lancifolia* dominance following clipping disturbance. *S. lancifolia* dominance increased faster under flooded, low salinity conditions than under any other treatment combination. The observation that *S. lancifolia* was quick to recover dominance from subsequent clipping disturbance was expected given that this plant dominated the community under the same flooded, low salinity environment during recovery from

salinity intrusion. No salinity x flooding treatment combination affected the degree to which the species recovered to pre-clipping dominance levels, indicating that the pre-clipping community was stable with respect to *S. lancifolia* dominance. Total aboveground biomass was also stable, with no treatment combination causing a significant difference in the degree of recovery to pre-clipping levels.

I hypothesized only highly salt-tolerant species would dominate the plant community immediately following the removal of intrusion stress, and that the combination of low water level, nutrient enrichment, and low salinity would favor high species diversity and productivity during recovery from saltwater intrusion. These hypotheses were not well supported; *S. lancifolia*, a moderately salt-sensitive plant (Howard and Mendelssohn 1999a), dominated the plant community immediately following saltwater intrusion, while more salt-tolerant species such as *S. patens*, were less dominant. Further, no single combination of water level, salinity, and nutrient treatment significantly affected diversity or aboveground production. Rather, water level was the most important driver of post-intrusion community characteristics. I also hypothesized that low water level, low salinity, and nutrient enrichment would interact to affect plant community resilience and stability for a subsequent disturbance (clipping). This hypothesis was partially supported, with greatest total cover stability occurring with under the conditions, though cover stability values were statistically similar to other flooding x nutrient x salinity combinations.

CONCLUSIONS

This research demonstrated that water level was the chief driver of plant community structure and growth following hurricane-induced salt water intrusion. In

areas such as coastal Louisiana, large expanses of wetlands are increasingly inundated by water due to the combination of eustatic sea level and local subsidence (Bjerstedt 2011, Day et al. 2011). In these sediment-starved wetlands, marsh platforms cannot maintain elevation, and continue to collapse below sea level (Reed et al. 2012). Further building on these impacts, past and current canal dredging along the Gulf Coast has increased channel flow, and has resulted in more direct connections between inland marshes and ocean (Turner 1997). As a result, brackish water is better able to penetrate inland into freshwater and oligohaline wetlands during surge events. In areas that have been impounded or semi-impounded by dredge spoil, flood water is retained and water levels remain high for extended periods of time (Morton and Barras 2001). The results of my study indicate that these periods of high flooding and salinity cause immediate shifts in plant community composition and structure. Gaps left by species unable to tolerate such stressful conditions are replaced by others that have maintained viability via belowground structures or seeds. For example, aboveground shoots of *S. lancifolia* withered during saltwater intrusion, but quickly regenerated once stressful conditions were relieved. Rapid regeneration of *S. lancifolia* was likely possible due to the survival of the plant's rhizomes. In addition to causing shorter-term changes in plant community structure and growth, hurricane mega-disturbances also cause long-term shifts in environmental conditions vital to these communities. Among those examined in this investigation, post-intrusion water level was the most important in shaping community recovery. Long periods of flooding following salt water intrusion resulted in the dominance of *S. lancifolia*, resulting in lower end-of-season aboveground biomass and relatively low species richness. Although recovery salinity and nutrient status did not play a major role

in controlling post-recovery ecological structure, these results will likely differ depending on the specific salinity and nutrient levels during any particular recovery period, as well as other potentially interacting abiotic and biotic stressors.

Because oligohaline wetlands provide vital ecological services in many coastal regions (Rozas and Hackney 1983, Peterson and Meador 1994), great effort should be put forth to understand both natural and human impacts to these systems. Information gained through research should be applied in a way that encourages the maintenance of healthy, productive, and diverse wetland communities. Because many water control structures have been previously emplaced, coastal Louisiana may already have some of the tools necessary to manage wetlands threatened by hurricane mega-disturbances. Opening freshwater diversions along Mississippi River following storm surge should be considered as a way to minimize salt stress following storm event, although the effect of high nutrient levels in Mississippi River water must be considered (Turner 2011). Other management activities such as the breaching of impoundments may alleviate extended flooding stress by allowing water drainage away from these areas. Through proper management and corrective action, diverse, productive wetlands can be supported, and important coastal ecological services can be preserved.

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CHAPTER 3

POST SALINITY-INTRUSION CONDITIONS DETERMINE OLIGOHALINE WETLAND SOIL STRUCTURE AND CONDITION

INTRODUCTION

Hurricane landfall often has profound impacts on the structure and function wetlands. Associated storm surges push salty ocean water into low-lying areas, resulting in elevations in porewater salinity for weeks or months (Maltby, E. Blood et al. 1991, Michener et al. 1997, Dix et al. 2008). These pulses of high salinity are detrimental to plant health and alter soil chemistry (Blood et al. 1991, Neyland 2007). When wetland plants that are adapted to low salinity environments are exposed to ocean water, they experience osmotic stress, ion toxicity, and reduced nutrient uptake (Mitsch and Gosselink 2000). Salinity exposure may therefore lead to reduced growth, necrosis, or even plant death (Guntenspergen et al. 1995, Martin and Shaffer 2005). Excessive rainfall associated with hurricanes can increase nutrient loads to coastal areas from soil leaching, erosion, leakage from wastewater treatment facilities, and runoff from landfill and animal feeding operations (Mallin and Corbett 2006). These nutrients may accelerate organic matter mineralization, weaken soils, and result in loss of soil strength, making wetland soils more susceptible to erosion during future storms (Turner 2011). Hurricanes may also alter the geomorphology of the wetland landscape, causing changes in hydrological connectivity and affecting longer-term salinity and flooding patterns (Morton and Barras 2011). Extended periods of flooding cause wetland soils to become greatly reduced and have deleterious impacts to plant health, thereby reducing accumulation of belowground plant structures.

Land use changes in areas surrounding northern Gulf of Mexico (GOM) coastal wetlands further magnify hurricane impacts to this region. For example, extensive canal dredging throughout the 20th century has increased hydrological connectivity, allowing for more geographically extensive saltwater intrusion (Craig et al. 1979, Day et al. 2000, Day et al. 2007). Dredge spoil from canal building has impounded wetlands causing storm water to be retained in these areas for extended periods of time. Also, deforestation, agricultural expansion, the increased use of fertilizer, and a reduction in riparian buffer zones in the Mississippi River drainage basin have resulted in increasing nutrient enrichment in wetlands in the northern GOM region. By potentially fueling decomposition and reducing belowground production, increased nutrient loading may weaken soils, making them more susceptible to future storm impacts (Turner 2011).

As human populations continue to grow and Earth's climate continues to change, impacts to coastal areas are likely to strengthen (Michener et al. 1997). For this reason, it is crucial that we gain a better understanding of how climactic and anthropogenic factors interact to affect the well-being of wetland systems. Because post-hurricane conditions can be dramatically different from pre-storm conditions, much uncertainty exists about how and to what extent wetland soils recover following such events. Critical to their recovery is the ability of coastal wetlands throughout the salinity gradient, from fresh to saline, to build and maintain elevation through both sediment accretion and the buildup of organic matter. Organic matter accumulation in coastal freshwater and oligohaline wetlands exposed to storm disturbances may be heavily dependent on post-storm conditions. Making these wetlands even more vulnerable to storm impacts is the fact that

freshwater wetland plants are shallowly rooted and therefore more susceptible to physical damage by hurricane storm surge (Rybczyk and Cahoon 2002).

The goal of this investigation was to determine how and to what extent post-storm conditions affect oligohaline wetland soils following hurricane-induced salinity intrusion. To achieve this goal, I exposed sods of wetland plants and soils to a simulated salt water intrusion. After the simulated intrusion, I studied the impacts of nutrient status, water level, and salinity on the recovery of various soil structural and functional attributes. Previous investigations of the impacts of salt water intrusion into wetland soils adapted to low salinities have found that rates of organic matter mineralization increase with increasing salinity (van der Valk 1994, Mallin and Corbett 2006). Further, Turner (2011) documented that increasing nutrient loads speeds cellulose decomposition rate and may thereby weaken soils. Therefore, I hypothesized that nutrient enrichment and high salinity would interact to cause faster decomposition of belowground organic matter, would cause a decrease in soil organic matter content, and would reduce soil strength. I also expected that flooding would lessen these responses to elevated nutrients and salinity and have an important impact on soil structure, function, and condition following disturbance. Because few wetland plants thrive under extended periods of flooding following a major disturbance (Baldwin and Mendelssohn 1998), and belowground root and rhizome growth is important for maintaining soil structure (Nyman et al. 1990, Reed 1995), I hypothesized that flooding would cause a reduction in belowground biomass and would thereby reduce soil strength.

METHODOLOGY

Experimental Design

A greenhouse mesocosm experiment was implemented to determine the influence of post-intrusion nutrient status, water level, and salinity on the capacity of oligohaline marsh soils to recover from short-term salinity intrusion. Sods of intact vegetation and soil were collected from an oligohaline marsh near Madisonville, LA located on the west bank of the Tchefuncte River (30° 23' 12.87" N, 90° 09' 34.38" W) in June 2009. Soils here are classified as a Kenner series Histosol and are of the textural class clayey/silty loam (Table 3.1; Slocum and Mendelssohn 2008). The average interstitial salinity is 0.96 \pm 0.03 psu (Baldwin and Mendelssohn 1998).

Table 3.1 Particle distribution (%) and textural classes of sod soils gathered from a marsh near Madisonville, LA.

	Sand	Silt	Clay	Textural Class
	29.1	49.0	21.9	Loam
	27.4	50.4	22.2	Silty Loam
	20.2	51.8	28.0	Clayey Loam
	31.9	44.6	23.5	Loam
	24.0	51.5	24.5	Silty Loam
Mean	26.5	49.5	24.0	
S.E.	2.0	1.3	1.1	

Once sods were transported to a Louisiana State University greenhouse, they were exposed to a 20 ppt simulated salinity intrusion for 5 weeks (see Chapter 2 for further detail). Synthetic sea water (Instant Ocean, Spectrum Brands, Inc. Atlanta, GA) was used as the salinity source. These sods are referred to as “treatment” sods. Additionally, 5 sods of soil and vegetation were maintained at ambient salinity during this time and for the duration of the experiment. These sods are referred to as “control” sods. After the 5 week

salt-water exposure, treatment and control sods were flushed with freshwater until ambient salinity was reached.

After this time of simulated salinity intrusion, treatment sods received an application of a combination of three post-intrusion treatments: (1) nutrient status (ambient and enriched) (2) water-level (drained or flooded), and (3) recovery salinity (low and high). Each treatment level combination was replicated 5 times. Two recovery phase salinity levels [low (2.0 ± 0.5 ppt) and high (6.0 ± 0.5 ppt)], in combination with two different water level regimes [drained (-12 cm) and flooded (+12 cm)], in combination with two nutrient regimes (ambient and elevated [equivalent of $20 \text{ g N m}^{-2} \text{ y}^{-1}$ and $3 \text{ g P m}^{-2} \text{ y}^{-1}$]) were established using a completely randomized factorial design. Ammonium nitrate and potassium phosphate were used as nutrient sources. Sods were maintained in the greenhouse for 34 months in order to assess both short and longer-term effects on soil structure (e.g., percent organic matter, bulk density, sod depth, shear strength, and belowground biomass), as well as functional attributes (e.g., decomposition rate) and edaphic conditions (e.g., extractable nutrient concentration, and soil physico-chemical response). Impacts on plant community dynamics were assessed during this time and are reported in Chapter 2.

Analytical Methods

At the conclusion of the greenhouse experiment in January 2012, soil cores (5.1 cm diameter by 12 cm deep) were collected from each sod, immediately sealed in water-tight plastic bags, and stored at 4°C. With the exception of extractable N, soil extractable ions were analyzed on field-moist soils by the LSU Soil Testing Laboratory to characterize the sods used in the experiments. Extractable P was extracted by mixing 2 g

soil with 40 ml of 0.03 M $\text{NH}_4\text{-F}$ and 0.1 M HCl (Byrnside and Sturgis 1958).

Extractable K, Ca, Mg, Na, S, Zn, and Cu were extracted by mixing 2 g of soil with 20 ml of 1 M NH_3OAc at neutral pH (Thomas 1982). Elemental concentrations in the extractions were determined on a Spectro Ciros^{CCD} inductively-coupled argon plasma emission spectrophotometer (ICP). Extractable N was extracted by mixing 10 g of soil with 25 ml of 2 N KCl. NO_2^- , NO_3^- and NH_4^+ concentrations were determined by the Department of Oceanography and Coastal Sciences (DOCS) Analytical Services Laboratory using an OI Analytical Flow Solution IV autoanalyzer (Strickland and Parsons 1972; Parsons et al. 1984).

A second soil core was collected from each sod (5.1 cm diameter by 12 cm deep) for soil texture, bulk density, and percent organic matter determinations at the end of the greenhouse experiment (Carter 1993).

A third core (7.6 cm diameter by 12 cm deep) was collected from each sod for belowground (BG) biomass determination. Following removal from the sod, soil cores were stored at 4 °C until processing. Each core was vigorously sprayed with water over a 0.2 mm sieve to remove all sediment contained in the core. After washing, live and dead belowground roots and rhizomes were dried together at 60 °C to a constant weight, and then weighed. Belowground biomass is expressed as grams of dry weight per square meter based on the 12 cm diameter of the core taken.

Porewater pH, conductivity, and sulfide concentration was measured quarterly throughout the duration of the experiment. Interstitial water samples were collected from each greenhouse sod at 10 – 15 cm below the soil surface within the center of the root zone with plastic syringe sippers (Koch and Mendelssohn 1989, McKee and

Mendelssohn 1989). A 20 ml porewater sample was collected and used for pH and conductivity determinations. Conductivity was measured using a Cole-Parmer conductivity meter and pH with an Orion pH meter and combination pH electrode. A second interstitial water sample (3.5 ml) was collected and immediately added to 3.5 ml of sulfide antioxidant buffer. This second water sample was analyzed for sulfide in the laboratory with an Orion sulfide electrode. Soil oxidation-reduction potential (Eh) was also measured seasonally. Duplicate Eh measurements were taken in each sod quarterly using brightened platinum-tip electrodes and a calomel reference electrode using standard methods.

Belowground organic matter decomposition was determined in each sod using two methods: the litter bag method (McKee and Seneca 1982) with belowground litter as substrate and the cotton strip method (Maltby 1987). Using the litter bag method, roots and rhizomes of plants representative of the source marsh community were collected in the field, allowed to die, placed in nylon litter bags (0.4 mm mesh) divided into depth sections of 0 – 12 cm and 12 – 24 cm, and inserted into the soil to a depth of 24 cm. One bag was inserted into each sod in August 2010 and they were removed in May 2011 (266 days). Decomposition data are expressed as percent mass remaining in the litter bags after the 266 day duration. In addition to the litter bag technique, soil cellulose decomposition was determined using the cotton strip technique based on the decay of a standardized cotton fabric comprising 97% cellulose (Maltby 1987, Slocum et al. 2009). This technique evaluated decomposition (cellulytic microbial activity) by measuring loss of tensile strength of the cotton fibers making up the strips over time. Measurements of tensile strength loss rates have been undertaken and proven successful in a wide range of

wetlands (Maltby 1987, Slocum et al. 2009) and non-wetland environments throughout the world. Methods for installation, measurement, and calculation of percent loss of tensile strength per day followed Mendelssohn et al. (1999). Differences in cellulose decomposition with depth and treatment were quantified.

Soil shear strength was measured at the conclusion of the greenhouse experiment in Jan. 2012 using a hand vane and torque gauge with a 34 cm wide x 5 cm long blade (Geotechnics, Auckland, New Zealand) in each of the greenhouse sods. Shear strength was measured in the top 5 to 20 cm of soil in 5 cm increments. Shear strength was not measured at 0 – 5 cm due to the uneven surface of some sod soils. The blade, attached to the rod and gauge assembly, was inserted to the shallowest desired depth (5 – 10 cm) and the assembly top was turned until maximum shear strength was reached. At this point, the blade broke through the surrounding soil and the torque reading was recorded on the assembly gauge. The blade was then pushed to the next desired depth and shear strength measurements were taken for the 10 – 15 cm and 15 – 20 cm depth ranges. This process was repeated two more times in each sod such that three replicate measurements were made at each depth for each sod. Replicate measurements within a sod were averaged for each depth for statistical analysis.

Data Analysis

Statistical analyses were conducted using SAS (version 9.2, SAS Institute). A univariate analysis of variance (PROC MIXED) was used to determine significant overall effects of flooding, nutrient status, recovery salinity, and their interactions on dependent variables including percent organic matter, bulk density, percent soil water, sod depth, belowground biomass, and the ratio of aboveground to belowground biomass. In

addition, the effects of depth and its interactions with the previously listed independent variables on shear strength and decomposition were also considered.

I used a factor analysis (PROC FACTOR) with the principal-axis extraction method to examine the dimensionalities correlated with soil physico-chemical response variables including Eh, porewater conductivity, porewater pH, porewater sulfide concentration, and extractable nutrient concentration. All response variables used in the factor analysis with the exception of extractable nutrient concentration were time-averaged. Factors with eigenvalues > 1 were retained and orthogonally rotated with a Varimax rotation (Willis and Hester 2004). Dependent variables with correlation coefficients ≥ 0.6 or ≤ -0.6 were used to define the retained factors. Factors scores generated for each plot were then analyzed using an ANOVA (PROC MIXED) with flooding, nutrient status, and recovery salinity as the fixed effects.

Individual ANOVAs were used to elucidate the effect of time and its interaction with flooding, nutrient status, and recovery salinity on Eh, conductivity, pH, and sulfide concentration.

All measures of significance were identified at $P < 0.05$. Where significant overall effects were identified, Tukey's post hoc adjustment was used to examine pair-wise differences. Residuals were checked for normality using the Shapiro-Wilk test, and for homogeneity of variance using the Levene's test. Where residuals were found not to be normally-distributed or residual variances were not homogeneous, I transformed the data. Soil shear strength, sulfide concentration, and aboveground to belowground biomass was log-transformed. Conductivity square-root transformed. Residuals for conductivity and pH were normally-distributed, but residual variance was not homogenous. Residuals for

decomposition rate using the litter-bag technique were homogenous, but not normally-distributed. Residuals for pH were neither normally-distributed nor homogenous, but transformation did not improve variance homogeneity of variance, so I did not transform these data ($P < 0.05$). ANOVA is relatively robust concerning deviations in residual normality and homogeneity of residual variance, especially when sample sizes are equal (Eisenhart 1947, Box 1953).

RESULTS

Post-Intrusion Effects on Soil Structure

Drained soils contained less organic matter by weight than did flooded soils, and soils maintained at a low salinity also contained a lower percent organic matter than did soils with greater salinity (Table 3.2A and B). Nutrient status did not impact organic matter content and there were no significant interactive effects. Mean organic matter content in control sods was 29.3 ± 0.74 % (mean \pm 1 S.E.). Soil bulk density was significantly greater in drained treatments than in flooded treatments, and there was not a significant effect of nutrients, salinity, or any two- or three-way interaction (Table 3.2A). Mean bulk density for those sods that were exposed to a salinity intrusion was 0.164 ± 0.059 g cm⁻³, while mean bulk density for control sods was 0.196 ± 0.015 g cm⁻³. Soil moisture under drained conditions was lower than under flooded conditions, and soils exposed to low salinity also contained less water by weight (Table 3.2A and B).

Whether sods were flooded or drained had a significant impact in the change in sod depth (distance from top to bottom of sod) over the course of the experiment (Table 3.2A). When the sods were originally harvested from the marsh, average sod was 33.5 ± 0.2 cm. By the end of the experiment, sods that had been maintained with drained water

levels had lost about 8.6 ± 0.7 cm in depth whereas the sods that had been maintained with flooded water levels had lost only 0.2 ± 0.4 cm in depth. Control sods, which were maintained with water levels equivalent to those in the drained treatment, lost 6.7 ± 1.8 cm in depth over the course of the experiment.

When all depths were averaged, shear strength was significantly greater in low salinity treatments than in high salinity treatments, but was unaffected by nutrients (Table 3.2A). However, at the shallowest depth (5 – 10 cm), the effect of salinity on shear strength was dependent on nutrient status (Table 3.2A and B, Fig. 3.1A). Nonetheless, shear strength at the shallowest depth was greater in the low salinity treatment than in the high salinity treatment, regardless of nutrient status (Fig. 3.1A and B). Flooding significantly interacted with depth such that shear strength was greatest in flooded treatments at the shallowest depth (Fig. 3.1C). However, shear strength was greater at the deepest depth when water level was drained. Shear strength in flooded and drained treatments was similar at the mid-level depth. When averaged across all depths, shear strengths for treatment and control sods were 7.47 ± 0.35 kPa and 8.77 ± 1.39 kPa, respectively.

Elevated water level had a positive impact on belowground biomass, while high salinity resulted in a decrease in BG biomass (Table 3.2A and B). There was no significant impact of nutrients on BG biomass. Mean BG biomass in treatment sods was 2.75 ± 0.17 kg m⁻². Mean BG biomass for control sods was 2.31 ± 0.30 kg m⁻². The ratio of aboveground to belowground biomass (AG:BG) was greater under drained conditions than when flooded (Table 3.2A and B). There was no nutrient or salinity impact on AG:BG (Table 3.2A).

Table 3.2 Univariate analysis of variance (ANOVA) results and means (± 1 S.E.) for treatment effects on wetland soil characteristics. Bolded values indicate the presence of significant differences ($P < 0.05$). Drained = water level maintained 12 cm below soil surface. Flooded = water level maintained 12 cm above soil surface. Ambient = no additional nutrients added. Enriched = 20 g N m⁻² yr⁻¹ and 3 g P m⁻² yr⁻¹ added. Low salinity = 2 ± 0.5 ppt. High salinity = 6 ± 0.5 ppt.

A. ANOVA		%					
Results		Organic Matter	Bulk Density	% Soil Water	Change in Sod Depth	Shear Strength	BG Biomass
Effect		p-value	p-value	p-value	p-value	p-value	p-value
Flooding (F)		0.0008	<0.0001	<0.0001	<0.0001	0.9546	<0.0001
Nutrients (N)		0.3266	0.9877	0.5974	0.9553	0.5781	0.0925
Salinity (S)		0.0478	0.0714	0.0005	0.2582	0.0002	0.0349
F x N		0.7112	0.6390	0.5322	0.2512	0.9438	0.2413
F x S		0.0677	0.7984	0.5189	0.9622	0.4818	0.6675
N x S		0.6675	0.1219	0.4252	0.1016	0.9553	0.9443
F x N x S		0.9779	0.9333	0.8175	0.9794	0.1947	0.4169
Depth (D)		n.a. [†]	n.a.	n.a.	n.a.	<0.0001	n.a.
F x D		n.a.	n.a.	n.a.	n.a.	<0.0001	n.a.
N x D		n.a.	n.a.	n.a.	n.a.	0.4322	n.a.
S x D		n.a.	n.a.	n.a.	n.a.	0.2574	n.a.
F x N x D		n.a.	n.a.	n.a.	n.a.	0.0667	n.a.
F x S x D		n.a.	n.a.	n.a.	n.a.	0.6937	n.a.
N x S x D		n.a.	n.a.	n.a.	n.a.	0.0015	n.a.
F x N x S x D		n.a.	n.a.	n.a.	n.a.	0.7130	n.a.
B. Means		%					
		Organic Matter	Bulk Density	% Soil Water	Change in Sod Depth	Shear Strength	BG Biomass
			g cm ⁻³		cm	kpa	g m ⁻²
Flooding							
Drained		28.4 (0.8)	0.186 (0.006)	74.6 (4.4)	-8.6 (0.67)	7.32 (0.45)	1931 (144)
Flooded		33.6 (1.2)	0.141 (0.007)	81.2 (3.7)	-0.2 (1.6)	7.62 (0.53)	3564 (214)
Nutrients							
Ambient		31.6 (1.1)	0.165 (0.008)	78.0 (4.9)	-4.4 (0.92)	7.67 (0.49)	2473 (240)
Enriched		30.5 (1.3)	0.163 (0.009)	77.7 (5.6)	-4.4 (1.3)	7.27 (0.50)	2622 (278)
Salinity							
Low		29.6 (0.9)	0.172 (0.008)	75.7 (5.3)	-4.8 (1.16)	9.26 (3.99)	3028 (297)
High		32.3 (1.4)	0.156 (0.009)	80.0 (4.2)	-3.9 (1.0)	5.68 (2.51)	2468 (200)

[†] n.a. refers to 'not applicable' because there was no referenced effect for this response

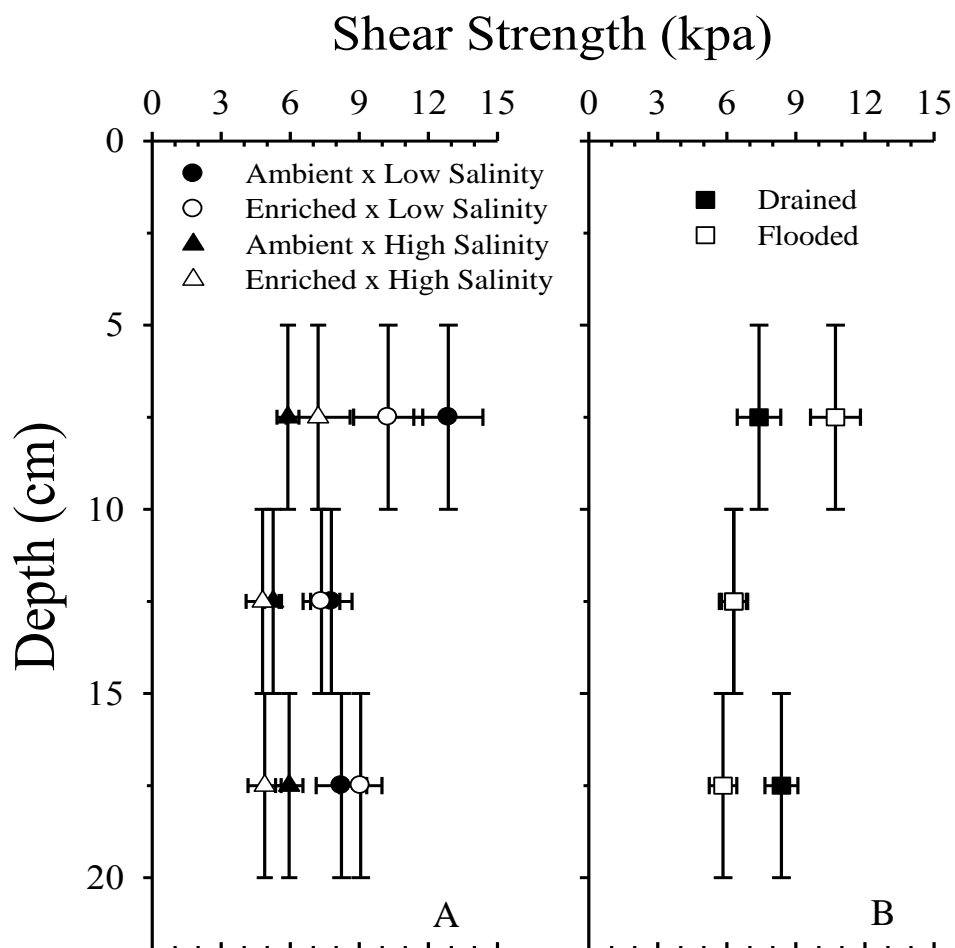


Figure 3.1 Soil shear strength by (A) nutrient (ambient or enriched) and salinity treatment (low salinity or high salinity) and (B) flooding treatment measured at three different depth increments (vertical bars). Horizontal error bars indicate 1 standard error (S.E.). Drained = water level maintained 12 cm below soil surface. Flooded = water level maintained 12 cm above soil surface. Ambient = no additional nutrients added. Enriched = 20 g N m⁻² yr⁻¹ and 3 g P m⁻² yr⁻¹ added. Low salinity = 2 ± 0.5 ppt. High salinity = 6 ± 0.5 ppt.

Edaphic Conditions and Decomposition Rate

A factor analysis of response variables characterizing marsh soil and porewater chemistry identified that calcium (Ca), Eh, sulfur (S), manganese (Mn), sodium (Na), phosphorus (P), nitrate (NO_x—N), and copper (Cu) were highly correlated with factor 1 (F1; Table 3.3). These indicator variables defined F1, which accounted for 59.4 % of variability in the dataset. Only conductivity defined factor 2 (F2) and conductivity was

highly correlated with this factor. F2 accounted for 17.8% of variability in the dataset. A univariate analysis of variance (ANOVA) on the effects of flooding, nutrients, salinity, and their interactions on F1 showed that flooding and salinity were important drivers of the defining response variables for this factor (Table 3.4). Ca, S, Mg, Na, P, NO_x—N, and Cu concentrations and Eh tended to be lower under flooded conditions than when soils were drained (Table 3.5). The results of the ANOVA also showed that salinity was an important driver of the response variables defining F1. Ca, Mg, and P concentrations were greater under low salinity conditions, while S, Na, NO_x—N, and Cu concentrations and Eh tended to be similar despite different salinity treatments (Table 3.5). Another separate ANOVA on the effects of flooding, nutrients, salinity, and their interactions on factor 2 showed that salinity was driver of the response variable defining F2 (Table 3.4). Conductivity was greater when the high salinity treatment was applied than when salinity was low (Table 3.5).

To elucidate treatment impacts over time, individual ANOVAs were used to determine the effects of flooding, nutrient status, and recovery salinity on soil Eh, porewater pH, porewater conductivity, and porewater sulfide concentration from Jan. 2010 to April 2011 (Table 3.6). Soil conditions were more reducing (lower Eh) under flooded conditions compared to drained, and this effect changed with time (Fig. 3.2A); Eh decreased over time under flooded conditions but remained relatively consistent under drained conditions. Porewater pH was greater under high salinity conditions when compared to pH under low salinity conditions, however, this difference was minor and not likely of ecological significance (Table 3.6). Flooding also impacted pH and this

Table 3.3 Correlations between indicator variables and retained factors for soil physico-chemical characteristics. Bolded values indicate variables with correlations ≥ 0.60 that define the factors.

Indicator Variables	Factor 1	Factor 2
Ca	0.8970	-0.1507
Eh	0.8304	-0.0551
S	0.8055	0.3006
Mg	0.7993	0.1143
Na	0.7928	0.4122
P	0.7597	-0.0169
NO _x ⁻ -N	0.7429	-0.1267
Cu	0.7199	-0.0023
Conductivity	0.0146	0.7281
K	-0.1327	0.5210
H ₂ S	0.1145	0.2235
pH	-0.0157	-0.3880
Zn	-0.0970	-0.3065
NH ₄ ⁺ -N	-0.0048	0.0160
Eigenvalue	5.14	1.54
% Variance Explained	59.4	17.8

impact changed with time such that flooding conditions resulted in a greater increase in pH over time than did drained conditions (Fig. 3.2B). Conductivity was greater under elevated recovery-salinity and increased over time when salinity was low and water level was low (Fig. 3.2C). Interstitial hydrogen sulfide concentrations were greater when salinity was high (Table 3.6).

Decomposition rate measured using the litter bag assay was reduced by flooding and low salinity, but was not significantly affected by nutrient status or by depth (Table 3.7). There was a significant flooding x depth interaction such that decomposition was greatest in the drained treatments at 0-12 cm depth, and least in the flooded treatments at

Table 3.4 Univariate analysis of variance (ANOVA) results and means (± 1 S.E.) for main effects on retained factors. Bolded values indicate the presence of significant differences ($P < 0.05$). Drained = water level maintained 12 cm below soil surface. Flooded = water level maintained 12 cm above soil surface. Low salinity = 2 ± 0.5 ppt. High salinity = 6 ± 0.5 ppt.

A. ANOVA Results		
	Factor 1	Factor 2
Effect	p-value	p-value
Flooding (F)	<0.0001	0.9686
Nutrients (N)	0.7034	0.1897
Salinity (S)	0.0411	<0.0001
F x N	0.2640	0.7325
F x S	0.6699	0.8173
N x S	0.6564	0.5250
F x N x S	0.3007	0.9300
B. Means		
F	Drained	0.76 (0.69) n.a.
	Flooded	-0.85 (0.36) n.a.
S		0.14 -0.59
	Low	(1.08) (0.51)
		-0.16 0.66
	High	(0.87) (0.79)

0-12 cm (Fig. 3.3). Decomposition rates were intermediate in the 12 – 24 cm range for drained and flooded treatments. There was also a significant salinity x depth interaction such that low-salinity soils at a depth of 0-12 cm had significantly lower decomposition rates than any other depth x salinity combination (Fig. 3.3). Although not significant at the $\alpha = 0.05$ level, there was a flooding x salinity x depth interaction ($p = 0.0528$) by which flooded soils also receiving a low salinity treatment had lower decomposition rates

Table 3.5: Mean values (± 1 S.E.) of soil physico-chemical response variables measured under different flooding, nutrient, and salinity treatments. Drained = water level maintained 12 cm below soil surface. Flooded = water level maintained 12 cm above soil surface. Ambient = no additional nutrients added. Enriched = 20 g N m⁻² yr⁻¹ and 3 g P m⁻² yr⁻¹ added. Low salinity = 2 \pm 0.5 ppt. High salinity = 6 \pm 0.5 ppt.

	Eh [†]	Cond. [†]	pH [†]	H ₂ S [†]	NO _x ⁻ -N	NH ₄ ⁺ -N	P	Ca	Cu	Mg	K	Na	S	Zn
	mV	mS cm ⁻¹		μM	(mg kg ⁻¹ dry soil)	(mg kg ⁻¹ dry soil)	(mg kg ⁻¹ dry soil)	(mg kg ⁻¹ dry soil)	(mg kg ⁻¹ dry soil)	(mg kg ⁻¹ dry soil)	(mg kg ⁻¹ dry soil)	(mg kg ⁻¹ dry soil)	(mg kg ⁻¹ dry soil)	(mg kg ⁻¹ dry soil)
Flooding														
Drained	169.0 (12.2)	8.47 (0.66)	6.8 (0.03)	89.2 (24.3)	57.8 (10.2)	184.7 (17.4)	0.831 (0.10)	27.6 (1.6)	0.054 (0.005)	21.2 (0.8)	2.74 (0.27)	88.3 (6.6)	8.47 (0.87)	0.051 (0.004)
Flooded	-50.4 (9.9)	7.64 (0.71)	6.8 (0.02)	68.3 (10.1)	4.7 (1.2)	189.5 (33.7)	0.306 (0.04)	16.0 (1.0)	0.025 (0.004)	15.5 (0.7)	3.33 (0.50)	52.8 (3.7)	4.70 (0.49)	0.064 (0.006)
Nutrients														
Ambient	55.4 (26.0)	8.04 (0.69)	6.8 (0.02)	78.8 (14.6)	25.5 (7.0)	159.7 (19.8)	0.518 (0.06)	23.3 (1.8)	0.049 (0.005)	19.2 (1.0)	2.24 (0.22)	67.1 (6.0)	5.72 (0.68)	0.059 (0.006)
Enriched	63.2 (28.9)	8.07 (0.69)	6.8 (0.02)	78.7 (22.2)	39.1 (11.4)	211.5 (28.9)	0.64 (0.12)	21.1 (1.9)	0.032 (0.006)	18.0 (1.0)	3.72 (0.44)	75.4 (7.5)	6.99 (1.01)	0.055 (0.005)
Salinity														
Low	74.5 (26.9)	5.31 (0.25)	6.84 (0.02)	59.75 (14.8)	36.7 (10.1)	190.6 (30.5)	0.654 (0.12)	24.5 (1.9)	0.042 (0.007)	19.2 (0.9)	2.57 (0.26)	69.8 (7.1)	6.18 (0.95)	0.065 (0.006)
High	44.1 (27.7)	10.80 (0.31)	6.7 (0.02)	97.7 (21.2)	28.2 (9.3)	183.0 (18.8)	0.503 (0.05)	19.4 (1.7)	0.038 (0.004)	17.7 (1.1)	3.52 (0.49)	73.4 (6.7)	6.62 (0.82)	0.048 (0.004)

[†]values for these variables are means averaged over multiple sampling times from Jan. 2010 to April 2011. All other values were measured from samples gathered during a single sampling time in Jan. 2012.

Table 3.6: Univariate analysis of variance (ANOVA) results for the main effects on wetland soil characteristics and means (± 1 S.E.). Bolded values indicate significant differences ($P < 0.05$).

	Eh	Conductivity	pH	H ₂ S
Effect	p-value	p-value	p-value	p-value
Flooding (F)	<0.0001	0.0202	0.1864	0.5506
Nutrients (N)	0.3199	0.7765	0.4210	0.3421
Salinity (S)	0.0724	<0.0001	0.0085	0.0030
F x N	0.7000	0.2322	0.8650	0.9774
F x S	0.8659	0.1241	0.3292	0.6915
N x S	0.6528	0.7636	0.5597	0.7529
F x N x S	0.1293	0.7736	0.1864	0.4460
Time (T)	<0.0001	<0.0001	<0.0001	0.0002
F x T	<0.0001	0.1450	<0.0001	0.0019
N x T	0.3709	0.3567	0.2669	0.6825
S x T	0.4972	0.0005	0.2461	0.9686
F x N x T	0.8734	0.5996	0.7612	0.4676
F x S x T	0.4779	0.0104	0.1637	0.0076
N x S x T	0.8426	0.8974	0.6642	0.1792
F x N x S x T	0.4485	0.8272	0.3868	0.9450

at the 0-12 cm depth than any other flooding x salinity combination at any depth (Tukey; $p < 0.0001$; Fig. 3.3).

Decomposition rate measured using the cotton strip technique was affected by depth such that the decomposition rate at the shallowest depth (0 – 2 cm) was slower than decomposition rates at intermediate depths (4 – 16 cm), but were similar to those at greater depths (16 – 24 cm) (Table 3.7; Fig. 3.4). There was also a significant depth x flooding interaction. Among the drained sods, the decomposition rates at the shallowest depth (0 -2 cm) were slower than decomposition rates at intermediate depths (4 – 16 cm), but were similar to those at 2 – 4 cm and 16 – 24 cm (Fig. 3.4A). Among the flooded sods, decomposition rates tended to be greater at shallower depths (0 – 10 cm) than at deeper depths (10 – 24 cm), but only when nutrient conditions were ambient and salinity

was low (Fig. 3.4B). Decomposition rates were relatively similar for all depths under flooded, nutrient-enriched conditions.

DISCUSSION

Flooding was the most important driver of post-salinity intrusion soil structure in this experiment. Under persistently flooded conditions, soils had greater percent organic matter, lower bulk density, and did not experience a loss in sod depth as did drained treatments. These structural attributes are likely the outcome of both belowground plant biomass accumulation and a shift toward soil physico-chemical conditions that are not conducive to decomposition of organic matter. Flooded treatments were dominated by *S. lancifolia* (see Chapter 2), a species known for its flood tolerance and for prolific belowground biomass growth (Martin and Shaffer 2005). The large roots and rhizomes produced by *S. lancifolia* constituted the majority of the belowground biomass and were nearly ubiquitous in all flooded sods. Alternatively, drained treatments contained a more mixed community which had less prolific above- and belowground plant growth. *S. lancifolia* was present in some, but not all drained treatments (see Chapter 2), and roots and rhizomes of this plant were not consistently dense.

Soil edaphic conditions such as low Eh also contributed to the maintenance of high organic matter under flooded conditions. High water level impeded oxygen permeability, reducing oxidation-reduction potential (Pezeshki et al. 1987). Because organic matter mineralization likely relied on the use electron acceptors less efficient than oxygen, decomposition rate was slowed (Box 1953), helping to maintain structural integrity of the belowground organic matter and sustain sod depth. Alternatively, drained soils were characterized by greater reduction-oxidation potential, allowing for faster

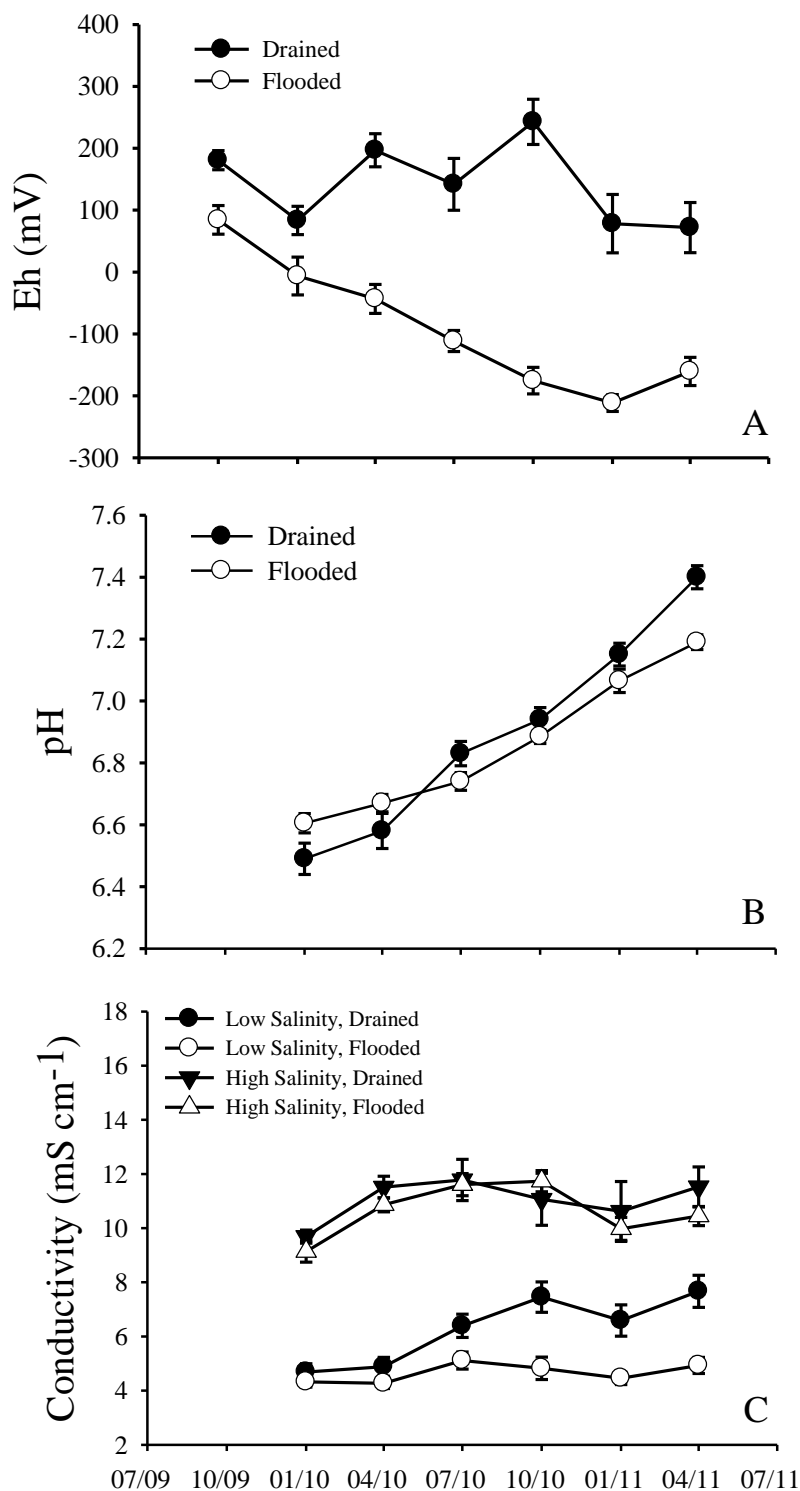
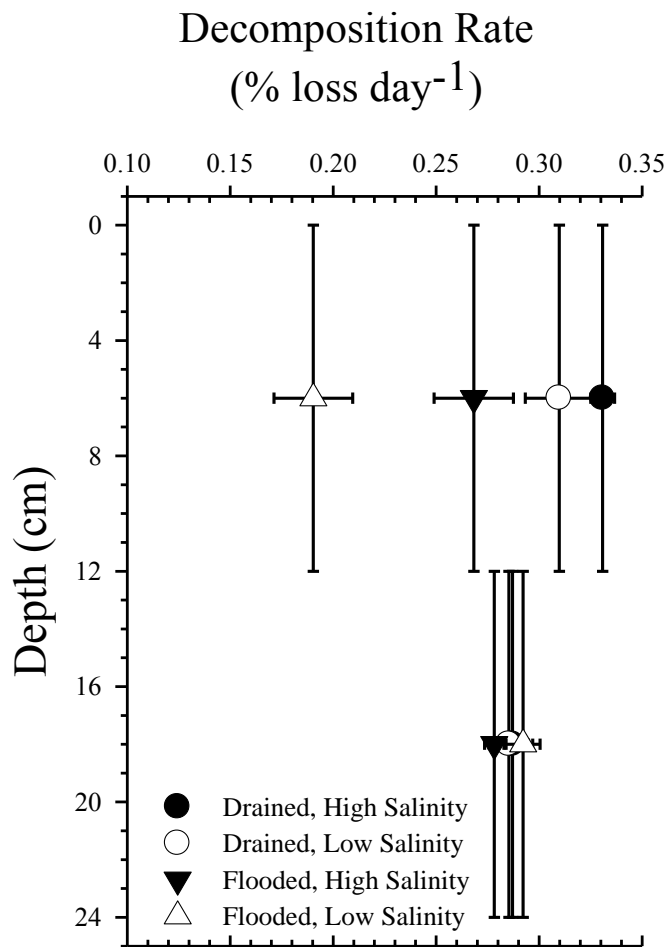


Figure 3.2 Soil physico-chemical variables by sampling date (mean \pm 1 S.E.). Drained = water level maintained 12 cm below soil surface. Flooded = water level maintained 12 cm above soil surface. Low salinity = 2 ± 0.5 ppt. High salinity = 6 ± 0.5 ppt.



Depth (cm)	Drained	Flooded
0 - 12	$0.320 \pm 8.83e^{-3}$	$0.229 \pm 15.9e^{-3}$
12 - 24	$0.286 \pm 6.67e^{-3}$	$0.285 \pm 4.88e^{-3}$

Depth (cm)	Low Salinity	High Salinity
0 - 12	$0.250 \pm 18.4e^{-3}$	$0.299 \pm 12.1e^{-3}$
12 - 24	$0.289 \pm 6.19e^{-3}$	$0.283 \pm 5.40e^{-3}$

Figure 3.3 Belowground decomposition rate measured using the litter bag technique at two depth increments (horizontal bars) for flooding x salinity treatments (top; mean \pm 1 S.E.) and decomposition rate for flooding and salinity treatments by depth (bottom; mean \pm 1 S.E.). Drained = water level maintained 12 cm below soil surface. Flooded = water level maintained 12 cm above soil surface. Low salinity = 2 ± 0.5 ppt. High salinity = 6 ± 0.5 ppt.

Table 3.7 Univariate analysis of variance (ANOVA) results and means (± 1 S.E.) for the main effects on wetland soil characteristics. Bolded values indicate significant differences ($P < 0.05$).

A. ANOVA	Litter	Cotton	B. Means		
Results	Bag	Strip		Litter Bag	Cotton Strip
	Decomp.	Decomp.		Decomp.	Decomp.
	Rate	Rate		Rate	Rate
Effect	p-value	p-value		% loss d ⁻¹	% CTSL d ⁻¹
Flooding (F)	< 0.0001	0.5557	Flooding		
Nutrients (N)	0.7977	0.1918	Drained	0.303	5.79
Salinity (S)	0.0214	0.7361		(0.006)	(0.12)
F x N	0.5173	0.4045	Flooded	0.257	5.63
F x S	0.2684	0.3090		(0.009)	(0.10)
N x S	0.8178	0.5441	Nutrients		
F x N x S	0.3925	0.0953	Ambient	0.281	5.48
Depth (D)	0.2404	< 0.0001		(0.056)	(0.09)
F x D	< 0.0001	0.0020	Enriched	0.279	5.95
N x D	0.3769	0.3096		(0.055)	(0.12)
S x D	0.0036	0.7305	Salinity		
F x N x D	0.4671	0.9040	Low	0.269	5.76
F x S x D	0.0528	0.3213		(0.010)	(0.11)
N x S x D	0.2818	0.3046	High	0.291	5.66
F x N x S x D	0.1334	0.0008		(0.007)	(0.12)

organic matter decomposition, and leading to a loss in sod depth due to the break-down of belowground organic matter.

That flooded conditions favored the maintenance of soil elevation has important implications for the ability of wetlands to survive relative sea level rise (RSLR) following hurricane disturbance. Belowground production of organic matter is important for building soil elevation because roots and rhizomes form a dense interlocking net that

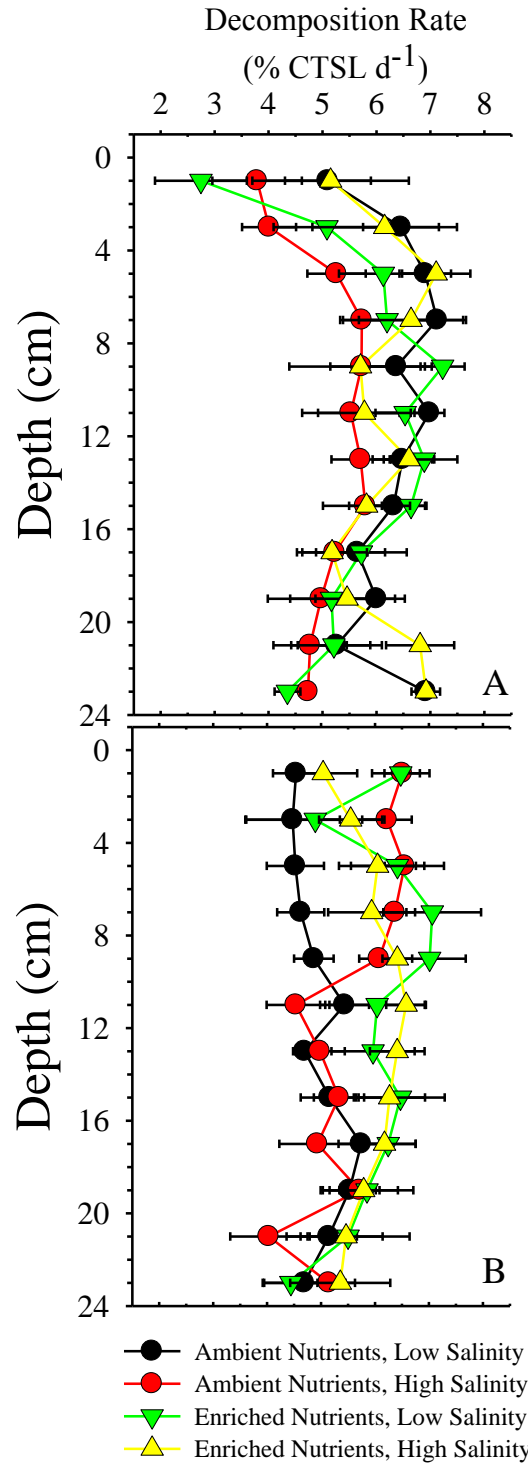


Figure 3.4 Decomposition rate using the cotton strip technique by nutrient and salinity treatment with (A) drained with (B) flooded water levels (mean \pm 1 SE). Drained = water level maintained 12 cm below soil surface. Flooded = water level maintained 12 cm above soil surface. Ambient = no additional nutrients added. Enriched = 20 g N m⁻² yr⁻¹ and 3 g P m⁻² yr⁻¹ added. Low salinity = 2 \pm 0.5 ppt. High salinity = 6 \pm 0.5 ppt.

contributes to soil volume and integrity (Nyman et al. 1990, Reed 1995, Rybczyk and Cahoon 2002). Therefore, wetlands dominated by prolific producers of belowground biomass are more likely to survive RSLR by this gain in elevation. Further, when soils are flooded, organic matter mineralization is generally slower and dead roots and rhizomes remain relatively intact buried as peat (Eisenhart 1947). However, flooded conditions do not ensure a greater production of belowground biomass. The flood tolerance of the dominant plant species and the degree of flooding are important considerations, as flooding of a flood-intolerant plant community may result in loss of both above- and belowground vegetation (van der Valk 1994). Such a decline in belowground biomass may result in an elevation loss due to plant death and resultant peat collapse (Nyman and Patrick 1994).

Post-intrusion salinity regime was also an important determinant of soil structure, function, and condition. Recovery-salinity elevated to 6 ppt resulted in less belowground (BG) biomass, faster decomposition, and relatively low shear strength. *S. lancifolia* showed greater dominance and produced more aboveground biomass under low salinity conditions (see Chapter 2). This information combined with the observation that there was no shift in the ratio of aboveground to belowground (AG:BG) biomass with a change in salinity leads me to deduce that the decrease in belowground biomass under elevated salinity is mainly due to a reduction in *S. lancifolia* BG biomass. The negative impacts of salinity on *S. lancifolia* belowground biomass have been documented. Martin and Shaffer (2005) found that although *S. lancifolia* is relatively salt tolerant when compared to other *Sagittaria* species, *S. lancifolia* biomass decreased significantly from 3 to 6 psu. Howard and Mendelssohn (1999) found that elevated salinity reduced *S. lancifolia* belowground

biomass over a 3 month duration of exposure. A reduction in belowground biomass allocation when exposed to elevated salinity has been demonstrated for other wetland plant species. Hester et al. (2001) found that sub-lethal salinity stress reduced *Panicum hemitomon*, *Spartina patens*, and *Spartina alterniflora* BG biomass. Willis and Hester (2004) also reported that an increase in salinity from zero to 1.5 and 3 psu salinity significantly reduced *P. hemitomon* BG biomass. In previous studies of the impacts of elevated salinity on *S. lancifolia*-dominated communities, researchers found that a sulfide concentration of 780 μM caused a reduction in vegetative growth (Webb and Mendelssohn 1996). In our experiment, the mean concentration of hydrogen sulfide for low- and high-salinity treatments never reached levels toxic to *S. lancifolia* and sulfide concentrations were not significantly different between salinity treatments (Table 7). Therefore, it is not likely that a reduction in belowground biomass was the result of a build-up of sulfide. However, conductivity was greater when salinity was high, indicating greater ionic concentration, which may have caused water stress and toxic ion effects on growing plants and may have contributed to a loss in BG biomass (Noble and Slatyer 1980, Krairapanond et al. 1992).

An increase in recovery salinity resulted in faster litter decomposition rate. Many factors influence organic matter decomposition rate including the quality and quantity of organic matter, oxidation-reduction potential (Eh), temperature, and nutrient availability (Reddy and DeLaune 2008). However, none of these factors explain faster decomposition in our high salinity treatment. The quality and quantity of organic matter used in both salinity treatments was the same and soil oxidization-reduction potential was not significantly different between salinity treatments. Further, temperature was not different

between treatments, as all sods were maintained in the same greenhouse. Additionally, extractable N and P concentrations were not different between salinity treatments. However, the greater availability of electron acceptors with higher reduction potentials in the seawater mix that was added in the high-salinity treatment may have allowed for faster litter decomposition. Previous studies of organic matter decomposition have indicated similar tendencies. Craft (2007) describes a positive relationship between decomposition and salinity in U.S. coastal wetlands. This and other studies have identified the more readily-available supply of sulfate in saltier water as the reason for faster decomposition (Weston et al. 2006, Weston et al. 2011). Sulfate is a more energetically-efficient electron acceptor than carbon dioxide, an alternate electron acceptor used more commonly in freshwater wetland environments, and is therefore used preferentially to carbon dioxide. Although I did not observe a statistically significant greater amount of sulfide (a product of sulfate reduction) in the porewater of the 6 ppt treatment, sulfate supply was greater to high salinity treatments and sulfide concentration tended to be greater. These findings suggest and I hypothesize that litter decomposition was faster in high salinity treatments because sulfate supply and reduction was greater.

Low shear strength in conditions of high recovery salinity was likely the result of less BG biomass and faster decomposition, especially at shallow depths. Soil shear strength is a function of the structural integrity of the root mat. When plants exhibit greater amounts of root and rhizome growth, soils are stronger (Nyman and Patrick 1994, Turner 2011). Under more saline conditions, belowground biomass was lower suggesting that the root mat was not as strong as under fresher conditions when belowground

biomass was greater. Furthermore, decomposition was higher under more saline conditions, leading to a decomposed root mat and lower soil strength.

Nutrient addition had only a minor impact on soil structure, function, and edaphic condition following short-term salinity intrusion. Under low recovery salinity conditions, nutrient enrichment resulted in a slight decline in shear strength at the 5 – 10 cm depth. Some previous research investigating the impacts of nutrient enrichment have found that under conditions of elevated nutrient delivery, decomposition rate is greater and the root mat is more decomposed, leaving these marshes more susceptible to erosional impacts such as storm events (Swarzenski et al. 2008, Turner 2011). In our experiment, shear strength was lower at very shallow depths but there was no apparent difference in decomposition rate at those depths when nutrient levels were enriched. Therefore, this difference in shear strength was likely due to an overall difference in plant root distribution. Although I did not measure root distribution by depth, it is possible that belowground plant structures were more dense in the 5 – 10 cm depth when salinity was low and nutrients were ambient than when salinity was low and nutrients were enriched. A greater density in plant roots would elevate shear strength under these conditions.

CONCLUSIONS

Prolonged exposure to flooded water levels following a short-term salinity intrusion disturbance resulted in a greater proliferation of belowground biomass, the maintenance of soil elevation, and reduced decomposition rate. Alternatively, soils that were exposed to relatively low water levels during recovery from salinity intrusion contained less belowground biomass, exhibited peat collapse, and a faster decomposition rate. Low salinity also favored buildup of belowground biomass and high shear strength.

These observations were likely due to the proliferation of the dominant plant, *S. lancifolia*, under flooded and low-salinity conditions. The use of *S. lancifolia* for marsh restoration has been suggested in the past due to the plant's ability to thrive when water level is high. Further, *S. lancifolia* is also relatively salt-tolerant, with belowground tubers surviving exposure to salinities of 20 ppt for 6 weeks, and with aboveground tissues regenerating relatively quickly after intrusion-exposure (personal observation). These relatively unique abilities should be taken advantage of. Many coastal wetlands are being threatened by global sea level rise and local subsidence, resulting in increased flooding and longer-term salinity intrusion. The use of *S. lancifolia* in managed and restored marshes should be considered in order to build belowground biomass and maintain marsh soil elevation.

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CHAPTER 4

EFFECTS OF FLOODING, GRAZING, AND SEDIMENT SUBSIDY ON AN OLIGOHALINE WETLAND RECOVERING FROM STORM-DRIVEN SALTWATER INTRUSION

INTRODUCTION

Coastal wetlands are under threat world-wide from numerous anthropogenic and natural stressors and disturbances. For example, eustatic sea level rise drowns once-healthy marshes where sediment and organic matter do not accumulate at an adequate pace (FitzGerald et al. 2008, Blum and Roberts 2009). The rate of sea level rise and wetland loss is accelerated where local soil subsidence occurs due to faulting or geological compaction, or other natural or human-induced processes (White and Tremblay 1995, Ko and Day 2004, Marriner et al. 2012). Anthropogenic alterations to marsh hydrology including canal dredging, emplacement of tidal control structures, building of berms and dikes, and impoundment or infilling the marsh platform, permanently change the extent and duration of flooding of the affected area (Sklar and Browder 1998, Bolduc and Afton 2004, Dimitriou and Zacharias 2010, Taylor 2012). Urbanization has also had extensive impacts on the size and functionality of coastal wetlands. For example, shoreline development may remove wetland buffer areas, allowing greater freshwater and nutrient inflow to wetlands from surrounding areas, altering plant community structure and function (Hopkinson and Vallino 1995, Lee et al. 2006). Residential developments and infrastructure along the fringes of coastal wetlands prevent the natural landward migration of wetland systems with continued sea level rise, resulting in fewer and smaller wetlands (Nicholls et al. 2008, Schleupner 2008). Cumulative effects of these disturbances have been a dramatic loss of coastal wetlands worldwide.

One especially significant natural disturbance that challenges the sustainability of coastal wetlands is storms and tropical cyclones (hurricanes). Strong winds can uproot and defoliate vegetation, and excessive rainfall can scour wetland surfaces, converting wetlands to open-water (Lugo et al. 1983, Smith et al. 1994, Guntenspergen et al. 1995, Barras 2006). Surge-associated increases in porewater salinity are detrimental to plant health and may alter soil chemistry, especially in wetlands adapted to low salinity. Excessive rainfall can increase nutrient loads to coastal areas due to soil leaching, erosion, leakage from wastewater treatment facilities, and runoff from landfill and animal feeding operations (Mallin and Corbett 2006). These nutrients may accelerate organic matter mineralization and weaken soils, making them more susceptible to erosion during future storms (Turner 2011). Hurricanes may also alter the geomorphology of the wetland landscape, causing changes in hydrological connectivity and affecting longer-term salinity and flooding patterns (Morton and Barras 2011).

Wetland condition and recovery trajectories after storms are controlled, in part, by the post-disturbance environment. For example, hurricane-impacted wetlands may be subject to high water levels and prolonged submergence, especially when impediments to natural hydrology exist. Also, herbivory and overgrazing may accelerate after hurricane disturbance due to a reduction in available living plant material and general habitat degradation (Spiller and Agrawal 2003). However, not all impacts resulting from hurricanes are detrimental. Sediment pulses provided by increased river input during and after storm events and delivery of near shore coastal sediments to the marsh platform during hurricanes provide enormous amounts of beneficial sediment to large expanses of drowning coastlines (Nyman et al. 1990, Turner et al. 2006, McKee and Cherry 2009,

Day et al. 2011). For example, in 2005, Hurricanes Katrina and Rita passed through the Louisiana coast in the northern Gulf of Mexico, delivering more than 131×10^6 metric tons of inorganic sediments to coastal wetlands, resulting in an average accretion depth of 5.18 cm (Turner et al. 2006). Even brackish marshes as far inland as about 125 km from the Gulf of Mexico, on the north shore of Lake Pontchartrain, experienced sediment deposition as great as 13 cm during the 2005 hurricane season (McKee and Cherry 2009). Not only can these sediments contribute directly to marsh elevation, but sediment addition also stimulates belowground biomass growth, further promoting wetland survival and lessening the impact of herbivore grazing by improving marsh condition (McKee and Cherry 2009).

However, experimental research assessing the importance of storm-generated sediment subsidies in counterbalancing post-hurricane barriers, like high water level and herbivory, to marsh recovery has not been investigated under field conditions. Thus, I examined the effects of flooding, grazing, and sediment subsidy, and their interactions, on an oligohaline wetland plant community following saltwater intrusion to address this information gap. This 26-month study aimed at answering the questions: (1) How does post-saltwater intrusion flooding and herbivory affect plant community recovery? and (2) Does sediment subsidy ameliorate the impacts of high flooding that are associated with storm surge? I hypothesized that high post-intrusion water level would interact with herbivory to limit plant biomass and species richness. I also expected that sediment subsidy would offset the impacts of high flooding such that species richness would be greater under highly flooded conditions when sediment was added than under highly flooded conditions when sediment was not added. Previous experiments suggest that

conditions of high flooding after short-term salinity intrusion results in low species richness, favoring the recovery of only one or two dominant species (Chapter 2). Alternatively, low flooding enhances species richness in intrusion-impacted communities, but speeds decomposition, resulting in loss of soil elevation (Chapter 3). However, the contribution of storm-derived sediment to the marsh platform may help to offset conditions of high flooding by raising elevation and enhancing plant growth.

METHODOLOGY

Experimental Design

I evaluated in the field the influence of post-saltwater intrusion grazing, extent of flooding, and sediment subsidy on the capacity of oligohaline marsh sods to recover from short-term salinity impact, similar to what occurs during hurricane-induced saltwater intrusion. The experimental design was a nested arrangement with three post-intrusion treatments: (1) grazing (ungrazed or grazed) (2) water-level (low flooding or high flooding), and (3) sediment subsidy (no sediment added or sediment added). Each treatment level combination was replicated 5 times.

Forty sods of intact vegetation and soil were collected from an oligohaline marsh near Madisonville, LA located on the west bank of the Tchefuncte River (30° 23' 12.88" N, 90° 09' 34.34" W) during April 2010. The marsh sods, approximately 36 cm in diameter and 30 cm in depth, were placed in 10 gallon plastic containers with 2.5 cm holes throughout the container sides to allow for water exchange in and out of the containers. The sods of vegetation were transported to a tented concrete slab in a greenhouse complex on the campus of Louisiana State University. Plant dominance was assessed (see Analytical Methods for details) prior to salt water exposure. The sods then

received a salinity (20 ppt) application (as in Flynn et al. 1995) by submerging the potted sods in large pools of synthetic sea water to a depth of approximately 10 cm (Instant Ocean, Spectrum Brands, Inc. Atlanta, GA). Saltwater-flooded sods were allowed to rest undisturbed for approximately seven weeks. Salinity of the pool water was monitored during this time, and fresh tap water was added to maintain the target salinity and flooding level. After seven weeks, dead biomass was removed, plant dominance was reassessed, and the sods were returned to the field (see details below). Five additional potted sods served as controls. Control sods were collected and potted in the same manner and at the same time as treatment sods in April 2010. However, unlike treatment sods, control sods were returned directly to the donor wetland instead of being exposed to the simulated salinity intrusion. One control mesocosm was established in each plot described below.

Five plots, each 2 m x 8 m in size and containing four treatment sods and one control sod, were randomly designated as either grazed or ungrazed for a total of 10 main plots. Panels constructed from crab trap wire and 1" PVC pipe were affixed to ground-driven PVC poles to create herbivore exclosures around ungrazed plots. Within each plot, four treatment sods were randomly assigned to a flooding (low or high) x sediment treatment (no sediment added or sediment added). High flooding was accomplished by excavating 12 cm of soil from beneath the potted sod, and laterally staking the sod pot into the surrounding wetland soil such that the sod surface was situated 12 cm below the wetland platform. Sods with the low flooding treatment were similarly staked such that the sod soil surface was situated at the same elevation as the surrounding marsh platform. Water level relative to the soil surface was measured hourly between April 2010 and July

2012 using a RDS Ecotone WM Water Level Instrument (Navassa, NC). Low and high flooding treatments were flooded above the sod surface approximately 60% and 98% of the study period, respectively. Mean water depths of the low and high flooding treatments were 4.1 and 16.1 (± 12.1) cm, respectively. Sediment from nearby Lake Pontchartrain, the physico-chemical properties of which are presented in Table 4.1, was transferred using 5 gallon buckets to those sods receiving a sediment addition until the added soil depth reached 6 cm. Because some adjustment of sod elevation was necessary, sod treatment application was not complete until Oct. 2012, and seasonal monitoring of plant and soil responses began in March 2010.

Table 4.1 Mean values (± 1 S.E.) of physico-chemical variables measured in sediment samples from Lake Pontchartrain used to subsidize wetland soil. Bulk density is expressed as g cm^{-3} and extractable nutrients are expressed as mg kg^{-1} dry soil.

Bulk Density	0.99 (0.01)
$\text{NH}_4^+\text{-N}$	17.8 (0.9)
P	11.6 (1.0)
K	21.0 (1.2)
Ca	79.7 (0.9)
Mg	60.4 (3.1)
Na	47.0 (2.0)
S	23.8 (1.7)
Fe	187 (12.8)
Mn	89.9 (7.2)
Zn	0.858 (0.035)
Cu	0.024 (0.004)

Analytical Methods

Plant community structure and growth during recovery

The methods used for measuring plant cover, dominance, and species richness are described in Chapter 2. These plant responses were measured during Spring, Summer, and Fall seasons beginning in March 2010 and ending in July 2012. Aboveground

biomass (AGB) was measured once during Oct. 2011 (end of season biomass) and once during July 2012 (peak season). To determine AGB (g sod^{-1}), all vegetation within the sod was clipped at the sod soil surface, divided according to species, dried to a constant weight at 60°C , and weighed.

Structure and function during recovery

At the conclusion of the field experiment in July 2012, soil cores (5.1 cm diameter by 12 cm deep) were collected from each sod, immediately sealed in water-tight plastic bags, and stored at 4°C . With the exception of extractable N, soil extractable ions were analyzed on field-moist soils by the LSU Soil Testing Laboratory to characterize the sods used in the experiments. Extractable P was extracted by mixing 2 g soil with 40 ml of 0.03 M $\text{NH}_4\text{-F}$ and 0.1 M HCl (Byrnside and Sturgis 1958). Extractable K, Ca, Mg, Na, S, Zn, and Cu were extracted by mixing 2 g of soil with 20 ml of 1 M NH_3OAc at neutral pH (Thomas 1982). Extractable Mn and Fe, were extracted by mixing 10 g of soil with 20 ml 0.005 M DTPA at 7.3 pH (Baker and Amacher 1982). Elemental concentrations in the extractions were determined on a Spectro Ciros^{CCD} inductively-coupled argon plasma emission spectrophotometer (ICP). Extractable N was extracted by mixing 10 g of field-moist soil with 25 ml of 2 N KCl. NO_2^- , NO_3^- and NH_4 concentrations were determined by the Department of Oceanography and Coastal Sciences (DOCS) Analytical Services Laboratory using an OI Analytical Flow Solution IV autoanalyzer (Strickland and Parsons 1972; Parsons et al. 1984).

A second soil core was collected from each sod (5.1 cm diameter by 12 cm deep) for bulk density and percent organic matter determinations at the end of the field experiment using methods described in Chapter 3 (from Carter 1993). Porewater pH,

conductivity, and sulfide concentration and soil oxidation-reduction potential (Eh) were measured three times per year as described in Chapter 3.

To determine belowground biomass (BGB) production, in-growth bags (6 cm diameter x 30 cm deep) containing root and rhizome free organic matter (finely ground peat) were inserted into each sod during March 2011. From this time until July 2012, plant roots and rhizomes could grow into the bags. At the conclusion of the experiment, the in-growth bags were removed from the soil, and roots extending from the bag were cut. Once returned to the lab, samples were washed of all peat, and all roots and rhizomes were dried to constant weight at 60°C and weighed.

Belowground organic matter decomposition was determined in each sod using two methods: the litter bag method (McKee and Seneca 1982) with belowground litter as substrate, and the cotton strip method (Maltby 1987) as modified by Slocum et al. (2009). For the litter bag method, roots and rhizomes of plants representative of the source marsh community were collected in the field, allowed to die, placed in nylon litter bags (0.4 mm mesh) divided into depth sections of 0 – 5, 5 – 10, and 10 – 15 cm, and inserted into the soil to a depth of 15 cm. One bag was inserted into each sod in June 2011 and the bags were removed in July 2012 (384 days). Litter decomposition data are expressed as percent mass lost in the litter bags after the 384 day duration. In addition to the litter bag technique, soil cellulose decomposition was determined using the cotton strip technique based on the decay of a standardized cotton fabric comprising 97% cellulose (Maltby 1987, Slocum et al. 2009). This technique further described in Chapter 3. Soil cellulose decomposition rate was determined during May 2011 and July 2012, and expressed as percent cotton tensile strength loss per day.

Net community CO₂ exchange

A 62.5 L clear plastic cylindrical chamber equipped with two 10.2-cm fans was connected to a CO₂ gas analyzer via clear flexible polyvinyl chloride tubing (*EGM-4 Environment gas monitor for CO₂ PP System Version 4.15, Amesbury, MA, USA*). The initial air CO₂ concentration in the chamber was recorded before lowering the chamber onto the marsh soil surface inside the potted sod. Care was taken to minimize disturbance of the wetland soil, and all plants were gently arranged to fit inside the chamber. Chamber air CO₂ concentration was recorded after two minutes, and the change in CO₂ concentration was calculated. Once the chamber was disconnected from a sod pot, CO₂ concentration in the chamber was allowed to stabilize to near-ambient before capping the next pot with the chamber. This procedure was repeated for each of 50 sods during June 2011. Net community CO₂ exchange was calculated as the change in CO₂ concentration per unit area over time.

Data Analysis

I used a multivariate analysis of variance (MANOVA; PROC GLM) to determine the overall and interactive effects of grazing, flooding level, and sediment treatment on dominance and biomass (end of season and peak season) of the four most commonly-occurring plant species (SAS version 9.2, SAS Institute). Treatment effects were determined using the Wilks' lambda test statistic. Where significant effects were identified, an individual mixed model ANOVA (PROC MIXED) with repeated measures was used to identify the specific dependent variables (i.e. plant species) that contributed to the significant overall effect (Graham and Mendelssohn 2010). For example, because there was an overall impact of time on dominance for the four most commonly-occurring

plant species (MANOVA), an ANOVA was performed to identify which of the four plant species were impacted by flooding.

I used a factor analysis (PROC FACTOR) with the principal-axis extraction method to examine the dimensionalities correlated with soil physico-chemical response variables including Eh, porewater conductivity, pH, porewater sulfide concentration, and soil-extractable nutrient concentrations. All response variables used in the factor analysis with the exception of extractable nutrient concentration were averaged for all sampling times by sod. Factors with eigenvalues > 1 were retained and orthogonally rotated with a varimax rotation (Willis and Hester 2004). Dependent variables with correlation coefficients ≥ 0.6 were used to define the retained factors. Factors scores generated for each plot were then analyzed using an ANOVA (PROC MIXED) with grazing, flooding level, and sediment treatments as the fixed effects. Individual ANOVAs were also used to elucidate the effect of time and its interaction with grazing, extent of flooding, and sediment subsidy on Eh, conductivity, pH, and sulfide concentration.

For all other response variables (e.g. total cover, species richness, total aboveground biomass, etc.), a mixed model ANOVA was used to determine significant overall effects. All measures of significance were identified at $p < 0.05$.

Residuals were checked for normality using the Shapiro-Wilk test, and for homogeneity of variance using the Levene's test. Where residuals were found not to be normally-distributed or variances were found to be heterogeneous, I transformed the data. Total plant canopy cover and cellulytic decomposition rate measured in 2012 were square root-transformed. Total belowground biomass, bulk density, and Eh were \log_{10} -transformed. Bulk density, Eh, conductivity, pH, and sulfide concentration did not meet

the normality assumption, but their residual variances were homogeneous. Total belowground biomass residual variances did not meet the assumption of homogenous variances, but residuals were normally-distributed. However, ANOVA is relatively robust concerning deviations in residual normality and homogeneity of residual variance, especially when sample sizes are equal (Eisenhart 1947, Box 1953). Control sods were excluded from all statistical analyses (e.g. MANOVA, ANOVA, and factor analysis).

RESULTS

Plant Community Response to Intrusion

The sods collected from the field contained 14 plant species, with *S. lancifolia* dominating the community (Table 4.2). The average species richness was 4.98 ± 0.22 plants sod^{-1} , with an overall canopy cover of 31.6 ± 2.1 % sod^{-1} . Once sods were exposed to elevated salinity for an extended period of time, plants became necrotic. Species richness decreased to 3.82 ± 0.24 species sod^{-1} and overall canopy cover decreased to 25 ± 2.7 % sod^{-1} . *S. lancifolia* remained dominant from pre- to post-intrusion, but canopy cover for the plant was reduced from 17.25 ± 0.97 to 3.04 ± 0.72 percent sod^{-1} . The post-intrusion plant community contained a total of nine plant species spread throughout the potted sod community, with the community having lost six species and gained one during the saltwater intrusion event (Table 4.2).

Plant Community Structure and Function during Recovery

I identified 16 species from 10 families in the intrusion-exposed community, and 15 species from 12 families in the control community during the recovery period (Table 4.3). In general, the most commonly occurring species throughout all treatment-combinations through time included *Alternanthera philoxeroides*, *Eleocharis fallax*,

Polygonum punctatum, and *Sagittaria lancifolia*. These species were also commonly observed in the control treatment. *Typha sp.*, *Schoenoplectus tabernaemontani*, and *Solidago sempervirens* were present only in the intrusion-exposed treatment, whereas *Vigna luteola*, and *Amaranthus sp.* were present only in the control treatment. *S. lancifolia* exhibited the greatest dominance of all observed species in intrusion-exposed and control treatments, though total dominance of *S. lancifolia* was generally greater in control sods (Table 4.3).

Table 4.2 Plant species and frequency of occurrence (%) for those plants present pre- and post-saltwater intrusion (June and August, respectively) in intrusion-impacted sods, and species lost or gained during intrusion period.

June 2010	August 2010	Species Lost	Species Gained
<i>A. philoxeroides</i> (40)	<i>A. philoxeroides</i> (52.5)	<i>Galium sp.</i>	<i>E. crus-galli</i>
<i>Amaranthus sp.</i> (45)	<i>Amaranthus sp.</i> (62.5)	<i>P. punctatum</i>	
<i>E. fallax</i> (72.5)	<i>E. crus-galli</i> (75)	<i>P. monspelenis</i>	
<i>Galium sp.</i> (7.5)	<i>E. fallax</i> (50)	<i>P. capillacium</i>	
<i>I. sagittata</i> (22.5)	<i>I. sagittata</i> (20)	<i>Sacciolepus sp.</i>	
<i>L. lineare</i> (47.5)	<i>L. lineare</i> (35)	<i>V. luteola</i>	
<i>P. punctatum</i> (12.5)	<i>S. lancifolia</i> (100)		
<i>P. monspelenis</i> (20)	<i>S. patens</i> (7.5)		
<i>P. capillacium</i> (60)	<i>S. subulatum</i> (27.5)		
<i>Sacciolepus sp.</i> (12.5)			
<i>S. lancifolia</i> (100)			
<i>S. patens</i> (5)			
<i>S. subulatum</i> (22.5)			
<i>V. luteola</i> (22.5)			

Percent cover

The effect of flooding on total canopy cover of the intrusion-exposed (treatment) sods was dependent on time of the year (Table 4.4; Fig. 4.1A). Total canopy cover was most reduced by high flooding compared to low flooding during Spring (April) and Summer (July) with little affect in the Fall (October) (Fig. 4.1A). Canopy cover remained nearly constant in highly flooded sods and did not exhibit seasonal variation

(Fig. 4.1A). There was no significant impact of grazing, sediment addition, or any of their two- or three-way interactions (Table 4.4). Percent cover in control sods (not exposed to intrusion) averaged $41.31 \pm 2.95 \text{ sod}^{-1}$ and percent cover in treatment sods averaged $31.9 \pm 1.8 \text{ sod}^{-1}$ through time.

Table 4.3 Plant species identified within study sods and their dominance values presented as the average and maximum for sods which were exposed to a salinity intrusion and those which were not.

Species	Family	Intrusion Exposed ^a		Control	
		Mean	Max.	Mean	Max.
<i>Sagittaria lancifolia</i>	Alismataceae	708	5,312	1,663	5,000
<i>Spartina patens</i>	Poaceae	282	11,050	129	1,875
<i>Ptilimnium capillaceum</i>	Apiaceae	180	5,625	34	450
<i>Symphotrichum subulatum</i>	Asteraceae	166	2,500	47	900
<i>Eleocharis fallax</i>	Cyperaceae	142	3,750	274	3,000
<i>Typha sp.</i>	Typhaceae	129	10,938	0	0
<i>Polypogon monspeliensis</i>	Poaceae	126	5,313	10	180
<i>Polygonum punctatum</i>	Polygonaceae	123	1,500	197	2,063
<i>Alternanthera philoxeroides</i>	Ameranthacea	98	1,875	140	1,125
<i>Galium sp.</i>	Rubiaceae	87	6,563	3	90
<i>Echinochloa crus-galli</i>	Poaceae	53	2,250	9	315
<i>Cyperus sp.</i>	Cyperaceae	32	3,375	2	120
<i>Schoenoplectus tabernaemontani</i>	Cyperaceae	13	2,025	0	0
<i>Lythrum lineare</i>	Lythraceae	13	1,575	47	750
<i>Ipomea sagittata</i>	Convolvulaceae	3	120	7	135
<i>Solidago sempervirens</i>	Asteraceae	1	105	0	0
<i>Vigna luteola</i>	Fabaceae	0	45	2	60
<i>Amaranthus sp.</i>	Amaranthaceae	0	45	1	30

^aMinimum dominance values for all species was zero.

Species richness

Sediment addition had a positive influence on species richness, but this effect was not constant over time (Table 4.4; Fig. 4.1B). Species richness peaked during July 2011 in sods that received a sediment subsidy, but was generally low among sods that did not receive sediment (Fig. 4.1B). After July 2011, species richness was not significantly different between sediment treatments, though richness was generally greater throughout

time in sediment-subsidized sods. Flooding also had a significant impact on species richness (Table 4.4); species richness averaged 2.5 ± 0.1 species sod⁻¹ in highly flooded treatments and 3.96 ± 0.2 species sod⁻¹ in treatments with relatively low levels of flooding. The impact of flooding tended to vary with time ($p = 0.0648$) such that species richness was greatest during Spring (April) and Summer (July) under conditions of low flooding, and tended to decrease through time under highly flooded conditions (Fig. 4.1C). Mean species richness for control sods was 4.2 ± 0.2 species sod⁻¹, while mean richness in treatment sods was 3.2 ± 0.1 species sod⁻¹. There was no significant impact of grazing or any interaction with grazing on species richness (Table 4.4).

Table 4.4 Univariate analysis of variance results for the main and interactive effects on various plant community characteristics. Bolded values indicate the presence of significant differences. ESAG = end of season aboveground. PSAG = peak season aboveground.

	Total Canopy Cover	Species Richness	Total ESAG Biomass	Total PSAG Biomass	CO ₂ Exchange
Effect	p-value	p-value	p-value	p-value	p-value
Flooding (F)	0.0019	<0.0001	0.2542	0.1152	0.9254
Grazing (G)	0.9181	0.3788	0.2643	0.7395	0.4584
Sediment Addition (SA)	0.1044	0.0581	0.0266	0.4256	0.0989
F x G	0.6100	0.6850	0.1758	0.3954	0.9491
F x SA	0.7452	0.1506	0.3894	0.9119	0.3564
G x SA	0.8596	0.3372	0.9736	0.7043	0.5396
F x G x SA	0.8276	0.5962	0.6206	0.9436	0.1421
Time (T)	<0.0001	<0.0001	-	-	-
F x T	0.0016	0.0648	-	-	-
G x T	0.1793	0.8453	-	-	-
SA x T	0.6774	0.0052	-	-	-
F x G x T	0.3019	0.2889	-	-	-
F x SA x T	0.4846	0.1903	-	-	-
H x SA x T	0.7573	0.6669	-	-	-
F x G x SA x T	0.7590	0.5341	-	-	-

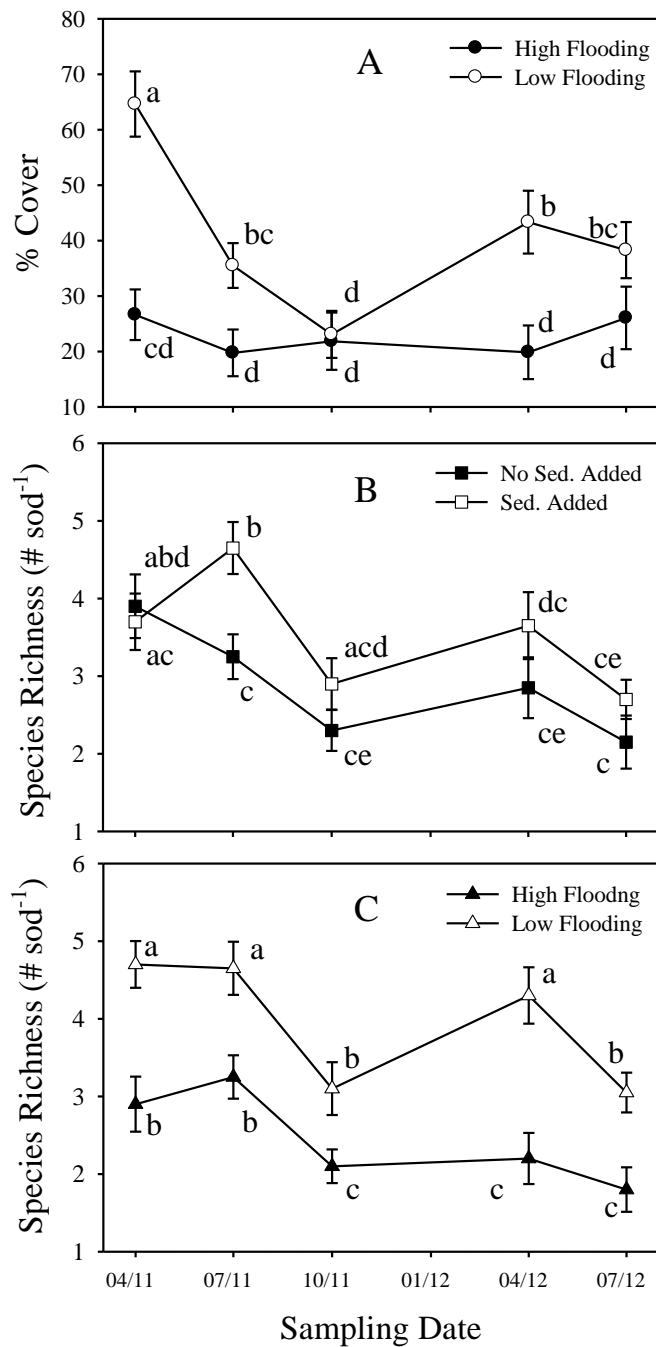


Figure 4.1 (A) Total percent canopy cover (mean \pm 1 S. E.) by sampling date for different flooding treatments, (B) species richness by sampling date for different sediment addition treatments, and (C) species richness by sampling date for different flooding treatments during recovery from salt water intrusion. Different lower-case letters represent significant differences (Tukey's; $p < 0.05$). High flooding = sods 12 cm below wetland platform elevation. Low flooding = sods at wetland platform elevation. Sed. added = 5 cm sediment added.

Biomass

End-of-season aboveground biomass (ESAB) summed for all species in a single sod was unaffected by flooding and grazing, but was significantly impacted by sediment addition (Table 4.4). Adding sediment resulted in a mean ESAB of $123.3 \pm 14.9 \text{ g sod}^{-1}$, while mean ESAB was $64.0 \pm 20.4 \text{ g sod}^{-1}$ for sods not receiving a sediment subsidy. Total peak season aboveground biomass (PSAB) was unaffected by all treatments and their interactions. Mean ESAB and PSAB were 68.6 ± 13.4 and $59.8 \pm 4.7 \text{ g sod}^{-1}$, respectively, for control sods and 93.7 ± 13.3 and $43.0 \pm 5.5 \text{ g sod}^{-1}$, respectively, for treatment sods.

When ESAB for the four most commonly-occurring plant species (*A. philoxeroides*, *E. fallax*, *P. punctatum*, and *S. lancifolia*) was analyzed together, MANOVA results indicated a significant flooding x grazing interaction, but no significant flooding, grazing, or sediment treatment effects on PSAB (Table 4.5A and B). When the interactive effect of flooding and grazing on ESAB from the MANOVA was explored further, the univariate ANOVA's indicated that this interaction was an important determinant of *A. philoxeroides* biomass, but was not important for *E. fallax*, *P. punctatum*, or *S. lancifolia* ESAB biomass (Table 4.5A). Although post-hoc analysis of pairwise comparisons revealed no significant differences between treatments ($p \geq 0.1642$; Tukey's), grazing tended to reduce *A. philoxeroides* biomass under conditions of low flooding, but had a lesser impact under highly flooded conditions (Fig. 4.2).

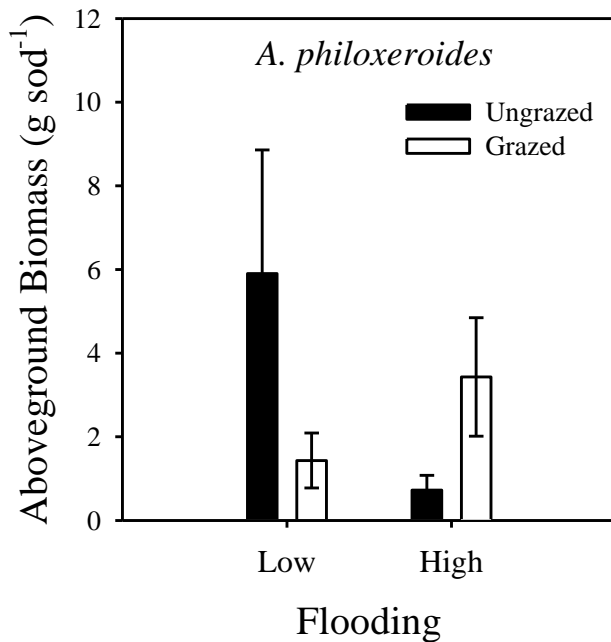


Figure 4.2 *Alternanthera philoxeroides* biomass (mean \pm 1 S. E.) represented for flooding x grazing treatments averaged for all post-intrusion sampling events.

Dominance

For intrusion-impacted and control sods, mean dominance was greater for *S. lancifolia* than for any other species (Table 4.3). *Spartina patens* and *Typha* sp. achieved the highest maximum dominance when compared to all other species in intrusion-impacted sods, while *S. lancifolia* achieved highest maximum dominance within the control treatment (Table 4.3). Because no species was present in all sods at all times, minimum dominance for all species was zero.

When dominance for the four most commonly-occurring plant species was analyzed together, MANOVA results indicated an overall effect of flooding over time (Table 4.5C). Grazing and sediment subsidy had no significant impact on the four most-commonly occurring plant species, nor did any of their two- or three-way interactions.

Table 4.5 Multivariate and univariate analysis of variance results for the main and interactive effects on plant community characteristics. The four most commonly-occurring plant species were used in the analyses, including *Alternanthera philoxeroides*, *Eleocharis fallax*, *Polygonum punctatum*, and *Sagittaria lancifolia*. ESAG = end of season aboveground. PSAG = peak season aboveground. Bolded values indicate the presence of significant differences ($P < 0.05$).

A. ESAG Biomass					
	MANOVA Effects			ANOVA Effects	
	d.f.	p-value		d.f.	p-value
F	4,5	0.2031	F x G		
G	4,5	0.4501	<i>A. philoxeroides</i>	1,32	0.0445
SA	4,5	0.4384	<i>E. fallax</i>	1,32	0.6501
F x G	4,5	0.0385	<i>P. punctatum</i>	1,32	0.7465
F x SA	4,5	0.4221	<i>S. lancifolia</i>	1,24	0.9387
G x SA	4,5	0.4435			
F x G x SA	4,5	0.5749			
B. PSAG Biomass					
	MANOVA Effects			ANOVA Effects	
	d.f.	p-value		d.f.	p-value
F	4,5	0.1864			
G	4,5	0.4902			
SA	4,5	0.4451			
F x G	4,5	0.2599			
F x SA	4,5	0.2277			
G x SA	4,5	0.7901			
F x G x SA	4,5	0.9931			
C. Dominance					
	MANOVA Effects			ANOVA Effects	
	d.f.	p-value		d.f.	p-value
Flooding (F)	4,5	0.2217	T		
Grazing (G)	4,5	0.2320	<i>A. philoxeroides</i>	4,128	0.0014
Sediment Addition (SA)	4,5	0.4178	<i>E. fallax</i>	4,128	0.0365
F x H	4,5	0.3628	<i>P. punctatum</i>	4,128	0.3617
F x SA	4,5	0.3963	<i>S. lancifolia</i>	4,128	<0.0001
G x SA	4,5	0.1817	F x T		
F x H x SA	4,5	0.9436	<i>A. philoxeroides</i>	4,128	0.0006
Time (T)	16,382	<0.0001	<i>E. fallax</i>	4,128	0.1405
F x T	16,382	<0.0001	<i>P. punctatum</i>	4,128	0.0161
G x T	16,382	0.4928	<i>S. lancifolia</i>	4,128	0.3070
SA x T	16,382	0.2015			
F x G x T	16,382	0.7876			
F x SA x T	16,382	0.7974			
G x SA x T	16,382	0.9345			
F x G x SA x T	16,382	0.5341			

When these four species were analyzed individually (ANOVA; Table 4.5C), I found that low flooding had a stimulatory impact on *P. punctatum* dominance and a mixed impact on *A. philoxeroides* dominance (Fig. 4.3A and B). *P. punctatum* dominance under low flooding conditions peaked during April 2012, generally increasing over time following salt intrusion disturbance. *P. punctatum* dominance changed little during recovery from intrusion disturbance under highly flooded conditions (Fig. 4.3A). Likewise, *A. philoxeroides* dominance remained nearly constant through time under highly flooded conditions (Fig. 4.3B). Mean dominance values for *P. punctatum* and *A. philoxeroides* were 68.1 ± 22.1 and 78.6 ± 16.8 for highly flooded sods, respectively, and 177.8 ± 22.1 and 116.7 ± 27.4 for sods under lower flooding conditions, respectively. Average dominance for the control treatment was 196.9 ± 63.8 and 139.6 ± 36.6 during the recovery period for *P. punctatum* and *A. philoxeroides*, respectively.

Net community CO₂ exchange rates

There was no significant impact of flooding, grazing, or sediment treatments, or any of their two- or three-way interactions on net community CO₂ exchange rates (Table 4.4). Mean CO₂ exchange rate for control sods was $9.59 \pm 4.90 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, and mean exchange rate for treatment sods was $8.78 \pm 2.29 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

Soil Structure and Function during Recovery

Soil structure and belowground biomass

Percent soil organic matter was more than four times greater in sods that did not receive a sediment subsidy than in those that did (Table 4.6B). However, soil organic matter content was not impacted by flooding, grazing, or any of their two- or three-way interactions (Table 4.6A). Bulk density varied significantly with sediment addition and

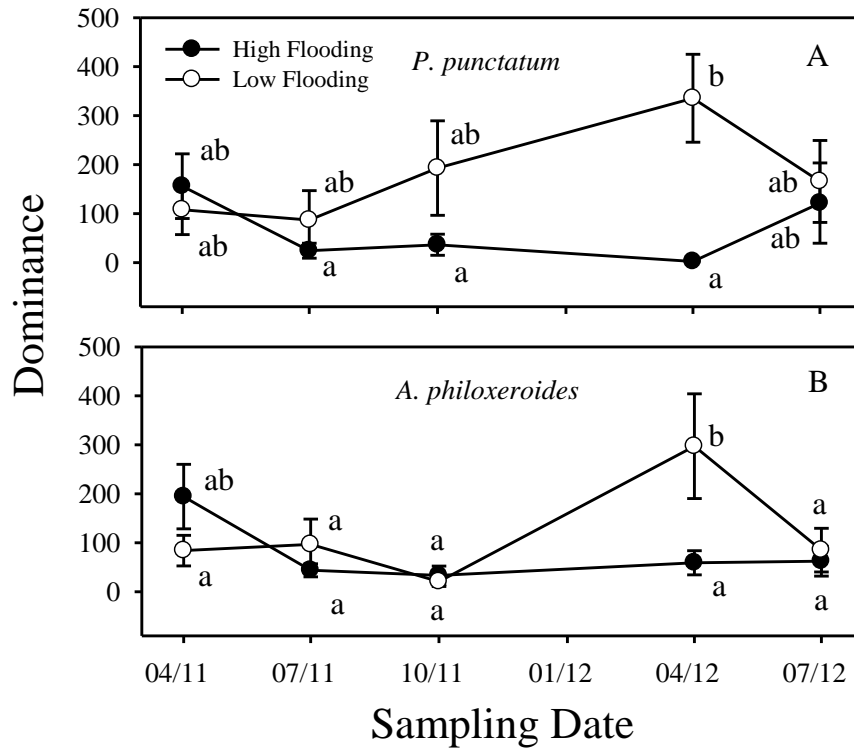


Figure 4.3 Plant species dominance by flooding treatment (mean \pm 1 S. E.) for (A) *P. punctatum* and (B) *A. philoxeroides* by sampling date. Different letters represent significant treatment differences within a species (Tukey's; $p < 0.05$). High flooding = sods 12 cm below wetland platform elevation. Low flooding = sods at wetland platform elevation.

flooding x grazing treatments (Table 4.6A). Bulk density was lowest when no sediment was added following intrusion exposure, and was greatest when sediment was added.

Sediment subsidy elevated bulk density by a factor of four (Table 4.6B). There was a significant flooding x grazing interaction effect on bulk density such that grazing lowered bulk density under highly flooded conditions, but grazing had no effect on bulk density under low flooding conditions (Table 4.6A; Fig. 4.4A). Total belowground (BG) biomass was greater under lesser flooded conditions, but was unaffected by grazing, sediment subsidy, or any of their two- or three-way interactions (Table 4.6A and B).

Table 4.6 Univariate analysis of variance (ANOVA) results and means (± 1 S.E.) for the main and interactive effects on wetland soil characteristics. Bolded values indicate the presence of significant differences ($p < 0.05$). BG = belowground. High flooding = sods 12 cm below wetland platform elevation. Low flooding = sods at wetland platform elevation. Sed. added = 5 cm sediment added.

A. ANOVA Results		%		Total BG
		Organic Matter	Bulk Density	Biomass Production
Effect		p-value	p-value	p-value
Flooding (F)		0.2035	0.0896	0.0013
Grazing (G)		0.4682	0.2686	0.8127
Sediment Addition (SA)		<0.0001	<0.0001	0.2361
F x G		0.1395	0.0409	0.1028
F x SA		0.6503	0.2750	0.2736
G x SA		0.2114	0.2292	0.1994
F x G x SA		0.2658	0.1160	0.6440
B. Means		%		Total BG
		Organic Matter	Bulk Density	Biomass Production
			g cm ⁻³	mg cm ⁻³
Flooding				
	Low	28.4 (4.6)	0.279 (0.046)	0.407 (0.091)
	High	31.7 (4.8)	0.238 (0.038)	0.192 (0.081)
Grazing				
	Ungrazed	29.0 (4.8)	0.252 (0.046)	0.235 (0.064)
	Grazed	31.1 (4.6)	0.266 (0.039)	0.376 (0.108)
Sediment Addition (SA)				
	None	48.9 (1.6)	0.102 (0.004)	0.281 (0.087)
	Added	11.2 (9.2)	0.425 (0.030)	0.332 (0.094)

† n.a. refers to 'not applicable' because there was no referenced effect for this response variable.

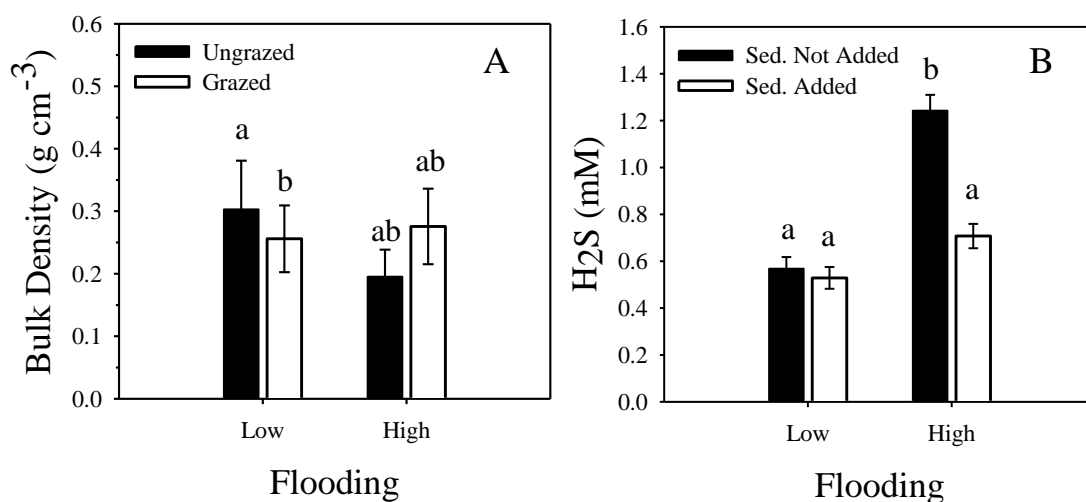


Figure 4.4 (A) Wetland soil bulk density (mean \pm 1 S. E.) for different flooding treatments when ungrazed or grazed by vertebrate herbivores, and (B) interstitial sulfide concentration for wetland low and highly flooded soils that did or did not receive a sediment subsidy following salt water intrusion. Different letters represent significant differences (Tukey's; $p < 0.05$). Sed. added = 5 cm sediment added.

Edaphic Conditions and Decomposition Rate

Four factors explaining 89.1% of the variance were identified as having eigenvalues greater than 1 (Table 4.7A). The variables defining factor 1 (F1) included calcium (Ca), magnesium (Mg), potassium (K), sodium (Na), sulfur (S) and phosphorus (P), all of which were highly positively correlated with F1. F1 explained 48.7% of the variance and was interpreted as a primarily a salinity-related factor that included phosphorus. Factor 2 (F2) explained 19.7% of the variance and was defined by porewater sulfide (H_2S) concentration, porewater pH, and soil Eh. Porewater sulfide and pH were positively correlated with F2, but Eh was negatively correlated with F2; hence, this factor was related to flooding. The variables defining factor 3 (F3) included manganese (Mn) and zinc (Zn), both of which were positively correlated with F3. F3 explained 10.6% of the variance. Iron (Fe) defined and was positively correlated with factor 4 (F4). F4

explained 10.1% of the variance. The last two factors can be interpreted as micronutrient-related factors.

A univariate analysis of variance (ANOVA) on the effects of flooding, grazing, and sediment addition, and their interactions on F1 showed that sediment addition, the flooding x grazing interaction, and the sediment x flooding x grazing interaction significantly impacted F1 (Table 4.7B). Adding sediment generally resulted in elevated concentrations of the F1 defining variables (Ca, Mg, K, Na, S, and P), and excluding grazing also elevated F1 defining variable concentrations (Table 4.8). However, the effects of flooding on F1 defining variables were inconsistent.

A separate ANOVA on the effects of flooding, grazing, and sediment addition, and their interactions on factor 2 showed that the main effects of flooding and sediment addition significantly affected F2 (Table 4.7B). When treatment effects on porewater sulfide concentration were explored over time (ANOVA), I found that sulfide concentration was significantly greater when soils were highly flooded, but sediment addition ameliorated the impacts of high flooding (Tables 4.8 and 4.9; Fig. 4.4A). pH and Eh were also significantly greater when flooding was low (Table 4.8 and 4.9). Sediment addition had a significant effect on F3 (Table 4.7). When comparing mean concentrations of the F3 defining variables, Mn and Zn concentrations were generally greater when sediment was added than when it was not (Table 4.8). There was no significant impact of flooding, grazing, sediment addition or their two- or three-way interactions on F4 (Table 4.7). However, high flooding tended to elevate Fe concentration ($p = 0.0833$; Tables 4.7 and 4.8). Although conductivity was not included as a defining variable for any of the identified factors (F1 through F4), conductivity was significantly affected by flooding

over time such that conductivity was significantly greater in highly flooded treatments during Oct. 2011, but was similar during other sampling times (Fig. 4.5). Conductivity peaked during July 2011 in both flooding treatments.

Table 4.7 (A) Correlations between indicator variables and retained factors for soil physico-chemical characteristics and (B) univariate analysis of variance (ANOVA) results for main effects on retained factors. (A) Bolded values indicate variables with correlations ≥ 0.60 that define the factors or (B) the presence of significant difference between means.

<i>A. Factor Analysis</i>				
Indicator Variables	Factor1	Factor2	Factor3	Factor 4
Ca	0.94996	-0.1722	0.08271	-0.1886
Mg	0.93942	-0.1738	0.06633	-0.0087
K	0.92688	-0.2327	0.02879	0.07281
Na	0.91642	-0.1614	0.05135	0.28214
S	0.77403	-0.129	0.56587	-0.1649
P	0.73374	0.0454	0.07835	-0.2557
H ₂ S	-0.2088	0.85076	-0.1798	0.06634
pH	0.05512	0.84947	-0.0597	-0.1608
NH ₄ N ⁺	-0.285	0.59489	-0.271	0.04158
NO _x N ⁻	-0.2305	0.55189	-0.2378	-0.1286
Eh	0.01234	-0.8749	-0.1485	-0.0338
Mn	-0.0299	-0.1764	0.91073	0.2353
Zn	0.59686	-0.0874	0.61348	-0.3161
Fe	-0.2283	0.06421	0.10447	0.86905
Conductivity	0.19639	-0.3209	0.00508	0.54278
Cu	0.33434	-0.3515	0.37678	-0.3971
Eigenvalue	6.65	2.69	1.45	1.37
% Variance Explained	48.7	19.7	10.6	10.1

Table 4.8 Mean values (\pm 1 S.E.) of soil physico-chemical response variables measured under different flooding, nutrient, and salinity treatments. High flooding = sods 12 cm below wetland platform elevation. Low flooding = sods at wetland platform elevation. Sed. added = 5 cm sediment added.

		Eh*	Cond.*	pH*	H ₂ S*	NO _x ⁻ -N	NH ₄ ⁺ -N	P	K
		mV	mS cm ⁻¹		mM	(mg kg ⁻¹ dry soil)	(mg kg ⁻¹ dry soil)	(mg kg ⁻¹ dry soil)	(mg kg ⁻¹ dry soil)
Flooding									
	Low	21.9 (8.1)	5.35 (0.11)	6.67 (0.54)	0.549 (0.043)	0.284 (0.77)	16.2 (6.5)	0.538 (0.089)	3.68 (0.58)
	High	-39.4 (6.4)	5.48 (0.19)	6.29 (0.03)	0.979 (0.019)	0.617 (0.213)	38.7 (11.4)	0.635 (0.140)	3.64 (0.61)
Grazing									
	Grazed	-9.6 (9.4)	5.38 (0.15)	6.21 (0.04)	0.756 (0.097)	0.477 (0.149)	31.6 (10.6)	0.503 (0.0873)	3.31 (0.56)
	Ungrazed	-7.9 (10.8)	5.45 (0.16)	6.73 (0.54)	0.771 (0.074)	0.424 (0.179)	23.2 (8.4)	0.671 (0.139)	4.01 (0.62)
Sediment Addition									
	None	-16.1 (9.5)	5.25 (0.12)	6.77 (0.54)	0.909 (0.099)	0.761 (0.197)	47.5 (11.7)	0.320 (0.028)	1.84 (0.12)
	Added	-1.4 (10.4)	5.58 (0.18)	6.18 (0.03)	0.618 (0.054)	0.140 (0.073)	7.3 (2.0)	0.853 (0.139)	5.48 (0.59)
		Ca	Mg	Na	S	Fe	Mn	Zn	Cu
		(mg kg ⁻¹ dry soil)	(mg kg ⁻¹ dry soil)	(mg kg ⁻¹ dry soil)	(mg kg ⁻¹ dry soil)	(mg kg ⁻¹ dry soil)	(mg kg ⁻¹ dry soil)	(mg kg ⁻¹ dry soil)	(mg kg ⁻¹ dry soil)
Flooding									
	Low	13.0 (1.7)	14.8 (2.1)	19.1 (2.7)	2.99 (0.40)	1.51 (0.09)	0.234 (0.015)	0.093 (0.019)	0.019 (0.003)
	High	12.8 (1.79)	15.1 (1.9)	21.8 (2.8)	3.02 (0.51)	1.91 (0.16)	0.229 (0.018)	0.114 (0.263)	0.015 (0.003)
Grazing									
	Grazed	12.1 (1.67)	14.2 (2.2)	19.9 (2.7)	2.62 (0.40)	1.65 (0.11)	0.217 (0.014)	0.074 (0.017)	0.016 (0.003)
	Ungrazed	13.7 (1.8)	15.7 (1.8)	21.0 (2.7)	3.39 (0.50)	1.78 (0.16)	0.245 (0.018)	0.132 (0.026)	0.018 (0.003)
Sediment Addition									
	None	7.40 (0.39)	8.99 (0.50)	13.0 (0.7)	1.51 (0.11)	1.79 (0.08)	0.204 (0.106)	0.030 (0.004)	0.011 (0.001)
	Added	18.4 (1.6)	20.9 (2.0)	27.9 (2.9)	4.50 (0.42)	1.64 (0.17)	0.258 (0.019)	0.176 (0.022)	0.023 (0.003)

* values for these variables are means averaged over multiple sampling times from April 2011 to June 2012. All other values were measured from samples gathered during a single sampling time in July 2012.

Table 4.9 Univariate analysis of variance (ANOVA) results for the main effects on wetland soil characteristics. Bolded values indicate the presence of significant differences.

	H ₂ S	pH	Eh	Cond
	p-value	p-value	p-value	p-value
Flooding (F)	0.0016	0.0001	<0.0001	0.5850
Grazing (G)	0.2055	0.5968	0.9237	0.7625
Sediment Addition (SA)	0.0331	0.3283	0.1547	0.1642
F x G	0.1677	0.4568	0.4572	0.9842
F x S	0.0072	0.0801	0.3888	0.7140
G x SA	0.2657	0.6319	0.9093	0.8528
F x G x SA	0.8948	0.6319	0.0989	0.6087
Time (T)	<0.0001	<0.0001	0.0003	<0.0001
F x T	0.1457	0.0024	<0.0001	0.0008
G x T	0.3005	0.2334	0.1843	0.1102
SA x T	0.3055	0.6537	0.1310	0.4539
F x G x T	0.7238	0.4265	0.8118	0.3646
F x SA x T	0.6895	0.9330	0.4292	0.9486
SA x G x T	0.9823	0.5053	0.4478	0.8981
F x G x SA x T	0.9986	0.4265	0.7995	0.8626

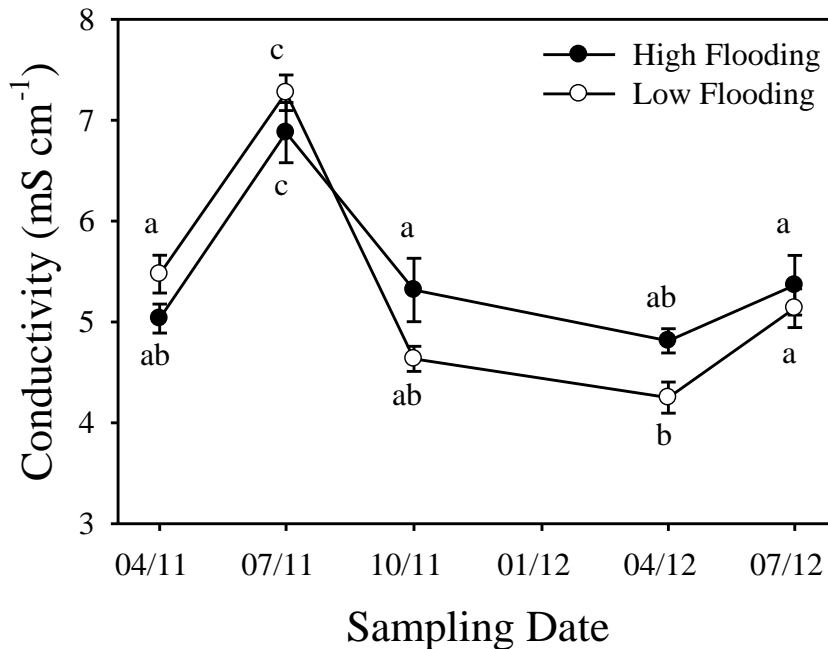


Fig. 4.5 Porewater conductivity (mean \pm 1 S. E.) for different flooding treatments by sampling date. Different letters represent significant differences (Tukey's; $p < 0.05$). High flooding = sods 12 cm below wetland platform elevation. Low flooding = sods at wetland platform elevation.

Decomposition rate measured using the litter bag assay was impacted by grazing with depth, and by the interaction of sediment addition and depth, but was unaffected by flooding (Table 4.10). Sediment addition slowed decomposition rate in the 0 – 5 cm depth, but had no impact at depths below 5 cm (Tukey's; Fig. 4.6A). Grazing resulted in an increase in decomposition rate at depths ≥ 5 cm, whereas grazing had no significant impact at 0 – 5 cm (Fig. 4.6B). Decomposition rate generally slowed with depth, with the greatest rate of decomposition occurring at the shallowest depth.

Table 4.10 Univariate analysis of variance (ANOVA) results for the main effects on wetland soil characteristics. Bolded values indicate the presence of significant differences.

		2011	2012
	Litter	Cotton	Cotton
	Bag	Strip	Strip
	Decomp.	Decomp.	Decomp.
	Rate	Rate	Rate
Effect	p-value	p-value	p-value
Flooding (F)	0.7962	0.0750	0.1005
Grazing (G)	0.1150	0.2790	0.7334
Sediment Addition (SA)	0.1083	0.1111	0.8354
F x G	0.6930	0.8437	0.2238
F x SA	0.3998	0.9382	0.1072
G x SA	0.4062	0.1702	0.5189
F x G x SA	0.2739	0.9792	0.9582
Depth (D)	<0.0001	<0.0001	<0.0001
F x D	0.3915	0.0123	0.4976
G x D	0.0263	0.5636	0.8380
SA x D	0.0114	0.9276	0.6297
F x G x D	0.6197	0.1697	0.0462
F x SA x D	0.8055	0.5567	0.2915
G x SA x D	0.9610	0.9259	0.3808
F x G x SA x D	0.9931	0.5776	0.3687

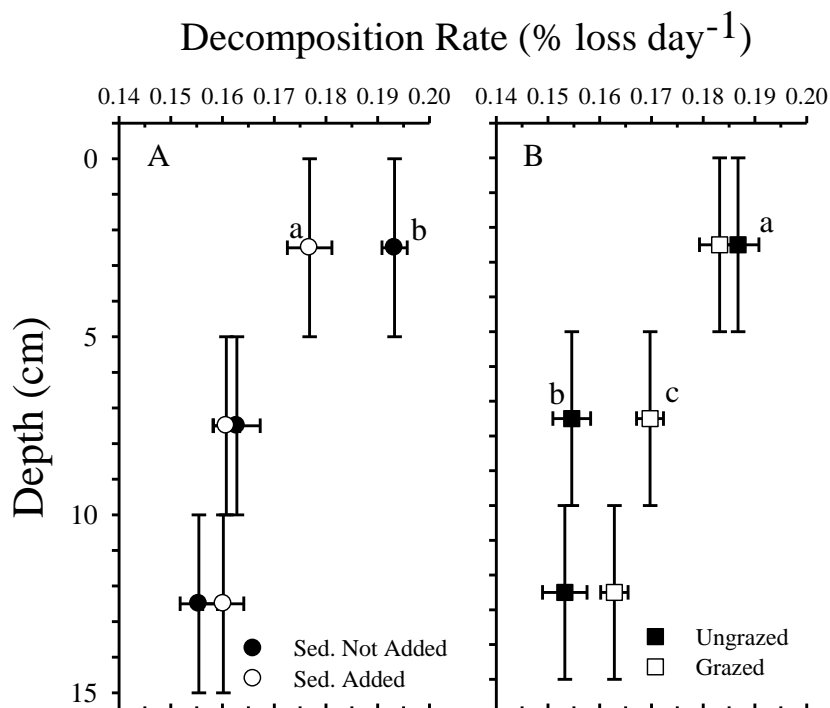


Figure 4.6 Mean litter decomposition rate between 0 and 15 cm below the soil surface by (A) sediment treatments and (B) grazing treatments. Vertical bars represent depth intervals and horizontal bars represent standard error. Different lower-case letters indicate significant differences within sediment or grazing treatments (Tukey's; $p < 0.05$). Sed. added = 5 cm sediment added.

Cellulose decomposition measured using the cotton strip technique during 2011 was affected by the interaction of flooding and depth such that at intermediate depths (4 – 12 cm), decomposition rate was faster under highly flooded conditions (Table 4.10; Fig. 4.7A). Flooding had no discernible impact on cellulose decomposition at shallow and deeper depths during 2011. There was a significant interaction between grazing, flooding, and depth during 2012 (Table 4.10). Although this interaction is difficult to interpret, decomposition rate steadily decreased with depth (2 – 22 cm) when sods were flooded and grazed, but the same trend was not observed when sods were not grazed under conditions of low flooding (Fig. 4.7B). Conversely, grazing generally had little impact on

the change in cellulytic decomposition rate with depth (2 – 22 cm) under conditions of high flooding (Fig. 4.7C).

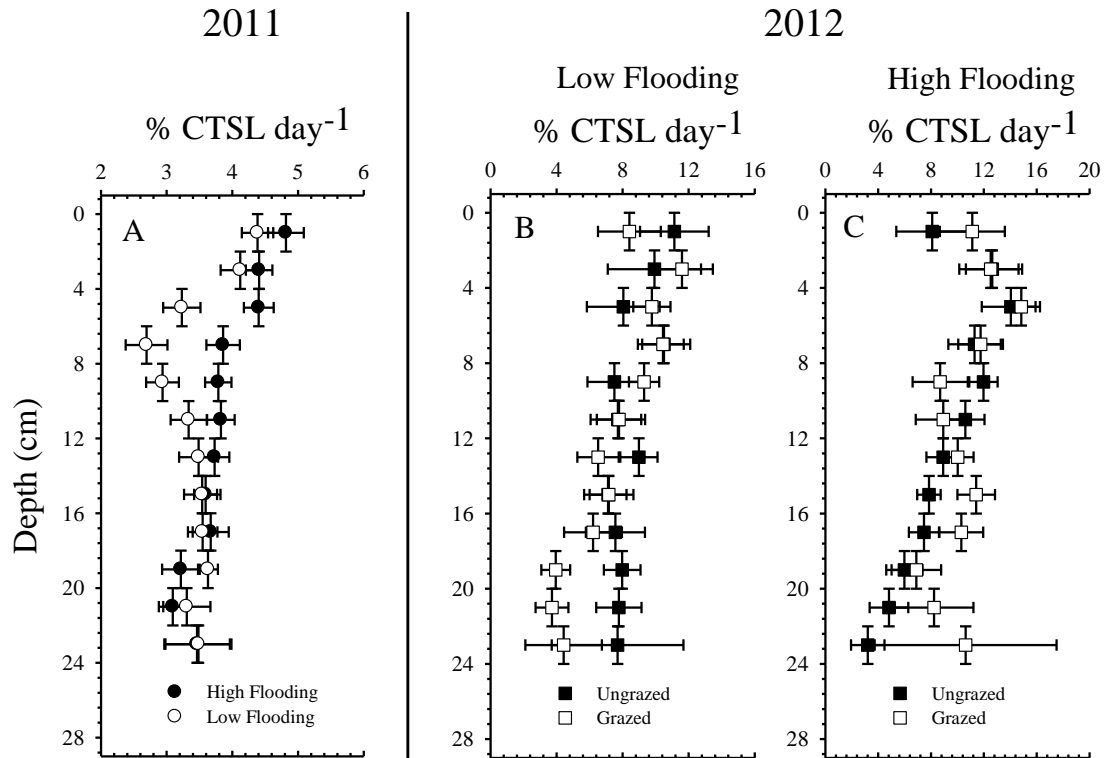


Figure 4.7 Cellulytic decomposition rate between 0 and 24 cm depth below the soil surface during May 2011 and July 2012. Vertical bars represent depth intervals and horizontal bars indicate standard error. CTSL = cotton tensile strength loss. High flooding = sods 12 cm below wetland platform elevation. Low flooding = sods at wetland platform elevation.

DISCUSSION

Exposing oligohaline wetland plants and soils to high salinity and flooding conditions, similar to those experienced during and after hurricane landfall, resulted in loss of aboveground vegetation and a decrease in plant species richness during and immediately after intrusion. Once intrusion conditions were alleviated, the physical environment (i.e. flooding level, grazing, and sediment subsidy) controlled the nature of plant recovery and the soil physico-chemical characteristics during recovery. For

example, sustained high flooding caused soils to become waterlogged and reduced, resulting in number of detrimental impacts to the plant community. The effects of post-intrusion grazing on the plant community were less prominent, interacting with flooding to impact the biomass of only one of the four most dominant plant species. Some conditions, such as high porewater sulfide concentration, produced by high flooding, were ameliorated by sediment subsidy, and greater species richness was favored when wetland soils were amended with additional sediment.

High flooding resulted in negative impacts to plant community structure, including less canopy cover and lower species richness. End of season *A. philoxeroides* aboveground biomass (AGB), and dominance of *A. philoxeroides* and *P. punctatum*, suffered when flooding was high. Because oxygen diffuses slowly in water-logged soils, plants growing under these conditions often become stressed due to a deficiency of oxygen, which plants require for photosynthesis. Although many wetland plants have developed adaptations to deal with poorly oxygenated soils, slow growth rate and low biomass are common for poorly-adapted plants when highly flooded conditions persist (Clevering et al. 1996, Baldwin and Mendelssohn 1998, Childers et al. 2006).

Furthermore, stressed communities are typically less species rich, with only the most stress-tolerant plants persisting, and therefore (co-) dominating (Grime 1977). For example, under conditions of high water, van der Valk (1994) found that species richness and Shannon's diversity index declined when water level was high, with richness decreasing over time. Raulings et al. (2010) found similar trends of decreasing diversity with deeper and longer inundation time, concluding that low light and anoxic soils caused by high water determined species richness by inhibiting survival of less flood-tolerant

plants. Previous experiments in *S. lancifolia*-dominated oligohaline wetlands have demonstrated the ability of the species to thrive during extended periods of high flooding, partially due to physiological adaptations that allow for a more oxidized rhizosphere and therefore a greater ability to survive long periods of flooding (Baldwin et al. 1996, Baldwin and Mendelssohn 1998, Ch. 2). Evidence from this experiment suggests that the difference in magnitude of flooding in high and low flooding treatments was not great enough to produce observable differences in *S. lancifolia* ABG or dominance; this species was dominant throughout the plant community regardless of experimental treatment.

Total belowground biomass (BGB) production under lesser flooded conditions was twice that of BGB production under highly flooded conditions. A reduction of belowground resource allocation under more highly flooded conditions is common among wetland plants (Blanch et al. 1999, Miller and Zedler 2003, Webb et al. 2012 and refs therein). Under conditions of sustained high water, wetland plants tend to produce more aboveground structures to maximize photosynthetically active aerial tissues such as shoots and leaves (Coops et al. 1996). Consequently, fewer resources are available for belowground production. In addition, flooded soils and highly reduced soil conditions impair root elongation due to root oxygen deficiencies (Pezeshki 1997). Although I did not determine shoot density, evidence from a variety of wetland plant studies supports the general conclusion that shoot density decreases with increasing water depth (Webb et al. 2012 and refs therein). Because suspended sediment retention is, in part, a function of stem density (Gleason et al. 1979), communities with low stem density trap less sediment and therefore are less sustainable because they are not able to build marsh platform

elevation. Also, belowground biomass production is an integral part of building and maintaining wetland platform elevation, therefore wetlands that experience high flooding are less likely to be able to combat sea level rise. These observations suggest that long periods of flooding that may follow hurricane occurrence are detrimental to elevation maintenance and wetland persistence. Further supporting this generalization is the observation that high flooding tended to speed cellulytic decomposition at intermediate depths, potentially contributing further to wetland elevation loss under highly flooded conditions.

Impacts of grazing on the plant canopy were somewhat complicated and difficult to predict. Under conditions of low flooding, grazing resulted in a decrease in *A. philoxeroides* aboveground biomass, but there was no difference in impact on the species' aboveground biomass under conditions of high flooding. Effects on *A. philoxeroides* biomass due to interactions between flooding and grazing were previously reported (Lu and Ding 2012). Non-flooded plants compensated for grazing by producing more biomass than ungrazed plants when maintained without flooding, but flooded plants showed no differential grazing effect (Lu and Ding 2010). The later observation is comparable to results of high flooding in this study; there was no difference between grazed and ungrazed treatments when flooding was high. There are a variety of potential explanations for this observation. The first is that the ability of *A. philoxeroides* to maintain aboveground biomass is diminished with the stress of high flooding, and may therefore not be productive enough to support grazing. Alternatively, highly flooded plants may be more difficult to graze, especially if they are underwater, and may therefore show no grazing impact. Grazing impacts were observed under lesser flooded

conditions such that *A. philoxeroides* biomass was less when grazing occurred. This is not surprising as previous studies have found that nutria selectively graze aboveground shoots, preferring certain species to others, and resulting in noticeable shifts in plant community structure (Shaffer et al. 1992, Johnson and Foote 1997, Ford and Grace 1998b). Conversely, grazing did not affect total aboveground biomass, nor did it impact biomass of the other three most dominant species. It is possible that herbivores were not numerous enough to exert significant top-down pressure on the plant community (Slocum and Mendelsohn 2008). While the extent to which they are hunted it is not documented for this particular marsh, nutria and other vertebrate herbivores in the area are targeted by hunters, trappers, and others regularly (pers. communication). Further, *S. lancifolia* is a rapidly-regenerating plant and quickly regrows after being damaged and may therefore be resistant to top-down control (Grace and Ford 1996).

Grazing also impacted a small number of soil characteristics including bulk density and litter decomposition rate, and the inter-correlation of a variety of extractable nutrients. A previous study of the effects of vertebrate herbivory on wetland soil characteristics have found no measurable impact on soil bulk density (Ford and Grace 1998a). Although I measured a significant decrease in bulk density due to grazing under low flooding conditions, the magnitude of this change is small and is not likely to be ecologically important. Litter decomposition rate was greater in grazed treatments than in ungrazed treatments at depths below 5 cm. Generally, grazers cause faster decomposition of soil organic matter in a variety of ways. By removing plant canopy, light penetration and soil temperature increase, causing an increase in organic matter decomposition rate (Wetzel 1983; Godshalk and Wetzel 1978). Furthermore, animals often leave scat in

areas that they have grazed, providing soil nutrients and delivering microbial decomposers, and thereby possibly speeding decomposition (van Soest 1982, Frank and Groffman 1998, Vanni 2002); scat was often observed along experiment walkways, suggesting use of the area.

Sediment subsidy following saltwater intrusion resulted in an increase in end-of-season aboveground (ESAG) biomass. While there was no species-specific impact, total ESAG biomass doubled when sediment was added, supporting other research demonstrating the positive effect of sediment pulses in promoting plant growth in healthy marshes (Slocum et al. 2005). Although McKee and Cherry (2009) found that storm-delivered sediment stimulated belowground root production, resulting in an accumulation of soil organic matter, I found no significant impact on belowground biomass production. Also, both belowground root and rhizome biomasses into ingrowth bags during the recovery period were indistinguishable between subsidized and unsubsidized treatments. The absence of any significant root growth in sediment-subsidized soils may be attributable to the dieback of vegetation that occurred during the initial intrusion disturbance. During this period of my experiment, once-healthy plants became necrotic. While the impacts of the initial saltwater intrusion to belowground roots and rhizomes were not studied, the condition of at least some belowground plant structures likely suffered during intrusion. Sediment subsidy also favored high species richness, with community richness reaching pre-intrusion during the summer following intrusion when sediment was added, but never returning to pre-intrusion richness when sediment was not added.

Subsidizing wetlands sods with sediment resulted in changes in the soil physico-chemical environment that were beneficial to the plant community, producing greater aboveground biomass and a richer plant community. For example, soils that received a sediment addition were less reduced, contained less hydrogen sulfide, and contained greater amounts of extractable minerals such as K and P. Such conditions, which are beneficial to wetland plant health, are often associated with sediment addition to wetlands because they provide better-aerated soils, supply metals which can precipitate toxic hydrogen sulfide, and deliver critical plant nutrients (Nyman et al. 1990, Mendelsohn and Kuhn 2003, Slocum et al. 2005). These results indicate that large amounts of sediment that may be delivered to a coastal wetland during hurricane landfall may be of critical importance to wetland survival. Because sediment addition can directly contribute to wetland elevation and also stimulate plant production, coastal wetlands may be better able to combat rising water and survive in the face of sea level rise. Without sediment subsidy however, wetlands affected by salt water intrusion and extended flooding due to hurricane landfall may succumb to the combined detrimental effects of reduced soils, low oxygen availability, and poor plant productivity, possibly transitioning to mudflats or open water. Furthermore, continuous grazing by vertebrate herbivores reduces the aboveground biomass of certain plant species, causing shifts in community composition and effects on wetland soil function and may contribute to wetland loss. Because coastal wetland survival and ability to thrive following mega-disturbances depend on post-disturbance conditions, wetlands should be managed in ways that promotes sediment delivery, controls herbivore pressure, and allows for drainage of excessively flooded areas to restore normal hydrology as quickly as possible after hurricane landfall.

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CHAPTER 5

BIOGEOCHEMICAL RECOVERY OF OLIGOHALINE WETLAND SOILS EXPERIENCING A SALINITY PULSE

INTRODUCTION

The Mississippi River Deltaic Plain is characterized by freshwater, brackish, and saltwater wetlands that transition from inland bottomland hardwood forests and tidal freshwater marshes to *Spartina alterniflora*-dominated salt marshes located on the fringes of the Gulf of Mexico (Box 1953). These wetlands are both ecologically and functionally diverse with dynamic eco-clines along a river-to-ocean salinity gradient (Eisenhart 1947). While the coastal wetlands within the Delta Plain are robust in their ability to adapt to typical edaphic changes, distinct differences in established ecological functionality occur at salinity gradient endpoints where salinity conditions are mostly stable and processes well-established (Odum 1988). For example, dominant biogeochemical pathways controlling catabolism of organic carbon in tidal freshwater wetlands and salt marshes are distinct from one another. Carbon mineralization in salt marshes is driven by the presence of sulfate in seawater, which is used as an alternative electron acceptor during microbial respiration under anaerobic conditions (Noble and Slatyer 1980, Krairapanond et al. 1992). Due to a greater availability of sulfate, organic matter decomposition in salt marshes produces a greater proportion of CO₂ than CH₄ (Odum 1988, White and Reddy 2003). Alternatively in freshwater marshes, sulfate availability is generally low, hence CH₄ production dominates due to the greater relative use of CO₂ as an alternative electron acceptor during anaerobic carbon mineralization (Noble and Slatyer 1980, Odum 1988). Chemical abundance and the pathways of nutrient cycling are also distinctive between fresh and saltwater estuarine environments. For example, ammonium (NH₄⁺) adsorption

is dependent on salinity (Davies 1974, Laursen 2004). NH_4^+ storage in freshwater sediments is relatively high due to relatively low activity of other ions, whereas NH_4^+ exchange in saline sediments is relatively high due greater ionic activity and greater competition for particle exchange sites (U.S.E.P.A. 1983, Peterson and Meador 1994). Further, microbially-mediated N cycling may also be affected by salinity due to inhibition in the conversion of NH_4^+ to NO_3^- by sulfide production in saline sediments and direct physiological effects of salts on nitrifiers and denitrifiers (Brookes et al. 1985, U.S.E.P.A. 1993, White and Reddy 2000). Therefore, wetlands adapted to low-salinities may experience strong functional shifts when exposed to higher salinities.

Increasing sea level rise (SLR) and decreasing freshwater input, in part due to changes in precipitation patterns are expected to cause an up-estuary migration of freshwater-saltwater mixing zones, causing intrusion of saltier water into wetlands that were once fresh (Vepraskas and Faulkner 2001, White et al. 2009). This press of SLR-associated saltwater intrusion is predicted to be an increasing chronic stress to tidal freshwater marshes (TFM), causing permanent changes in vegetation regimes, altering biogeochemical cycling, and deterioration of wetland health (Neubauer and Craft 2009, Weston et al. 2010). Previous experiments in TFMs have shown that encroaching saltwater will likely result in the replacement of methanogenesis with sulfate reduction as the primary pathway of anaerobic organic matter mineralization, and saltwater intrusion will increase organic matter decomposition rates in these wetlands (Weston et al. 2006, Weston et al. 2011). Faster rates of organic matter decomposition in tidal freshwater marsh soils suggests that platform elevation loss may increase, resulting in more chronic inundation of these wetlands. Further, SLR-associated saltwater intrusion is expected to

elevate CO₂ production and may elevate CH₄ production from TFM soils due to faster rates of C mineralization (Weston et al. 2011). Sea level rise-associated saltwater intrusion may contribute to worsening impacts of global climate change by increasing the rate at which CO₂ and CH₄, strong greenhouse gasses, is released from coastal wetlands.

The biogeochemical functionality of low-salinity wetlands is also impacted by pulsed saltwater intrusion events (Peng et al. 2005, Li et al. 2008). Temporary increases in salinity may occur for a variety of reasons including decreases in river discharge, drought, and with the passage of large frontal systems. The combination of strong winds, waves, and tides push saline water inland, causing rapid elevations in water level and salinity that may last for weeks or months following storm occurrence (Blood et al. 1991, Michener et al. 1997, Dix et al. 2008). These pulsed salinity events can change porewater chemistry by introducing sulfate, changing ionic strength, and changing nutrient availability (Blood et al. 1991). Although the effects of chronic and pulsed salinity into TFMs have been well documented, little is known about the impacts of pulsed salinity intrusions on the biogeochemistry of oligohaline wetland soils. While freshwater and saline marsh systems experience relatively stable salinity conditions, intermediate salinity wetlands occupy a dynamic interface where changes in environmental conditions such as rainfall, temperature, river flow, wind direction, or tides may result in dramatic shifts in salinity. These systems are generally able to absorb such perturbations without causing significant stresses on wetland vegetation, but salinity levels greater than the normal range can damage plants and disrupt biogeochemical cycling (Ch. 2, Ch. 4, Baldwin and Mendelssohn 1998a, Li et al. 2008). As sea level continues to rise, storm-associated salinity pulses may become more frequent, intense, and have longer duration (Michener

et al. 1997). Therefore, it is important to understand how oligohaline wetland sediment biogeochemistry responds to pulsed salinity, and perhaps more importantly, to understand how resilient soils recover from these events.

The goal of this investigation was to determine how and to what extent a storm-associated saltwater pulse affected oligohaline soil biogeochemistry, and how soil biogeochemistry changed once intrusion pressure was relieved. Specifically, I sought to answer the questions: (a) Does salinity intrusion change the soil microbial biomass or activity of the soil microbes?; and if so, (b) Does soil microbial biomass and activity return to levels of non-impacted soils once salinity intrusion is relieved? To answer these questions, I measured a suite of variables related to microbially-mediated processes. Because the degree and nature of organic matter cycling in wetland soils is strongly related microbially-mediate processes, the results of our study may be useful in predicting the fate of oligohaline wetlands in the face of rising sea level and continued pulsed salinity intrusion.

METHODOLOGY

Experimental Design

Thirty-five unvegetated soil cores were collected during July 2010 from an oligohaline marsh near Madisonville, LA (30°23'10.5"N, 90°09'0.7"W) where average salinity concentrations are 0.96 ± 0.03 psu (mean \pm 1 SE) (Baldwin and Mendelssohn 1998b). Soils at this site are in the Kenner series which is described as very poorly drained with slow permeability and containing a highly organic surface layer stratified with a fluid clayey alluvium (NRCS 2009). Soil cores (7 cm in diameter) were collected to a minimum depth of 15 cm and were transported to Louisiana State University in

Baton Rouge, LA where they were placed in a 23°C water bath in the dark. All soil cores were flooded to 10 cm depth with irradiated Gulf of Mexico seawater diluted with deionized water to a salinity of 1.5 psu as was measured using a Hach HQ Series portable meter, and cores were left undisturbed for a 10-day acclimation period. The tops of all core tubes remained unsealed and floodwater was gently bubbled using aquarium air pumps and tubing to maintain aerobic conditions. The bottom of each core tube was plugged with a rubber stopper. Evaporated water was replaced with deionized water throughout the experiment prior to sampling to maintain a constant water column depth.

After 10 days, Eh was measured *in situ* in 5 of the 35 cores as described below, and these cores were then sectioned into 5-cm depth intervals for further processing. The intrusion status of these cores is referred to as “before impact (BI)”, and this sampling event will be referred to as Sampling Event 1 (Fig. 5.1; Table 5.1). Sectioned soils were stored at 4 °C and processed within 6 weeks of removal from core tubes. Cores used for one sampling event were not used for any later samplings because sample processing was destructive. Seventeen days after core collection from the field, all of the remaining cores (N = 30) were drained of all flood water by gently pouring the water from the top of the core tube. Flood water for 15 of the remaining 30 cores was replaced with irradiated Gulf of Mexico sea water diluted to 20 psu, as measured using a Hach HQ Series portable meter to simulate saltwater intrusion from a storm surge. These cores are referred to as having an intrusion status of “impacted (I)” (Fig. 5.1; Table 5.1). Flood water for the remaining 15 cores was replaced with sea water diluted to 1.5 psu. These cores are referred to as having an intrusion status of “reference (R)”. Water was drained and replaced in all cores two more times during the next week in order to ensure that the

replacement water penetrated the soil volume. Soil cores remained flooded to 10 cm depth for approximately 6 weeks.

After 66 days of incubation, Eh was measured *in situ* in 5 of the 15 impacted cores and 5 of the 15 reference cores. The cores were then sectioned as described previously, and stored at 4 °C. This sampling is designated as Sampling Event 2 (Fig. 5.1; Table 1). Following, all remaining cores ($N_I = 10$ and $N_R = 10$) were flushed with 1.5 psu salinity water three times over seven days until porewater salinities dropped to near the target levels. On day 101, Eh in 5 impacted and 5 reference cores were again measured and soils sectioned and stored. This sampling is designated as Sampling Event 3. The remaining 10 cores were maintained under flooded conditions for 20 more days and then processed during Sampling Event 4.

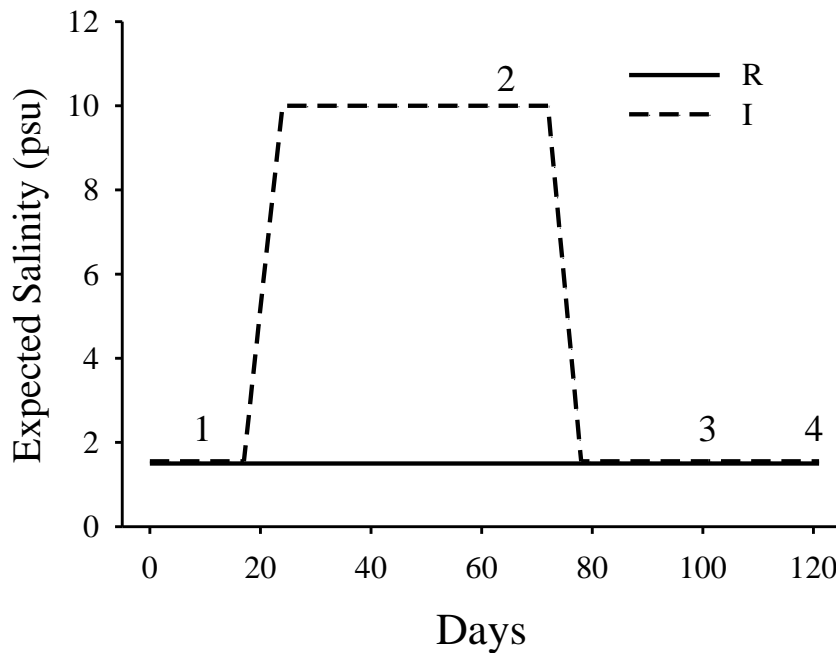


Figure 5.1 Expected salinity in reference (R) and impacted (I) wetland soil cores and Sampling Events (1, 2, 3, 4).

Table 5.1 Name, intrusions status, and sampling time of each treatment-level.

Treatment	Intrusion Status	Sampling Event
	Before	
BI	Impact	1
R2	Reference	2
I2	Impacted	2
R3	Reference	3
I3	Impacted	3
R4	Reference	4
I4	Impacted	4

Sample Collection and Analytical Methods

Soil Eh was measured at 10 cm below the soil surface with bright platinum electrodes and a calomel reference electrode attached to a Fisher Scientific accumet portable meter. Eh probes were inserted in the soil at least 24 hr before the first measurement was taken to equilibrate, and duplicate measurements were taken in each core.

Soil organic matter (OM), total nitrogen (TN), total carbon (TC), potentially mineralizable nitrogen (PMN), microbial biomass C and a select number of microbial activity were determined in three depth sections for all soil cores: 0 – 5, 5 – 10, 10 – 15 cm. Soil OM was determined by loss on ignition at 550 °C for two hours (Davies 1974). TN and TC were determined on a Costech Model 4010 Elemental Analyzer (Valencia, CA). PMN was determined by comparing time-zero extractable NH_4^+ -N concentrations to extractable NH_4^+ concentrations from an incubated sample from each depth section from each core. Soil samples were incubated at 40 °C for 10 days. NH_4^+ -N was extracted from 0.5 g of soil using 25 mL of 2M KCl and analyzed for NH_4^+ -N on the Seal AQ2 Discrete Analyzer using USEPA Method 351.2 (U.S.E.P.A. 1993). Microbial biomass carbon was determined by using a standard chloroform fumigation extraction method

(Brookes et al. 1985) with adaptations from White and Reddy (2000). Total organic carbon was measured using a Shimadzu Scientific Instrument TOC-VCSN (Columbia, MD).

Maximum basal and substrate-induced anaerobic respiration rates were measured using samples from depth-sectioned cores to determined microbial activity. For measurement of CH₄ and CO₂ production, 0.75 g dry weight equivalents of soil from each sample was added to 27 ml anaerobic tubes containing 12.5 ml of water. Tubes were sealed with a gas-impermeable butyl rubber stoppers and sealed with aluminum crimps. Each tube was flushed with 99.9% O₂-free N₂ for 3 – 5 minutes, evacuated to a pressure of -60 kPa, and then flushed again with 99.9% O₂-free N₂ for 2 – 5 minutes. Soil tubes were placed in the dark on an orbital shaker at at 25 °C. Samples were analyzed for CO₂ every 7 – 9 days using a Shimadzu GC-2014 fitted with a thermal conductivity detector at 160°C, utilizing a Poropak N column at 80°C. A 1% CO₂ gas mixture with an N₂ balance was used as a standard (Scott Specialty Gases). CH₄ samples were analyzed every 9-14 days using a Shimadzu GC-2014 with a flame ionization detector at 160°C, fitted with a Carboxyn 1000 column at 110°C. A 1% CH₄ gas mixture with an N₂ balance was used as a standard (Scott Specialty Gases). Substrate-induced incubations for CH₄ and CO₂ were identical to basal incubations, except 12.5 ml of sodium acetate solution (23 g C kg⁻¹ dry soil) was added to CH₄ vials while 12.5 ml glucose substrate (30 g C kg⁻¹ dry soil) was added to CO₂ vials. CO₂ samples were analyzed every 1 – 3 days, while CH₄ samples were analyzed every 2 – 7 days.

Interstitial water samples were taken from each core at 5 to 10 cm below the soil surface with plastic syringe sippers (Koch and Mendelssohn 1989, McKee and

Mendelssohn 1989) to determine porewater nutrient concentrations (NH_4^+ , NO_x^- , and PO_4^{3-}), porewater sulfide concentrations, and porewater pH and salinity. One 20 ml sample was immediately filtered through a 0.45 μm nylon syringe filter for determinations of NH_4^+ , NO_x^- , and PO_4^{3-} . All water samples were frozen until analysis. A second 20 ml sample was collected for salinity and pH measurements. Additionally, a 3 ml interstitial water sample was collected and immediately added to a sulfide antioxidant buffer. The sample was analyzed for sulfide concentration in the laboratory with an Orion sulfide electrode within 24 hours. Porewater salinity was determined by measuring conductivity, then converting these values to salinity using standard calculation methods. These values are reported in units of parts-per-thousand (ppt).

Data Analysis

To determine the effects of treatment (defined below) on soil biogeochemical responses, a one-way analysis of variance was performed using the PROC MIXED procedure in SAS v9.2. The statistical design was completely randomized with five cores assigned to each of seven treatments. Statistical significance was determined at the $\alpha = 0.05$ significance level. Tukey's post-hoc analysis was used to determine pair-wise differences when needed. Error variances were checked for homogeneity of variance using Levene's test and error variances were checked for normality using the Shapiro-Wilk test. Where residual variances were heterogeneous or not normally-distributed, a transformation was performed. The following variables were square-root transformed: OM, MBC, extractable NH_4^+ , PMN, and substrate-induced CH_4 production. The following variables were transformed using the inverse function: TN:TC, basal CO_2 production, basal CH_4 production, and substrate-induced CH_4 production. Extractable

NH_4^+ residuals were heterogeneous, and residuals for PMN, substrate-induced CO_2 production, basal CO_2 production and substrate-induced CO_2 production were not normally distributed. ANOVA is relatively robust concerning deviations in residual normality and homogeneity of residual variance, especially when sample sizes are equal (Eisenhart 1947, Box 1953).

Eh, pH, porewater (PW) NH_4^+ , porewater NO_x^- , porewater PO_4^{3-} , and porewater H_2S concentrations, and PW salinity were analyzed for the effect of treatment, where treatment is defined by the intrusion status and sampling event (Table 5.1). This approach resulted in seven treatment-levels (BI, R2, I2, etc.) with five replicate cores in each treatment. Soil OM, TN, TC, PMN, MBC, and microbial activity were analyzed for the effect of treatment, depth, and their interaction. This approach resulted in seven treatment-levels with five replicate cores in each treatment-level, three depths, and twenty-one treatment x depth interactions.

A factor analysis (PROC FACTOR) further reduced the dimensionalities of correlated soil and porewater chemical variables. Factors with eigenvalues greater than 1 were retained and orthogonally rotated with a varimax rotation (Kaiser 1958). Factor scores generated for each core were then analyzed using one-way ANOVA (PROC MIXED), with treatment as the independent variable. A correlation analysis (PROC CORR) was also used to explore the linear relationships between response variables.

RESULTS

Soil Properties

Soil organic matter (OM) content and soil bulk density changed significantly with depth, but neither was affected by treatment (Table 5.2, Fig. 5.2). Mean OM ranged from 28.8 to 39.7 % and mean bulk density ranged from 0.151 to 0.203 g cm⁻³. Organic matter density was unchanged by treatment or depth and averaged 0.059 ± 0.012 g cm⁻³ (mean \pm 1 SD). Mean soil Eh for the first sampling was -99.8 ± 56.3 . Although soil Eh was measured during each sampling time, a malfunctioning reference electrode compromised the Eh values measured during samplings 2, 3, and 4. Therefore, these values are not reported.

Microbial Biomass

Microbial biomass (MBC) was affected by treatment, depth, and their interactions (Table 5.2). A pairwise comparison of Reference (R) 2 and Impacted (I) 2 treatments (Table 5.1) showed that intrusion-impacted cores had greater MBC than reference cores during Sampling Event 2 (Fig. 5.3). When averaged over all depths, MBC in the I2 treatment-level averaged 11.3 ± 1.47 g kg⁻¹ soil, whereas mean MBC in the R2 treatment-level was 9.0 ± 1.09 g kg⁻¹ soil. The difference between R2 and I2 treatments was dependent on depth. There was a greater difference in MBC at the shallowest (0 – 5 cm) and deepest (10 – 15 cm) depths during sampling event 2, whereas the difference was minimal at the intermediate depth (5 – 10 cm). On average, MBC increased with depth with MBC significantly greater at the 10 – 15 cm depth than at shallower depths. There was no other significant differences between impacted and reference cores for any of the other sampling times.

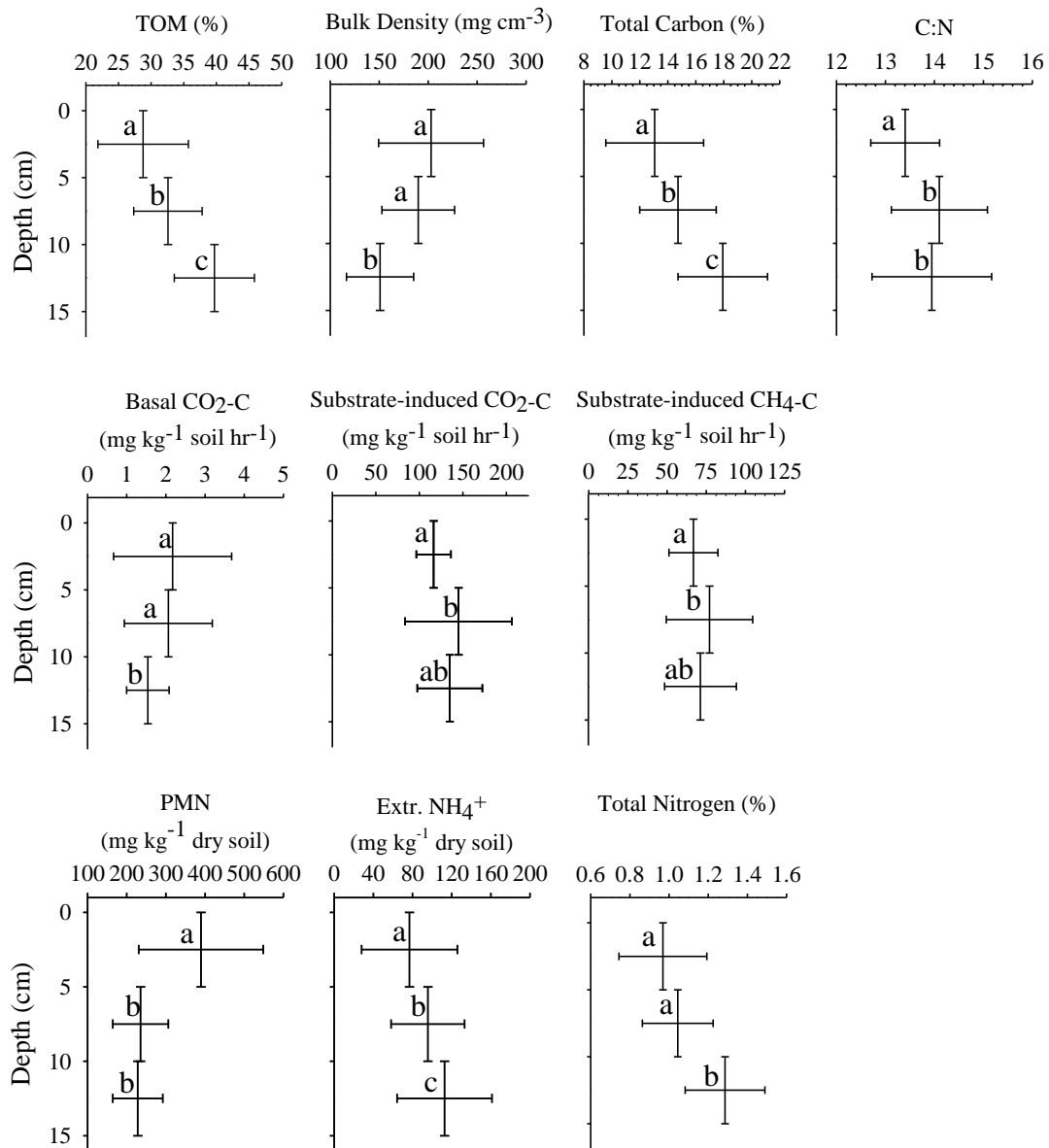


Figure 5.2 Oligohaline wetland soil and porewater response variables (mean ± 1 SD) measured in 5 cm increments (vertical bars) measured before, during, and after a saltwater intrusion. Significant differences by depth are indicated with different letters ($P < 0.05$). TOM = total organic matter; C:N = carbon to nitrogen ratio; PMN = potentially mineralizable nitrogen; Extr. = extractable.

Table 5.2 ANOVA results for evaluation of treatment and depth effects on soil responses to salinity intrusion. Significant effects are indicated by bolded text. OM = organic matter; MBC = microbial biomass carbon; TC = total carbon; TN = total nitrogen; C:N = total carbon to nitrogen ratio; PMN = potentially mineralizable nitrogen.

A. Soil Properties

		df ₁ , df ₂	p-value			df ₁ , df ₂	p-value
OM	Treatment (T)	6,28	0.8467	TC	Treatment (T)	6,84	0.6132
	Depth (D)	2,56	<0.0001		Depth (D)	2,84	<0.0001
	T x D	12,56	0.0820		T x D	12,84	0.3735
OM density	Treatment (T)	6,28	0.2316	TN	Treatment (T)	6,84	0.6200
	Depth (D)	2,56	0.4267		Depth (D)	2,84	<0.0001
	T x D	12,56	0.2038		T x D	12,84	0.1524
Bulk Density	Treatment (T)	6,28	0.1629	C:N	Treatment (T)	6,28	0.3851
	Depth (D)	2,56	<0.0001		Depth (D)	2,56	0.0046
	T x D	12,56	0.2673		T x D	12,56	0.4126
MBC	Treatment (T)	6,28	<0.0001	Extractable NH ₄ ⁺	Treatment (T)	6,28	< 0.0001
	Depth (D)	2,56	<0.0001		Depth (D)	2,56	< 0.0001
	T x D	12,56	<0.0001		T x D	12,56	0.0009
				PMN	Treatment (T)	6,28	0.0158
					Depth (D)	2,56	<0.0001
					T x D	12,56	0.7355

B. Microbial Activity

Substrate-added CH ₄	Treatment (T)	6,28	0.0009	Basal CH ₄	Treatment (T)	6,28	0.0309
	Depth (D)	2,56	0.0597		Depth (D)	2,56	0.1963
	T x D	12,56	0.0004		T x D	12,56	0.6145
Substrate-added CO ₂	Treatment (T)	6,27.7	0.0498	Basal CO ₂	Treatment (T)	6,28	0.0001
	Depth (D)	2,55.3	0.0106		Depth (D)	2,56	0.0552
	T x D	12,55.2	0.0022		T x D	12,56	0.4135

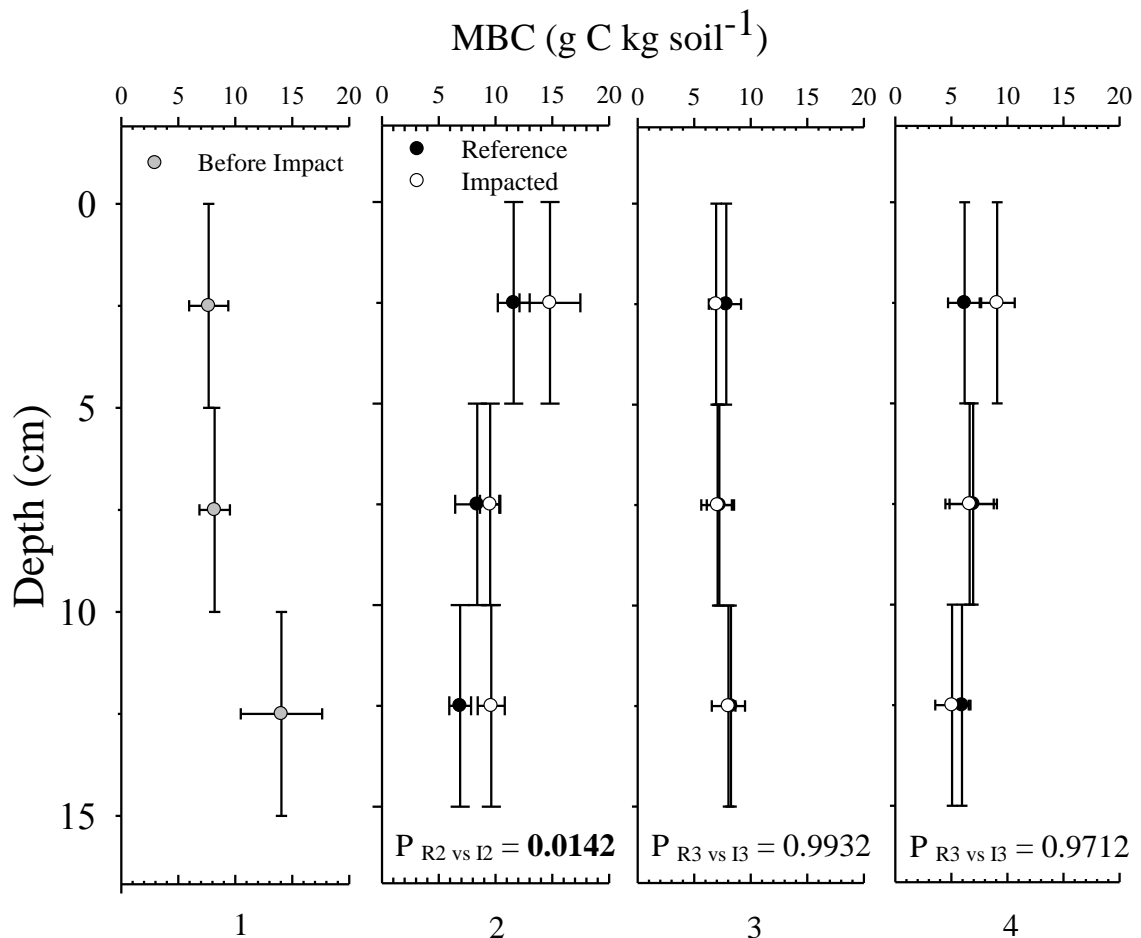


Figure 5.3 Microbial biomass carbon (MBC) (mean \pm 1 SD) by depth (vertical bars) for BI, R, and I intrusion status. P-values indicate Tukey's pair-wise comparisons between R and I statuses within each sampling event (sampling event listed at bottom).

Microbial Activity

There was a significant treatment effect observed for basal CO₂ production, basal CH₄ production, substrate-induced CO₂ production, and substrate-induced CH₄ production (Table 5.2B). However, there were no significant pair-wise differences in treatments within the same sampling event (i.e., R2 vs. I2, R3 vs. I3, R4 vs. I4) for basal CO₂ production, basal CH₄ production, or substrate-induced CO₂ production when post-hoc tests were performed. Substrate-induced CH₄ production was greater before saltwater intrusion (BI) than production in R2 and S2 treatments, but there were no other

significant pair-wise differences in treatments within the same sampling event when post-hoc tests were performed.

Basal CO₂ production, substrate-induced CO₂ production, and substrate-induced CH₄ production changed with depth (Table 5.2; $p < 0.05$). In general, basal CO₂ production decreased with increasing depth (Fig. 5.2). Substrate-induced CO₂ production and substrate-induced CH₄ production were greatest at the 5 – 10 cm depth range, intermediate at the 10 – 15 cm range, and lowest at the 0 – 5 cm depth range (Fig. 5.2). Basal CH₄ production did not vary with depth, and averaged 1.5 ± 0.6 mg C kg soil⁻¹ hr⁻¹. Although there was a significant interaction of treatment and depth for substrate-induced CO₂ production, substrate-induced CH₄ production, and basal CH₄ production (Table 5.2), post-hoc comparisons indicated that there were no significant pair-wise differences in treatments within the same sampling event.

Porewater and Soil Biogeochemistry

There were significant treatment and depth effects for soil potentially mineralizable nitrogen (PMN; Table 5.2). PMN in reference soils during sampling event 4 (218 ± 85.5 mg kg⁻¹ dry soil) was significantly lower than PMN in the impacted soils during sampling events 2 (322 ± 166 mg kg⁻¹ dry soil) and 3 (349 ± 189 mg kg⁻¹ dry soil). PMN decreased with depth, with the 0 – 5 cm depth section having greater PMN than either the 5 – 10 or 10 – 15 cm depth sections (Fig. 5.2). There were significant depth and treatment effects for soil extractable NH₄⁺, but there was no significant treatment x depth effect. Extractable NH₄⁺ was greatest in both soils (treatment and reference) during sampling event 3, and there was no difference in extractable NH₄⁺ in reference and impacted soils during any sampling event. Extractable NH₄⁺ increased with depth, (Fig.

5.2). Total percent carbon (TC), total percent nitrogen (TN), and C:N were unaffected by treatment-level and there was no depth x treatment interaction (Table 5.1). However, all were affected by depth (Fig. 5.2). Porewater salinity and porewater sulfide concentrations varied significantly by treatment ($p < 0.0001$), and values of both response variables were greatest in the I2 treatment (Fig. 5.4).

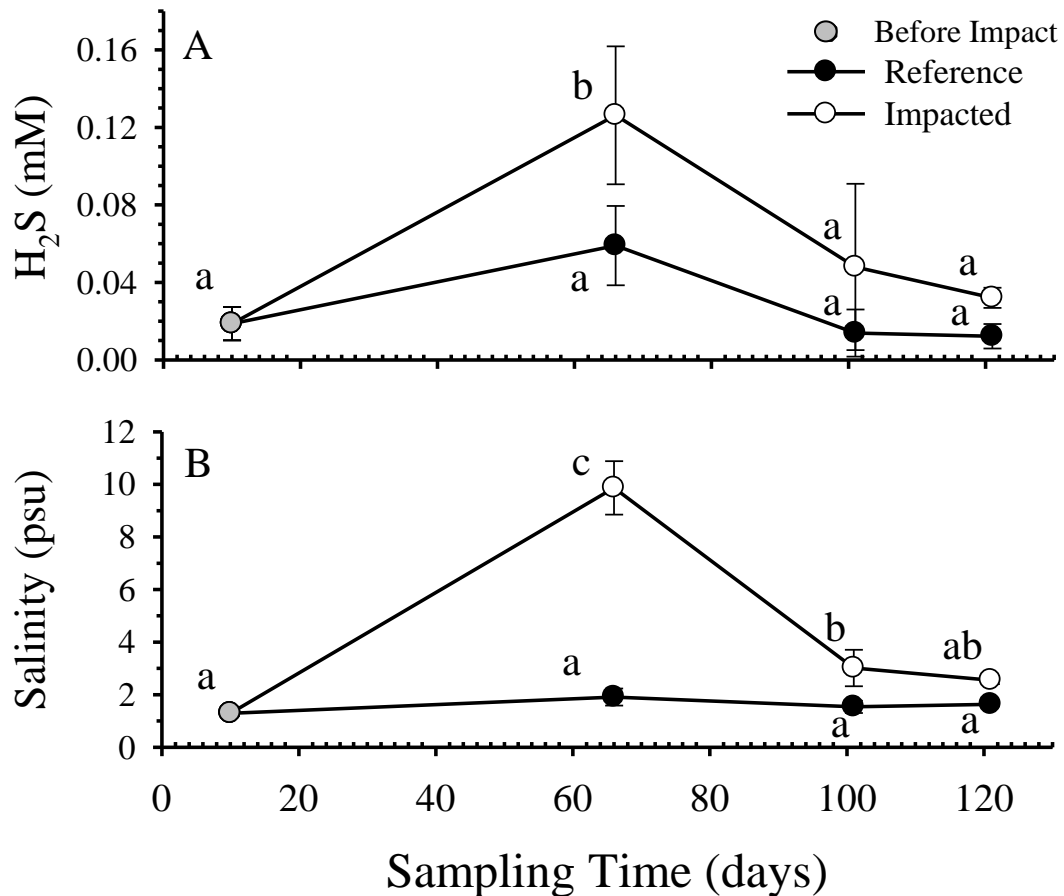


Figure 5.4: (A) Interstitial sulfide concentration and (B) salinity for BI, R, and I intrusion statuses over time (mean ± 1 S.D.). Different letters represent significant differences between treatments ($P < 0.05$). PW = Porewater.

Correlation of Soil and Porewater Variables

Five factors explaining 73% of the variance were identified as having eigenvalues greater than 1 (Table 5.3). The variables defining factor 1 (F1) included TC,

OM, and TN, all of which were highly positively correlated with F1. F1 explained 26% of the variance. Factor 2 (F2) explained 20% of the variance and was defined by porewater salinity, porewater sulfide, and substrate-induced CH₄ production. Porewater salinity and porewater sulfide were positively correlated with F2, but substrate-induced CH₄ production was negatively correlated with F2. The variables defining factor 3 (F3) included porewater SRP, basal CO₂, and basal CH₄, all of which were positively correlated with F3. F3 explained 12% of the variance. OM density, bulk density, and porewater NO_x⁻ defined factor 4 (F4) which explained 10% of the variance and all of the defining variables were positively correlated with F4. Factor 5 (F5) explained 6% of the variance and was defined by substrate-induced CO₂ production, MBC, and extractable NH₄⁺. Substrate-induced CO₂ production and MBC were positively correlated with F5, while extractable NH₄⁺ was negatively correlated with F5.

Correlation and regression analyses were used to further explore the relationship between soil response variables (Fig. 5.5). Factor 1 defining variables including TN, TC, and % OM were positively correlated with one another ($r = 0.76$ to 0.92 , $p \leq 0.0019$), and they were all significantly positively correlated with porewater sulfide concentration ($r = 0.37$, $p = 0.0465$; $r = 0.48$, $p = 0.0083$; $r = 0.42$, $p = 0.0230$, respectively). Low substrate-induced CH₄ production, a defining variable of F2, was associated with elevated porewater sulfide concentration and elevated salinity (Fig. 5.5A, B); sulfide concentration and salinity were also linearly related ($r = 0.81$, $p < 0.0001$). The defining variables of factor 3 including basal CO₂ production, basal CH₄ production, and porewater SRP were all positively correlated with one another ($r = 0.43$ to 0.64 , $p < 0.0180$), and while none of these variables were linearly related to porewater sulfide concentration, basal CH₄

Table 5.3 Factor analysis of depth-averaged soil variables and non-averaged porewater variables. Indicator variables corresponding to bolded correlation coefficients ($\geq \pm 0.6$) define the factor. PMN = potentially mineralizable nitrogen. SRP = soluble reactive phosphorus.

	Factor1	Factor2	Factor3	Factor4	Factor5
Total Carbon (TC)	0.9308	0.2150	0.0942	-0.0353	-0.0279
Organic Matter (OM)	0.9255	0.0783	0.0583	-0.0075	0.0184
Total Nitrogen (TN)	0.8609	0.0963	0.0575	0.2273	-0.1708
PMN	0.4335	0.3898	-0.0892	-0.0221	0.1130
Porewater Salinity	0.1392	0.9094	-0.1099	-0.0130	0.0866
Porewater H ₂ S	0.3122	0.8417	0.1769	0.0085	0.1160
Substrate-induced CH ₄	-0.1348	-0.7346	-0.0281	-0.2472	0.2398
Porewater SRP	-0.0045	0.0885	0.7781	0.0416	0.0178
Basal CO ₂	0.0584	-0.1788	0.7294	-0.2946	0.2717
Basal CH ₄	-0.0240	-0.3366	0.6001	-0.0118	0.5241
Porewater pH	-0.3932	-0.0867	-0.5852	-0.0070	-0.0058
OM Density	0.2684	0.1916	-0.3405	0.7729	0.2199
Bulk Density	-0.3743	0.1195	-0.4004	0.7157	0.2353
Porewater NO _x ⁻	0.1695	-0.0038	0.1895	0.6436	-0.0939
Porewater NH ₄ ⁺	-0.1456	0.3194	0.4610	0.5042	-0.3007
TC:TN	0.5436	0.3105	0.1384	-0.5517	0.2417
Substrate-induced CO ₂	-0.1675	0.1036	0.2997	-0.0435	0.7080
MBC	-0.0192	0.3928	-0.2077	0.1235	0.7026
Extractable NH ₄ ⁺	-0.1477	0.3773	-0.1071	0.0454	-0.6079
Eigenvalue	4.46	3.41	2.17	1.84	1.67
Variance explained	26%	20%	11%	10%	6%

production was moderately negatively correlated with porewater salinity ($r = -0.35$, $p = 0.064$). Factor 4 defining variables were also inter-correlated, and none of the factor 4 defining variables were linearly related to porewater salinity or sulfide concentration. Lastly, the defining variables for F5 were also intercorrelated. High extractable NH₄⁺ concentration was associated with low substrate-induced CO₂ production and low MBC ($r = -0.36$, $p = 0.0316$ and $r = -0.37$, $p = 0.0301$, respectively). MBC increased and extractable NH₄⁺ decreased linearly with increasing porewater salinity and increasing

sulfide concentration (Fig. 5.5B, C), but substrate-induced CO₂ production was unrelated to salinity or sulfide.

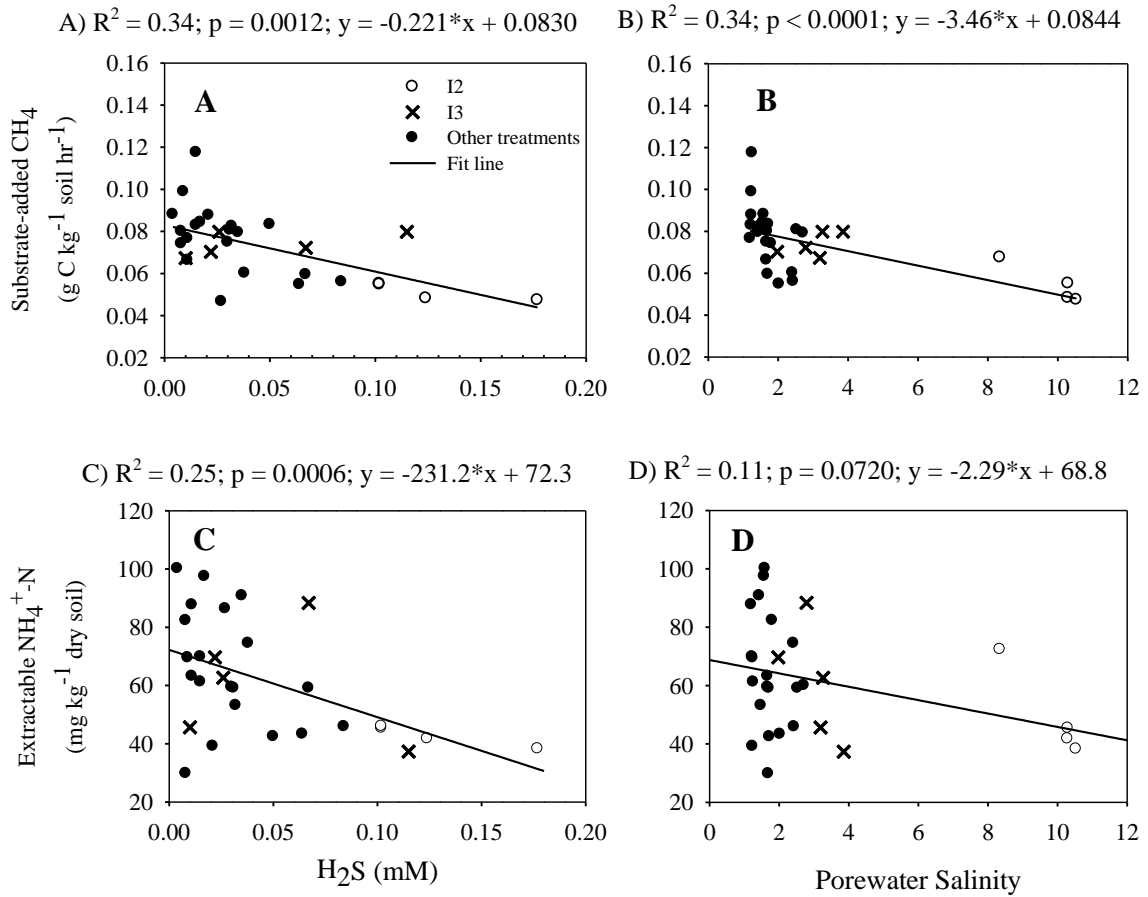


Figure 5.5 Microbial activity (A and B) and extractable NH₄⁺ concentrations (C, and D) measured before during and after a saltwater intrusion pulse. Linear regression coefficients, significance, and regression equations are listed for figures A – D. I2 = impacted soils during Sampling Event 2. I3 = impacted soils during Sampling Event 3.

DISCUSSION

Saltwater intrusion into oligohaline wetland soils caused porewater salinity and sulfide to increase, but CO₂ production was not related to salinity. Previous investigations of the effects of long-term saltwater intrusion in tidal freshwater marsh (TFM) soils have observed accelerated microbial organic matter mineralization due to saltwater exposure, causing CO₂ and CH₄ emissions from TFM soils to increase (Weston et al. 2011). Due

the greater presence of more efficient alternative electron acceptors in intruding saltwater (mainly SO_4^{2-}), organic mineralization rates in TFM soils increased. That oligohaline wetland soils and TFM soils react differently to saltwater intrusion isn't surprising. TFM soils contain a relatively small pool of SO_4^{2-} under normal conditions, so anaerobic organic matter mineralization relies more heavily on the use of CO_2 as an alternative electron acceptor than do more saline soils. In contrast, oligohaline wetlands typically contain a larger pool of SO_4^{2-} ; therefore, adding saltwater to these soils may not cause an observable increase in organic matter mineralization. Although I did not directly measure SO_4^{2-} concentration of the interstitial or flood water of our soil cores, I can estimate that interstitial SO_4^{2-} concentrations in our reference cores were likely between 55 mg l^{-1} , the average concentration of typical flood water at the donor marsh site (Blum and Roberts 2009), and 119 mg l^{-1} , the concentration of SO_4^{2-} in seawater diluted to 1.5 psu salinity. These values are between five and twelve times greater than SO_4^{2-} concentrations measured in TFM reference soils (Weston et al. 2011). Given these estimates, it is possible that reference and intrusion-impacted cores had a readily-available source SO_4^{2-} for use in carbon mineralization; therefore, adding 20-psu saltwater produced no observable change in CO_2 production in these soils.

Short-term seawater exposure resulted in a significant increase in sulfide and microbial biomass carbon (MBC) concentration during exposure, but concentrations returned to levels near those in soils prior to impact once the more saline water was replaced with water of ambient salinity. A build-up of hydrogen sulfide in wetland soils during exposure to seawater indicates the use of SO_4^{2-} by microbes as an alternative electron acceptor during organic matter mineralization (Vepraskas and Faulkner 2001).

Previous investigations of the impacts of salinity exposure on microbial assemblages have shown that salinity exposure increases microbial diversity, but depressed microbial functional activity (FitzGerald et al. 2008). In our study, functional activity (methanogenesis) was depressed when soils were exposed to saltwater intrusion, but changes in overall CH_4 production were likely the result of a shift away from CO_2 reduction during organic matter mineralization to reduction of other alternative electron acceptors in the added seawater. This relationship between methanogenesis and porewater salinity was stronger when acetate was added to the soil, suggesting that the additional C substrate fueled higher rates of methanogenesis when salinity was low, but not when salinity was high. Although there was no apparent relationship between CO_2 production and salinity or sulfide concentration, CO_2 production when glucose was added was strongly positively correlated with MBC, suggesting that saltwater intrusion may indirectly affect CO_2 production when an energetically efficient mineralizable substrate is present by regulating microbial biomass. Soil depth was also an important determinant of MBC. Before intrusion impact, MBC was greatest at the deepest depth measured (10 – 15 cm) than at either of the two shallower depth sections. This trend is opposite that of relationships observed in many soils (White and Reddy 2003, Peng et al. 2005, Poret-Peterson et al. 2007). One possible explanation of this altered trend is that water flow at shallow depths within the wetland has reduced the pool of mineralizable C at these shallow depths, and that root exudates at deeper depths provides microbes with a more available C source. However, this concept is not explored in our investigation. Nutrient availability may have been an important determinant of MBC, as MBC concentration was highly correlated with extractable NH_4^+ , and extractable NH_4^+ also increased with depth.

Porewater NO_x^- concentration and porewater NH_4^+ concentration were not related to salinity, but extractable NH_4^+ was negatively related to salinity level and sulfide concentration, suggesting that short-term salinity intrusion into oligohaline wetland soils does affect N availability in these soils. This observation supports other research demonstrating that elevations in salinity cause the release of NH_4^+ from adsorption sites, resulting in greater fluxes NH_4^+ from estuarine sediments when subjected to greater salinity (Weston et al. 2010). Soil depth also affected extractable NH_4^+ concentration, with concentration increasing with depth. Our observation that PMN decreased with depth is consistent with the typical pattern in wetland soils because nitrogen mineralization rate typically increases linearly with extractable NH_4^+ (White and Reddy 2001) and extractable NH_4^+ increased with depth.

While there was no treatment effect on soil structural components such as bulk density or percent OM, these characteristics changed significantly with depth. That bulk density decreased with depth and organic matter density remained unchanged suggests that mineral sediment density was greater in shallower depths than at deeper depths. Because of the proximity of our site to Lake Pontchartrain (~ 800 m) and the Tchefuncte River (~ 160 m), sediment delivery to the marsh surface is likely dependent on total suspended sediment (TSS) concentrations in the lake and river water that floods the marsh. Though elevated TSS concentration in Lake Pontchartrain is largely controlled by wave action during high wind events (Li et al. 2008), the opening of the Bonnet Carré Spillway in 2008 and 2011 resulted in a significant increase in suspended sediment within the Spillway plume (White et al. 2009, Roy et al. 2013). These types of internal

and external loading events in the recent past may have contributed to elevated sediment levels at shallow depths within our cores.

Although OM density was unchanged with depth, percent OM was greater at the 10 – 15 cm depth range, and percent OM density was significantly correlated with TN and TC. Further, the C:N ratio increased with depth, and this ratio correlated significantly with percent OM. Because the C:N ratio of wetland plant detritus typically decreases over time due to decomposition, measuring the C:N ratio in a soil can be a good indicator of how decomposed the soil is. The main detrital source for the marsh where the soil cores originated was likely the dominant herbaceous plant, *S. lancifolia*, which has a C:N of about 20 under typical conditions (Laursen 2004). The measured soil C:N values ranged from about 13 – 14, indicating a moderate degree of decomposition. Because labile carbon may not have been readily available to microbes in these soils, adding glucose or acetate resulted in a marked response in microbial activity, especially at intermediate and deeper depths (5 – 15 cm) where microbial biomass was generally greatest.

CONCLUSIONS

The goal of this investigation was to determine how and to what extent a storm-associated salinity pulse would affect oligohaline soil biogeochemistry, and how soil biogeochemistry changed once salinity pressure was relieved. Saltwater intrusion had mixed impacts on microbial responses. Oligohaline wetland soils did not experience increased organic matter mineralization rate when exposed to pulsed salinity intrusion, as was evident by no significant increase in CO₂ or CH₄ production, and there was no apparent effect of salinity intrusion on organic matter mineralization once salinity intrusion was removed. However, saltwater exposure resulted in an increase in MBC,

especially at shallow soil depths where MBC concentration doubled, but MBC concentration returned to near pre-intrusion levels once saltwater intrusion was removed. These observations were surprising given that prior investigations of the impacts of encroaching saltwater in TFMs as a result of rising sea level has consistently shown that organic matter mineralization rate and associated gaseous C emission will likely increase as saline water intrudes up-estuary.

However, given the differences in ambient soil conditions between TFMs and oligohaline wetlands and the fact that salinity presses (sea level rise) and salinity pulses (storm surge), may be very different in extent, severity, and length of effect, generalizations concerning the potential impacts of rising sea-levels on these wetland-types must be made with caution. Nevertheless, pulsed saltwater intrusion had no effect or only transient effects on microbial processes in cores collected from an oligohaline wetland under the experimental conditions in our study suggesting a biogeochemical resilience to a salinity pulse.

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CHAPTER 6 CONCLUSIONS

The primary focus of this research was to explore how and to what extent storm-driven saltwater intrusion and post-intrusion conditions affect oligohaline wetland plants and soils. I found that exposing oligohaline wetland plants and soils to high salinity and flooding conditions, similar to those experienced during and immediately after hurricane events, reduced plant cover by up to 71% and plant species richness by up to 39%. In some cases, percent cover and species richness never recovered to pre-intrusion conditions during the course of the study. Gaps left by species unable to tolerate the stress of high intrusion salinity and flooding were replaced by others that maintained viability via belowground structures or seeds. For example, aboveground shoots of *Sagittaria lancifolia* withered during saltwater intrusion, but quickly regenerated once stressful conditions were relieved. Rapid regeneration of *S. lancifolia* was likely possible due to the survival of the plant's rhizomes. Saltwater intrusion also altered soil biogeochemistry, raising porewater salinity and sulfide concentration, and changing the distribution of microbial biomass carbon (MBC) in the soil. Saltwater intrusion had little effect on organic matter mineralization rate in these soils, and once saltwater intrusion was removed, soil biogeochemistry quickly returned to pre-intrusion condition unless the post-intrusion condition (e.g., flooding level.) was manipulated.

Possibly more importantly, I found that the oligohaline wetland plant community and soil structure and function was determined by post-intrusion environmental conditions. Of the post-intrusion factors studied, flooding level was the most important driver of post-intrusion wetland condition. This generalization is supported by both greenhouse and field observations. In the greenhouse, drained water level favored a more

diverse plant community with greater aboveground biomass, while flooding favored the dominance of only a few species, mainly *S. lancifolia*. In the field, high water level stressed the recovering plant community, resulting in less canopy cover and low species richness. However, soil elevation and strength was impacted in the greenhouse when water level was consistently drained. Under drained conditions, decomposition rate was high and soils lost elevation due to increased rates of decomposition and less prolific belowground biomass production. Conversely, the dominance of *S. lancifolia* when flooding was high appeared to contribute substantially to soil volume due to greater production of belowground biomass, and decomposition rate was relatively low when soils were highly flooded. The combination of high belowground biomass production and low decomposition rate helped to maintain soil elevation under highly flooded conditions. I also found that *S. lancifolia* was resilient and stable when exposed to subsequent disturbance. Furthermore, *S. lancifolia* is also relatively salt-tolerant, with belowground tubers surviving exposure to salinities of 20 psu for 6 weeks, and with aboveground tissues regenerating relatively quickly after intrusion-exposure (personal observation). These relatively unique abilities should be taken advantage of; many coastal wetlands are being threatened by global sea level rise and local subsidence, resulting in increased flooding and longer-term salinity intrusion. The use of *S. lancifolia* in managed and restored marshes should be considered in order to build belowground biomass and maintain marsh soil elevation.

Past and current canal dredging along the Gulf Coast has increased channel flow, and has resulted in more direct connections between inland marshes and ocean (Turner 1997). As a result, brackish water is better able to penetrate inland into freshwater and

oligohaline wetlands during storm surge events. Wetland impoundments may exacerbate the impact of these pulsed intrusions by trapping saline water in affected wetlands for long periods of time. Therefore, it is important to consider the potential impacts of long-term salinity regime changes on wetland plants and soils following saltwater intrusion. Although belowground structures of *S. lancifolia* were able to survive short-term saltwater intrusion and aboveground biomass regenerated quickly once intrusion stress was removed, high recovery salinity caused lower *S. lancifolia* dominance, stem elongation rate, and aboveground biomass. High salinity also affected community resilience following subsequent disturbance. Under conditions of high flooding and low salinity, *S. lancifolia* recovered more quickly than under any other flooding x salinity combination. The combination of drained water level and high salinity slowed canopy cover resilience, and high salinity also lessened community stability regardless of flooding condition. Post-intrusion salinity regime was also an important determinant of soil structure, function, and condition. High recovery salinity resulted in less belowground biomass, faster decomposition, and relatively low shear strength. These combined results suggest strongly that long-term shifts in salinity regime toward more saline conditions are an overall detriment to oligohaline wetland health, threatening plant community resilience and stability and the ability of wetlands to maintain platform elevation to combat rising sea level.

I found that nutrient status impacted only a single plant growth response among those measured within the recovering oligohaline wetland plant community following saltwater intrusion; adding nutrients to greenhouse mesocosms increased community-wide annual production. Nutrient addition also had only minor impacts on recovery of

soils from saltwater intrusion, causing a slight decline in shear strength at the 5 – 10 cm depth, but nutrient status did not affect decomposition rate or belowground biomass production. Furthermore, nutrient status had no significant impact on plant community resilience and stability. Therefore, I conclude that nutrient status was of relatively little importance to wetland recovery when compared to other post-intrusion conditions (i.e. flooding and salinity). However, it is important to note that wetland response will likely differ depending on the specific nutrient and nutrient level during any particular recovery period, as well as other potentially interacting abiotic and biotic stressors. Because land use changes in the Mississippi River drainage basin have resulted in increasing nutrient enrichment in wetlands in the northern GOM region, eutrophication of coastal systems and the potential for ecosystem-level changes, especially following disturbance, continues to be a serious threat. Therefore, continued study, monitoring, and responsible management of affected areas are necessary.

When the impacts of herbivory on wetland condition following saltwater intrusion were studied in the field, I found that grazing was of lesser importance than post-intrusion flooding level, but sometimes interacted with flooding to affect wetland recovery. For example, under conditions of low flooding, grazing resulted in a decrease in *A. philoxeroides* biomass. However, grazing did not affect the aboveground biomass of this species under conditions of high flooding. I also found that grazing sped litter decomposition rate. Generally, continuous grazing by vertebrate herbivores reduces the aboveground biomass of certain plant species, causing shifts in community composition and effects of wetland soil function that may contribute to wetland loss. However, these impacts may be offset by sediment pulses provided by increased river input during and

after storm events, and delivery of near shore coastal sediments to the marsh platform during hurricanes provide enormous amounts of beneficial sediment to large expanses of drowning coastlines (Nyman et al. 1990, Turner et al. 2006, McKee and Cherry 2009, Day et al. 2011). In the field, subsidizing wetland soils with sediment resulted in a greater production of aboveground biomass, a richer plant community, less sulfide buildup, and greater amounts of mineral nutrients. Taken together, the results of this dissertation indicate that the large amounts of sediment that may be delivered to coastal wetlands during hurricane landfall may be of critical importance to wetland survival. Because sediment addition can directly contribute to wetland elevation and also stimulate plant production, coastal wetlands may be better able to combat rising water level and survive in the face of sea level rise. Without sediment subsidy however, wetlands affected by saltwater intrusion and extended flooding due to hurricane landfall may succumb to the combined detrimental effects of reduced soils, low oxygen availability, and poor plant productivity, possibly transitioning to mudflats or open water.

In conclusion, because oligohaline wetlands provide vital ecological services in many coastal regions (Rozas and Hackney 1983, Peterson and Meador 1994), great effort should be put forth to understand both natural and human impacts to these systems. Information gained through research should be applied in a way that encourages the maintenance of healthy, productive, and diverse wetland communities. Because many water control structures have been previously emplaced, coastal Louisiana may already have some of the tools necessary to manage wetlands threatened by hurricane mega-disturbances. Opening freshwater diversions along Mississippi River following storm surge should be considered as a way to minimize salt stress following storm events,

although the effect of high nutrient levels in Mississippi River water must be considered (Turner 2011). Other management activities such as the breaching of impoundments may alleviate extended flooding stress by allowing water drainage away from these areas. Furthermore, wetlands should also be managed in ways that promotes sediment delivery in efforts to promote wetland health. Through proper management and corrective action, diverse, productive wetlands can be supported, and important coastal ecological services can be preserved.

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VITA

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