

2009

Remediating impacts of global climate change-induced submergence on salt marsh ecosystem functions

Camille LaFosse Stagg

Louisiana State University and Agricultural and Mechanical College

Follow this and additional works at: https://digitalcommons.lsu.edu/gradschool_dissertations



Part of the [Oceanography and Atmospheric Sciences and Meteorology Commons](#)

Recommended Citation

Stagg, Camille LaFosse, "Remediating impacts of global climate change-induced submergence on salt marsh ecosystem functions" (2009). *LSU Doctoral Dissertations*. 3289.

https://digitalcommons.lsu.edu/gradschool_dissertations/3289

This Dissertation is brought to you for free and open access by the Graduate School at LSU Digital Commons. It has been accepted for inclusion in LSU Doctoral Dissertations by an authorized graduate school editor of LSU Digital Commons. For more information, please contact gradetd@lsu.edu.

REMEDIATING IMPACTS OF GLOBAL CLIMATE CHANGE-INDUCED
SUBMERGENCE ON SALT MARSH
ECOSYSTEM FUNCTIONS

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
Camille LaFosse Stagg
B.S., Christian Brothers University, 2002
M.S., Clemson University, 2004
May 2009

For Henry

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my major advisor, Dr. Irving Mendelssohn for his vital academic and personal support. This accomplishment would not have been possible without his scientific insight and guidance. I would also like to thank my advisory committee, Drs. Jaye Cable, John Day, John Fleeger and Robert Gambrell for their continuous assistance and direction throughout this stage of my academic career. Additionally, I thank Louisiana Sea Grant, whose financial support made this research possible. Special thanks to all of my fellow graduate students and colleagues, Joe Baustian, Jane Buck, Sean Graham, Carey Perry, Josh Roberts, Angela Schrift and Matthew Slocum, whose help in the field and laboratory was indispensable and made this an especially enjoyable experience. I owe the greatest debt of gratitude to my family, especially my husband, Philip; my father and mother, Thomas and Gayle; and my brother and sisters, Clayton, Emily and Lauren, who gave unwavering motivation and support throughout my entire academic career. Their continuous encouragement has provided me with the confidence to accomplish anything. Thank you.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS.....	iii
LIST OF TABLES.....	vii
LIST OF FIGURES.....	viii
ABSTRACT.....	x
CHAPTER 1	
INTRODUCTION	1
1.1 Global Climate Change and Wetland Submergence.....	1
1.2 Restoration of Submerged Wetlands with Sediment Addition.....	3
1.3 Rationale.....	4
1.4 Objectives.....	7
1.5 Literature Cited.....	8
CHAPTER 2	
IMPACTS OF SEDIMENT ADDITION ON ABOVE- AND BELOWGROUND PRIMARY PRODUCTION.....	17
2.1 Introduction.....	17
2.2 Materials and Methods.....	19
2.2.1 Site Description and Experimental Design.....	19
2.2.2 Primary Production.....	21
2.2.3 Soil Physico-Chemical Characterization.....	22
2.2.4 Statistical Analysis.....	24
2.3 Results.....	26
2.3.1 Primary Production.....	26
2.3.2 Soil Physico-Chemical Characteristics.....	28
2.3.3 Determinants of Primary Production.....	32
2.4 Discussion.....	33
2.5 Conclusions.....	40
2.6 Literature Cited.....	41
CHAPTER 3	
EFFECT OF SEDIMENT ADDITION ON DECOMPOSITION OF BELOWGROUND ORGANIC MATTER.....	49
3.1 Introduction.....	49
3.2 Materials and Methods.....	51
3.2.1 Site Description and Experimental Design.....	51
3.2.2 Root and Rhizome Decomposition.....	53
3.2.3 Cellulose Decomposition.....	55
3.2.4 Soil Physico-Chemical Measurements.....	56
3.2.5 Statistical Methods.....	58
3.3 Results.....	59

3.3.1 Root and Rhizome Decomposition.....	59
3.3.2 Cellulose Decomposition.....	60
3.3.3 Soil Conditions.....	61
3.3.4 Determinants of Decomposition.....	63
3.4 Discussion and Conclusions.....	66
3.5 Literature Cited.....	73

CHAPTER 4

GROWTH, SURVIVAL AND PRODUCTION OF *LITTORARIA IRRORATA* IN A SALT MARSH RESTORED WITH SEDIMENT ADDITION.....

4.1 Introduction.....	80
4.2 Materials and Methods.....	81
4.2.1 Site Description and Experimental Design.....	81
4.2.2 Enclosure Construction and Sampling Procedures.....	83
4.2.3 Growth, Survival and Production Calculations.....	86
4.2.4 Vegetation Estimates.....	87
4.2.5 Soil Physico-Chemical Measurements.....	87
4.2.6 Statistical Analyses.....	89
4.3 Results.....	90
4.3.1 <i>Littoraria irrorata</i>	90
4.3.2 <i>Spartina alterniflora</i>	92
4.3.3 Soil Conditions.....	93
4.3.4 Determinants of <i>L. irrorata</i> Growth, Survival and Production.....	95
4.4 Discussion.....	97
4.5 Conclusions.....	103
4.6 Literature Cited.....	104

CHAPTER 5

CONTROLS ON RESILIENCE AND STABILITY IN A SEDIMENT SUBSIDIZED SALT MARSH AND DETERMINATION OF LONG-TERM SUSTAINABILITY.....

5.1 Introduction.....	108
5.2 Materials and Methods.....	111
5.2.1 Site Description and Experimental Design.....	111
5.2.2 Resilience and Stability.....	114
5.2.3 Soil Physico-Chemical Parameters.....	116
5.2.4 Statistical Analyses.....	117
5.3 Results.....	119
5.3.1 Total Cover.....	119
5.3.2 Recovery Rate.....	121
5.3.3 Stability.....	123
5.3.4 Soil Physico-Chemical Characteristics.....	126
5.3.5 Determinants of Resilience.....	128
5.4 Discussion.....	131
5.4.1 Venice Total Cover and Resilience.....	131
5.4.2 Fourchon Total Cover and Resilience.....	134
5.4.3 Venice and Fourchon Stability.....	136

5.4.4 Venice vs. Fourchon.....	138
5.5 Conclusions.....	140
5.6 Literature Cited.....	140
CHAPTER 6	
CONCLUSIONS.....	146
6.1 Conclusions.....	146
6.2 Literature Cited.....	151
VITA.....	152

LIST OF TABLES

2.1 Principle component analysis of soil variables	30
2.2 Soil physic-chemical characteristics of the restored and natural marshes in 2005 and 2006	32
2.3 Multiple regression parameters that explain variance associated with response variables, above- and belowground production	33
3.1 Correlations between indicator variables and principle components (PCs) for soil characteristics.....	64
3.2 Multiple regression models for root+rhizome and cellulose decomposition as selected from all possible models by the stepwise selection method.....	66
4.1 Correlations between indicator variables and principle components (PCs) for soil characteristics.....	94
4.2 Multiple regression analyses describing relationships between <i>L. irrorata</i> responses and environmental characteristics.....	97
4.3 Correlations between <i>L. irrorata</i> biological responses and environmental variables	98
5.1 Correlations between indicator variables and principal components (PCs) for soil characteristics at Venice and Fourchon restoration sites	127
5.2 Multiple regression parameters that explain variance associated with response variables, total cover and recovery rate, at each of the two restoration sites 1) Venice and 2) Fourchon	130

LIST OF FIGURES

2.1 Sediment subsidy treatment site (blocks 1-4) and references (blocks 5-8)	21
2.2 Interactive effect of time and above- versus belowground production.....	27
2.3 Effect of sediment addition on total <i>Spartina alterniflora</i> production as well as ratios of below versus aboveground live biomass.....	28
2.4 Turnover rates of above- and belowground materials at different levels of sediment addition	29
2.5 Effect of sediment addition on soil characteristics representing 1) Soil moisture and salinity (PC1) and 2) Iron and phosphorus (PC2)	31
3.1 Sediment subsidy treatment site (blocks 1-4) and references (blocks 5-8).	53
3.2 The interactive effects of sediment subsidy and tissue type on the rate of belowground decomposition	60
3.3 The effect of sediment subsidy on belowground decomposition of total belowground biomass (root+rhizome tissue).....	61
3.4 Decomposition of cellulose (% CTSL·day ⁻¹) as effected by sediment subsidy	62
3.5 Graph showing the interactive effects of depth and elevation on cellulose decomposition (% CTSL·day ⁻¹)	63
3.6 Effect of sediment subsidy on 1) Soil moisture and salinity (PC1), 2) Iron and phosphorus (PC2) and 3) Redox Potential	65
4.1 Sediment subsidy treatment site (blocks 1-4) and references (blocks 5-8)	83
4.2 Snail enclosures located at each STL and reference block	85
4.3 Effect of sediment subsidy on <i>L. irrorata</i> 1) Growth rate, 2) Survival rate and 3) Production.....	91
4.4 <i>Spartina alterniflora</i> canopy cover at different levels of sediment addition.	93
4.5 Effect of sediment subsidy on 1) Soil moisture and salinity (PC1), 2) Iron and phosphorus (PC2) and 3) Redox Potential	96
5.1 Sediment addition at 1) Fourchon (sediment addition: 2002) and 2) Venice (sediment addition: 1992) restoration sites.....	112

5.2 The effect of sediment subsidy and disturbance intensity on total (live and dead) <i>S. alterniflora</i> cover one year after applied disturbances. 1) Interaction of sediment subsidy and disturbance intensity on total cover at Venice. Main effects of 2) sediment subsidy and 3) disturbance intensity on total cover at Fourchon	120
5.3 Effect of sediment subsidy on recovery rate at 1) Venice and 2) Fourchon. Effect of disturbance intensity on recovery rate at 3) Venice and 4) Fourchon.	122
5.4 Effect of sediment subsidy on odds of stability at Venice (Type 3 Likelihood Ratio test, $p < 0.05$).....	124
5.5 Effect of disturbance intensity on stability at Fourchon (1). Effect of sediment subsidy on stability after 2) non-lethal and 3) lethal disturbances at Fourchon (Type 3 Likelihood Ratio test, $p < 0.05$).....	125
5.6 Effect of sediment subsidy on PC1s at 1) Venice: PC1 (Salinity), and 2) Fourchon: PC1 (Soil Moisture/Salinity). Effect of sediment subsidy on PC2s at 3) Venice: PC2 (Reduction), and 4) Fourchon: PC2 (Fe/P)	129

ABSTRACT

Impacts of global climate change, such as sea level rise and severe drought, have altered the hydrology of coastal salt marshes resulting in submergence and subsequent degradation of ecosystem function. A potential method of rehabilitating these systems is the addition of sediment-slurries to increase the elevation of the marsh surface, thus ameliorating the effects of excessive inundation. Although this technique is growing in popularity, the successful restoration of ecological function after sediment addition has received little attention. The purpose of this research was to determine if sediment subsidized salt marshes are functionally equivalent to natural marshes and whether salt marshes restored with this technique are sustainable over time. This research addressed the following questions: 1) Does sediment-slurry addition restore important ecological functions such as primary production, organic matter decomposition and secondary production?, 2) If so, what level of sediment addition results in optimal function?, 3) What soil physico-chemical parameters associated with sediment addition influence these ecological functions? and 4) How does vegetation resilience in sediment subsidized marshes change over time?

Moderate intensities of sediment-slurry addition, resulting in elevations at the mid to high intertidal zone (42-53 cm NAVD 88), successfully restored ecological function to degraded salt marshes. Additionally, salt marshes that received intermediate levels of sediment addition were more resilient than natural marshes, and maintained their resilience over time. However, all ecological functions showed a sediment addition threshold that was characterized by a decline in production and resilience and accelerated decomposition in areas of intense sediment addition, or high elevation (> 53 cm NAVD 88). The primary regulator of enhanced ecological function in the restored marshes was the alleviation of flooding stress observed in the degraded marsh.

Declines in ecological function above the sediment addition threshold were principally influenced by dry conditions that resulted from insufficient and infrequent flooding at high elevations. Therefore, the addition of intermediate levels of sediment to submerging salt marshes increases marsh surface elevation, ameliorates impacts of prolonged inundation and increases production and resilience. However, too much addition of sediment results in diminished ecological function that is equivalent to the submerged or degraded system

CHAPTER 1

INTRODUCTION

1.1 Global Climate Change and Wetland Submergence

The deterioration of coastal wetlands is a significant concern in Louisiana's Mississippi River Delta complex, where wetland loss occurs at a rate of $77 \text{ km}^2 \cdot \text{y}^{-1}$ (Barras *et al.*, 2003). A multitude of factors have contributed to the decline of these vegetated systems, including canal dredging, levee construction, geological subsidence, eustatic sea level rise and severe weather events, such as hurricanes and drought (Boesch *et al.*, 1994; Jelgersma, 1996; Turner, 1997; Day *et al.*, 2000; Barras, 2006; Alber *et al.*, 2008). Furthermore, these events do not occur in isolation, but it is the interaction of anthropogenic activities and global climate change which has lead to significant alteration of the natural hydrology of coastal salt marshes (see Day *et al.*, 2008). Climate change will result in increased sea level rise, elevated temperatures, and associated increases in severe weather events such as hurricanes and drought (IPCC, 2007), all of which have the potential to impact coastal ecosystems.

Sea level rise, which is projected to increase from 0.8 m to 1.5 m depending on ice sheet contributions (Pfeffer *et al.*, 2008; Rohling *et al.*, 2008; Mitrovica *et al.*, 2009), results in the excessive inundation of salt marshes that are not able to accrete mineral and organic matter at a pace equal to or greater than the rate of sea level rise (Cahoon *et al.*, 1995; Day *et al.*, 1997). Higher flood duration leads to anoxic sediment conditions (DeLaune *et al.*, 1983; Wilsey *et al.*, 1992; Mendelssohn and Kuhn 2003), resulting in the formation of phyto-toxic sulfides (Patrick and DeLaune, 1972; Linthurst, 1979; Mendelssohn and McKee, 1988) and the inhibited growth and potential mortality of *Spartina alterniflora* (Linthurst, 1980; Mendelssohn and McKee, 1988; Bradley and Dunn, 1989; Koch and Mendelssohn, 1989). Furthermore, the vulnerability

of salt marshes to sea level rise may be even greater in areas like Louisiana, which experience higher rates of relative sea level rise ($1.2\text{--}1.65\text{ cm}\cdot\text{y}^{-1}$; Ramsey and Penland, 1992) due to geological subsidence (Penland and Ramsey, 1990; Ramsey and Penland, 1992; Dokka and Shinkle., 2004; Dokka, 2006). Anthropogenic activities, such as canal dredging and levee construction, further exacerbate the effects of sea level rise through inhibiting the natural deposition of mineral sediments in the salt marsh (Turner, 1985; Swenson and Turner, 1987; Boesch *et al.*, 1994; Turner 1997; Day *et al.*, 2000), which aid in positive elevation change (Nyman *et al.*, 1990; DeLaune *et al.*, 1992; DeLaune *et al.* 2003). Additionally, subsurface fluid withdrawal may also intensify relative sea level rise by enhancing rates of geological subsidence (Morton *et al.*, 2002), while dredging of pipeline canals results in the immediate loss of vegetation and alteration of salt marsh hydrology (Turner, 1997).

In addition, severe weather events, including hurricanes and droughts, are predicted to increase in both intensity and frequency (IPCC, 2007). Hurricanes have the potential to cause both negative and positive impacts on coastal wetlands. For example scouring can cause substantial land loss and decreased marsh surface elevation (Stone and Finkle, 1995; Barras, 2006); however, sediments may be re-deposited elsewhere, potentially aiding in the progradation and increased elevation of other systems (Stone and Finkle, 1995; Turner *et al.*, 2006a). In contrast, extreme drought causes negative impacts to coastal salt marshes, without positive effects (McKee *et al.*, 2004; Brown and Pezeshki, 2007). For example, in 2000 a severe drought caused the sudden dieback of over 100,000 acres of *S. alterniflora* salt marsh in southern Louisiana (McKee *et al.*, 2004; Lindstedt *et al.*, 2006; Alber *et al.*, 2008). Although some areas recovered after this expansive disturbance, in many cases, salt marshes were converted to unvegetated mudflats that eventually subsided. Materne and Mendelssohn (2006) documented up

to a 15 cm decrease in elevation at dieback-affected areas relative to unaffected salt marshes. Thus, drought-induced subsidence altered the natural hydrology of the affected areas, resulting in longer periods of inundation (Materne and Mendelssohn, 2006) accompanied by low redox potentials, high sulfide concentrations and minimal vegetative recovery (Schrift *et al.*, 2008).

1.2 Restoration of Submerged Wetlands with Sediment Addition

Although several factors interact to influence wetland loss in southern Louisiana, all of these scenarios ultimately result in a decrease in marsh surface elevation and excessive inundation of the salt marsh. Therefore, restoration methods that increase marsh elevation and reduce inundation may prove suitable in promoting marsh vigor (Mendelssohn and McKee, 1988, DeLaune *et al.* 1990, Wilsey *et al.* 1992). One potentially sound approach for accomplishing these goals, and thereby reducing wetland loss, is the application of sediment-slurries to degraded wetlands. This method of salt marsh restoration is based on the self-design concept (Mitsch and Wilson, 1996; Mitsch *et al.*, 1998) and the related concept of self-organization (Odum, 1989), which propose that an open ecosystem will optimize itself through natural recruitment and facilitation of those species which are best adapted to the system. Thus, abiotic intervention (Harris and Hobbs, 2001) resulting in restoration of hydrological and physico-chemical components, provides a template for the development of salt marsh community structure and ecosystem function.

The success of a restoration is often measured by the ecological equivalency between restored and natural systems. This concept of ecological equivalency provides a set of indices, which are used to measure the health of an ecosystem, and include organization, vigor and resilience (Rapport *et al.*, 1998). Several studies have demonstrated that the addition of sediment to degraded salt marshes results in the successful restoration of vegetation structure

(organization) (Mendelssohn and Kuhn, 2003; Slocum *et al.*, 2005; Schrifft *et al.*, 2008). The use of hydraulically dredged sediments decreases flood duration (Materne and Mendelssohn, 2006) and increases bulk density and soil nutrient concentrations (Mendelssohn and Kuhn, 2003), resulting in greater aboveground biomass, plant density and cover (Mendelssohn and Kuhn, 2003; Slocum *et al.*, 2005; Schrifft *et al.*, 2008). However, with the exception of Edwards and Mills (2005), little evidence is available concerning the successful restoration of ecological function.

1.3 Rationale

The goals of restoration aim to return a degraded system to previous conditions based on services and values, which depend not only on ecological structure, but also on ecosystem function. Additionally, quality ecological functions and resulting services have not always been present after successful restoration of structural characteristics (Zedler and Callaway, 1999; Rozas and Minello, 2001). Therefore, to determine the success of sediment addition in restoring degraded salt marshes, more information is needed on whether restoration of ecological function and resilience actually occurs. Thus, the objective of my research was to measure several ecological functions, primary production, organic matter decomposition, secondary production, and resilience, in a salt marsh restored using sediment addition, and to determine if these functions are equivalent to those in ambient marshes in the area.

As a salt marsh develops, several key attributes of ecosystem function interact to create a sustainable system. As a principle contributor of organic matter to salt marsh trophic systems, primary production plays a pivotal role in the overall productivity of the salt marsh (Teal, 1962; Wiegert, 1979; Woodwell *et al.*, 1979; Houghton and Woodwell, 1980). Additionally, primary production significantly influences organic matter accumulation in the salt marsh and is a critical

factor controlling elevation change (McCaffrey and Thompson, 1980; Hatton *et al.*, 1983; DeLaune *et al.*, 1990; Nyman *et al.*, 1993; Calloway, 1994; Turner *et al.*, 2001; Rybczyk and Cahoon, 2002; DeLaune and Pezeshki, 2003; Turner *et al.*, 2004). The limits on primary production in a salt marsh are largely physical, primarily driven by the frequency and duration of tidal inundation, which result in complex interactions of soil anoxia, soluble sulfide and salinity to affect nutrient uptake by *Spartina alterniflora* (Mendelssohn and Morris, 2000). Thus, although salt marsh plants are nitrogen-limited, concentrations of available nitrogen are often high in areas of low growth and excessive inundation (Mendelssohn, 1979), suggesting that primary production is not only limited by processes that control nutrient availability, but also by physical conditions that affect efficiency of nutrient uptake.

Nitrogen availability is primarily limited by *in situ* mineralization of organic matter (DeLaune and Patrick, 1979), which in turn is also strongly dependent upon inundation frequency and resultant aerobic/anaerobic soil conditions (Kirby, 1971; Reddy and Patrick, 1975; Kruczynski *et al.*, 1978; Tate, 1979; Montagna and Ruber, 1980; DeLaune *et al.*, 1981; Mackey and Smail, 1996). Decomposition plays an important role in influencing energy flow through the salt marsh (Teal, 1962; Good *et al.*, 1982; Davis *et al.*, 2006) and can contribute to accretion dynamics and potential elevation change (Hackney and Clearly, 1987; Bricker-Urso *et al.*, 1989). Decomposition of organic matter releases nutrients through mineralization, promoting primary production (Abd. Aziz and Newell, 1979; Henriksen and Jensen, 1979; Valiela and Teal, 1979), which in turn affects organic matter accumulation and vertical accretion (McCaffrey and Thomson, 1980; Neyman *et al.*, 2006; Turner *et al.*, 2006b). However, accelerated rates of decomposition may decrease soil volume and organic matter accumulation (Morris and Bradley, 1999), potentially resulting in a net negative elevation change. Therefore, restoration resulting in

balanced decomposition dynamics, such that rates of decay are not only optimal for nutrient release but also favorable for organic matter accretion, is important in maintaining ecosystem processes that promote sustainability.

As a detritus based system, the majority of primary production in the salt marsh is decomposed by bacteria and fungi (Teal, 1962). The grazing of detritivores stimulates decomposition through the physical breakdown of plant litter, thus providing more surface area for microbial colonization, and increased decay rates (Gosselink and Kirby, 1974; Fenchel, 1970). Recent studies have illustrated that *Littoraria irrorata*, a rasping detritivore, expedites the decomposition of *S. alterniflora* through facilitating fungal invasion on the wounds of live *S. alterniflora* leaves (Silliman and Newell, 2003). Additionally, the grazing of *L. irrorata* on fungal biomass (Silliman and Zieman, 2001) creates a positive feedback mechanism, where deposition of fecal pellets by *L. irrorata* further stimulates fungal biomass production (Silliman and Newell, 2003). Although, traditionally, herbivores were thought to play a minor role in limiting salt marsh primary production (Odum and Smalley, 1959; Teal, 1962), recent evidence suggests that consumers, such as *L. irrorata*, have the potential to significantly impact *S. alterniflora* production through this indirect interaction (Silliman and Zieman, 2001; Silliman and Bertness, 2002). Additionally, synergistic effects of climate change and grazing pressure may lead to ecosystem collapse in salt marshes (Silliman *et al.*, 2005), underlining the importance of understanding controls on herbivore production.

The ability of a system to recover after disturbance is often used as a measure to indicate ecosystem health (Costanza, 1992; Costanza *et al.*, 1998; Rapport *et al.*, 1998). As an emergent property of the ecosystem, resilience is influenced by the interaction of multiple factors and processes, thus providing an integrated measure of ecological status (Gunderson, 2000).

Stability, defined as the ability to recover to a steady state after disturbance, and resilience, defined as the return time, or recovery rate, to a steady state after disturbance (Grimm and Wissel, 1997), is described as the engineering definition of resilience (Holling, 1996). Implicit in this definition of resilience is the assumption of global stability, or a singular equilibrium state. In contrast, the concept of ecological resilience assumes multiple steady states, where resilience is defined as the amount of disturbance a system can take before re-organization to an alternate steady state (Holling, 1996). In the context of ecological restoration, where success is measured by the return of a system to pre-degradation conditions, the steady state is necessarily singular and is constrained by the objectives of the restoration. Thus, engineering resilience, or recovery rate to a steady state, is an appropriate measure of ecosystem health in a restored system.

As an application of the engineering resilience concept, measurements of recovery after experimental disturbances can be used to accurately reflect the underlying stress in salt marsh systems (Slocum and Mendelssohn, 2008). Additionally, this method provides insight into not only the present ecological status of the salt marsh, but also potential responses to future natural and anthropogenic disturbances before they occur (Underwood, 1989). Because sediment subsidy is an increasingly popular wetland remediation technique, there are a growing number of newly restored sediment subsidized marshes (Louisiana Coastal Area Beneficial Use of Dredged Material Program, 2006). Therefore, it is important to determine not only how resilience is maintained in older marshes, but also how the increasing number of young marshes will respond to disturbance.

1.4 Objectives

The overall goal of this research was to provide insight into the viability of sediment addition as a successful restoration technique and the sustainability of these restored systems over time.

Specific research questions include:

- (a) How are wetland functions influenced by various intensities of sediment addition?
- (b) Are wetlands, restored via sediment addition, functionally equivalent to natural wetlands, and what level of sediment addition results in functional equivalency?
- (c) What physico-chemical characteristics resulting from sediment addition influence ecological function?
- (d) How does resilience and stability of sediment subsidized salt marshes change over time?

I hypothesize that sediment additions, within a specific range, will restore productivity, decomposition and resilience to levels equivalent to natural marshes. However, beyond this range, additional sediment addition will result in a sediment subsidy threshold that will impede the attainment of functional equivalency. These questions and over-arching hypothesis are addressed in the following chapters:

Chapter two investigates the effects of sediment addition on above- and belowground net primary production of the dominant salt marsh grass *Spartina alterniflora*. Chapter three elucidates the effects of sediment addition on decomposition of belowground organic matter, and compares decomposition dynamics of root and rhizome tissues and cellulose. In chapter four, I examine the growth, survival and production of *Littoraria irrorata* exposed to different elevations within the sediment subsidized and reference marshes. Chapter five discusses the resilience and stability of sediment subsidized marshes of differing age, and chapter six provides overall conclusions.

1.5 Literature Cited

Abd. Aziz, S.A. and Newell, D.B. 1979. Microbial nitrogen transformations in the salt marsh environment. In Jeffries, R.L. and Davy A.J. editors, *Ecological processes in coastal environments*, Blackwell: Oxford, England.

- Alber, M., Swenson, E.M., Adamowicz, S.C. and Mendelssohn, I.A. 2008. Salt marsh dieback: an overview of recent events in the US. *Estuarine, Coastal and Shelf Science*, 80: 1–11.
- Barras, J., Beville, S., Britsch, D., Hartley, S., Hawes, S., Johnston, J., Kemp, P., Kinler, Q., Martucci, A., Porthouse, J., Reed, D., Roy, K., Sapkota, S. and Suhayda, J. 2003. Historical and projected coastal Louisiana land changes: 1978-2050. USGS Open File Report 03-334.
- Barras, J. A. 2006. Land area change in coastal Louisiana after the 2005 hurricanes—a series of three maps: U.S. Geological Survey Open-File Report 06-1274.
- Boesch, D., Mehta, A., Morris, J., Nuttle, W., Simenstad, C. and Swift, D. 1994. Scientific assessment of coastal wetland loss, restoration and management in Louisiana. *Journal of Coastal Research* special issue, 20: 1-103.
- Bradley, P.M. and Dunn, E.L. 1989. Effects of sulfide on the growth of 3 salt marsh halophytes of the southeastern United States. *American Journal of Botany*, 76: 1707-1713.
- Bricker-Urso, S., Nixon, S.W., Cochran, J.K., Hirschberg, D.J. and Hunt, C. 1989. Accretion rates and sediment accumulation in Rhode Island salt marshes. *Estuaries*, 12: 300-317
- Brown, C.E. and Pezeshki, S.R. 2007. Threshold for recovery in the marsh halophyte *Spartina alterniflora* grown under the combined effects of salinity and soil drying. *Journal of Plant Physiology*, 164: 274-282.
- Cahoon, D., Reed, D. and Day, J. 1995. Estimating shallow subsidence in microtidal salt marshes of the southeastern United States: Kaye and Barghoorn revisited. *Marine Geology*, 128: 1-9.
- Calloway, J.C. 1994. Sedimentation processes in selected coastal wetlands from the Gulf of Mexico and Northern Europe. Ph.D. Dissertation, Louisiana State University, Baton Rouge, LA.
- Costanza, R., 1992. Toward an operational definition of health. In Costanza, R., Norton, B., Haskell, B., editors. *Ecosystem Health, New Goals for Environmental Management*. Island Press, Washington, DC, USA. pp. 239–256.
- Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.J., Sutton, P. and van den Belt, M. 1998. The value of the world's ecosystem services and natural capital. *Ecological Economics*, 25: 3-15.
- Davis, S.E. III, Childers, D.L. and Noe, G.B. 2006. The contribution of leaching to the rapid release of nutrients and carbon in the early decay of wetland vegetation. *Hydrobiologia*, 569: 87-97.

- Day, J., Martin, J., Cardoch, L. and Templet, P. 1997. System functioning as a basis for sustainable management of deltaic ecosystems. *Coastal Management*, 25: 115–154.
- Day, J. W., G. P. Shaffer, L. D. Britsch, D. J. Reed, S. R. Hawes and D. R. Cahoon. 2000. Pattern and process of land loss in the Mississippi Delta: a spatial and temporal analysis of wetland habitat change. *Estuaries*, 23: 425-438.
- Day, J.W., Christian, R.R., Boesch, D.M., Yáñez-Arancibia, A., Morris, J., Twilley, R., Naylor, L., Schaffner, L. and Stevenson, C. 2008. Consequences of climate change on the ecogeomorphology of coastal wetlands. *Estuaries and Coasts*, 31: 477–491.
- DeLaune, R.D. and Patrick, W.H. Jr. 1979. Nitrogen and phosphorus cycling in a Gulf Coast salt marsh. In Kennedy, V.S., editor. *Estuarine perspectives*. Academic Press, New York, U.S.A. pp. 143-151.
- DeLaune, R. D., Reddy, C. N. and Patrick, W. H. Jr. 1981. Organic matter decomposition in soil as influenced by pH and redox conditions. *Soil Biology and Biochemistry*, 13: 533-534.
- DeLaune, R. D., Smith, C. J. and Patrick, W. H. Jr. 1983. Relationship of marsh elevation, redox potential, and sulfide to *Spartina alterniflora* productivity. *Soil Science Society of America*, 47: 930-935.
- DeLaune, R. D., Pezeshki, S. R., Pardue, J. H., Whitcomb, J. H. and Patrick, W. H. Jr. 1990. Some influences of sediment addition to a deteriorating salt marsh in the Mississippi River deltaic plain: A pilot study. *Journal of Coastal Research*, 6: 181-188.
- DeLaune, R.D., Patrick, W.H. Jr. and Smith, C.J. 1992. Marsh aggradation and sediment distribution along rapidly submerging Louisiana Gulf Coast. *Environmental Geology and Water Science*, 20: 57-64.
- Delaune, R. D., Jugsujinda, A., Peterson, G. W. and Patrick, W. H. Jr. 2003. Impact of Mississippi River freshwater reintroduction on enhancing marsh accretionary processes in a Louisiana estuary. *Estuarine, Coastal and Shelf Science*, 58: 653-662.
- DeLaune, R.D. and Pezeshki, S.R. 2003. The role of soil organic carbon in maintaining surface elevation in rapidly subsiding U.S. Gulf of Mexico coastal marshes. *Water, Air and Soil Pollution*, 3: 167-179.
- Dokka, R.K. and Shinkle, K.D. 2004. Rates of vertical displacement at benchmarks in the lower Mississippi valley and the northern Gulf coast. NOAA Technical Report NOS/NGS 50.
- Dokka, R.K. 2006. Modern-day tectonic subsidence in coastal Louisiana. *Geology*, 34: 281-284.

- Edwards, K.R. and Mills, K.P. 2005. Aboveground and belowground productivity of *Spartina alterniflora* (Smooth Cordgrass) in natural and created Louisiana salt marshes. *Estuaries*, 28: 252-265.
- Fenchel, T. 1970. Studies on the decomposition of organic detritus derived from the turtle grass *Thalassia testudinum*. *Limnology and Oceanography*, 15: 14-20.
- Good, R. E., Good, N. F. and Frasco, B. R. 1982. A review of primary production and decomposition dynamics of the belowground marsh component. *Estuarine Comparisons*, 139-157.
- Gosselink, J.G. and Kirby, C.J. 1974. Decomposition of salt marsh grass *Spartina alterniflora* Loisel. *Limnology and Oceanography*, 19: 825-832.
- Grimm, V. and Wissel, C. 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia*, 109: 323–334.
- Gunderson, L. 2000. Ecological resilience – in theory and application. *Annual Review of Ecology and Systematics*, 31: 425–39.
- Guntenspergen, G.R., Cahoon, D.R., Grace, J., Steyer, G.D., Fournet, S., Townson, M.A. and Foote, A.L. 1995. Disturbance and recovery of the Louisiana coastal marsh landscape from the impacts of Hurricane Andrew. *Journal of Coastal Research* (Special Issue) 21: 324-339
- Hackney, C.T. and Cleary, W.J. 1987. Salt marsh loss in southeaster North Carolina lagoons: importance of sea level rise and human activities. *Journal of Coastal Research*, 3: 93-97
- Hatton, R.S., DeLaune, R.D. and Patrick, W. H. Jr. 1983. Sedimentation, accretion, and subsidence in marshes of Barataria Basin, Louisiana. *Limnology and Oceanography*, 18: 494-502.
- Harris, J.A. and Hobbs, R.J. 2001. Clinical practice for ecosystem health: the role of ecological restoration. *Ecosystem Health*, 7: 195-202.
- Henriksen, K. and Jensen, A. 1979. Mineralization in a salt marsh ecosystem dominated by *Halimione portulacoides*. In Jeffries, R.L. and Davy, A.J., editors. *Ecological processes in coastal environments*, Blackwell: Oxford, England.
- Holling, CS. 1996. Engineering resilience vs. ecological resilience. In Schulze, P.C., editor. *Engineering Within Ecological Constraints*, pp. 31–43. Washington, DC: National Academy.
- Houghton, R.A. and Woodwell, G.M. 1980. The Flax Pond ecosystem study: exchanges of carbon dioxide between a salt marsh and the atmosphere. *Ecology*, 61: 1434-1445.

- IPCC. 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). Solomon, S., Qin, D., Manning, M., Marquis, M., Averyt, K., Tignor, M.M.B., Miller, H.L. Jr., and Chen, Z., editors. Cambridge University Press, UK.
- Jelgersma, S. 1996. In Milliman, J.D. and Haq, B.U., editors. *Sea Level and coastal subsidence. Causes, consequences, and strategies*. Kluwer, Dordrecht. pp. 47-62.
- Kirby, C. J. 1971. The annual net primary production and decomposition of the salt marsh grass *Spartina alterniflora* Loisel. in the Barataria Bay estuary of Louisiana. Ph.D. Dissertation. Louisiana State University, Baton Rouge. 74 p.
- Koch, M.S. and Mendelsohn, I.A., 1989. Sulphide as a soil phytotoxin: differential responses in two marsh species. *Journal of Ecology*, 77: 565-578.
- Kruczynski, W. L., Subrahmanyam, C. B. and Drake, S. H. 1978. Studies on the plant community of a north Florida salt marsh. *Bulletin of Marine Science*, 28: 707-715.
- Lindstedt, D.M., Swenson, E.M., Reed, D., Twilley, R. and Mendelsohn, I.A. 2006. Marsh dieback technical synthesis report. Technical Report, Coastal Restoration Division, Louisiana Department of Natural Resources.
- Linhurst, R. A. 1979. The effect of aeration on the growth of *Spartina alterniflora* Loisel. *American Journal of Botany*, 66: 685-691.
- Linhurst, R.A. 1980. A growth comparison of *Spartina alterniflora* Loisel. Ecophenes under aerobic and anaerobic conditions. *American Journal of Botany*, 67: 883-887.
- Louisiana Coastal Area-Beneficial Use of Dredged Material Program, 2006. Supplemental environmental impact statement scoping program. United States Army Core of Engineers, Louisiana Department of Natural Resources.
- Mackey, A.P. and Smail, G. 1996. The decomposition of mangrove litter in a subtropical mangrove forest. *Hydrobiologia*, 332: 93-98.
- Materne, M.D. and Mendelsohn, I.A. 2006. Beneficial use of hydraulically dredged sediment-slurries for wetland restoration: II. Spatial, hydrologic and vegetative assessment. Governor's Applied Coastal Research and Development Program.
- McCaffrey, R.J. and Thompson, J. 1980. A record of the accumulation of sediment and trace metals in a Connecticut salt marsh. *Advances in Geophysics*, 22: 165-236.
- McKee, K.L., Mendelsohn, I.A. and Materne, M.D. 2004. Acute salt marsh dieback in the Mississippi River Deltaic Plain: a drought-induced phenomenon? *Global Ecology and Biogeography*, 13: 67-73.

- Mendelssohn, I.A. 1979. The influence of nitrogen level, form, and application method on the growth response of *Spartina alterniflora* in North Carolina. *Estuaries*, 2: 106-112.
- Mendelssohn, I. A. and McKee, K. L. 1988. *Spartina alterniflora* die-back in Louisiana: Time-course investigation of soil waterlogging effects. *Journal of Ecology*, 76: 509-521.
- Mendelssohn, I. A. and Morris, J.T. 2000. Eco-physiological constraints on the primary productivity of *Spartina alterniflora*. In *Concepts and Controversies*. Elsevier Press.
- Mendelssohn, I.A. and Kuhn, N.L. 2003. Sediment subsidy: effects on soil-plant responses in a rapidly submerging coastal salt marsh. *Ecological Engineering*, 21: 115-128.
- Mitrovica, J.X., Gornex, N. and Clark, P.U. 2009. The sea-level fingerprint of West Antarctic collapse. *Science*, 323: 753.
- Mitsch, W.J and Wilson, R.F. 1996. Improving the success of wetland creation and restoration with know-how, time and self-design. *Ecological Applications*, 6: 77-83.
- Mitsch, W.J., Wu, X., Nairn, R.W., Weihe, P.E., Wang, N., Deal, R. and Boucher, C.E. 1998. Creating and restoring wetlands: a whole-ecosystem experiment in self-design. *Bioscience*, 48: 1019-1030.
- Montagna, P. A. and Ruber, E. 1980. Decomposition of *Spartina alterniflora* in different seasons and habitats of a northern Massachusetts salt marsh, and a comparison with other Atlantic regions. *Estuaries*, 3: 61-64.
- Morton, R.A., Buster, N. and Krohn, M.D. 2002. Subsurface controls on historical subsidence rates and associated wetland loss in south-central Louisiana. *Gulf Coast Association of Geological Societies*, 52: 767-778.
- Morris, J.T. and Bradley, P.M. 1999. Effects of nutrient loading on the carbon balance of coastal wetland sediments. *Limnology and Oceanography*, 44: 699-702.
- Nyman, J.A., DeLaune, R.D. and Patrick, W.H. Jr. 1990. Wetland soil formation in the rapid subsiding Mississippi River Deltaic Plain: mineral and organic matter relationships. *Estuarine, Coastal and Shelf Science*, 31: 57-69.
- Nyman, J.A., DeLaune, R.D., Roberts, H.H. and Patrick, W.H. Jr. 1993. Relationship between vegetation and soil formation in a rapidly submerging coastal marsh. *Marine Ecology Progress Series*, 96: 296-279.
- Nyman, J.A., Walters, R.J., DeLaune, R.D. and Patrick, W.H. Jr. 2006. Marsh vertical accretion via vegetative growth. *Estuarine, Coastal and Shelf Science*, 69: 370-380.

- Odum, E.P. and Smalley, A.E. 1959. Comparison of population energy of an herbivorous and a deposit-feeding invertebrate in a salt marsh ecosystem. *Proceedings of the National Academy of Science*, 45: 617-622.
- Odum, H.T. 1989. Ecological engineering and self-organization. In Mitsch, W.J. and Jorgenson, S.E., editors. *Ecological Engineering*. John Wiley and Sons, New York, U.S.A. pp. 79-101.
- Patrick, W.H. Jr. and DeLaune, R.D. 1972. Characterization of the oxidized and reduced zones in flooded soil. *Proceedings of the Soil Science Society of America*, 36: 573-576.
- Penland, S. and Ramsey, K.E. 1990. Relative sea level rise in Louisiana and the Gulf of Mexico 1908-1988. *Journal of Coastal Research*, 6: 323-342.
- Pfeffer, W.T., Harper, J.T. and O'Neel, S. 2008. Kinematic constraints on glacier contributions to 21st century sea level rise. *Science*, 321: 1340-1343.
- Ramsey, K.E. and Penland, S. 1992. Sea level rise and subsidence in Louisiana and the Gulf of Mexico. In Williams, S.J., Cichon, H.A., Westpal, K. and Ramsey, K., editors. *Representative publications from the Louisiana barrier island erosion study*. U.S. Department of the Interior, U.S.G.S. Open File Report pp. 92-530.
- Rapport, D.J., Costanza, R. and McMichael, A.J. 1998. Assessing ecosystem health. *TREE*, 13: 397-402.
- Reddy, K.R. and Patrick, W.H., Jr. 1975. Effect of alternate aerobic and anaerobic conditions on redox potential, organic matter decomposition and nitrogen loss in a flooded soil. *Soil Biology and Biochemistry*, 7: 87-94.
- Rohling, E.J., Grant, K., Hemleben, C.H., Siddall, M., Hoogakker, B.A.A., Bolshaw, M. and Kucera, M. 2008. High rates of sea level rise during the last interglacial period. *Nature Geoscience*, 1: 38-42.
- Rozas, L.P. and Minello, T.J. 2001. Marsh terracing as a wetland restoration tool for creating fishery habitat. *Wetlands*, 21: 327-341.
- Rybczyk, J.M. and Cahoon, D.R. 2002. Estimating the potential for submergence for two wetlands in the Mississippi River Delta. *Estuaries*, 25: 985-998.
- Schrift, A.M., Mendelsohn, I.A. and Materne, M.D. 2008. Salt marsh restoration with sediment-slurry amendments following a drought-induced large-scale disturbance. *Wetlands*, 28: 1071-1085.
- Silliman, B.R. and Zieman, J.C. 2001. Top-down control of *Spartina alterniflora* production by periwinkle grazing in a Virginia salt marsh. *Ecology*, 82: 2830-2845.

- Silliman, B.R. and Bertness, M.D. 2002. A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Science*, 99: 10500-10505.
- Silliman, B.R. and Newell, S.Y. 2003. Fungal farming in a snail. *Proceedings of the National Academy of Science*, 100: 15643-15648.
- Silliman, B.R., van de Koppel, J., Bertness, M.D., Stanton, L.E. and Mendelssohn, I.A. 2005. Drought, snails and large-scale die-off of southern U.S. salt marshes. *Science*, 310: 1803-1806.
- Slocum, M.G., Mendelssohn, I.A. and Kuhn, N.L. 2005. Effects of sediment slurry enrichment on salt marsh rehabilitation: plant and soil responses over seven years. *Estuaries*, 28: 519-528.
- Slocum, M.G. and Mendelssohn, I.A. 2008. Use of experimental disturbances to assess resilience along a known stress gradient. *Ecological Indicators*, 8: 181-190.
- Stone, G.W. and Finkle, C.W. 1995. Preface. *Journal of Coastal Research*, Special Issue, 21: 1-5.
- Swenson, E.M. and Turner, R.E. 1987. Spoil banks: effects on a coastal marsh water-level regime. *Estuarine and Coastal Shelf Science*, 24: 599-609.
- Tate, R.L. 1979. Effect of flooding on microbial activities in organic soils: carbon metabolism. *Soil Science*, 128: 267-272.
- Teal, J.M. 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology*, 43: 614-624.
- Turner, R. E. 1985. Coastal land loss, canals, and canal levee relations in Louisiana. US Fish and Wildlife Service Biological Program Report 85(14).
- Turner, R. E. 1997. Wetland loss in the Northern Gulf of Mexico: multiple working hypotheses. *Estuaries*, 20: 1-13.
- Turner, R.E., Swenson, E.M. and Milan, C.S. 2001. Contrasting organic and inorganic content in recently accumulated salt marsh sediments. In Weinstein, M. and Kreeger, D.D., editors. *Concepts and controversies in tidal marsh ecology*, Kluwer Academic Publishers: Dordrecht, The Netherlands. pp. 583-595.
- Turner, R.E., Swenson, E.M., Milan, C.S., Lee, J.M. and Oswald, T.A. 2004. Below-ground biomass in healthy and impaired marshes. *Ecological Research*, 19: 29-35.
- Turner, R. E., Baustian, J. J., Swenson, E. M. and Spicer, J.S. 2006a. Wetland sedimentation from Hurricanes Katrina and Rita. *Science*, 314: 449-452.
- Turner, R.E., Milan, C.S. and Swenson, E.M. 2006b. Recent volumetric changes in salt marsh soils. *Estuarine, Coastal and Shelf Science*, 69: 352-359.

- Underwood, A.J. 1989. The analysis of stress in natural populations. *Biological Journal of the Linnean Society* 37: 51-78.
- Valiela, I. and Teal, J.M. 1979. Inputs, outputs and interconversions of nitrogen in a salt marsh ecosystem. In Jeffries, R.L. and Davy, A.J., editors. *Ecological processes in coastal environments*, Blackwell: Oxford, England.
- Wiegert, R.G. 1979. Ecological processes characteristics of coastal *Spartina marshes* of the southeastern U.S.A. In Jeffries, R.L. and Davy, A.J., editors. *Ecological processes in coastal environments*, Blackwell Publishers: Oxford, England. pp. 467-490.
- Wilsey, B. J., McKee, K. L. and Mendelssohn, I. A. 1992. Effects of increased elevation and macro- and micronutrient additions on *Spartina alterniflora* transplant success in salt-marsh dieback areas in Louisiana. *Environmental Management*, 16: 505-511.
- Woodwell, G.M., Houghton, R.A., Hall, C.A.S., Whitney, D.E., Moll, R.A. and Juers, D.W. 1979. The Flax Pond ecosystem study: the annual metabolism and nutrient budgets of a salt marsh. In Jeffries, R.L. and Davy, A.J., editors. *Ecological processes in coastal environments*, Blackwell Publishers: Oxford, England. pp. 491-511.
- Zedler, J.B. and Callaway, J.C. 1999. Tracking wetland restoration: Do mitigation sites follow desired trajectories? *Restoration Ecology*, 7: 69-73.

CHAPTER 2

IMPACTS OF SEDIMENT ADDITION ON ABOVE- AND BELOWGROUND PRIMARY PRODUCTION

2.1 Introduction

The deterioration of coastal wetlands is a significant concern in Louisiana's Mississippi River Delta complex, where wetland loss occurs at a rate of $77 \text{ km}^2 \cdot \text{y}^{-1}$ (Barras *et al.*, 2003). A multitude of factors have contributed to the decline of these vegetated systems, including canal dredging, levee construction, geological subsidence, and eustatic sea level rise (Boesch *et al.*, 1994; Jelgersma, 1996; Turner, 1997; Day *et al.*, 2000). Additionally, severe weather events, such as hurricanes and drought, have been linked to the acute and sudden loss of coastal wetlands (McKee *et al.*, 2004; Alber *et al.*, 2008; Day *et al.*, 2008). For example, in 2000 a severe drought caused the sudden dieback of over 100,000 ha of *S. alterniflora* salt marsh in southern Louisiana (McKee *et al.*, 2004; Lindstedt *et al.*, 2006; Alber *et al.*, 2008). Although some areas recovered after this expansive disturbance, in many cases, salt marshes were converted to unvegetated mudflats that eventually subsided. Materne and Mendelssohn (2006) documented up to a 15 cm decrease in elevation at dieback-affected areas relative to unaffected salt marshes. Thus, drought-induced subsidence altered the natural hydrology of the affected areas, resulting in longer periods of inundation (Materne and Mendelssohn, 2006) accompanied by low redox potentials, high sulfide concentrations and minimal vegetative recovery (Schrift *et al.*, 2008).

To ameliorate the effects of excessive inundation, hydraulically dredged sediments were added to a dieback-affected marsh, with the notion that an increase in elevation would improve soil drainage and ultimately vegetative growth (Mendelssohn and Seneca, 1980). The use of hydraulically dredged, fine-grain sediments can decrease flood duration (Materne and Mendelssohn, 2006) and increase bulk density and soil nutrient concentrations (Mendelssohn and

Kuhn, 2003), resulting in greater aboveground biomass, plant density and cover (Mendelssohn and Kuhn, 2003; Slocum *et al.*, 2005; Schrifft *et al.*, 2008). However, the effect of sediment restoration of coastal marshes on ecological function has received little attention (Edwards and Mills, 2005).

The goals of restoration are to return a degraded system to pre-degradation conditions based on functional ecological services, which depend not only on ecological structure, but also on ecosystem function. Quality ecological functions and resulting services have not always been present after successful restoration of structural characteristics (Zedler and Callaway, 1999; Rozas and Minello, 2001). Therefore, this study was designed to enhance our knowledge of the effects of sediment addition on an important ecological function, primary production.

As the principle contributor of organic matter to salt marsh trophic systems, primary production plays a pivotal role in the overall productivity of the salt marsh (Teal, 1962; Wiegert, 1979; Woodwell *et al.*, 1979; Houghton and Woodwell, 1980). Additionally, primary production significantly influences organic matter accumulation in salt marshes and is a critical factor controlling elevation change (McCaffrey and Thompson, 1980; Hatton *et al.*, 1983; DeLaune *et al.*, 1990; Nyman *et al.*, 1993; Calloway, 1994; Turner *et al.*, 2001; Rybczyk and Cahoon, 2002; DeLaune and Pezeshki, 2003; Turner *et al.*, 2004). As such, the restoration of primary production is of paramount importance in the successful restitution of ecosystem function and sustainability. However, Edward and Mills (2005) examined the functional trajectories of above- and belowground production in sediment subsidized marshes, and found that the restored marshes were not functionally equivalent to natural marshes.

In an effort to improve our ability to successfully restore marshes to functional equivalency with natural marshes, I have examined the physico-chemical factors that control

primary production along an elevation gradient resulting from differential sediment addition. This research addressed the following questions: 1) Does sediment-slurry addition restore primary production to natural marsh equivalency? 2) If so, what level of sediment addition results in optimum primary production? 3) How does sediment addition affect the physico-chemical character of the marsh soil? 4) What abiotic factors influence primary production at different elevations within the marsh? Based on previous studies (Mendelssohn and Kuhn, 2003; Slocum *et al.*, 2005; Schrifft *et al.*, 2008), I hypothesized that sediment addition would ameliorate the impacts of excessive inundation, resulting in greater primary production of *Spartina alterniflora*. However, I also hypothesized that a sediment addition threshold would limit primary production at elevations where inundation is relatively infrequent (Edwards and Mills, 2005; Slocum *et al.*, 2005; Schrifft *et al.*, 2008).

2.2 Materials and Methods

2.2.1 Site Description and Experimental Design

The study site (29° 10.58'N and 90° 14. 23'W) is located in Terrebonne Basin, a part of the Mississippi River Deltaic Plain. The specific area of interest was a submerging, degraded salt marsh located on the west bank of Bayou Lafourche near Leeville, LA. This area was affected by sudden marsh dieback (SMD), which was linked to extreme drought conditions documented during the summer of 2000 (McKee *et al.*, 2004; Lindstadt *et al.*, 2006; Alber *et al.*, 2008). In addition to the dieback marsh, natural marshes, unaffected by the SMD event, occur throughout the area. These ambient marshes were dominated by *S. alterniflora* and interspersed with *Salicornia virginica*.

Two years following the disturbance (2002), the dieback site was divided into four cells through the construction of small earthen dikes. The cells were hydraulically connected through

culverts and breaks in the levees that allowed for tidal exchange. Hydraulically dredged sediments from adjacent Bayou Lafourche were pumped into each cell resulting in four separate sediment subsidy treatment blocks (Figure 2.1). The sediment slurries were comprised of approximately 20-30 % solids and 70-80 % water by volume. Addition of differential volumes of sediments within each replicate block resulted in four separate sediment subsidy treatment levels (STLs): 1) High STL: 28-36 cm above ambient marsh, 2) Medium STL: 20-25 cm above ambient marsh, 3) Medium-Vegetated (Medium-Veg) STL: areas with 100 % vegetative cover in the fall of 2003 and an average elevation of 20 cm above ambient marsh and 4) Low STL: 13-18 cm above ambient marsh. Sediments in the sediment addition zone were comprised of 8.94 ± 0.20 % sand, 42.89 ± 0.54 % silt, 47.21 ± 0.60 % clay 10.90 ± 3.64 % organic matter and (Schrift *et al.*, 2008).

In addition to the sediment treatment areas, reference areas, which did not receive sediment subsidy, were also included in the experimental design (Figure 2.1). Two types of reference sites were used, each replicated twice: 1) an ambient reference marsh, which neither died back nor received sediment (2-5 cm above the ambient benchmark) and 2) a degraded reference marsh, which died back but did not receive sediment (-0.5 - -2.5 cm below the ambient benchmark). These elevations, in addition to the STL elevations, can all be related to the North American Vertical Datum of 1988 (NAVD 88) by adding 29.78 cm to the marsh surface elevations. Sediments in the reference zone (ambient and degraded) were comprised of 7.71 ± 2.55 % sand, 34.88 ± 1.77 % silt, 49.74 ± 10.25 % clay and 27.52 ± 1.24 % organic matter (Schrift *et al.*, 2008).

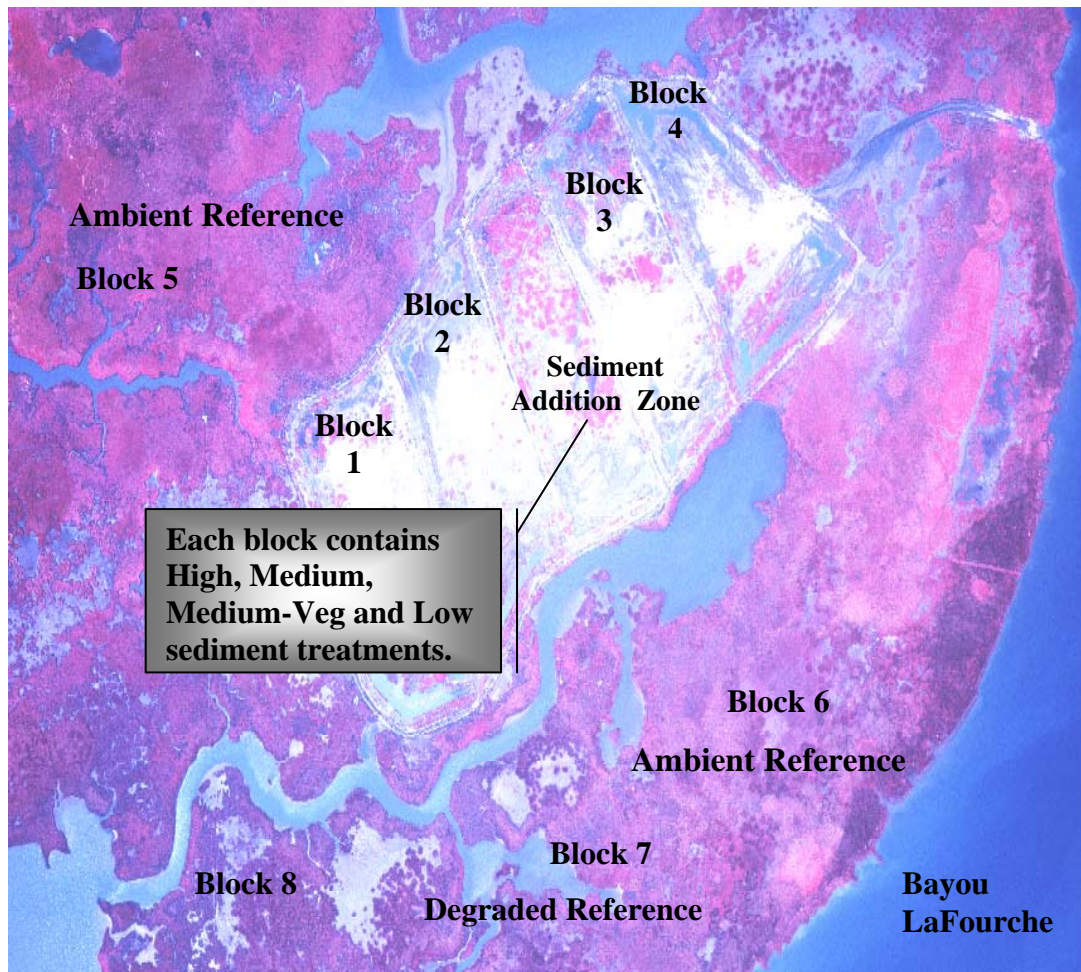


Figure 2.1. Sediment subsidy treatment site (blocks 1-4) and references (blocks 5-8).

2.2.2 Primary Production

Although other important primary producers such as benthic and epibenthic algae may respond differently to sediment addition, this study focused on the production of an emergent macrophyte, *Spartina alterniflora*, the dominant salt marsh grass and a primary contributor to organic matter production. Net primary production was estimated by measuring the change in live and dead biomass between seasonal sampling intervals (every three months) over a period of two years (2005-2007) (Smalley, 1958). Above- and belowground production were measured separately, and total net primary production (total NPP) was estimated as the sum of above- and belowground production. The root and rhizome to shoot ratio (R+R:S) was calculated using the

mean annual live biomass of belowground (roots + rhizomes) and aboveground (stems and leaves) materials. The mean annual above- and belowground production estimates and maximum live biomass values were used to calculate turnover rates at each sediment treatment level and reference block ($\text{NPP}/\text{max live biomass} = \text{y}^{-1}$).

Aboveground biomass was collected by harvesting all vegetation within a 0.25 m² quadrat randomly located within each STL and reference block. Biomass was rinsed free of sediment, separated into live and dead components and oven dried to a constant weight at 60 °C for one week (Mendelssohn and Marcellus, 1976). Belowground production was measured using the in-growth core method described by Gallagher *et al.* (1984). At the beginning of the study (April 2005), eight in-growth cores were created at each STL and reference block by replacing existing soil (7.5 cm x 30 cm soil volume) with root and rhizome-free sediment collected from adjacent unvegetated mudflats. The in-growth cores were retrieved seasonally and rinsed over a 1 mm² sieve, and all live roots, rhizomes and dead organic matter were separated and dried to a constant weight at 60 °C for one week.

2.2.3 Soil Physico-Chemical Characterization

Several soil physical and chemical properties were measured in 2005 and 2006. Sampling procedures were identical in 2005 and 2006, with the exception of sulfide collection, which only occurred in 2006. A core (5 cm diameter x 10 cm long) was taken at each STL and reference plot to measure soil bulk density, organic matter content, percent moisture and electrical conductivity. After collection, the cores were analyzed for wet weight, dried at 65 °C, and weighed again to determine bulk density and percent moisture. A portion of the dried soil was also used to measure electrical conductivity and organic matter content. To determine electrical conductivity, 5 g of dried soil was mixed vigorously with 30 ml of distilled water for one hour.

The mixture was then centrifuged at 2817 *g* for 5 minutes, and the supernatant was analyzed for electrical conductivity on a Cole Parmer 19820-00 meter. To determine organic matter content, approximately 2-3 grams of dry soil was treated with 1N HCl until all inorganic carbonates were volatilized. The soil was then analyzed for percent organic matter through loss on ignition at 550 °C in a Fisher Isotherm combustion oven (Programmable Forced Draft Furnaces, model 10-750-126) (Nelson and Sommers, 1996).

A second soil core (5 cm diameter x 15 cm long) was simultaneously taken at each STL and reference block to measure soil pH (moist sediment), soil extractable nutrients and other elements (NH₄-N, NO₃-N, P, Fe, K, Mg, Mn, Na, and S) The soil cores were immediately placed on ice in the field and transported back to the laboratory at Louisiana State University, where they were homogenized. After homogenization, several soil aliquots were collected to perform the following extractions: NH₄-N and NO₃-N (2 M KCl (Bremner and Kenney, 1966)); P (Bray-2 (Byrnside and Sturgis, 1958)); Ca, K, Mg and Na (ammonium acetate (Thomas, 1982)); and Fe and Mn (DTPA (Lindsay and Norvell, 1978)). Following extraction, NH₄-N and NO₃-N samples were filtered through a 0.45 µm filter and measured on a segmented flow AutoAnalyzer (Flow Solution IV AutoAnalyzer, O-I Analytical, USA). The remaining extracts were measured with an inductively coupled argon plasma emission spectrometer (ICP) (SpectroCiros CCE, Spectro Analytical Instruments, Germany).

Redox potential was also measured during the same sampling events using bright platinum electrodes, a calomel reference electrode and a portable Cole-Parmer digital pH-mV meter. Three platinum electrodes were placed 15 cm below the soil surface at each STL replicate, and the average of the three readings was used in statistical analysis.

An additional soil core was taken in February 2006 to measure soil sulfide concentrations. The cores (5 cm diameter x 10 cm long) were taken from each treatment replicate and immediately placed in a centrifuge tube (500 ml) containing air-tight septa. The core was purged with nitrogen gas for 2 minutes to maintain an anoxic environment and then stored on ice. Once the cores were returned to the laboratory, they were centrifuged at 2817 g for 20 minutes to extract porewater from the soil. The supernatant was decanted, stabilized with an anti-oxidant buffer and analyzed for total soluble sulfides (Lazar Model IS-146 sulfide electrode, Lazar Research Laboratories, Los Angeles, CA).

2.2.4 Statistical Analysis

The design of this study was a randomized incomplete block design (6 treatment levels, $n = 2, 4$) (Figure 2.1). The incomplete designation arises from the fact that not all treatment levels are found in every replicate block. For example, the four blocks containing the sediment addition treatments do not contain reference treatments, and the reference blocks do not contain sediment addition treatments.

There was no significant interaction between time, elevation and above- versus belowground production ($p < 0.2609$). Additionally, there was no significant interaction between time and elevation ($p < 0.7452$). Thus, in both years, 2005-2006 and 2006-2007, sediment addition had the same effect on above- and belowground production. Therefore, the mean annual total NPP (2005-2007) was used in statistical analyses to test the effect of sediment addition on primary production. I used one-way mixed model ANOVAs to test the effects of elevation on 1) total above- and belowground production and 2) the ratio of below and aboveground biomass, with sediment treatment level as the fixed effect and block as the random effect for both models. Two-way mixed model ANOVAs were used to test for interactive effects of 1) time on

differences between above- and belowground production, and 2) elevation and differences in above- and belowground turnover rates. In all two-way ANOVA tests, time or sediment treatment level were set as fixed effects, with block and corresponding block by time or elevation as random effects, depending on the parameter of interest.

To maintain consistency, individual soil variables were averaged over the two year period for principle component analysis, multiple regression and ANOVA tests. Soil physical and chemical analytes (mean of two year samples) were consolidated into composite variables using principle component analysis (PCA). Only principle components (PCs) with eigenvalues > 1 were used for subsequent analyses. To determine the effect of sediment subsidy on the rotated factor scores, I used a one-way mixed model ANOVA, with sediment subsidy as the fixed effect and block as the random effect. Additionally, I performed multiple regression analyses, with sediment treatment level and PCA factor scores as independent variables and either above- or belowground production as dependent variables to determine which environmental parameters most influenced primary production. Slope parameters were entered into the models through stepwise selection method (significance level $p < 0.15$). To determine what soil parameters influenced inter-annual variability (time x above- versus belowground interaction), I used a one-way mixed model ANOVA to test for differences in individual soil variables between 2005 and 2006 samples.

For all statistical tests, normality and homogeneity of variance were determined by using the Shapiro-Wilks test, and box-plots. Natural log and square root transformations were used to improve normality only in the PCA. Pairwise comparisons were made using Fisher's Protected LSD tests. All statistical tests were performed using the MIXED, FACTOR, or REG procedures of SAS 9.1.2 unless otherwise noted (SAS Institute Inc., 2004).

2.3 Results

2.3.1 Primary Production

Above- and belowground production rates were equivalent in the first year of sampling (2005-2006). However, over time belowground production significantly surpassed aboveground production, and was higher at all elevations in the reference and restored marshes (Figure 2.2). Additionally, sediment addition had a significant effect on the ratio of below- to aboveground biomass (R+R:S) ($p < 0.0045$), with the highest ratios in the degraded (30:1) and High STL (42:1) (Figure 2.3). The R+R:S ratio decreased at moderate elevations, and ranged from 0.62 to 0.88 (Figure 2.3).

Sediment addition also had a significant effect on above- and belowground production (Figure 2.3). Moderate levels of sediment addition restored above- and belowground production to natural marsh production rates. Additionally, areas of moderate sediment addition (Low and Medium-Veg STLs) and the natural ambient marsh had significantly higher above- and belowground production compared to the degraded marsh and High and Medium STLs (Figure 2.3). Aboveground net primary production (NPP) ranged from 642.0-841.2 $\text{g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ and belowground NPP ranged from 972.0-1469 $\text{g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ in areas of moderate elevation.

Mean turnover rates, calculated as the ratio of above- or belowground NPP to maximum live biomass, were $1.0\cdot\text{y}^{-1} \pm 0.12$ and $1.2\cdot\text{y}^{-1} \pm 0.09$ for above- and belowground materials, respectively. There was a significant interaction between above- and belowground turnover rates and sediment addition (Figure 2.4). Turnover rates of above- and belowground materials were equivalent except at the degraded reference, where aboveground turnover was significantly higher than belowground turnover. Furthermore, aboveground turnover at the degraded reference

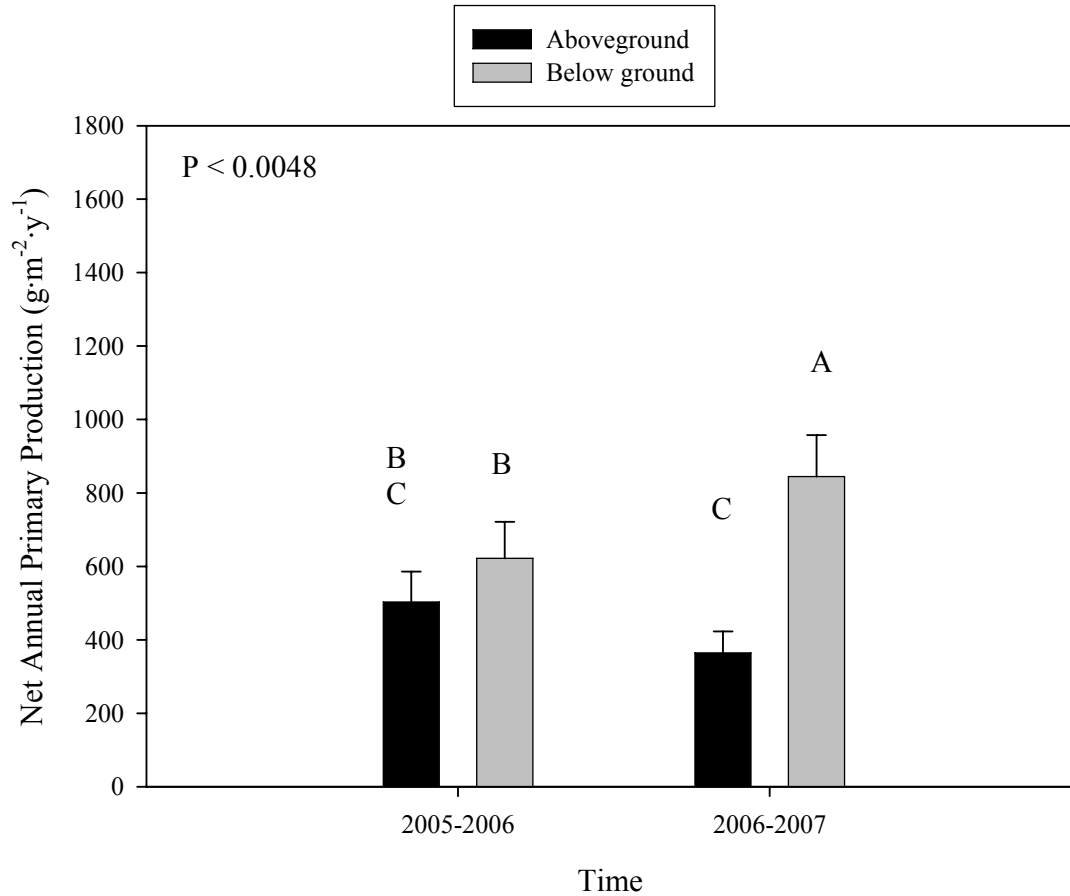


Figure 2.2. Interactive effect of time and above- versus belowground production. Error bars represent standard errors, and different letters denote significantly different means (Fisher's Protected LSD $p < 0.05$).

was significantly higher than turnover rates at all other STLs. In contrast, belowground turnover rates were not significantly affected by sediment addition (Figure 2.4).

There was no statistically significant difference between root and rhizome production ($p < 0.3153$, $701.9 \pm 107.6 \text{ g} \cdot \text{m}^{-2}$ and $786.3 \pm 116.6 \text{ g} \cdot \text{m}^{-2}$, respectively); however, live rhizome biomass exceeded live root biomass at all elevations in the restored and reference marshes. The average ratio of live rhizome to live roots across all STLs was 1.75, and live rhizomes accounted for 60% of the total live belowground biomass (roots+rhizomes) over the two year period.

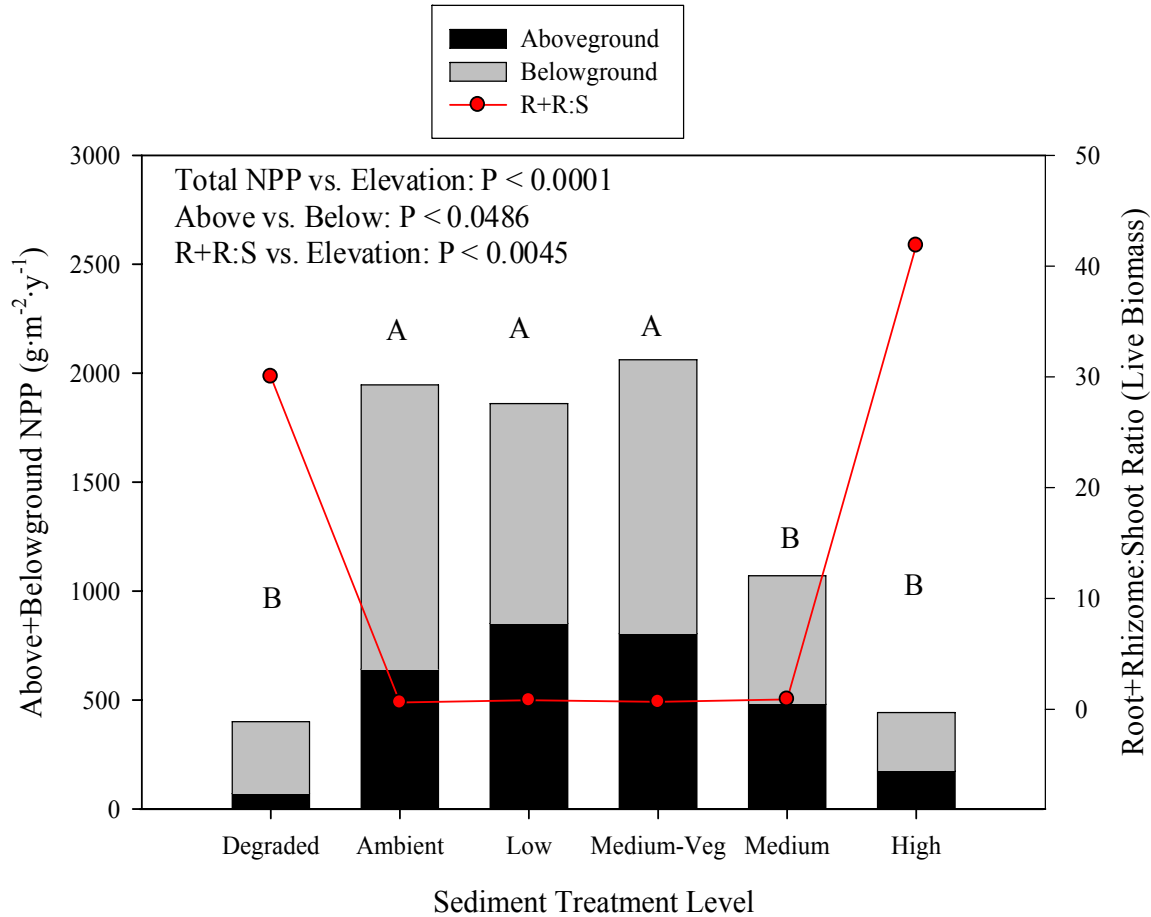


Figure 2.3. Effect of sediment addition on total *S. alterniflora* production (Bars = above+belowground NAPP), as well as ratios of below versus aboveground live biomass (line=R+R:S ratio). Different letters represent significantly different means, with respect to the effect of sediment addition on total production ($p < 0.0001$) (Fisher's Protected LSD $p < 0.05$). Shading denotes above- or belowground production, which is significantly different at all STLs ($p < 0.0486$). Red line represents root +rhizome: shoot ratio which is significantly higher at the degraded and High STL compared to all other STLs ($p < 0.0045$).

2.3.2 Soil Physico-Chemical Characteristics

The physico-chemical parameters characterizing the marsh soil were highly intercorrelated, and were combined into two principle components (PCs) that explained 89 % of the variability in the soil dataset (Table 2.1). The two PCs describing soil variables included a soil moisture/salinity component (PC1), an iron/phosphorus component (PC2). PC1 (Soil Moisture/Salinity) was loaded with parameters that commonly characterize flooded conditions, such as increased % moisture, ammonium, % organic matter, and sulfides and decreasing redox

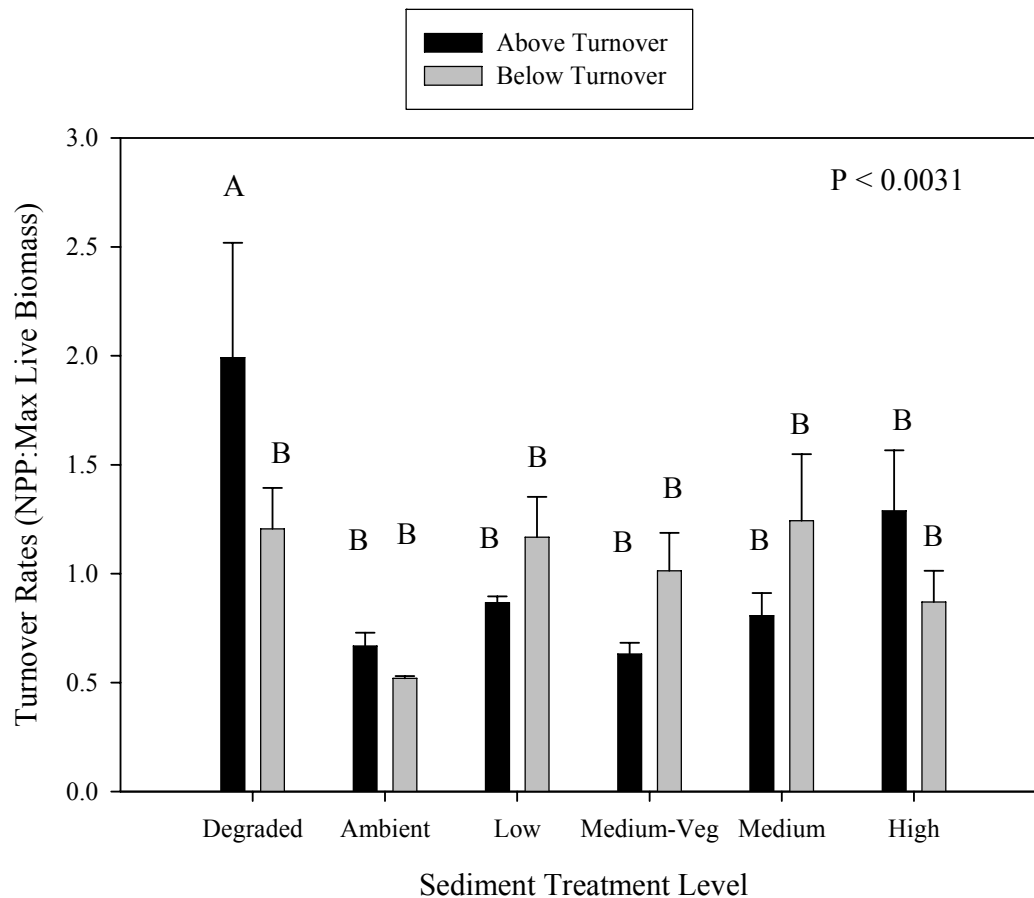


Figure 2.4. Turnover rates of above- and belowground materials at different levels of sediment addition. Error bars represent standard errors. Different letters represent significantly different means (Fisher's Protected LSD, $p < 0.05$).

potential and bulk density. Additionally, PC1 (Soil Moisture/Salinity) was also positively loaded with soil variables that are associated with increasing salinity, such as conductivity, magnesium, potassium, sodium, and sulfur. This PC explained 79 % of the variance in the soil dataset. The second PC (Fe/P) was positively loaded with iron and phosphorus and explained 10 % of the variance. Although manganese was negatively associated with PC1, it also had a high positive loading onto PC2 (Fe/P), suggesting that as iron and phosphorus concentrations increased, manganese concentrations increased as well (Table 2.1).

Sediment addition had a significant effect on the physico-chemical condition of the soil (Figures 2.5.1-2). Soil moisture and salinity (PC1) significantly decreased with increasing

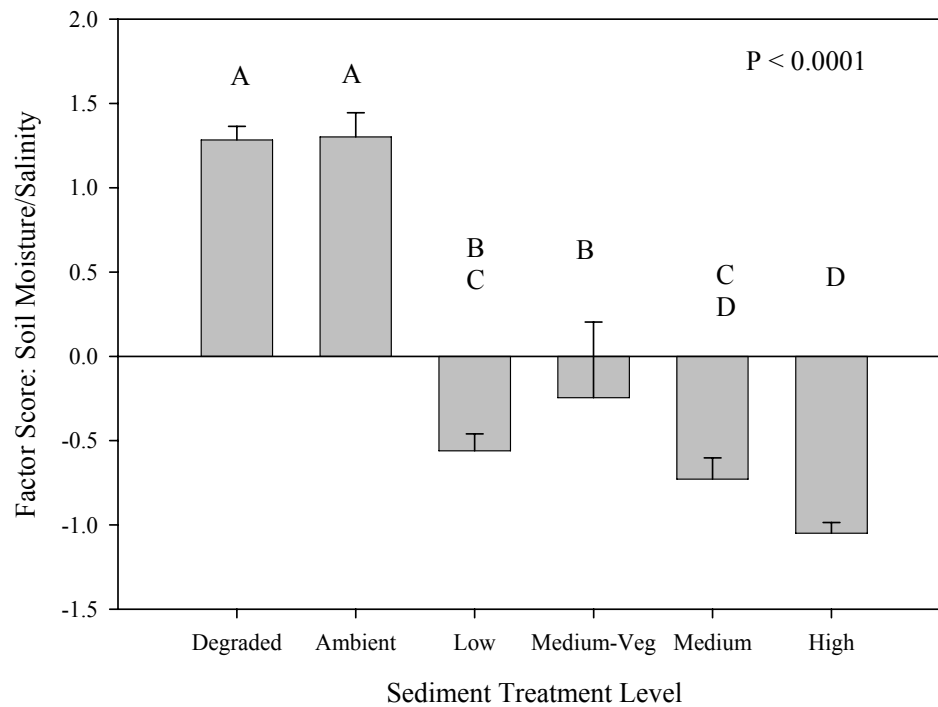
Table 2.1. Principle component analysis of soil variables. Bolded factor scores define the component. Natural log and square-root transformations were performed to improve normality on those parameters labeled with an ^{ln} or ^{-1/2}, respectively.

Indicator Variables	Principle Components	
	PC1 Soil Moisture /Salinity	PC2 Fe/P
Ammonium ^{ln}	0.93633	0.17026
Conductivity ^{ln}	0.96362	0.15768
Iron ^{ln}	0.50948	0.79941
Magnesium ^{ln}	0.94127	0.2537
Manganese ^{-1/2}	-0.78928	0.4358
Phosphorous ^{ln}	0.12103	0.89569
Potassium ^{ln}	0.89151	0.39422
Sodium ^{ln}	0.96357	0.20106
Sulfur ^{ln}	0.9412	0.29132
Sulfide ^{ln}	0.75169	0.31344
Eh	-0.82114	-0.4014
Bulk density	-0.93537	-0.3058
pH	-0.86456	-0.3336
% Moisture ^{ln}	0.92185	0.34823
% Organic Matter ^{ln}	0.94678	0.2187
Eigenvalue	11.9	1.55
% Variance Explained	79 %	10 %
Cumulative % Variance Explained	89 %	

sediment addition (Figure 2.5.1). Similarly, iron and phosphorus also decreased at the highest elevation (High STL), but otherwise remained constant between low and moderate elevations (Figure 2.5.2). Additionally, the character of the marsh soil changed over time (Table 2.2).

Several parameters associated with soil salinity, such as conductivity and sodium, increased from 2005 to 2006. Redox potential also increased in addition to soil exchangeable nutrients (ammonium, iron and manganese) and organic matter content.

1)



2)

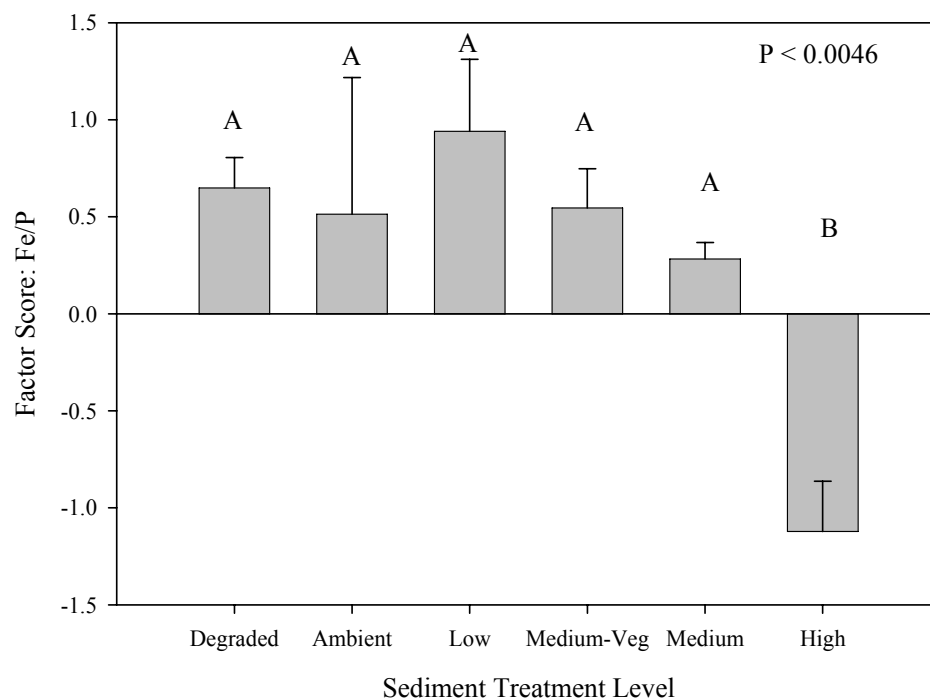


Figure 2.5. Effect of sediment addition on soil characteristics representing 1) Soil moisture and salinity (PC1) and 2) Iron and phosphorus (PC2). Error bars represent standard errors, and different letters denote significantly different means (Fisher's Protected LSD, $p < 0.05$).

Table 2.2. Soil physico-chemical characteristics of the restored and natural marshes in 2005 and 2006. Data are means (across all elevations) and standard errors in parentheses (n=6). Shared letters within the same row indicate no significant difference (Fisher's Protected LSD, $p < 0.05$).

Soil Parameter	Time	
	2005	2006
Conductivity (mS)	15.64 (0.67) a	13.99 (0.59) b
Sodium ($\mu\text{g}\cdot\text{cm}^{-3}$)	12770 (853.5) a	11400 (788.4) b
Potassium ($\mu\text{g}\cdot\text{cm}^{-3}$)	1251 (59.04) a	1017 (57.07) b
Magnesium ($\mu\text{g}\cdot\text{cm}^{-3}$)	2196 (127.3) a	1987 (118.5) b
Sulfur ($\mu\text{g}\cdot\text{cm}^{-3}$)	1003 (83.10) a	1169 (102.4) b
pH	7.257 (0.0487) a	7.048 (0.0710) a
Ammonium ($\mu\text{g}\cdot\text{cm}^{-3}$)	6.90 (0.94) a	9.72 (1.47) b
Phosphorus ($\mu\text{g}\cdot\text{cm}^{-3}$)	37.34 (1.527) a	35.43 (5.104) a
Iron ($\mu\text{g}\cdot\text{cm}^{-3}$)	225 (10.2) a	274 (17.5) b
Manganese ($\mu\text{g}\cdot\text{cm}^{-3}$)	34.41 (2.434) a	50.98 (3.151) b
% Moisture	47.16 (1.23) a	47.13 (1.29) a
Bulk Density ($\mu\text{g}\cdot\text{cm}^{-3}$)	0.87 (0.02) a	0.89 (0.03) a
% Organic Matter	9.94 (0.51) a	13.69 (0.57) b
Reox Potential (mV)	79 (8) a	165 (9) b

2.3.3 Determinants of Primary Production

Changes in soil moisture and salinity as well as iron and phosphorus significantly influenced above- and belowground production and explained 48 % of aboveground production (Table 2.3). Belowground production was also significantly correlated to elevation, which together with PC1 (Soil Moisture/ Salinity) and PC2 (Fe/P) explained 59 % of the variance (Table 2.3). Above- and belowground production were similarly influenced by the physical and chemical conditions of the soil. Both above- and belowground production were negatively associated with increasing soil moisture and salinity and positively correlated with iron and phosphorus. Iron and phosphorus explained the majority of variance for both above- and belowground production (31 % and 30 %, respectively). Additionally, increasing elevation had a negative influence on belowground production, and explained more of the variance for belowground production than did soil moisture and salinity.

Table 2.3. Multiple regression parameters that explain variance associated with response variables, above- and belowground production. Models were derived using the stepwise selection method, which took into account elevation and all principle components.

Response Variable	Independent Variable	Parameter Estimate	Partial R²	R²	P-value
Aboveground Production	Soil Moisture/Salinity (PC1)	-2.40E+02	0.1709	0.4830	0.0071
	Fe/P (PC2)	3.73E+02	0.3120		
Belowground Production	Sediment Addition	-389.62485	0.2382	0.5871	0.0051
	Soil Moisture/Salinity (PC1)	-726.16935	0.0472		
	Fe/P (PC2)	1.96E+02	0.3017		

2.4 Discussion

Sediment addition at moderate intensities resulted in the functional restoration of total NPP compared to the ambient natural marsh. Above- and belowground NPP were significantly greater at moderate elevations compared to extreme low (degraded reference) and extreme high (High STL) marsh elevations. Increasing elevation with sediment addition decreased salinity and soil moisture resulting in a significant increase in above- and belowground production. However, further addition of sediment, resulting in elevations greater than 20 cm above ambient marsh, resulted in insufficient flooding and decreased primary production to levels equivalent to the degraded marsh.

Intermediate additions of sediment resulted in a significant decrease in flood duration, sulfide concentration and salinity, all of which likely contributed to increased primary production. It has been well documented that excessive inundation, resulting in decreased redox potential (DeLaune *et al.*, 1983; Wilsey *et al.*, 1992; Mendelssohn and Kuhn 2003) and sulfide accumulation (Patrick and DeLaune, 1972; Linthurst, 1979; Mendelssohn and McKee, 1988), is

directly linked to growth inhibition and mortality of *S. alterniflora* (Linthurst, 1980; Mendelssohn and McKee, 1988; Bradley and Dunn, 1989; Koch and Mendelssohn, 1989). Additionally, increased salinity negatively impacts *S. alterniflora* production through osmotic stress (Shalhevet, 1993; Glen and Brown, 1998; Brown and Pezeshki, 2007) and limited nutrient uptake (Bradley and Morris, 1991). Furthermore, the interaction of high salinity and anaerobic conditions may further reduce metabolic efficiency (Knott, 1977), which is already limited in excessively flooded soils (Mendelssohn *et al.*, 1981). Therefore, increasing the elevation of the marsh surface improved drainage and aeration as well as decreased salinity, alleviating both salinity and flooding stresses, resulting in increased primary production (Mendelssohn and Seneca, 1980; Linthurst and Seneca, 1981; Brown and Pezeshki, 2007).

Primary production was also positively correlated with soil extractable iron and phosphorus concentrations. Iron and phosphorus concentrations were highest in areas of low to moderate elevation, which also coincided with significant increases in above- and belowground production. The availability of iron in flooded soils is linked to increased growth of *S. alterniflora* and a decrease in free sulfides (King *et al.*, 1982; Ornes and Kaplan, 1989), which are precipitated by iron in a non-bioavailable form (Gambrell and Patrick, 1978). Additionally, although nitrogen is the predominant limiting nutrient in salt marsh plants (Darby and Turner, 2008b), extractable phosphorus is positively correlated with aboveground biomass (DeLaune *et al.*, 1979; Mendelssohn and Kuhn, 2003). Therefore, the combination of decreased sulfide availability and phosphorus stimulation may have also attributed to greater production in areas of moderate sediment addition (Gambrell and Patrick, 1978; Mendelssohn and Kuhn, 2003).

In contrast to the positive effect of moderate sediment addition on primary productivity, too much added sediment, resulting in relatively high elevations, generated a low primary

productivity that was equivalent to that in the degraded marsh. Hence, the response of primary productivity to sediment addition follows a threshold model, whereby above a specific sediment addition level, productivity is negatively impacted by sediment addition. The mechanism for this negative effect on primary productivity involved decreases in soil moisture and salinity as well as soil nutrients. Also, at the higher elevations, soil redox potentials were high and sulfide concentrations low (0.08 ± 0.07 mM), below that known to impair plant growth (1.0 mM; Koch and Mendelssohn, 1989). Although iron concentrations were lowest at the highest elevations, iron is not generally limiting to *S. alterniflora* growing in fine-grain sediments. However, ammonium and phosphorus were significantly lower at elevations above 20 cm, and may have played a role in lower primary productivity at the High STL. It is well documented that nitrogen limits the aboveground production of *S. alterniflora* (Squiers and Good, 1974; Valiela and Teal, 1974; Sullivan and Daiber, 1974; Gallagher 1975; Patrick and DeLaune, 1976 and Mendelssohn, 1979). However, at high elevations, where redox potentials are maximal, nitrification and subsequent leaching may have promoted ammonium loss (Patrick and Wyatt, 1964). Similarly, precipitation of phosphorus with ferric iron, calcium or aluminum can decrease the availability of phosphorus in aerobic soils (Mitsch and Gosselink, 2000) potentially resulting in both ammonium and phosphorus limitation at the High STL.

However, the effects of nutrient limitation on belowground production are less clear. Several studies have shown that the absolute mass of belowground roots and rhizomes increases with nitrogen addition (Haines and Dunn, 1976; Linthurst and Seneca, 1981; Ornes and Kaplan, 1989); although in some cases root biomass is not significantly affected (Broome *et al.*, 1975; Morris, 1982), or decreases with increased nitrogen availability (Valiela *et al.*, 1976). Additionally, effects of phosphorus on root and rhizome biomass are also variable (Broome *et*

al., 1975; Ornes and Kaplan, 1989; Darby and Turner, 2008b), although many studies indicate that a decrease in nutrient availability coincides with greater belowground biomass production for foraging (Haines and Dunn, 1976; Valiela *et al.*, 1976; Morris, 1980; Morris, 1982; Schubauer and Hopkinson, 1984). Therefore, the sediment addition threshold may have resulted in nutrient limitation of above- and belowground production, although other factors may also be limiting belowground growth and foraging ability of *S. alterniflora*.

Sediment addition caused a significant drop in soil moisture, which resulted in higher production at the moderate elevations. However, insufficient flooding may be restricting both above- and belowground production at high elevations. Although *S. alterniflora* responds positively to well-drained soils in the field (King *et al.*, 1982; Mendelssohn and Seneca, 1980), experimental evidence shows that production of *S. alterniflora* is better under flooded conditions when soil toxins are not present (Mendelssohn and Seneca, 1980). Additionally, periods of prolonged soil drying can cause a decrease in stomatal conductance, photosynthesis, biosynthate production and growth (Brown and Pezeshki, 2007).

At the present restoration site, Materne and Mendelssohn (2006) observed a significant decrease in flood duration and frequency at the High and Medium STLs compared to all other elevations. The High STL was only flooded 3.4 % of the time, with a frequency of 12 %, which corresponds to only 50 flood events in 15 months. Even if these events occurred at regular intervals over the 15 month period, the marsh surface would have remained dry for a period of at least eight days between flooding events. In a study that simulated drought conditions, Brown and Pezeshki (2007) observed a significant decrease in above- and belowground *S. alterniflora* biomass after eight, sixteen and twenty-four days of soil drying compared to plants in regularly flooded soils. Furthermore, after re-hydration, recovery of stomatal conductance and

photosynthesis did not occur in plants exposed to prolonged drought conditions (24 days). Therefore, it is probable that above- and belowground production at the high elevations were negatively impacted by drought conditions that lasted for periods of eight days, and possibly longer. In summary, the elevation gradient created by sediment addition resulted in a bell-shaped pattern of primary production, which was principally controlled by alterations in tidal flooding. The initial increase in elevation decreased flooding, relieved salinity and water-logging stress, and increased primary production; however, above this elevation threshold, further reductions in flooding resulted in lower nutrient availability, drought-like conditions and a decrease in primary production.

I observed a similar pattern in the ratio of belowground to aboveground biomass ($R+R:S$), which was significantly higher in areas of extreme low (degraded reference) and high elevations (High STL). An increase in the ratio of belowground to aboveground biomass has been observed for plants in stressful environments (Bray, 1963; Valiela *et al.*, 1976; Smith *et al.*, 1979; Hopkinson and Schubauer, 1984), which increase allocation of carbon to belowground biomass when resources are limited, or uptake per unit of root surface is less efficient (Shaw, 1952; Shaver and Billings, 1975). In contrast, $R+R:S$ ratios were less than 1:1 in areas of moderate elevation, which also had the highest primary production. Morrison (1982) also observed a decrease in $R+R:S$ ratio with increasing nitrogen availability and total NPP, concluding that the main determinant of total NPP was the effect of nitrogen on development, or the differential allocation of carbon to photosynthesizing organs versus roots and rhizomes. For example, in a resource-limited system, allocation of carbon to roots increases to enhance uptake; however aboveground production decreases along with photosynthesis and total NPP. In contrast, as resources become more available, the relative biomass of roots decreases as

aboveground biomass, photosynthesis and total NPP increase (Morris, 1982). Therefore, it appears that in areas of moderate elevation, increased nutrient availability and decreased flooding and salinity stress allow *S. alterniflora* to allocate more carbon to aboveground, photosynthesizing organs resulting in an increase in total NPP.

Although the ratio of belowground to aboveground live biomass was less than 1:1 at moderate elevations, belowground NPP was greater than aboveground NPP at all elevations. Annual production was measured as the change in live and dead biomass over time, and thus the relative difference in live biomass and production between above- and belowground parts is likely due to the slower turnover of belowground dead material (Schubauer and Hopkins, 1984; Lana *et al.*, 1991).

Conversely, belowground turnover of live biomass was not significantly different from aboveground live turnover at moderate-high elevations (Figure 2.4). The mean aboveground turnover rate ($1.2 \cdot \text{y}^{-1} \pm 0.10$) from this study is slightly lower than those reported for marshes in this region ($1.38\text{-}3.5 \cdot \text{y}^{-1}$; Kirby and Gosselink, 1976; Hopkins *et al.*, 1978; Kaswadji *et al.*, 1990; Darby and Turner, 2008a), but the mean belowground turnover rate ($1.0 \cdot \text{y}^{-1} \pm 0.11$) is within the range of literature values for this region ($0.67\text{-}10.7 \cdot \text{y}^{-1}$; Gallagher and Plumely, 1979; Schubauer and Hopkins, 1984; Darby and Turner, 2008a). Thus, the equivalent turnover between above and belowground materials is due to lower aboveground turnover rates, not high belowground turnover. Slow aboveground turnover rates may be a result of low tidal amplitude and decreased flooding, resulting in less organic matter removed from the marsh surface by tidal flushing (Hopkins *et al.*, 1978; Turner, 1976). Nevertheless, the slightly higher rates of aboveground turnover and the significantly higher rates of belowground production suggest that

the production of organic matter by roots and rhizomes is the primary contributor to organic matter accretion (Blum, 1993; Turner *et al.*, 2001).

In addition, belowground production increased over time. I observed inter-annual variation in belowground production, which was equivalent to aboveground production in the first year of measurements, but significantly surpassed aboveground production by 2006. In contrast, I observed no change in aboveground production over time. Inter-annual variation of belowground production in natural marshes is thought to be primarily controlled by climactic conditions, such as rainfall, as opposed to changes in soil fertility (Dame and Kenny, 1986; Blum, 1993; Darby and Turner, 2008a). However, I observed a significant increase in exchangeable soil nutrients (iron, manganese and ammonium) with corresponding increases in belowground production over time.

Therefore, belowground production in sediment subsidized marshes may be responding to changes in the marsh soil that are a result of the maturation of the system as a whole. For example, as the restored marsh ages, organic matter production and decomposition will influence nutrient dynamics and alter the physical character of the soil, thus having a directional effect on belowground production. Edward and Mills (2005) found that belowground production in a restored marsh increased exponentially for several years following sediment addition and continued to increase to levels above natural marshes nine years after restoration. In contrast, aboveground production was negatively correlated with marsh age, such that production in restored marshes was greater than natural marshes after sediment addition, but began to decrease over time, approaching functional equivalency of the natural marsh (Edwards and Mills, 2005). These results indicate that the addition of sediments positively affects belowground production through ameliorating flooding stress, and continues to optimize belowground production over

time as the marsh matures, and emphasizes the importance of belowground production in marsh sustainability.

Additionally, although above- and belowground primary production were not significantly different between the natural and moderately subsidized marshes, I believe that over time the marshes restored using moderate amounts of sediment subsidy will be functionally superior to these natural marshes. As with many of the salt marshes in this region (Day *et al.*, 1993; Turner, 1997), the natural reference marsh appears to be declining. Flood duration and frequency, as well as sulfide concentrations, are significantly higher at the ambient natural marsh (50% time flooded, 1.63 ± 0.50 mM sulfide) compared to the Low and Medium-Veg STLs (10-20% time flooded, 0.03 ± 0.01 mM sulfide). In comparison to *S. alterniflora* production reported for the southeastern U.S., which ranges between 1113 and 1281 $\text{g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ for aboveground (Kirby and Gosselink, 1976; Kaswadji *et al.*, 1990; Darby and Turner, 2008a) and 770-5500 $\text{g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ for belowground (Gallagher and Plumley, 1976; Dame and Kenny, 1986; Blum, 1993), aboveground production in the ambient marsh is relatively low (641 $\text{g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ aboveground, 1469 $\text{g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ belowground), further supporting the notion that the natural marshes in this area are in decline. Additionally, resilience, measured as the recovery rate of *S. alterniflora* after experimental disturbances, is significantly lower in the ambient marsh compared to the moderately subsidized marshes (Stagg, 2009). Based on these observations, it is probable that the ambient marsh will begin to deteriorate, or at least become less productive than the subsidized marshes.

2.5 Conclusions

In summary, sediment subsidy increased the elevation of the marsh surface, and alleviated stress associated with excessive inundation and high salinity. Primary production was

maximal at elevations ranging from 5-20 cm above ambient marsh (35-50 cm NAVD 88), and decreased at elevations above 20 cm (50 cm NAVD 88), where primary production was limited by insufficient flooding. Both above- and belowground production in areas of moderate sediment addition was functionally equivalent to the natural marsh. Therefore, sediment addition that results in elevations within the mid to high intertidal zone can successfully restore ecological function to a degraded system. Additionally, belowground production at moderate levels of sediment addition will likely increase over time, suggesting that these areas will continue to accrete organic matter and maintain their intertidal position, potentially resulting in functional superiority to the natural marshes in Louisiana, which are rapidly subsiding and deteriorating.

2.6 Literature Cited

- Alber, M., Swenson, E.M., Adamowicz, S.C. and Mendelssohn, I.A. 2008. Salt marsh dieback: an overview of recent events in the US. *Estuarine, Coastal and Shelf Science*, 80: 1–11.
- Barras, J., Beville, S., Britsch, D., Hartley, S., Hawes, S., Johnston, J., Kemp, P., Kinler, Q., Martucci, A., Porthouse, J., Reed, D., Roy, K., Sapkota, S. and Suhayda, J. 2003. Historical and projected coastal Louisiana land changes: 1978-2050. USGS Open File Report 03-334.
- Barras, J. A. 2006. Land area change in coastal Louisiana after the 2005 hurricanes-a series of three maps: U.S. Geological Survey Open-File Report 06-1274.
- Blum, L.K. 1993. *Spartina alterniflora* root dynamics in a Virginia marsh. *Marine Ecology Progress Series*, 102: 169-178
- Boesch, D., Mehta, A., Morris, J., Nuttle, W., Simenstad, C. and Swift, D. 1994. Scientific assessment of coastal wetland loss, restoration and management in Louisiana. *Journal of Coastal Research* special issue, 20: 1-103.
- Bradley, P.M. and Dunn, E.L. 1989. Effects of sulfide on the growth of 3 salt marsh halophytes of the southeastern United States. *American Journal of Botany*, 76: 1707-1713.
- Bradley, P.M. and Morris, J.T. 1990. Influence of oxygen and sulfide concentration on nitrogen uptake kinetics in *Spartina alterniflora*. *Ecology*, 71: 282-287.
- Bradley, P.M. and Morris, J.T. 1991. The influence of salinity on the kinetics of NH_4^+ uptake in *Spartina alterniflora*. *Oecologia*, 85: 375-380.
- Bray, J. R. 1963. Root production and the estimation of net productivity. *Canadian Journal of Botany*, 41: 65-72.

- Bremner, J. M. and Kenney, D.R. 1966. Determination and isotope-ratio analysis of different forms of nitrogen in soils: 3. Exchangeable ammonium, nitrate, and nitrite by extraction-distillation methods. *Soil Science Society of America Proceedings*, 30: 577-582.
- Broome, S. W., Woodhouse, W. W. Jr. and Seneca, E. D. 1975. The relationship of mineral nutrients to growth of *Spartina alterniflora* in North Carolina: II. The effects of N, P and Fe fertilizers. *Soil Science Society of America*, 39: 295-301.
- Brown, C.E. and Pezeshki, S.R. 2007. Threshold for recovery in the marsh halophyte *Spartina alterniflora* grown under the combined effects of salinity and soil drying. *Journal of Plant Physiology*, 164: 274-282.
- Byrnside, D.S. Jr. and Sturgis, M.B. 1958. Soil phosphorus and its fractions as related to response of sugar cane to fertilizer phosphorus. Bull No. 513, Louisiana State University Agriculture Experiment Station, Baton Rouge, Louisiana, USA.
- Calloway, J.C. 1994. Sedimentation processes in selected coastal wetlands from the Gulf of Mexico and Northern Europe. Ph.D. Dissertation, Louisiana State University, Baton Rouge, LA.
- Dame, R. F. and Kenny, P. D. 1986. Variability of *Spartina alterniflora* primary production in the euhaline North Inlet estuary. *Marine Ecology Progress Series*, 32: 71-80.
- Darby, F. A. and Turner, R.E. 2008a. Below- and aboveground *Spartina alterniflora* production in a Louisiana salt marsh. *Estuaries and Coasts: JCERF*, 31: 223-231.
- Darby, F.A. and Turner, R.E. 2008b. Below- and aboveground biomass of *Spartina alterniflora*: response to nutrient addition in a Louisiana salt marsh. *Estuaries and Coasts*, 31: 326-334.
- Day, J. W., Conner, W. H., Costanza, R., Kemp, G. P. and Mendelssohn, I. A. 1993. Impacts of sea level rise on coastal systems with special emphasis on the Mississippi River deltaic plain. In Warrick, R. A., Barrow, E. M. and Wigley, T. M. L., editors. *Climate and Sea Level Change: Observations, Projections, and Implications*. Cambridge University Press: Cambridge, Great Britain. pp. 276-296
- Day, J. W., Shaffer, G.P., Britsch, L.D., Reed, D.J., Hawes, S.R., and Cahoon, D.R. 2000. Pattern and process of land loss in the Mississippi Delta: a spatial and temporal analysis of wetland habitat change. *Estuaries*, 23: 425-438.
- Day, J.W., Christian, R.R., Boesch, D.M., Yáñez-Arancibia, A., Morris, J., Twilley, R., Naylor, L., Schaffner, L. and Stevenson, C. 2008. Consequences of climate change on the geomorphology of coastal wetlands. *Estuaries and Coasts*, 31: 477-491.

- DeLaune, R.D., Buresh, R.J. and Patrick W.H. Jr. 1979. Relationship of soil properties to standing crop biomass of *Spartina alterniflora* in a Louisiana marsh. *Estuarine and Coastal Marine Science*, 8: 477–487.
- DeLaune, R. D., Smith, C. J. and Patrick, W. H. Jr. 1983. Relationship of marsh elevation, redox potential, and sulfide to *Spartina alterniflora* productivity. *Soil Science Society of America*, 47: 930-935.
- DeLaune, R. D., Pezeshki, S. R., Pardue, J. H., Whitcomb, J. H. and Patrick, W. H. Jr. 1990. Some influences of sediment addition to a deteriorating salt marsh in the Mississippi River deltaic plain: A pilot study. *Journal of Coastal Research*, 6: 181-188.
- DeLaune, R.D. and Pezeshki, S.R. 2003. The role of soil organic carbon in maintaining surface elevation in rapidly subsiding U.S. Gulf of Mexico coastal marshes. *Water, Air and Soil Pollution*, 3: 167-179.
- Edwards, K.R. and Mills, K.P. 2005. Aboveground and belowground productivity of *Spartina alterniflora* (Smooth Cordgrass) in natural and created Louisiana salt marshes. *Estuaries*, 28: 252-265.
- Gallagher, J. L. 1975. Effect of an ammonium nitrate pulse on the growth and elemental composition of natural stands of *Spartina alterniflora* and *Juncus roemerianus*. *American Journal of Botany*, 62: 644-648.
- Gallagher, J. L. and Plumley, F.G. 1979. Underground biomass profiles and productivity in Atlantic coastal marshes. *American Journal of Botany*, 66: 156-161.
- Gallagher, J. L., Wolf, P.L. and Pfeiffer, W.J. 1984. Rhizome and root growth rates and cycles in protein and carbohydrate concentrations in a Georgia *Spartina alterniflora* Loisel marsh. *American Journal of Botany*, 71: 165-169.
- Gambrell, R. P. and Patrick, W. H. Jr. 1978. Chemical and microbiological properties of anaerobic soils and sediments. In Hook, D. D. and Crawford, R. M. M., editors. *Plant Life in Anaerobic Environments*. Ann Arbor Scientific Publishing, Inc., Ann Arbor, MI, USA, pp. 375-423.
- Glenn, E. and Brown, J. 1998. Effects of soil salt levels on the growth and water use efficiency of *Atriplex canescens* (*Chenopodiaceae*) varieties in drying soil. *American Journal of Botany*, 85: 10–6.
- Haines, B. L. and Dunn, E.L. 1976. Growth and resource allocation responses of *Spartina alterniflora* Loisel. to three levels of NH₄-N, Fe, and NaCl in solution culture. *Botanical Gazette*, 137: 224-230.

- Hatton, R.S., DeLaune, R.D. and Patrick, W.H. Jr. 1983. Sedimentation, accretion, and subsidence in marshes of Barataria Basin, Louisiana. *Limnology and Oceanography*, 18: 494-502.
- Hopkinson, C.S., Gosselink, J.G. and Parrondo, R.T. 1978. Aboveground production of seven marsh plant species in coastal Louisiana. *Ecology*, 59: 760-769.
- Hopkinson, C.S. and Schubauer, J. P. 1984. Static and dynamic aspects of nitrogen cycling in the salt marsh graminoid, *Spartina alterniflora* Loisel. *Ecology*, 65: 961-969.
- Houghton, R.A. and Woodwell, G.M. 1980. The Flax Pond ecosystem study exchanges of carbon dioxide between a salt marsh and the atmosphere. *Ecology*, 61: 1434-1445.
- Jelgersma, S. 1996. In Milliman, J.D. and Haq, B.U., editors. *Sea Level and coastal subsidence. Causes, consequences, and strategies*. Kluwer, Dordrecht. pp. 47-62.
- Kaswadji, R.F., Gosselink, J.G. and Turner, R.E. 1990. Estimation of primary production using five different methods in a *Spartina alterniflora* salt marsh. *Wetlands Ecology and Management*, 1: 57-64.
- King, G.M., Klug, M.J., Wiegert, R.G. and Chalmers, A.G. 1982. Relation of soil water movement and sulfide concentration to *Spartina alterniflora* production in a Georgia salt marsh. *Science*, 218: 61-63.
- Kirby, C.J. and Gosselink, J.G. 1976. Primary production in a Louisiana gulf coast *Spartina alterniflora* marsh. *Ecology*, 57: 1052-1059.
- Knott, W. M. 1977. The response of *Spartina alterniflora* Loisel, to various salinities under simulated marsh conditions in the greenhouse. Ph.D. Thesis. North Carolina State University, Raleigh, NC. 93 p.
- Koch, M.S. and Mendelssohn, I.A., 1989. Sulphide as a soil phytotoxin: differential responses in two marsh species. *Journal of Ecology*, 77: 565-578.
- Koch, M.S., Mendelssohn, I.A. and McKee, K.L. 1990. Mechanism for the hydrogen sulfide-induced growth limitation in wetland macrophytes. *Limnology and Oceanography*, 35: 399-408.
- Lana, P. da Cunha, Guiss, C. and Disaro C.T. 1991. Seasonal variation of biomass and production dynamics for above- and belowground components of a *Spartina alterniflora* marsh in the euhaline sector of Paranaguá (SE Brazil). *Estuarine, Coastal and Shelf Science*, 32: 231-241.
- Lindsay, W. L. and Norvell, W.A. 1978. Development of a DTPA soil test for zinc, iron, manganese, and copper. *Soil Science Society of America* 42: 421-428.

- Lindstedt, D.M., Swenson, E.M., Reed, D., Twilley, R. and Mendelssohn, I.A. 2006. Marsh dieback technical synthesis report. Technical Report, Coastal Restoration Division, Louisiana Department of Natural Resources.
- Linthurst, R. A. 1979. The effect of aeration on the growth of *Spartina alterniflora* Loisel. *American Journal of Botany*, 66: 685-691.
- Linthurst, R.A. 1980. A growth comparison of *Spartina alterniflora* Loisel. Ecophenes under aerobic and anaerobic conditions. *American Journal of Botany*, 67: 883-887.
- Linthurst, R. A. and Seneca, E. D. 1981. Aeration, nitrogen and salinity as determinants of *Spartina alterniflora* Loisel growth response. *Estuaries*, 4:53-63.
- Livingstone, D.C. and Patriquin, D.G. 1981. Belowground growth of *Spartina alterniflora* Loisel: habit, functional biomass and non-structural carbohydrates. *Estuarine Coastal Shelf Science*, 12: 579-588.
- Materne, M.D. and Mendelssohn, I.A. 2006. Beneficial use of hydraulically dredged sediment-slurries for wetland restoration: II. Spatial, hydrologic and vegetative assessment. Governor's Applied Coastal Research and Development Program.
- McCaffrey, R.J. and Thompson, J. 1980. A record of the accumulation of sediment and trace metals in a Connecticut salt marsh. *Advances in Geophysics*, 22: 165-236.
- McKee, K.L., Mendelssohn, I.A. and Materne, MD. 2004. Acute salt marsh dieback in the Mississippi River Deltaic Plain: a drought-induced phenomenon? *Global Ecology and Biogeography*, 13: 67-73.
- Mendelssohn, I.A. and Marcellus, K. L. 1976. Angiosperm production of three Virginia marshes in various salinity and soil nutrient regimes. *Chesapeake Science*, 17: 15-23.
- Mendelssohn, I.A. 1979. The influence of nitrogen level, form, and application method on the growth response of *Spartina alterniflora* in North Carolina. *Estuaries*, 2: 106-112.
- Mendelssohn, I. A. and Seneca, E. D. 1980. The influence of soil drainage on the growth of salt marsh cordgrass *Spartina alterniflora* in North Carolina. *Estuarine and Coastal Marine Science*, 11: 27-40.
- Mendelssohn, I. A., McKee, K. L. and Patrick, Jr., W. H. 1981. Oxygen deficiency in *Spartina alterniflora* roots: Metabolic adaptation to anoxia. *Science*, 214: 439-441.
- Mendelssohn, I. A. and McKee, K. L. 1988. *Spartina alterniflora* die-back in Louisiana: Time-course investigation of soil waterlogging effects. *Journal of Ecology*, 76: 509-521.
- Mendelssohn, I. A. and Morris, J.T. 2000. Eco-physiological constraints on the primary productivity of *Spartina alterniflora*. In *Concepts and Controversies*. Elsevier Press.

- Mendelssohn, I.A. and Kuhn, N.L. 2003. Sediment subsidy: effects on soil-plant responses in a rapidly submerging coastal salt marsh. *Ecological Engineering*, 21: 115-128.
- Mitsch, W.J. and Gosselink, J.G., editors. 2000. Wetlands, third edition. John Wiley and Sons, Inc. New York, U.S.A. 920p.
- Morris, J. T. 1980. The nitrogen uptake kinetics of *Spartina alterniflora* in culture. *Ecology*, 61: 1114-1121.
- Morris, J.T. 1982. A model of growth responses by *Spartina alterniflora* to nitrogen limitation. *Journal of Ecology*, 70: 25-42.
- Morris, J.T. and Dacey, J.W.H. 1984. Effects of O₂ on ammonium uptake and root respiration by *Spartina alterniflora*. *American Journal of Botany*, 71: 979-985.
- Nelson, D.W. and Sommers, L.E. 1996. Carbon and organic matter: loss on ignition method. In *Methods of Soil Analysis, Part 3, Chemical Methods*, Soil Science Society of America, Inc., American Society of Agronomy, Inc., Madison, WI. pp. 1001-1010.
- Nyman, J.A., DeLaune, R.D., Roberts, H.H. and Patrick, W.H. Jr. 1993. Relationship between vegetation and soil formation in a rapidly submerging coastal marsh. *Marine Ecology Progress Series*, 96: 296-279.
- Ornes, W.H. and Kaplan, D.I. 1989. Macronutrient status of tall and short forms of *Spartina alterniflora* in a South Carolina salt marsh. *Marine Ecology Progress Series*, 55: 63-72.
- Patrick, W.H. Jr. and DeLaune, R.D. 1972. Characterization of the oxidized and reduced zones in flooded soil. *Proceedings of the Soil Science Society of America*, 36: 573-576.
- Patrick, W. H. Jr. and Delaune, R.D. 1976. Nitrogen and phosphorus utilization by *Spartina alterniflora* in a salt marsh in Barataria Bay, Louisiana. *Estuarine and Coastal Marine Science*, 4: 59-64.
- Rozas L.P. and Minello T.J. 2001. Marsh terracing as a wetland restoration tool for creating fishery habitat. *Wetlands*, 21: 327-341.
- Rybczyk, J.M. and Cahoon, D.R. 2002. Estimating the potential for submergence for two wetlands in the Mississippi River Delta. *Estuaries*, 25: 985-998.
- SAS Institute Inc., 2004. SAS® 9.1.2. *Qualification Tools User's Guide*, Cary, NC.
- Schrift, A.M., Mendelssohn, I.A. and Materne, M.D. 2008. Salt marsh restoration with sediment-slurry amendments following a drought-induced large-scale disturbance. *Wetlands*, 28: 1071-1085.

- Schubauer, J.P. and Hopkins, C.S. 1984. Above- and belowground emergent macrophyte production and turnover in a coastal marsh ecosystem, Georgia. *Limnology and Oceanography*, 29: 1052–1063.
- Shalhevet, J. 1993. Plants under water and salt stress. In: Fowden L, Mansfield, T. and Stoddart, J., editors. *Plant adaptation to environmental stress*. New York: Chapman & Hall. pp.133–54.
- Shaver, G. R. and Billings, W. D. 1975. Root production and root turnover in a wet tundra ecosystem, Barrow, Alaska. *Ecology*, 56: 401-409.
- Shaw, B. T., editor. 1952. Soil physical conditions and plant growth. Academic Press.
- Slocum, M.G., Mendelssohn, I.A. and Kuhn, N.L. 2005. Effects of sediment slurry enrichment on salt marsh rehabilitation: plant and soil responses over seven years. *Estuaries*, 28: 519-528.
- Smalley, A. E. 1958. The role of two invertebrate populations, *Littorina irrorata* and *Orchelimum fificinium*, in the energy flow of a salt marsh ecosystem. Ph.D. thesis, Univ. Georgia, Athens. 126 p.
- Smith, K. K., Good, R.E. and Good, F.N. 1979. Production dynamics for above- and belowground components of a New Jersey *Spartina alterniflora* tidal marsh. *Estuarine, Coastal and Marine Science*, 9: 189-201.
- Squiers, E. R. and Good, R.E. 1974. Seasonal changes in the productivity, caloric content, and chemical composition of a population of salt-marsh cord-grass (*Spartina alterniflora*). *Chesapeake Science*, 15: 53-71.
- Stagg, C.L. 2009. Remediating impacts of global climate change-induced submergence on salt marsh ecosystem functions. Ph.D. dissertation. Louisiana State University, Baton Rouge, LA.
- Sullivan, M. J. and Daiber, F.C. 1974. Response in production of cord grass, *Spartina alterniflora*, to inorganic nitrogen and phosphorus fertilizer. *Chesapeake Science*, 15: 121-123.
- Teal, J.M. 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology*, 43: 614-624.
- Thomas, G. W. 1982. Exchangeable cations. In Page, A. L., Miller, R. H., and Keeney, D. R., editors. *Methods of soil analysis: Part 2--chemical and microbiological properties*, second edition. American Society of Agronomy, Inc. and Soil Science Society of America, Inc., Madison, WI. pp.159-165.
- Turner, R.E. 1976. Geographic variations in salt marsh macrophyte production: a review. *Contributions in Marine Science*, 20: 47–68.

- Turner, R. E. 1997. Wetland loss in the Northern Gulf of Mexico: multiple working hypotheses. *Estuaries*, 20: 1-13.
- Turner, R.E., Swenson, E.M. and Milan, C.S. 2001. Contrasting organic and inorganic content in recently accumulated salt marsh sediments. In Weinstein, M. and M. Kreeger, D.D., editors. *Concepts and controversies in tidal marsh ecology*, Kluwer Academic Publishers: Dordrecht, The Netherlands. pp. 583-595.
- Turner, R.E., Swenson, E.M., Milan, C.S., Lee, J.M. and Oswald, T.A. 2004. Below-ground biomass in healthy and impaired marshes. *Ecological Research*, 19: 29–35.
- Valiela, I.I. and Teal, J.M. 1974. Nutrient limitation in salt marsh vegetation. In Reimold, R.J. and Queen, W. H., editors. *Ecology of halophytes*, Academic Press: New York, U.S.A.
- Valiela, I., Teal, J.M., Persson, N.Y. 1976. Production and dynamics of experimentally enriched salt marsh vegetation: Belowground biomass. *Limnology and Oceanography*, 21: 245-252.
- Wiegert, R.G., Chalmers, A.G. and Randerson, P.F. 1983. Productivity gradients in salt marshes – the response of *Spartina alterniflora* to experimentally manipulated soil-water movement. *Oikos*, 41: 1-6.
- Wiegert, R.G. 1979. Ecological processes characteristics of coastal *Spartina marshes* of the southeastern U.S.A. In Jefferies, R.L. and Davy, A.J., editors. *Ecological processes in coastal environments*, Blackwell Publishers: Oxford, England. pp. 467-490.
- Wilsey, B. J., McKee, K. L. and Mendelsohn, I. A., 1992. Effects of increased elevation and macro- and micronutrient additions on *Spartina alterniflora* transplant success in salt-marsh dieback areas in Louisiana. *Environmental Management*, 16: 505-511.
- Woodwell, G.M., Houghton, R.A., Hall, C.A.S., Whitney, D.E., Moll, R.A. and Juers, D.W. 1979. The Flax Pond ecosystem study: the annual metabolism and nutrient budgets of a salt marsh. In Jefferies, R.L. and Davy, A.J., editors. *Ecological processes in coastal environments*, Blackwell Publishers: Oxford, England. pp. 491-511.
- Zedler, J.B. and Callaway, J.C. 1999. Tracking wetland restoration: Do mitigation sites follow desired trajectories? *Restoration Ecology*, 7: 69-73.

CHAPTER 3

EFFECT OF SEDIMENT ADDITION ON DECOMPOSITION OF BELOWGROUND ORGANIC MATTER

3.1 Introduction

Along the northern Gulf of Mexico, Louisiana is losing coastal wetland area at a rate of $77 \text{ km}^2 \cdot \text{y}^{-1}$ (Barras *et al.*, 2003). Several factors have been contributed to this extensive land loss, including canal dredging, levee construction, geological subsidence, eustatic sea level rise (Boesch *et al.*, 1994; Turner, 1997; Jelgersma, 1996; Day *et al.*, 2000), as well as hurricanes and drought-induced subsidence (McKee *et al.*, 2004; Barras, 2006; Lindstedt *et al.*, 2006; Alber *et al.*, 2008). Recent evidence suggests that severe drought is at least partly responsible for the Sudden Marsh Dieback (SMD) event observed in the Southeastern United States in 2000 (Alber *et al.*, 2008). This dieback event was characterized by the death of over 100,000 hectares of *S. alterniflora* dominated salt marsh in Louisiana (Lindstedt *et al.*, 2006). Not only did this event cause vegetation mortality, but also, in many cases, salt marshes were converted to unvegetated mudflats that eventually subsided. Materne and Mendelssohn (2006) documented up to a 15 cm decrease in elevation at SMD-affected areas compared to unaffected salt marshes. Thus, drought-induced subsidence alters the natural hydrology of the affected areas, resulting in longer periods of inundation (Materne and Mendelssohn, 2006) accompanied by low redox potentials, high sulfide concentrations and minimal vegetative recovery (Schrift *et al.*, 2008).

One method of salt marsh restoration, sediment subsidy, aims to ameliorate effects of submergence through increasing the elevation of the marsh surface. This approach is based on the understanding that excessive inundation can lead to inhibited growth, or even mortality, of *S. alterniflora* (Mendelssohn and McKee, 1988), whereas increasing soil drainage can improve plant production (Mendelssohn and Seneca, 1980; Wilsey *et al.*, 1992). The addition of

hydraulically dredged sediment-slurries to degraded salt marshes increases the elevation of the salt marsh, and increases mineral content, soil aeration and nutrient availability, decreases toxic sulfides and restores vegetative structure (Mendelssohn and Kuhn, 2003; Slocum *et al.*, 2005; Schrifft *et al.*, 2008). The long term effects of sediment subsidy were investigated by Slocum *et al.*, (2005) who found that, seven years after restoration, sediment subsidized areas of moderate elevations (~ 12 cm above ambient marsh) had the highest plant cover and biomass compared to areas receiving lesser or greater sediment additions. Additionally, canopy cover and species richness were also measured at a drought-induced dieback site by Schrifft *et al.* (2008), who found that structural characteristics of the salt marsh were restored in areas of moderate sediment subsidy.

The goals of restoration aim to return a degraded system to previous conditions based on ecological services and values, which depend not only on ecological structure, but also on ecosystem function. However, ecological functions and resulting services have not always been restored after successful restoration of structural characteristics (Zedler and Callaway, 1999; Rozas and Minello, 2001). Therefore, my goal was to determine if the use of sediment subsidy can successfully restore ecosystem function to previously degraded marshes.

Decomposition is a key ecological function, which influences energy flow through the salt marsh (Teal, 1962; Good *et al.*, 1982; Davis *et al.*, 2006) and may also contribute to accretion dynamics and potential elevation change (Hackney and Clearly, 1987; Bricker-Urso *et al.*, 1989). The *in situ* decomposition of organic matter releases nutrients through mineralization, thus promoting primary production (Henriksen and Jensen, 1979; Abd. Aziz and Newell, 1979; Valiela and Teal, 1979), which in turn affects organic matter accumulation and vertical accretion (McCaffrey and Thomson, 1980; Neyman *et al.*, 2006; Turner *et al.*, 2006). However,

accelerated rates of decomposition may decrease soil volume and organic matter accumulation (Morris and Bradley, 1999), potentially resulting in a net negative elevation change.

Therefore, restoration resulting in balanced decomposition dynamics, such that rates of decay are not only optimal for nutrient release but also favorable for organic matter accretion, is important in maintaining ecosystem processes that promote sustainability during periods of sea level rise. To determine how sediment subsidy affects decomposition dynamics, I asked the following questions: 1) How do varying intensities of sediment subsidy affect decomposition of belowground biomass? 2) Is there a differential effect of sediment subsidy on root versus rhizome tissue decomposition? 3) How does sediment subsidy differentially affect the decomposition of relatively recalcitrant organic material (roots and rhizomes) versus more labile cellulose? 4) What environmental factors influence decomposition of plant tissue (roots and rhizomes) and cellulose? 5) Does restoration via sediment subsidy result in functional equivalency, in terms of decomposition, between restored salt marshes and natural salt marshes?

Based on results from previous studies (Mendelssohn and Kuhn, 2003; Slocum *et al.*, 2005; Schrifft *et al.*, 2008), I predict that moderate levels of sediment subsidy will provide the environmental conditions necessary to promote decomposition. Also, given the sediment-deprived status of Louisiana's coastal marshes and their high degree of submergence (Bauman *et al.*, 1984; Boesch *et al.*, 1994; Day *et al.*, 2000), I hypothesize that areas receiving sediment additions may be functionally superior to natural reference marshes.

3.2 Materials and Methods

3.2.1 Site Description and Experimental Design

The study site (29° 10.58'N and 90° 14. 23'W) was located in Terrebonne Basin, a part of the Mississippi River Deltaic Plain. The specific area of interest was a submerging, degraded salt

marsh located on the west bank of Bayou Lafourche near Leeville, LA. This area was affected by a sudden marsh dieback (SMD) event, which was linked to extreme drought conditions documented during the summer of 2000 (McKee *et al.*, 2004; Lindstast *et al.*, 2006). In addition to the dieback marsh, natural marshes, unaffected by the SMD event, occur throughout the area. These ambient marshes are dominated by *S. alterniflora* and interspersed with *Salicornia virginica*.

In 2002, after the SMD event, the dieback site was divided into four cells through the construction of small earthen dikes. The cells were hydraulically connected through culverts and breaks in the levees that allowed for tidal exchange. Hydraulically dredged sediment-slurries from adjacent Bayou Lafourche were pumped into each cell resulting in four separate sediment subsidy treatment blocks (Figure 3.1). The sediment slurries were comprised of approximately 20-30 % solids and 70-80 % water by volume. Addition of these sediment slurries at differential volumes within each replicate block resulted in four separate sediment subsidy treatment levels (STLs): 1) High STL: 28-36 cm above ambient marsh, 2) Medium STL: 20-25 cm above ambient marsh, 3) Medium-Vegetated (Medium-Veg) STL: areas with 100 % vegetative cover in the fall of 2003 and an average elevation of 20 cm above ambient marsh, and 4) Low STL: 13-18 cm above ambient marsh. . Sediments in the sediment addition zone were comprised of 8.94 ± 0.20 % sand, 42.89 ± 0.54 % silt, 47.21 ± 0.60 % clay 10.90 ± 3.64 % organic matter and (Schrift *et al.*, 2008).

In addition to the sediment treatment areas, reference areas, which did not receive sediment subsidy, were also included in the experimental design (Figure 2.1). Two types of reference sites were used, each replicated twice: 1) an ambient reference marsh, which neither died back nor received sediment (2-5 cm above the ambient benchmark) and 2) a degraded

reference marsh, which died back but did not receive sediment (-0.5 - -2.5 cm below the ambient benchmark). These elevations, in addition to the STL elevations, can all be related to the North American Vertical Datum of 1988 (NAVD 88) by adding 29.78 cm to the marsh surface elevations. Sediments in the reference zone (ambient and degraded) were comprised of 7.71 ± 2.55 % sand, 34.88 ± 1.77 % silt, 49.74 ± 10.25 % clay and 27.52 ± 1.24 % organic matter (Schrift *et al.*, 2008).

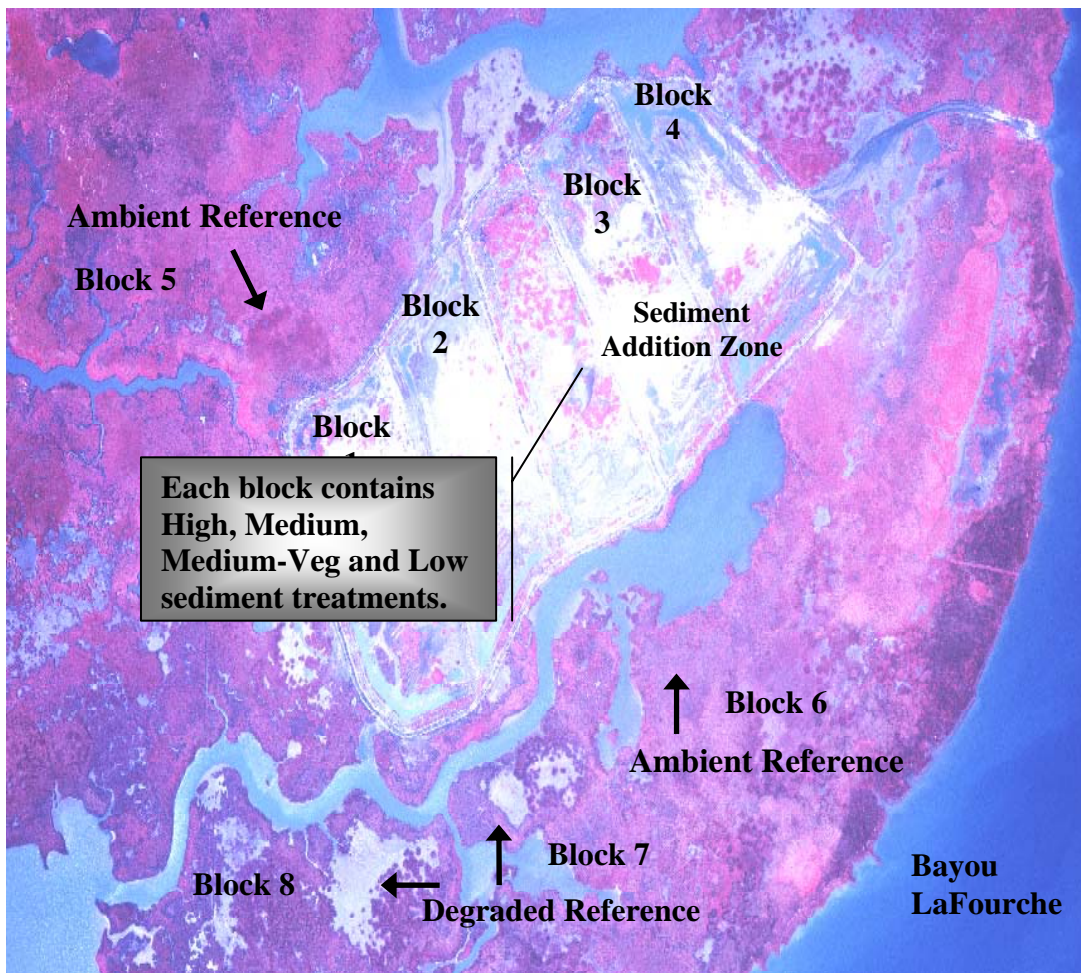


Figure 3.1. Sediment subsidy treatment site (blocks 1-4) and references (blocks 5-8).

3.2.2 Root and Rhizome Decomposition

Decomposition of roots and rhizomes was measured using the litter bag technique (Hackney and de la Cruz, 1980). Live *S. alterniflora* plants were collected from a nearby natural

marsh in June 2005. The live plants were transported in buckets back to the laboratory at Louisiana State University, where they were rinsed of all soil and extraneous material. Roots and rhizomes were then separated from the aboveground portion of the plant and rinsed a second time. Live roots and rhizomes were identified by color, turgidity and structural integrity and then separated and air dried to a constant mass. Nylon mesh bags (8 x 30 cm, 0.4 mm mesh size) were filled with the air-dried root (1.0 g) or rhizome tissue (1.0 g) and placed in the soil, so that the mid-point of the tissue was approximately 15 cm belowground.

The litterbags were collected over a period of 2 years (June 2005-July 2007), at a sampling interval of 2 weeks, 1 month, 2 months, 4 months, 8 months, 16 months and 25 months after installation. After retrieval, the litterbags were gently rinsed with deionized water over a 1mm sieve, and the tissue was oven dried to a constant mass at 60 °C. The tissue was then weighed and percent mass remaining (% MR) was calculated using the following equation:

$$\% \text{ MR} = (w_t/w_0) \cdot 100 \quad (3.1)$$

where w_0 is dry weight at time zero, and w_t is dry weight at time t (days after installation). After weighing air-dried tissue, drying at 60 °C and reweighing, an average moisture correction factor, was applied to the starting mass (w_0) of air-dried tissues. Separate moisture correction factors were calculated for roots and rhizomes.

To examine the decomposition of total belowground material (roots+rhizomes), individual root and rhizome % MR values were weighted with a relative volume correction factor and summed. To calculate the volume correction factor, roots and rhizomes were collected from cores (7.5 x 30 cm) taken from each STL and reference block, and their volume was measured by displacement. Relative volume (% V) was then calculated using the following equation:

$$\% V = (V_t / V_{Rt+Rz}) \cdot 100 \quad (3.2)$$

Where % V = relative volume, V_t = individual root or rhizome volume and V_{Rt+Rz} = sum total volume of root and rhizome tissues. The % V correction factor was then applied to the respective % MR value before summation so that percent mass remaining of total roots and rhizomes would not exceed 100 %.

For both individual roots and rhizomes, as well as for total belowground biomass (roots+rhizomes), the rate of decomposition was derived using a single negative exponential decay model:

$$Y = ae^{-kt} \quad (3.3)$$

where Y is percent mass remaining after time, t (days after installation), a is the parameter constant and $-k$ is the rate constant (% mass lost·day⁻¹) (Wieder and Lang, 1982). Regression analysis was performed using the nonlinear regression procedure, proc nlin, from SAS statistical software (version 9.1.2; SAS Institute, Inc., 2004).

3.2.3 Cellulose Decomposition

Cellulose decomposition was measured using the cotton strip technique (Maltby, 1988). This method provides information on cellulytic activity in the marsh, as compared to decomposition of whole plant tissues using the litterbag technique. Additionally, the use of cotton strips allows for examination of decomposition along a depth profile. The cotton strip technique employs the use of artist's canvas (12-ounce duck, very close construction, unprimed, raw, 100% cotton, un-dyed, style number 548; Tara Materials, Inc., Lawrenceville, GA) as a proxy for cellulose (Slocum *et al.*, in press). Cotton strips (10 cm wide x 30 cm long) were vertically inserted in the marsh soil using a sharp shooter shovel in June 2006. A horizontal incision was made at the top of the cotton strip indicating the location of the marsh surface. After

13 days in the marsh, the cotton strips were retrieved. Additionally, during collection of the test cotton strips, control strips were inserted and immediately retrieved to account for handling effects. These controls were processed in the same manner as the test strips and were used as the baseline for decomposition measurements of the test cotton strips.

After collection, the cotton strips were rinsed gently with deionized water and all soil and extraneous material was removed. The cotton strips were then allowed to air dry over night, after which they were cut into 2 cm subsections along the vertical profile (Slocum *et al.*, in press). Decomposition of the 2 cm subsections was measured as tensile strength lost, compared to the reference subsection, using a Dillon Quantrol™ Snapshot Tension Compression Motorized Test Stand tensometer connected to a Dillon Quantrol™ Advanced Force Gauge. The rate of decomposition was then calculated as percent cotton strip tensile strength lost per day (% CTSL·day⁻¹):

$$\% \text{ CTSL} \cdot \text{day}^{-1} = [(1-N/C)/t] \times 100 \quad (3.4)$$

where N is strength of the subsection (Newtons), C is mean strength of the reference substrips, and t is time (days) in the marsh.

3.2.4 Soil Physico-chemical Measurements

In November 2006, a core (5 x 10 cm) was taken at each STL and reference replicate to measure soil bulk density, % organic matter, % moisture and electrical conductivity. After collection, the cores were analyzed for wet weight, dried at 65 °C, and weighed again to determine bulk density and % moisture. A portion of the dried soil was also used to measure electrical conductivity and organic matter content. To determine electrical conductivity, 5 g of dried soil was mixed vigorously for one hour with 30 ml of distilled water. The mixture was then centrifuged at 2817 g for 5 minutes, and the supernatant was analyzed for electrical conductivity

on a Cole Parmer 19820-00 meter. To determine organic matter content, approximately 2-3 grams of dry soil was treated with 1N HCl until all inorganic carbonates were volatilized. The soil was then analyzed for percent organic matter through loss on ignition at 550 °C in a Fisher Isotherm combustion oven (Programmable Forced Draft Furnaces, model 10-750-126) (Nelson and Sommers, 1996).

A second soil core (5 x 15 cm) was simultaneously taken at each STL and reference block to measure soil pH (moist sediment), soil extractable nutrients and other elements (NH₄-N, NO₃-N, P, Fe, K, Mg, Mn, Na, and S). The soil cores were immediately placed on ice in the field and transported back to the laboratory at Louisiana State University, where they were homogenized. After homogenization, several soil aliquots were collected to perform the following extractions: NH₄-N and NO₃-N (2 M KCl (Bremner and Kenney, 1966)); P (Bray-2 (Byrnside and Sturgis, 1958)); Ca, K, Mg and Na (ammonium acetate (Thomas, 1982)); and Fe and Mn (DTPA (Lindsay and Norvell, 1978)). Following extraction, NH₄-N and NO₃-N samples were filtered through a 0.45 µm filter and measured on a segmented flow AutoAnalyzer (Flow Solution IV AutoAnalyzer, O-I Analytical, USA). The remaining extracts were measured with an inductively coupled argon plasma emission spectrometer (ICP) (Spectro Ciros CCE, Spectro Analytical Instruments, Germany).

Redox potential was also measured during the same sampling event using bright platinum electrodes, a calomel reference electrode and a portable Cole-Parmer digital pH-mV meter. Three platinum electrodes were placed 15 cm below the soil surface at each STL and reference block, and the average of the three readings was used in statistical analyses.

Additionally, a third soil core was taken in February 2006 to measure soil sulfide concentrations. The cores (5 x 10 cm) were taken from each treatment replicate and immediately

placed in a centrifuge tube (500 ml) containing air-tight septa. The core was purged with nitrogen gas for 2 minutes to maintain an anoxic environment and then stored on ice. Once the cores were returned to the laboratory, they were centrifuged at 2817 g for 20 minutes to extract porewater from the soil. The supernatant was decanted, stabilized with an anti-oxidant buffer and analyzed for total soluble sulfides (Lazar Model IS-146 sulfide electrode, Lazar Research Laboratories, Los Angeles, CA).

3.2.5 Statistical Methods

Sediment treatments were added in a randomized incomplete block design (6 treatment levels, $n=2-4$) (Figure 3.1). The incomplete designation arises from the fact that not all treatment levels are found in every replicate block. For example, the four blocks containing the sediment addition treatments do not contain reference treatments, and the reference blocks do not contain sediment addition treatments.

To determine how sediment addition affected decomposition of total belowground material (root+rhizome), I used a one-way mixed model ANOVA, with sediment treatment level as the fixed effect and block as the random effect. A two-way mixed model ANOVA was used to determine the effects of sediment subsidy and tissue type on individual decomposition rates for roots and rhizomes. To test the interactive effects of both sediment subsidy and depth on cellulose decomposition, a two-way mixed model ANOVA was used.

Soil physical and chemical analytes were consolidated into composite variables using principle component analysis (PCA). Only principle components (PCs) with eigenvalues > 1 were used for subsequent analyses. To determine the effect of sediment subsidy on the rotated factor scores, I used a one-way mixed model ANOVA, with sediment subsidy as the fixed effect and block as the random effect.

To determine which environmental factors most influenced decomposition, I conducted a multiple regression analysis including all PCs from the PCA. The model used in the multiple regression analysis was derived by using the stepwise selection method to include only those independent variables in the model that significantly ($p < 0.15$) influence the response variable, decomposition. Separate multiple regression analyses were performed for total root+rhizome decomposition and cellulose decomposition.

For all statistical tests, normality and homogeneity of variance were determined by using the Shapiro-Wilks test, and box-plots. Natural log and square root transformations were used to improve normality only in the PCA. Pairwise comparisons were made using Fisher's Protected LSD tests ($p < 0.05$). All statistical tests were performed using the MIXED, FACTOR, or REG procedures of SAS 9.1.2 unless otherwise noted (SAS Institute Inc., 2004).

3.3 Results

3.3.1 Root and Rhizome Decomposition

Sediment addition significantly affected decomposition of roots and rhizomes; however, the influence of elevation on decomposition was dependent upon tissue type (Figure 3.2). The rate of root decomposition in the sediment enhanced areas was not significantly different from decomposition rates in the reference areas. In contrast, rhizome tissue decomposition was significantly greater at the High and Medium sediment treatment levels (STLs) compared to the Low and Medium-Veg STLs, which were equivalent to the reference sites. Furthermore, rhizome decomposition was faster than root decomposition at all marsh locations, except for the Low STL (Figure 3.2). Thus, large amounts of sediment addition, resulting in elevations above 20 cm, caused rhizome decomposition to increase compared to the reference sites; whereas moderate

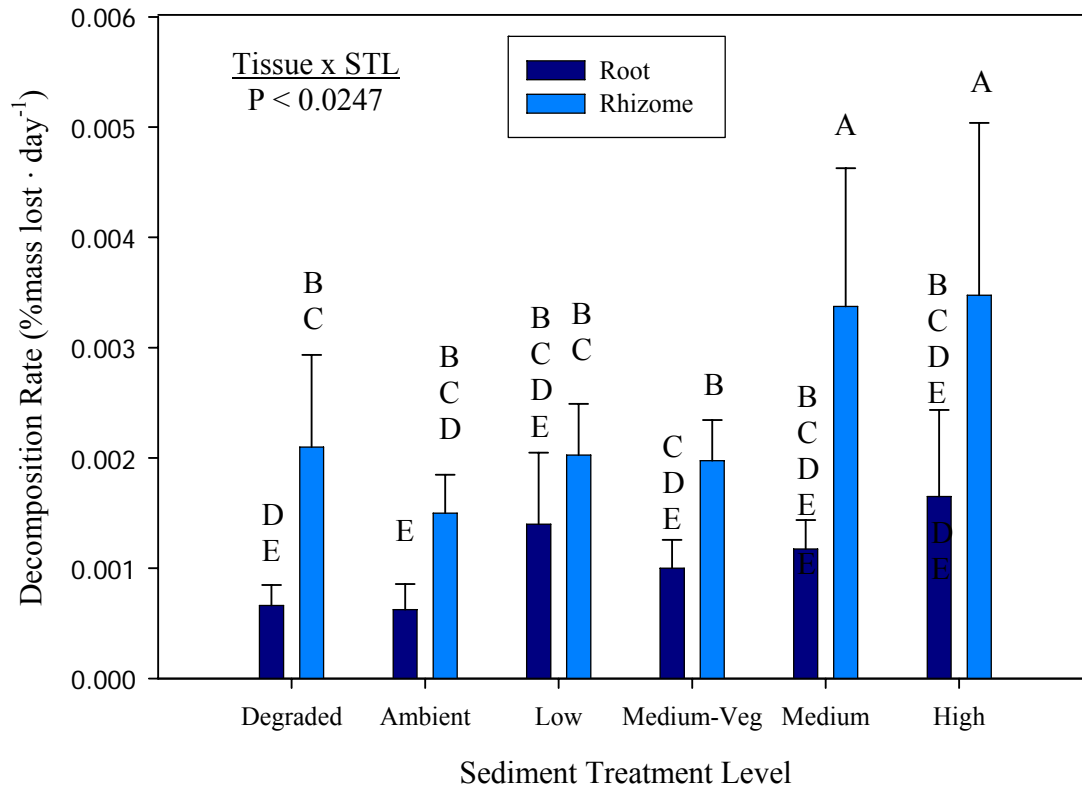


Figure 3.2. The interactive effects of sediment subsidy and tissue type on the rate of belowground decomposition. Error bars are standard errors and different letters represent significant differences among means (Fisher's Protected LSD, $p < 0.05$).

amounts of sediment addition resulted in equivalent decomposition rates compared to the reference sites.

Additionally, sediment subsidy significantly affected decomposition of total belowground biomass (roots+rhizomes) (Figure 3.3). I observed the highest decomposition rates in High and Medium STLs, moderate rates of decomposition in Low and Medium-Veg STLs and low rates of decomposition in both reference types (Figure 3.3).

3.3.2 Cellulose Decomposition

Cellulose decomposition significantly decreased with increasing sediment addition, with the lowest % CTS \cdot day $^{-1}$ at the High STL (Figure 3.4). The main effect of sediment addition, however, varied with depth (Figure 3.5). Below 12 cm depth, cellulose degradation did not

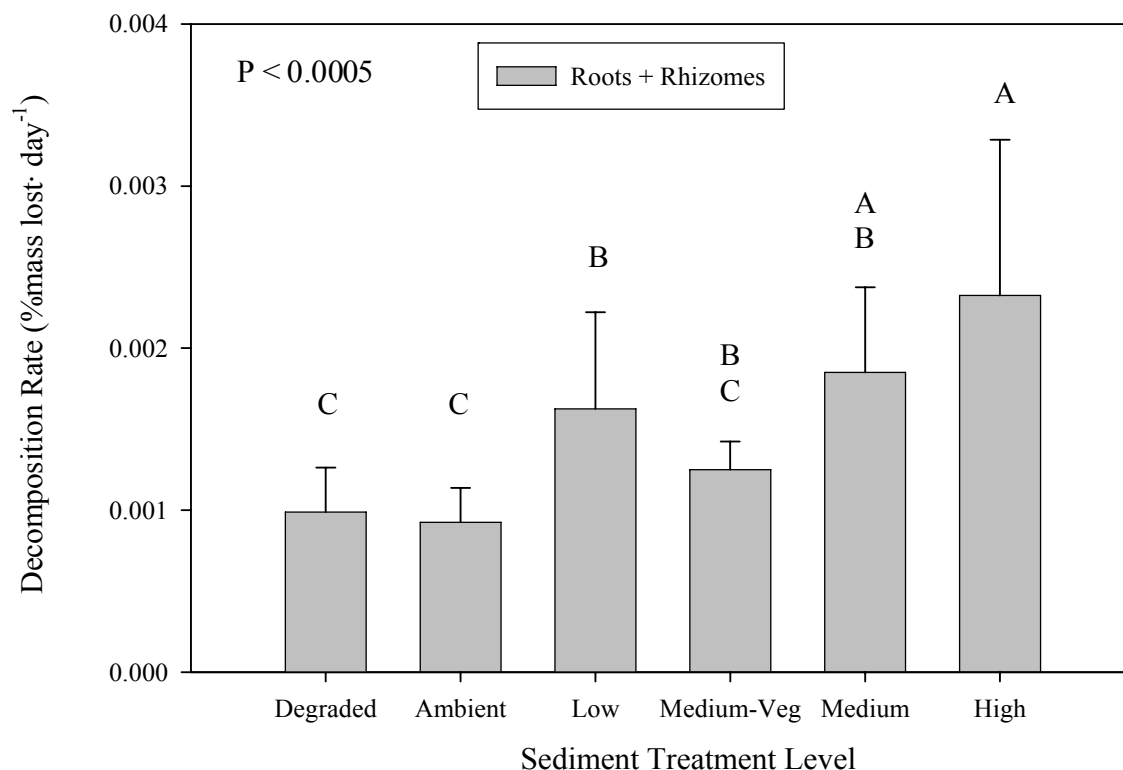


Figure 3.3. The effect of sediment subsidy on belowground decomposition of total belowground biomass (root+rhizome tissue). Error bars are standard errors and different letters represent significant differences among means (Fisher's Protected LSD, $p < 0.05$).

significantly differ with sediment addition. Above 12 cm, however, the treatments receiving greater sediment additions had lower decomposition compared to areas of moderate-low elevation. Additionally, significant changes in cellulose decomposition, in terms of depth, only occurred at depths above 12 cm and in areas of moderate sediment addition (Medium, Medium-Veg and Low STLs), where decomposition peaked between 6-12 cm depth (Figure 3.5).

3.3.3 Soil Conditions

The physico-chemical parameters characterizing the marsh soil were highly intercorrelated (Table 3.1). Principle component analysis of soil variables resulted in three principal components (PCs) accounting for 87 % of the variability in the dataset. The three PCs associated with the soil variables included a soil moisture/salinity component (PC1), an iron/phosphorus component (PC2) and an oxidation/nitrate component (PC3).

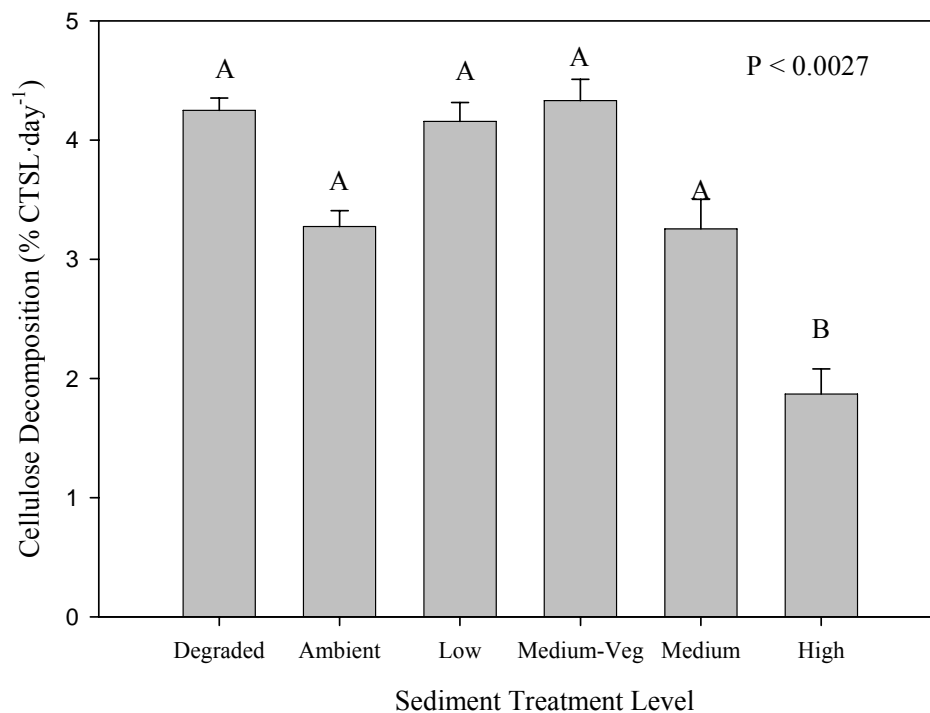


Figure 3.4. Decomposition of cellulose (% CTSL·day⁻¹) as effected by sediment subsidy. Error bars represent standard errors and different letters represent significant differences among means (Fisher's Protected LSD, $p < 0.05$).

PC1 (Soil Moisture/Salinity), which accounted for 65 % of variability in the dataset, was defined by variables associated with flooded soils such as increasing sulfide ammonium, % moisture, % organic matter and decreasing bulk density. Additionally, PC1 was also defined by variables associated with salinity such as conductivity, sodium, potassium and magnesium. PC2 (Fe/P) was positively loaded with iron and phosphorus and accounted for 15 % of the variance associated with the dataset. PC3 (Oxidation/NO₃) was defined by reduction-oxidation potential and nitrate concentrations and explained only 7 % of the variance in the soil dataset.

Sediment addition significantly affected soil characteristics as evidenced by the observed decrease in PC1 (Soil Moisture/Salinity) at the High, Medium, Medium-Veg and Low STLs compared to the reference areas (Figure 3.6.1). Iron and phosphorus concentrations (PC2) were

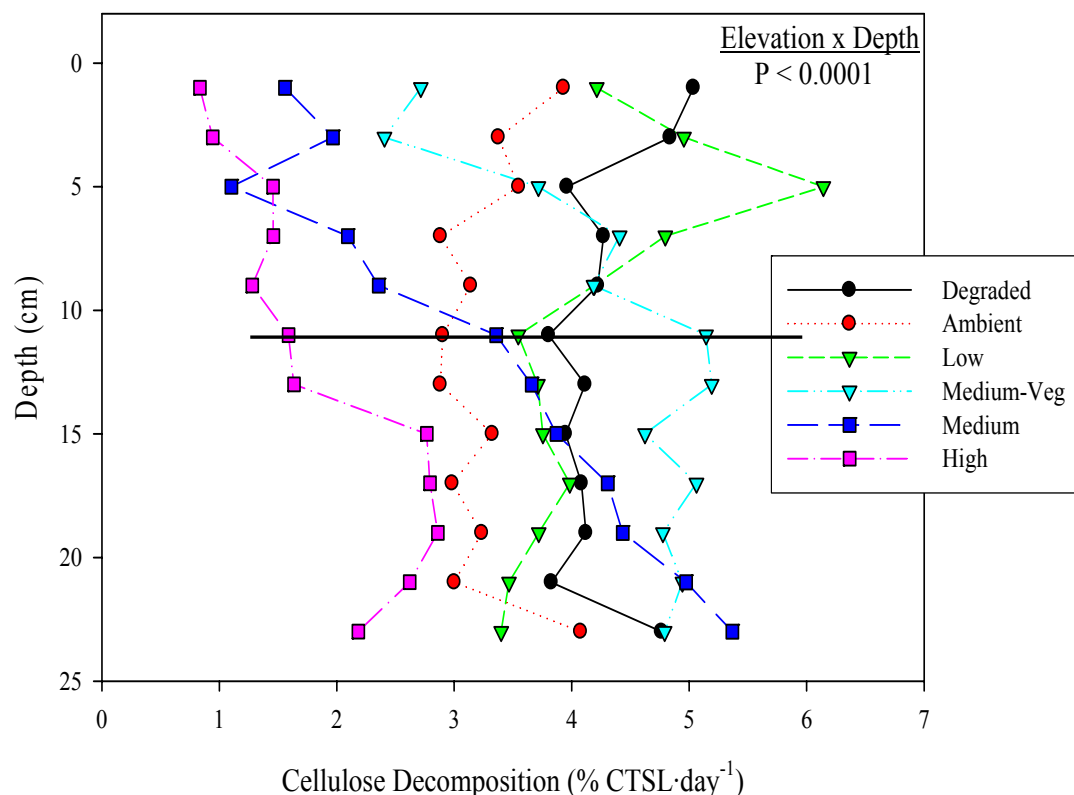


Figure 3.5. Graph showing the interactive effects of depth and elevation on cellulose decomposition (% CTSL·day⁻¹). Error bars were not included to maintain clarity of the graph. The solid black line represents the depth (12 cm) below which there is no significant difference across STL or depth treatment (except for Medium, which significantly increased at 23 cm). Significant differences among means reported in the text are based on Fisher's Protected LSD ($p < 0.05$).

equivalent between the reference sites and the Low and Medium-Veg STLs and significantly lower at the High and Medium STLs (Figure 3.6.2). In contrast no discernable trend was observed for PC3 (Oxidation/NO₃) (data not shown). However, sediment subsidy significantly affected redox potential, *per se*, with Eh values higher in areas receiving sediment addition compared to the reference sites (Figure 3.6.3).

3.3.4 Determinants of Decomposition

Oxidation, or redox potential, explained approximately 54 % of the variability associated with root and rhizome decomposition (Table 3.2). Redox potential was positively correlated to tissue decomposition, indicating that as soil oxidation increased, decomposition increased.

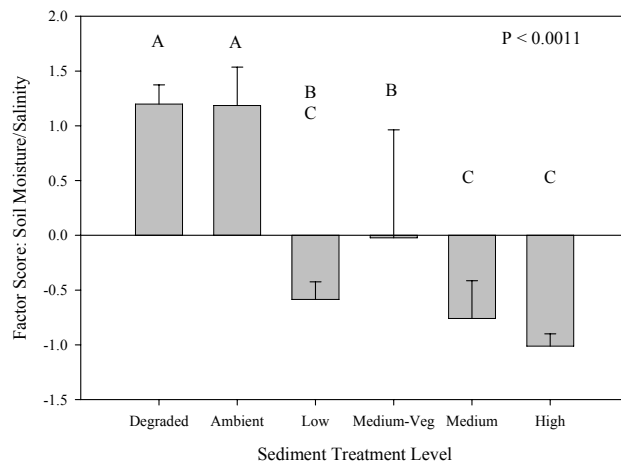
Table 3.1. Correlations between indicator variables and principal components (PCs) for soil characteristics. Eigen values and percent variation explained are included for each PC. Bolded loadings indicate variables that define the PC. Symbols ^{ln} and ^{-1/2} denote natural log transformation and square root transformation of the data, respectively.

Indicator Variables	PC1: Moisture/ Salinity	Soil PC2: Fe/ P	PC3: Oxidation/ NO₃
Ammonium ^{ln}	0.8325	-0.1852	-0.1649
Conductivity ^{ln}	0.8551	0.1038	-0.3816
Iron ^{-1/2}	0.1850	0.8374	-0.3706
Magnesium ^{ln}	0.9383	0.1213	-0.1465
Manganese ^{ln}	-0.8018	0.4350	-0.1905
Nitrate ^{ln}	0.1688	-0.3133	0.8882
Phosphorous ^{ln}	0.1674	0.8467	-0.0651
Potassium ^{ln}	0.8937	0.3370	-0.1435
Sodium ^{ln}	0.9517	0.0940	-0.1370
Sulfur ^{ln}	0.9485	0.1801	-0.1397
Sulfide ^{ln}	0.7437	-0.0859	-0.4241
Redox potential	-0.5248	-0.1365	0.7101
Bulk density	-0.9474	-0.2702	0.0344
Ph	-0.8529	-0.1962	-0.0986
% Moisture ^{ln}	0.9326	0.3010	-0.0456
% Organic Matter ^{ln}	0.9375	0.1998	0.0331
Eigenvalue	10.38	2.43	1.14
% Variance Explained	65 %	15 %	7 %
Cumulative % Variance Explained	87 %		

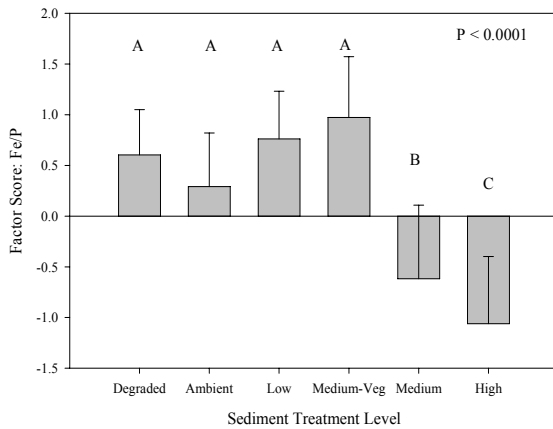
Additionally, redox potential and decomposition are significantly greater in areas that received sediment subsidy. Therefore, decomposition of roots and rhizomes is largely controlled by the aerobic condition of the soil, and is faster in those areas that received sediment subsidy compared to reference areas.

Sediment addition, soil moisture and salinity (PC1), and iron and phosphorus (PC2) explained the majority of variability (64 %) associated with cellulose decomposition (Table 3.2). Like root and rhizome decomposition, cellulose decomposition is largely influenced by elevation

1)



2)



3)

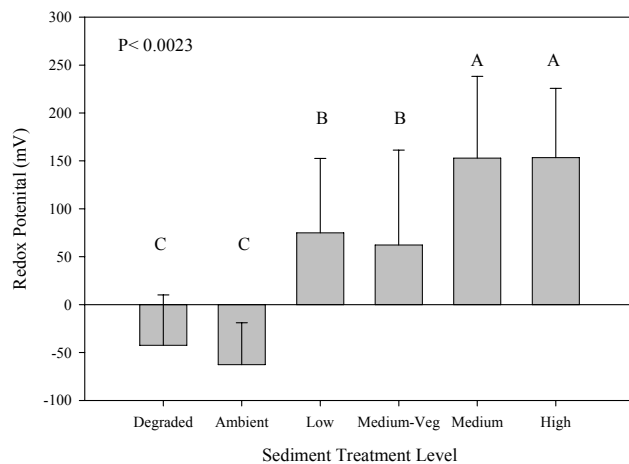


Figure 3.6. Effect of sediment subsidy on 1) Soil moisture and salinity (PC1), 2) Iron and phosphorus (PC2) and 3) Redox Potential. Error bars represent standard errors, and different letters denote significant differences among means (Fisher's Protected LSD, $p < 0.05$).

Table 3.2. Multiple regression models for root + rhizome and cellulose decomposition as selected from all possible models by the stepwise selection method ($p < 0.15$).

Response Variable	Independent Variable	Parameter Estimate	Partial R^2	R^2	P-Value
Root + Rhizome Decomposition	Oxidation	5.4E-06	.	0.5414	0.0002
Cellulose Decomposition	Sediment Addition	-0.7357	0.3714	0.6367	0.0008
	PC1 (Soil Moisture/Salinity)	0.77862	0.2316		
	PC2 (Fe/P)	0.23417	0.0338		

(sediment addition) and the resulting hydrology and moisture of the system. However, % CTSL·day⁻¹ is negatively correlated with sediment addition and positively correlated with soil moisture and salinity (PC1). This trend implies that cellulose decomposition is faster at lower elevations that receive more flooding, which supports the results from ANOVA tests. Additionally, cellulose decomposition is positively correlated with increasing iron and phosphorus concentrations (PC2), which are higher in areas of low-moderate elevation. In contrast to root and rhizome tissues, highly aerobic soils are not as important for cellulose decomposition, and other factors associated with flooded soils, such as soil moisture and fertility, may be more influential in driving cellulose decomposition.

3.4 Discussion and Conclusions

Sediment subsidy had a significant effect on decomposition of belowground organic matter, both for roots and rhizomes as well as for cellulose material. Decomposition of roots and rhizomes was significantly influenced by increasing redox potential, which was in turn

influenced by increasing elevations resulting from sediment addition. Areas that received more sediment had higher redox potential, lower soil moisture and higher rates of root and rhizome decomposition. It has been well documented that decomposition of organic matter increases under aerated conditions (Reddy and Patrick, 1975; DeLaune *et al.*, 1981), compared to slower rates of decomposition observed under anaerobic soil conditions (Waksman *et al.*, 1928; Waksman and Stevens, 1929; Tenney and Waksman, 1930; Reddy and Patrick, 1975; Tate, 1979; DeLaune *et al.*, 1981; McKee and Seneca, 1982). Additionally, Hemminga *et al.* (1988) reported similar results in which belowground decomposition of roots and rhizomes significantly increased with increasing marsh surface elevation.

Although decomposition of total belowground biomass (roots + rhizomes) was clearly influenced by increasing elevation, the effect of sediment addition was not uniform across tissue type. Root decomposition showed no effect of sediment addition, whereas rhizome decomposition was significantly higher in heavily subsidized STLs. Additionally, rhizome decomposition was faster than root decomposition at all but one marsh location.

Differential decomposition of roots versus rhizomes has been observed in other marsh species including *Carex lasiocarpa*, *Schoenoplectus americanus* and *Juncus roemerianus* (Hackney and de la Cruz, 1980; Scheffer and Aerts, 2000; Saunders, C.J. unpublished data/personal communication), which may be due to differences in tissue quality, including nutrient and lignin content (Valiela *et al.*, 1985; Ball and Drake, 1997; Scheffer and Aerts, 2000; Saunders *et al.*, 2006). In a study by Scheffer and Aerts (2000), *Carex lasiocarpa* rhizomes contained lower concentrations of structural compounds, such as lignin, cell wall material and holocellulose compared to roots. Furthermore, *C. lasiocarpa* rhizomes had higher concentrations of nitrogen and phosphorus, resulting in lower C:N ratios and higher

decomposition rates than roots of the same species. Saunders *et al.* (2006) also reported that *Schoenoplectus americanus* roots contained more holocellulose and lignin and had higher C:N and lignin:N ratios than rhizomes of the same species, which decomposed at a faster rate than roots (Saunders, C.J. unpublished data/personal communication). Additionally, in accordance with Hackney and de la Cruz (1980), I observed that, although rhizomes appeared to be more rigid than roots at the beginning of the experiment, after two years, roots still maintained their turgor, while rhizomes appeared to be flaccid and soft. Thus, it is likely that *S. alterniflora* roots contain more refractory compounds than rhizomes, resulting in faster decomposition of rhizomes compared to roots, fitting with the generally established relationship between decomposition and litter chemistry (Godshalk and Wetzel, 1978; Maccubin and Hodson, 1980; McKee and Seneca, 1982).

Furthermore, tissue type and elevation interact resulting in greater rates of rhizome decomposition at high elevations compared to areas of moderate-low elevation. The synergistic effect of sediment subsidy and tissue type on decomposition may have important impacts on vertical accretion, or positive elevation change in the marsh. Rhizome biomass represents the majority of belowground standing stock (Schubauer and Hopkinson, 1984; Darby and Turner, 2008; Stagg, 2009), and can exceed maximum aboveground biomass by five times (Darby and Turner, 2008). Given that several studies have illustrated the important role that belowground biomass plays in marsh vertical accretion, (Blum, 1993; Turner *et al.*, 2001; Rybczyk and Cahoon, 2002), it follows that disproportionately greater decomposition of the main contributor to belowground biomass, rhizomes, may have detrimental effects on the ability of the marsh to vertically accrete organic matter and thus incur positive elevation change.

Sediment subsidy also had a significant effect on belowground decomposition of cellulose. In contrast to roots and rhizomes, however, cellulose decomposition decreased in areas of greater sediment addition and resultant high elevation. Results from this study suggest that cellulose decomposition is primarily controlled by factors that vary with elevation, such as flooding, soil moisture and nutrient concentration. The opposite trend was observed for root and rhizome tissue, whose decomposition increased under drier and aerated conditions. The differential rates of decomposition between roots+rhizomes and cellulose can be attributed to the different types of organic matter comprising plant litter versus cotton strips.

In this study, as in several other studies (Latter and Howson, 1977; Harrison *et al.*, 1988; Maltby, 1988; Mendelssohn *et al.*, 1999), cotton strips are used as a proxy measurement of cellulose decomposition. Comprised of 97 % holocellulose, cotton strip decomposition reflects the processes and controlling factors associated with labile tissue decomposition. On the other hand, root and rhizome tissue is structurally more complex and is comprised of both labile organic matter and refractory material. The differential composition of the decomposing organic matter generally results in variable, but predictable, decomposition rates over time as the plant litter is broken down into detritus, with more labile fractions, such as cellulose, decomposing at a greater rate than more refractory compounds, such as lignin (Godshalk and Wetzel, 1978; Maccubin and Hodson, 1980).

Additionally, environmental factors controlling decomposition of organic matter will also vary depending on the degree of lignification. Decomposition of labile organic matter is more heavily influenced by temperature than the degree of oxidation, whereas decomposition of refractory organic matter takes place primarily under warm, aerobic conditions (Godshalk and Wetzel, 1978). Additionally, it appears that anoxic conditions inhibit the decomposition of

recalcitrant organics, such as lignin and aromatic hydrocarbons (Fenchel and Balckburn, 1979), whereas soil oxidation has minimal influence on the decomposition of more labile compounds such as cellulose and protein (Ferdele and Vestal, 1980; Hemminga *et al.*, 1988; Maltby, 1988; Mendelssohn *et al.*, 1999). Accordingly, I found that cellulose decomposition increased in marshes that were frequently flooded and had reduced soils, indicating that the controls on cellulose decomposition are more complex than simply availability of oxygen.

Several other factors have been shown to influence decomposition, including soil fertility and moisture (Mellilo *et al.*, 1982; Fenn, 1991; Halupa and Howes, 1995; Newell *et al.*, 1996; Morris and Bradley, 1999). In this study, decreasing elevation, longer flood duration and consequently greater soil moisture and nutrients (ammonium, iron and phosphorus) accounted for greater than 60% of the variation in cellulose decomposition. Site fertility significantly affects litter decomposition (Fenn, 1991; Royer and Minshall, 1997; Thormann and Bayley, 1997; Laursen, 2004), which can be limited by both nitrogen and phosphorus (Rybczyk *et al.*, 1996; Mendelssohn *et al.*, 1999; Laursen, 2004). Therefore, it is likely that, while reduced soil conditions do not inhibit cellulose decomposition, it is the higher nutrient concentrations at low-moderate elevations that accelerate decomposition. This conclusion was also reached by Mendelssohn *et al.*, (1999), who reported increased rates of cellulose decomposition in frequently flooded, reduced, soils containing high ammonium and phosphorus concentrations.

However, the influence of moisture on cellulose decomposition cannot be discounted, as several studies have reported a promoting effect of moisture on decomposition rates (Frasco and Good, 1982; Halupa and Howes, 1995; Newell, 1996). Furthermore, given the extreme dryness of the high elevations, which were flooded less than 10 % of the time (Materne and Mendelssohn, 2006), it is likely that the observed decrease in cellulose decomposition is in part

due to a lack of moisture. Halupa and Howes (1995) concluded that moisture content of *Spartina alterniflora* litter is directly related to flood duration and frequency and is principally responsible for high decay rates at lower marsh elevations. Although the authors did concede that submergence had a slight inhibitory effect on litter decomposition, this effect was much less prominent than the negative effect of low moisture content associated with infrequent flooding. In the present study, however, moisture related variables and ammonium are correlated (PC1), and iron and phosphorus also increase with increasing decay; therefore the relative effects of moisture and nutrient limitation cannot be separated, indicating that it is a combination of these factors, regulated by flood regime, that control cellulose decomposition.

However, sediment addition and resultant marsh elevation only affected cellulose decomposition above 12 cm depth, with greater cellulose decomposition occurring in areas of low-moderate elevation. Additionally, cellulose decomposition did not significantly change with depth at the High STL, or reference sites, but peaked 6-12 cm below the soil surface at the Low and Medium-Veg STLs. Trends of cellulose decomposition with increasing depth are variable, and have been shown to increase, decrease or remain constant as depth below the soil surface increases (Lawson, 1988; Mendelssohn *et al.*, 1999; Laursen, 2004; Mendelssohn and Slocum, 2004). However, in the two studies where cellulose decomposition increased with depth, similar peaks in decay rates were observed at 8-19 cm depth (Lawson, 1988; Laursen, 2004), which was attributed to increased microbial activity at the root zone where labile carbon sources are plentiful (Howarth and Hobbie 1982, Moriarty *et al.*, 1986).

The significance of the depth by elevation interaction can be interpreted through examining the effects of elevation on vegetative growth, which in turn influences the depth profile of the marsh soil (Hemminga *et al.*, 1988). Excretion of labile organic carbon by plant

roots stimulates microbial activity (Lynch, 1976; Howarth and Hobbie 1982), which may be limited in areas without easily available organic carbon, i.e. plant root leachates, resulting in lower mineralization rates (Clarholm, 1985). Accordingly, in the present study, cellulose decomposition was not affected by soil depth in areas where *S. alterniflora* belowground production was minimal (Stagg, 2009). Furthermore, the peak in decomposition observed in the vegetated marshes occurred within the root zone (0-20 cm) (de la Cruz and Hackney, 1977; Shubauer and Hopkinson, 1984; Darby and Turner, 2008), indicating that plant presence may significantly influence cellulose decomposition. Therefore, sediment addition at moderate intensities results in a flood regime that provides appropriate soil moisture, increased nutrients and belowground primary production, creating optimal conditions for plant-soil interactions and cellulose decomposition.

In conclusion, I determined that the more complex material of roots and rhizomes decomposes faster at levels of greater sediment subsidy and is principally influenced by soil oxidation. Moreover, at extremely high levels of sediment subsidy (> 20 cm above ambient marsh, 50 cm NAVD 88), rhizomes decompose at a disproportionately higher rate than roots and rhizomes at other STLs, which may result in negative elevation change over time. Therefore I suggest that moderate sediment subsidy be applied to achieve optimum mineralization and still allow for organic matter accumulation.

Additionally, cellulose decomposition is not primarily influenced by redox potential, as is root and rhizome tissue, but is accelerated by higher ammonium and phosphorus concentrations, soil moisture, and the interaction of these flood-related factors with plant presence. Therefore, the use of sediment subsidy at moderate intensities can restore hydrologic conditions necessary to achieve plant-soil interactions that will optimize decomposition.

3.5 Literature Cited

- Abd. Aziz, S.A. and Newell, D.B. 1979. Microbial nitrogen transformations in the salt marsh environment. In Jeffries, R.L. and Davy A.J., editors. *Ecological processes in coastal environments*, Blackwell: Oxford, England.
- Alber, M., Swenson, E.M., Adamowicz, S.C. and Mendelssohn, I.A. 2008. Salt marsh dieback: an overview of recent events in the US. *Estuarine, Coastal and Shelf Science*, 80: 1–11.
- Barras, J., Beville, S., Britsch, D., Hartley, S., Hawes, S., Johnston, J., Kemp, P., Kinler, Q., Martucci, A., Porthouse, J., Reed, D., Roy, K., Sapkota, S. and Suhayda, J. 2003. Historical and projected coastal Louisiana land changes: 1978-2050. USGS Open File Report 03-334.
- Barras, J. A. 2006. Land area change in coastal Louisiana after the 2005 hurricanes-a series of three maps: U.S. Geological Survey Open-File Report 06-1274.
- Baumann, R. H. and DeLaune, R. D. 1981. Sedimentation and apparent sea-level rise as factors affecting land loss in coastal Louisiana. In Proceedings of the Conference on Coastal Erosion and Wetland Modification in Louisiana: Causes, Consequences, and Options, US Department of Interior, USFWS: Washington DC, USA. pp. 2-13.
- Baumann, R. H., Day, J. W. Jr. and Miller, C.A. 1984. Mississippi deltaic wetland survival: Sedimentation versus coastal submergence. *Science*, 224: 1093-1095
- Blum, L.K. 1993. *Spartina alterniflora* root dynamics in a Virginia marsh. *Marine Ecology Progress Series*, 102: 169-178.
- Boesch, D.F., Josselyn, M.N., Mehta, A.J., Morris, J.T., Nuttle, W.K., Simenstach, C. A. and Swift, D.J.P. 1994. Scientific assessment of coastal wetland loss, restoration and management in Louisiana. *Journal of Coastal Research: Special Issue*, 20: 1–103.
- Bremner, J. M. and Kenney, D.R. 1966. Determination and isotope-ratio analysis of different forms of nitrogen in soils: 3. Exchangeable ammonium, nitrate, and nitrite by extraction-distillation methods. *Soil Science Society of America Proceedings*, 30: 577-582.
- Bricker-Urso, S., Nixon, S.W., Cochran, J.K., Hirschberg, D.J. and Hunt, C. 1989. Accretion rates and sediment accumulation in Rhode Island salt marshes. *Estuaries*, 12: 300-317
- Byrnside, D.S. Jr. and Sturgis, M.B. 1958. Soil phosphorus and its fractions as related to response of sugar cane to fertilizer phosphorus. Bull No. 513, Louisiana State University Agriculture Experiment Station, Baton Rouge, Louisiana, USA.
- Calloway, J.C., Nyman, J.A. and DeLaune, R.D. 1996. Sediment accretion in coastal wetlands: a review and a simulation of model processes. *Current Topics in Wetland Biogeochemistry*, 2: 2-23.
- Clarholm, M. 1985. Interactions of bacteria, protozoa and plants leading to mineralizations of soil nitrogen. *Soil Biology and Biochemistry*, 17: 181-187.

- Darby, F. A. and Turner, R.E. 2008. Below- and aboveground *Spartina alterniflora* production in a Louisiana salt marsh. *Estuaries and Coasts: JCERF*, 31: 223-231.
- Davis, S.E. III, Childers, D.L. and Noe, G.B. 2006. The contribution of leaching to the rapid release of nutrients and carbon in the early decay of wetland vegetation. *Hydrobiologia*, 569: 87-97.
- Day, J. W., Conner, W. H., Costanza, R., Kemp, G. P. and Mendelssohn, I. A. 1993. Impacts of sea level rise on coastal systems with special emphasis on the Mississippi River deltaic plain. In Warrick, R. A., Barrow, E. M. and Wigley, T. M. L. , editors. *Climate and Sea Level Change: Observations, Projections, and Implications*. Cambridge University Press: Cambridge, Great Britain. pp. 276-296
- de la Cruz, A. A. and Hackney, C. T. 1977. Energy value, elemental composition, and productivity of belowground biomass of a *Juncus* tidal marsh. *Ecology*, 58: 1165-1170
- DeLaune, R. D., Reddy, C.N. and Patrick, W. H. Jr. 1981. Organic matter decomposition in soil as influenced by pH and redox conditions. *Soil Biology and Biochemistry*, 13: 533-534.
- DeLaune, R. D., Pezeshki, S. R., Pardue, J. H., Whitcomb, J. H. and Patrick, W. H. Jr. 1990. Some influences of sediment addition to a deteriorating salt marsh in the Mississippi River deltaic plain: A pilot study. *Journal of Coastal Research*, 6: 181-188.
- Fenchel, T. and Blackburn, T. H. 1979. Bacteria and mineral cycling. Academic Press: New York, U.S.A.
- Fenn, M. 1991. Increased site fertility and litter decomposition rate in high-pollution sites in the San Bernardino Mountains. *Forest Science*, 37: 1163-1181.
- Ferdele, T.W. and Vestal, J.R. 1980. Lignocellulose mineralization by arctic lake sediments in response to nutrient manipulation. *Applied Environmental Microbiology*, 40: 32-39.
- Frasco, B.A. and Good, R.E. 1982. Decomposition dynamics of *Spartina alterniflora* and *Spartina patens* in a New Jersey salt marsh. *American Journal of Botany*, 69: 402-406.
- Godshalk, G.L. and Wetzel, R.G. 1978. Decomposition of aquatic angiosperms. III. *Zostera marina* L., and a conceptual model of decomposition. *Aquatic Botany*, 5: 329-354.
- Good, R. E., Good, N. F. and Frasco, B. R. 1982. A review of primary production and decomposition dynamics of the belowground marsh component. In Kennedy, V.S., editor. *Estuarine comparisons*, Academic Press: New York, U.S.A. pp. 139-158.
- Hackney, C T. and de la Cruz, A. A. 1980. *In situ* decomposition of roots and rhizomes of two tidal marsh plants. *Ecology*, 61: 226-231.

- Hackney, C. T. 1987. Factors affecting accumulation or loss of macroorganic matter in salt marsh sediments. *Ecology*, 68: 1109-1113
- Hackney, C.T. and Cleary, W.J. 1987. Salt marsh loss in southeastern North Carolina lagoons: importance of sea level rise and human activities. *Journal of Coastal Research*, 3: 93-97.
- Halupa, P.J. and Howes, B.L. 1995. Effects of tidally mediated litter moisture content on decomposition of *Spartina alterniflora* and *S. patens*. *Marine Biology*, 123: 379-391.
- Harrison, A.F., Latter, P.M. and Walton, D.W.H. 1988. Appendix I: Current method for preparation, insertion, and processing of cotton strips. In Harrison, A.F., Latter, P.M., and Walton, D.W.H., editors. *Cotton strip assay: an index of decomposition in soils*. Institute of Terrestrial Ecology: Grange-Over-Sands, UK pp. 166-171.
- Hemminga, M.A., Kok, C.J. and de Munck, W. 1988. Decomposition of *Spartina anglica* roots and rhizomes in a salt marsh of the Westerschelde Estuary. *Marine Ecology Progress Series*, 48: 175-184.
- Henriksen, K. and Jensen, A. 1979. Mineralization in a salt marsh ecosystem dominated by *Halimione portulacoides*. In Jeffries, R.L. and Davy, A.J., editors. *Ecological processes in coastal environments*, Blackwell: Oxford, England.
- Howarth, R.W. and Hobbie, J.E. 1982. The regulation of decomposition and heterotrophic microbial activity in salt marsh soils: A review. In Kennedy, V.S., editor. *Estuarine Comparisons*. Academic Press: New York, U.S.A. pp. 183-207.
- Ingold, A. and Havill, D.C. 1984. The influence of sulphide on the distribution of higher plants in salt marshes. *Journal of Ecology*, 72: 1043-1054.
- IPCC. 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). Solomon, S., Qin, D., Manning, M., Marquis, M., Averyt, K., Tignor, M.M.B., Miller, H.L. Jr., and Chen, Z., editors. Cambridge University Press: UK.
- Ivins, E.R., Dokka, R.K. and Blom, R.G. 2007. Post-glacial sediment load and subsidence in coastal Louisiana. *Geophysical Research Letters*, 34: L16303-L16308.
- Koch, M.S. and Mendelssohn, I.A., 1989. Sulphide as a soil phytotoxin: differential responses in two marsh species. *Journal of Ecology*, 77: 565-578.
- Laursen, K.R. 2004. The effects of nutrient enrichment on the decomposition of belowground organic matter in *Sagittaria lancifolia*-dominated oligohaline marsh. Masters Thesis, Louisiana State University, Baton Rouge, LA.
- Latter, P.M. and Howson, G. 1977. The use of cotton strips to indicate cellulose decomposition in the field. *Pedobiologia*, 17: 145-155.

- Lawson, G.J. 1988. Using the cotton strip assay to assess organic matter decomposition patterns in the mires of South Georgia. *In* Harrison, A.F., Latter, P.M. and Walton, D.W.H., editors. *Cotton strip assay: an index of decomposition in soils*. Institute of Terrestrial Ecology: Grange-Over-Sands, UK pp. 134-139.
- Lindsay, W. L. and Norvell, W.A. 1978. Development of a DTPA soil test for zinc, iron, manganese, and copper. *Soil Science Society of America* 42: 421-428.
- Lindstedt, D.M., Swenson, E.M., Reed, D., Twilley, R. and Mendelssohn, I.A. 2006. Marsh dieback technical synthesis report. Technical Report, Coastal Restoration Division, Louisiana Department of Natural Resources.
- Lynch, J. M. 1976. Products of soil microorganisms in relation to plant growth. *Critical Reviews in Microbiology*, 5: 67-107.
- Maccubbin, A.E. and Hodson, R.E. 1980. Mineralization of detrital lignocelluloses by salt marsh sediment microflora. *Applied Environmental Microbiology*, 40: 735-740.
- Maltby, E. 1988. Use of cotton strip assay in wetland and upland environments - an international perspective. *In* Harrison, A. F., Latter, P. M. and Walton, D. W. H., editors. *Cotton Strip Assay: An Index of Decomposition in Soils*. Institute of Terrestrial Ecology: Grange-Over-Sands, Great Britain. pp. 140-154.
- Materne, M.D. and Mendelssohn, I.A. 2006. Beneficial use of hydraulically dredged sediment-slurries for wetland restoration: II. Spatial, hydrologic and vegetative assessment. Governor's Applied Coastal Research and Development Program.
- McKee, K. L. and Seneca, E.D. 1982. The influence of morphology in determining the decomposition of two salt marsh macrophytes. *Estuaries*, 5: 302-309.
- McKee, K.L., Mendelssohn, I.A. and Materne, M.D. 2004. Acute salt marsh dieback in the Mississippi River Deltaic Plain: a drought-induced phenomenon? *Global Ecology and Biogeography*, 13: 67-73.
- Melillo, J. M., Aber, J. D. and Muratore, J. E. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology*, 63: 621-626.
- Mendelssohn, I. A. and Seneca, E. D. 1980. The influence of soil drainage on the growth of salt marsh cordgrass *Spartina alterniflora* in North Carolina. *Estuarine and Coastal Marine Science*, 11: 27-40.
- Mendelssohn, I. A., McKee, K. L. and Patrick, W. H. Jr. 1981. Oxygen deficiency in *Spartina alterniflora* roots: Metabolic adaptation to anoxia. *Science*, 214: 439-441.
- Mendelssohn, I. A. and McKee, K. L. 1988. *Spartina alterniflora* die-back in Louisiana: Time-

- course investigation of soil waterlogging effects. *Journal of Ecology*, 76: 509-521.
- Mendelssohn, I.A., Sorrell, B.K., Brix, H., Schierup, H.H., Lorenzen, B. and Maltby, E. 1999. Controls on soil cellulose decomposition along a salinity gradient in a *Phragmites australis* wetland in Denmark. *Aquatic Botany*, 64: 381-398.
- Mendelssohn, I.A. and Kuhn, N.L. 2003. Sediment subsidy: effects on soil-plant responses in a rapidly submerging coastal salt marsh. *Ecological Engineering*, 21: 115-128.
- Mendelssohn, I.A. and Slocum, M.G. 2004. Relationship between soil cellulose decomposition and oil contamination after an oil spill at Swanson Creek. *Maryland. Marine Pollution Bulletin*, 48: 359-370.
- Moriarty, D.J.W., Iverson, R.L. and Pollard, P.C. 1986. Exudation of organic carbon by the seagrass *Halodule wrightii* Aschers. and its effect on bacterial growth in the sediment. *Journal of Experimental Marine Biology and Ecology*, 96: 115-126.
- Morris, J.T. and Bradley, P.M. 1999. Effects of nutrient loading on the carbon balance of coastal wetland sediments. *Limnology and Oceanography*, 44: 699-702.
- Nelson, D.W. and Sommers, L.E. 1996. Carbon and organic matter: loss on ignition method. In *Methods of Soil Analysis, Part 3, Chemical Methods*, Soil Science Society of America, Inc., American Society of Agronomy, Inc., Madison, WI. pp. 1001-1010.
- Newell, S.Y., Arsuffi, T.L. and Palm, L.A. 1996. Misting and nitrogen fertilization of shoots of a salt marsh grass: effects upon fungal decay of leaf blades. *Oecologia*, 108: 459-460.
- Nyman, J.A., Walters, R.J., DeLaune, R.D. and Patrick, W.H. Jr. 2006. Marsh vertical accretion via vegetative growth. *Estuarine, Coastal and Shelf Science*, 69: 370-380.
- Ramsey, K.E. and Penland, S. 1992. Sea level rise and subsidence in Louisiana and the Gulf of Mexico. In Williams, S.J., Cichon, H.A., Westpal, K. and Ramsey, K., editors. *Representative publications from the Louisiana barrier island erosion study*. U.S. Department of the Interior, U.S.G.S. Open File Report 92-530.
- Reddy, K.R. and Patrick, W.H. Jr. 1975. Effect of alternate aerobic and anaerobic conditions on redox potential, organic matter decomposition and nitrogen loss in a flooded soil. *Soil Biology and Biochemistry*, 7: 87-94.
- Reed, D. J. 1995. The response of coastal marshes to sea-level rise: survival or submergence. *Earth Surface Process and Landforms*, 20: 39-48.
- Royer, T. V. and Minshall, G.W. 1997. Rapid breakdown of allochthonous and autochthonous plant material in a eutrophic river. *Hydrobiology*, 344: 81-86.
- Rozas, L.P. and Minello, T.J. 2001. Marsh terracing as a wetland restoration tool for creating

- fishery habitat. *Wetlands*, 21: 327-341.
- Rybczyk, J.M., Garson, G. and Day, J.W. Jr. 1996. Nutrient enrichment and decomposition in wetland ecosystems: models, analyses, and effects. *Current Topics in Wetland Biogeochemistry*, 2: 52-72.
- Rybczyk, J.M. and Cahoon, D.R. 2002. Estimating the potential for submergence for two wetlands in the Mississippi River Delta. *Estuaries*, 25: 985-998.
- SAS Institute Inc., 2004. *SAS® 9.1.2. Qualification Tools User's Guide*, Cary, NC.
- Schrift, A.M., Mendelssohn, I.A. and Materne, M.D. 2008. Salt marsh restoration with sediment-slurry amendments following a drought-induced large-scale disturbance. *Wetlands*, 28: 1071-1085.
- Schubauer, J.P. and Hopkins, C.S. 1984. Above- and belowground emergent macrophyte production and turnover in a coastal marsh ecosystem, Georgia. *Limnology and Oceanography*, 29: 1052-1063.
- Slocum, M.G., Mendelssohn, I.A. and Kuhn, N.L. 2005. Effects of sediment slurry enrichment on salt marsh rehabilitation: plant and soil responses over seven years. *Estuaries*, 28: 519-528.
- Slocum, M., Roberts, J. and Mendelssohn, I.A. *in press*. Artist canvas as a new standard for the cotton strip assay. *Journal of Plant Nutrition and Soil Science*.
- Stagg, C.L. 2009. Remediating impacts of global climate change-induced submergence on salt marsh ecosystem functions. Ph.D. dissertation. Louisiana State University, Baton Rouge, LA.
- Tate, R.L. 1979. Effect of flooding on microbial activities in organic soils: carbon metabolism. *Soil Science*, 128: 267-272.
- Teal, J.M. 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology*, 43: 614-624.
- Tenney, F. G. and Waksman, S. A. 1930. Composition of natural organic materials and their decomposition in the soil: V. Decomposition of various chemical constituents in plant materials under an-aerobic conditions. *Soil Science*, 30: 143-160.
- Thomas, G. W. 1982. Exchangeable cations. In Page, A. L., Miller, R. H., and Keeney, D. R., editors. *Methods of soil analysis: Part 2--chemical and microbiological properties*, second edition. American Society of Agronomy, Inc. and Soil Science Society of America, Inc., Madison, WI. pp.159-165.
- Thormann, M. N. and Bayley, S. E. 1997. Decomposition along a moderate-rich fen-marsh peatland gradient in boreal Alberta, Canada. *Wetlands*, 17: 123-137.

- Tornqvist, T.E., Wallace, D.J., Storms, J.E.A., Wallinga, J., Van Dam, R.L., Blaauw, M., Derksen, M.S., Klerks, J.W., Meijneken, C. and Snijders, E.M.A. 2008. Mississippi Delta subsidence primarily caused by compaction of Holocene strata. *Nature Geoscience*, 3: 173-176.
- Turner, R.E., Swenson, E.M. and Milan, C.S. 2001. Contrasting organic and inorganic content in recently accumulated salt marsh sediments. In Weinstein, M. and Kreeger, D.D., editors. *Concepts and controversies in tidal marsh ecology*, Kluwer Academic Publishers: Dordrecht, The Netherlands. pp. 583-595.
- Turner, R.E., Swenson, E.M., Milan, C.S., Lee, J.M. and Oswald, T.A. 2004. Below-ground biomass in healthy and impaired marshes. *Ecological Research*, 19: 29-35.
- Turner, R.E., Milan, C.S. and Swenson, E.M. 2006b. Recent volumetric changes in salt marsh soils. *Estuarine, Coastal and Shelf Science*, 69: 352-359.
- Valiela, I. and Teal, J.M. 1979. Inputs, outputs and interconversions of nitrogen in a salt marsh ecosystem. In Jeffries, R.L. and Davy A.J., editors. *Ecological processes in coastal environments*, Blackwell: Oxford, England.
- Waksman, S.A. and Stevens, K.R. 1929. Contribution to the chemical composition of peat: V. The role of microorganisms in peat formation and decomposition. *Soil Science*, 28: 315-340.
- Waksman, S.A., Tenney, F.G. and Stevens, K.R. 1928. Role of microorganisms in the transformation of organic matter in forest soils. *Ecology*, 9: 126-144.
- Webb, E. C., Mendelssohn, I. A. and Wilsey, B. J., 1995. Causes for the vegetation dieback in a Louisiana salt marsh: A bioassay approach. *Aquatic Botany*, 51: 281-289.
- Wieder, R.K. and Lang, G.E. 1982. A critique of the analytical methods used in examining decomposition data obtained from litter bags. *Ecology*, 63(6): 1636-1642.
- Wilsey, B. J., McKee, K. L. and Mendelssohn, I. A. 1992. Effects of increased elevation and macro- and micronutrient additions on *Spartina alterniflora* transplant success in salt-marsh dieback areas in Louisiana. *Environmental Management*, 16: 505-511.
- Zedler, J.B. and Callaway, J.C. 1999. Tracking wetland restoration: Do mitigation sites follow desired trajectories? *Restoration Ecology*, 7: 69-73.

CHAPTER 4

GROWTH, SURVIVAL AND PRODUCTION OF *LITTORARIA IRRORATA* IN A SALT MARSH RESTORED USING SEDIMENT ADDITION

4.1 Introduction

The salt marsh periwinkle, *Littoraria irrorata*, is a conspicuous inhabitant of intertidal salt marshes along the mid-Atlantic, southeastern and Gulf coasts of the United States (see Silliman and Zieman, 2001). Studies investigating the interactions between *L. irrorata* and *Spartina alterniflora* have dramatically changed our understanding of salt marsh energy flow (Silliman and Zieman, 2001; Silliman and Bertness, 2002; Silliman and Newell, 2003). Although the salt marsh has historically been viewed as a resource limited system (Odum and Smalley, 1959; Teal, 1962), recent studies have revealed that *L. irrorata* has the potential to exert top-down control on primary production (Silliman and Zieman, 2001; Silliman and Bertness, 2002) through facilitating fungal invasion of *S. alterniflora* (Silliman and Newell, 2003). However, nutrient stimulation of *S. alterniflora* is not eliminated in the presence of *L. irrorata*, suggesting that this system is simultaneously controlled through both bottom-up and top-down forces (Silliman and Zieman, 2001). Furthermore, *L. irrorata* may influence nutrient dynamics through expediting the decomposition of *S. alterniflora* (Kemp *et al.*, 1990; Silliman and Newell, 2003), indicating that *L. irrorata* has the potential to impact salt marsh production bi-directionally, i.e. through top-down control of *S. alterniflora* and bottom-up control in the detrital pathway.

Therefore, the multi-faceted role of *L. irrorata* in salt marsh energy flow makes it an important species in terms of ecosystem function, and it's restoration in degraded systems. However, with the exception of Knott *et al.* (1997), who measured population densities of *L. irrorata* in a restored salt marsh, little is known about the response of *L. irrorata* to salt marsh restoration.

To lessen this gap in scientific knowledge, I examined the survival, growth and production of *L. irrorata* in a marsh restored with the addition of hydraulically dredged sediments. The addition of sediments to degraded salt marshes has been shown to decrease flood duration (Materne and Mendelssohn, 2006) and increase bulk density and soil nutrient concentrations (Mendelssohn and Kuhn, 2003), resulting in greater aboveground biomass, plant density and cover (Mendelssohn and Kuhn, 2003; Slocum *et al.*, 2005; Schrifft *et al.*, 2008). However, this is the first study to examine the effect of sediment addition on the ecological function of a consumer species.

To provide a suitable habitat for *L. irrorata*, and ultimately restore function to a degraded marsh, it is important to understand the biotic and abiotic controls on production. Therefore, the objective of this study was to determine how environmental characteristics of the restored marsh varied with sediment addition, and which of these factors primarily influenced *L. irrorata* production. The differential addition of sediment created an elevation gradient in the restored marsh, which provided me the opportunity to determine (1) what environmental factors associated with elevation change affected *L. irrorata* production and (2) what level of sediment addition resulted in functional equivalency to the natural marsh.

4.2 Materials and Methods

4.2.1 Site Description and Experimental Design

The study site (29° 10.58'N and 90° 14. 23'W) was located in Terrebonne Basin, a part of the Mississippi River Deltaic Plain. The specific area of interest was a submerging, degraded salt marsh located on the west bank of Bayou Lafourche near Leeville, LA. This area was affected by a sudden marsh dieback (SMD) event, which was linked to extreme drought conditions during the summer of 2000 (McKee *et al.*, 2004; Lindstedt *et al.*, 2006; Alber *et al.*, 2008). Thousands

of acres of *Spartina alterniflora*-dominated salt marshes died and subsequently submerged. In addition to the dieback marsh, natural marshes, unaffected by the SMD event, occur throughout the area. These ambient marshes are dominated by *S. alterniflora* and interspersed with *Salicornia virginica*.

In 2002, the dieback site was divided into four cells through the construction of small earthen dikes. The cells were hydraulically connected through culverts and breaks in the levees that allowed for tidal exchange. Hydraulically dredged sediments from adjacent Bayou Lafourche were pumped into each cell resulting in four separate sediment subsidy treatment blocks (Figure 4.1). The sediment slurries were comprised of approximately 20-30 % solids and 70-80 % water by volume. Addition of these sediment slurries at differential volumes within each replicate block resulted in four separate sediment subsidy treatment levels (STLs): 1) High STL: 28-36 cm above ambient marsh, 2) Medium STL: 20-25 cm above ambient marsh, 3) Medium-Vegetated (Medium-Veg) STL: areas with 100 % vegetative cover in the fall of 2003 and an average elevation of 20 cm above ambient marsh, and 4) Low STL: 13-18 cm above ambient marsh. . Sediments in the sediment addition zone were comprised of 8.94 ± 0.20 % sand, 42.89 ± 0.54 % silt, 47.21 ± 0.60 % clay 10.90 ± 3.64 % organic matter and (Schrift *et al.*, 2008).

In addition to the sediment treatment areas, reference areas, which did not receive sediment subsidy, were also included in the experimental design (Figure 2.1). Two types of reference sites were used, each replicated twice: 1) an ambient reference marsh, which neither died back nor received sediment (2-5 cm above the ambient benchmark) and 2) a degraded reference marsh, which died back but did not receive sediment (-0.5 - -2.5 cm below the ambient benchmark). These elevations, in addition to the STL elevations, can all be related to the North

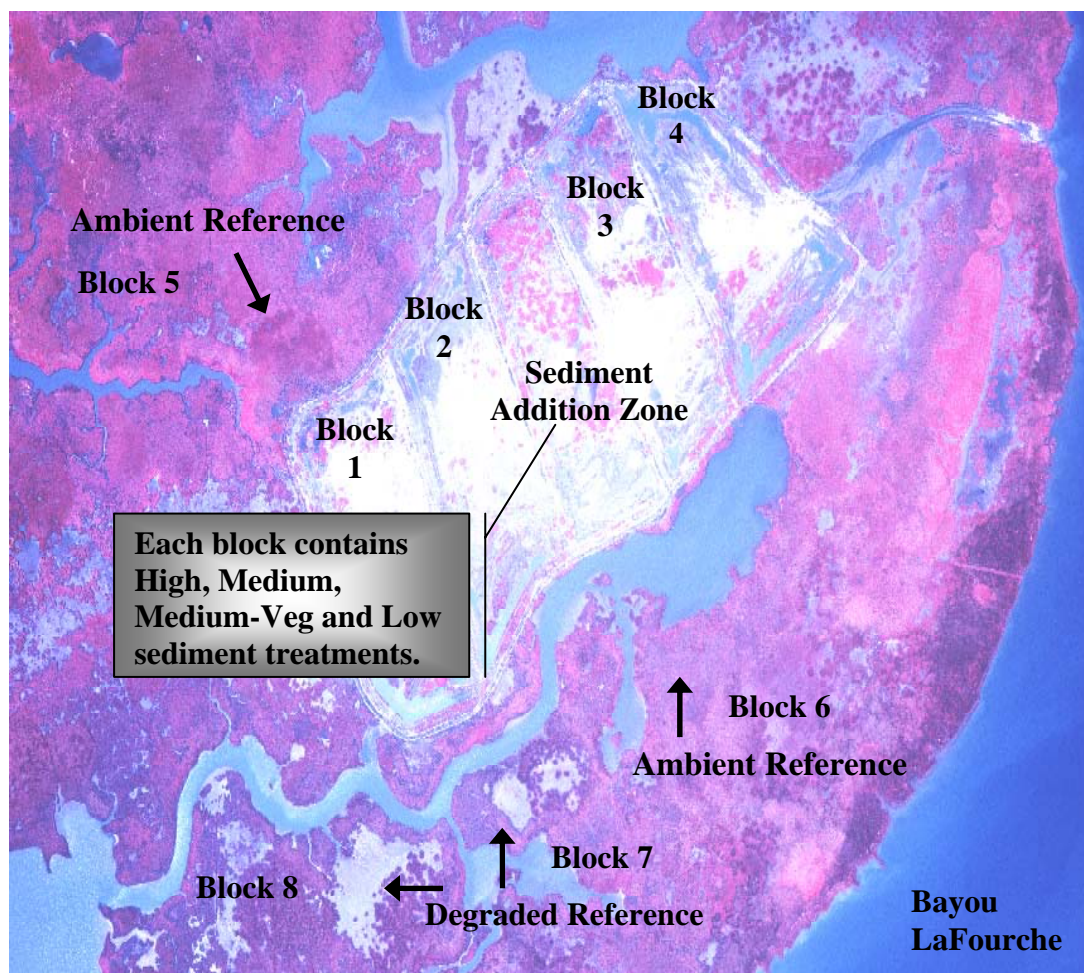


Figure 4.1. Sediment subsidy treatment site (blocks 1-4) and references (blocks 5-8).

American Vertical Datum of 1988 (NAVD 88) by adding 29.78 cm to the marsh surface elevations. Sediments in the reference zone (ambient and degraded) were comprised of 7.71 ± 2.55 % sand, 34.88 ± 1.77 % silt, 49.74 ± 10.25 % clay and 27.52 ± 1.24 % organic matter (Schrift *et al.*, 2008).

4.2.2 Enclosure Construction and Sampling Procedures

I used a bioassay approach to determine the effects of sediment addition on *L. irrorata* growth survival and production, which was measured for snails kept in enclosures at each STL. Thus, production estimates reflect habitat suitability and are not production estimates for the entire population of *L. irrorata*, but rather an index of secondary production at each sediment

treatment level. Although other consumer species such as infauna, epifauna and nekton may respond differently to sediment addition, *L. irrorata* is directly associated with the dominant salt marsh grass *S. alterniflora*, and plays an important role in salt marsh energy flow. Three 0.25 m² enclosures containing 25 snails were placed at each STL and reference plot (replicated in multiple blocks) (Figure 4.2). Snail densities in the enclosures (100 snails·m⁻²) approximated *L. irrorata* densities in the surrounding natural marshes (133 ± 17 snails·m⁻²). The 0.25 m² cages were constructed of galvanized mesh (3 mm opening) screening. The 1.5 m tall mesh panels were attached to 2-m PVC poles (1.5 in diameter), which were placed 30 cm into the sediment. I also buried the bottom of the mesh paneling approximately 10 cm below the marsh surface to prevent snails from escaping. To further re-enforce the bottom of the enclosure, I buried galvanized sheet metal around the perimeter of the cage, so that a 2-cm lip covered the bottom of the enclosure. This lip prevented snails from escaping, but it did not impede tidal flooding or drainage.

Snails, ranging in size from 6-13 mm, were collected from a nearby natural marsh in June of 2007. Snails in this size class are defined as sub-adults by Hamilton (1978) and were chosen for their increased sensitivity (Stiven and Hunter, 1976; Vaughn and Fisher, 1992; Henry *et al.*, 1993) and higher growth rates (Bingham, 1972a; Stiven and Hunter, 1976) compared to adult snails. Additionally, sub-adults are easier to locate than juveniles (< 6 mm), and were less likely to escape from the mesh enclosures. After collection, the snails were carefully transported to the laboratory in plastic containers that contained air holes and *S. alterniflora* leaves. In the laboratory, the snails remained in these containers for seven days, during which time I measured shell length and labeled the shells with acrylic paint. Clear aquarium glue (non-toxic) was

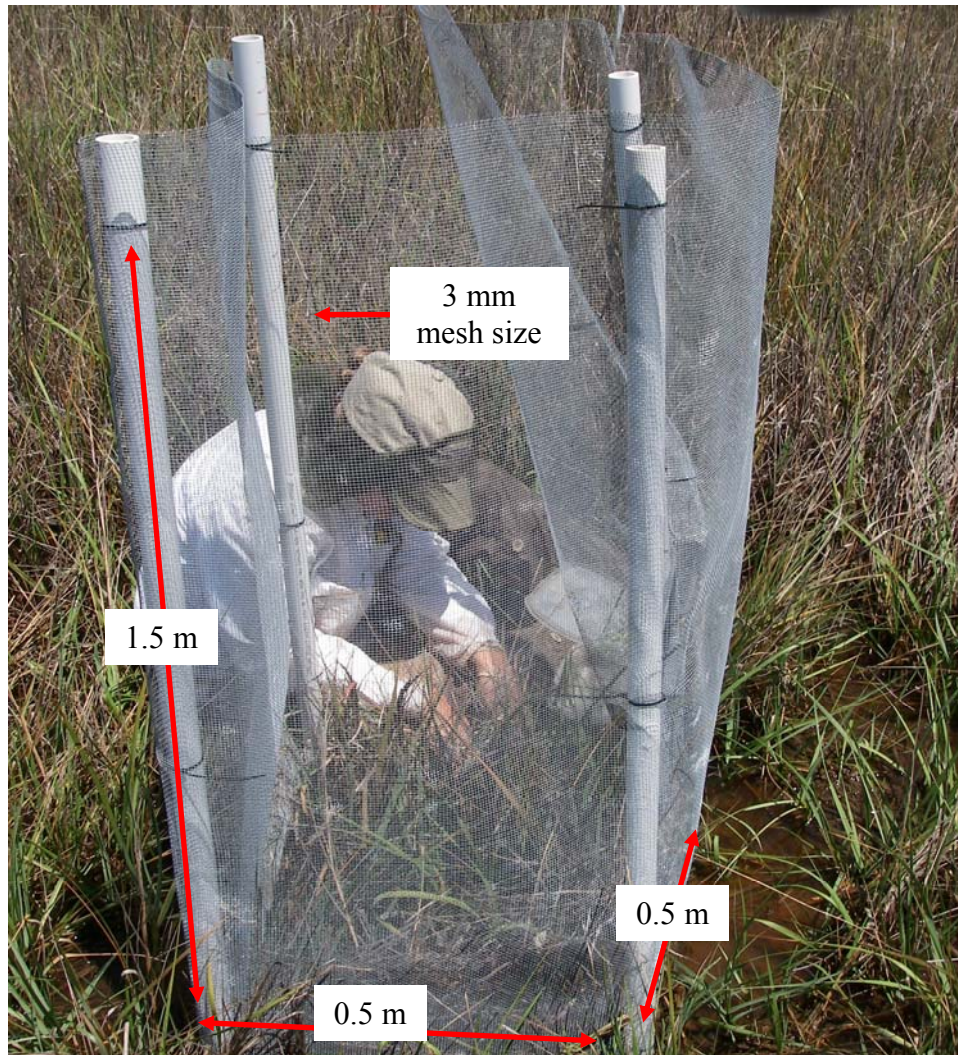


Figure 4.2. Snail enclosures (n=3) located at each STL and reference block (n=2-4).

applied over the paint mark to prevent removal. The snails were then transported back to the study site and placed in randomly designated enclosures.

Shell length was measured three times over a period of 92 days (6/07, 7/07 and 9/07). Using calipers, I measured length along the vertical axis of the shell (the longest portion) of each snail. I spent up to 20 minutes searching for snails in the enclosures, which I considered an adequate amount of time to ensure location of all snails that were present. Missing snails were considered dead, and all snails that were present were rinsed clean with water and examined to determine if they were alive or dead.

The mean length and number of surviving snails from each cage at each sampling period was used to determine growth, survival and production rates for each STL (3 subsamples = 1 rate for each STL replicate). Shell length was converted to biomass using a linear model derived from a log-linear regression of shell length and biomass as described by Crisp (1984). A separate sample of snails was collected to construct the regression model.

A random sample of 100 snails of varying sizes (3-15 mm) was collected from a nearby natural marsh and transported to the laboratory at Louisiana State University. In the laboratory, shell length was measured, and the soft tissue was then extracted by carefully crushing the shell using a small vice. I used tweezers to remove shell debris followed by a rinse with deionized water. The soft tissue was immediately placed in a desiccator until oven dried at 60 °C for four days. The length and corresponding biomass was then used in a log-linear regression to predict biomass from shell length. Regression of shell length and biomass resulted in a linear model with 96% variance explained ($p < 0.0001$). This model was then used to predict the mass of experimental snails based on field measurements of shell length.

4.2.3 Growth, Survival and Production Calculations

Growth rate was calculated using a log-linear regression of change in biomass over time as described by Crisp (1984):

$$G = 2.303 \cdot \Delta \log_{10}(w) / \Delta t \quad (4.1)$$

where G = weight-specific instantaneous growth rate (day^{-1}), w = biomass (mg) and t = time (days). An overall growth rate was calculated for the duration of the experiment ($\Delta t = 92$ days), and increment growth rates were calculated at each interval for production estimates ($\Delta t_1 = 28$ days, $\Delta t_2 = 64$ days). Similarly, survival rate was calculated using a log-linear regression of change in survivors over time (Crisp, 1984):

$$Z = 2.303 \cdot \Delta \log_{10}(N) / \Delta t \quad (4.2)$$

where Z = instantaneous mortality rate (or -survival rate) (day^{-1}), N = number of survivors and t = time (days). Again, an overall survival rate was calculated for the duration of the experiment (Δt = 92 days), and increment survival statistics ($\text{survivors} \cdot \text{m}^{-2}$) were calculated at each interval for production estimates (Δt_1 = 28 days, Δt_2 = 64 days). Production was estimated using the increment growth method described by Crisp (1984):

$$P = \sum_{(t=0-1)} G \cdot w \cdot N \cdot \Delta t \quad (4.3)$$

where P = biomass production ($\text{mg} \cdot \text{m}^{-2}$), which equals the sum of relative growth increments, $G \cdot w \cdot N \cdot \Delta t$, from each time interval. G = mass-specific instantaneous growth rate (day^{-1}), w = biomass (mg), N = survivors ($\text{N} \cdot \text{m}^{-2}$), and Δt = duration of interval (days).

4.2.4 Vegetation Estimates

Canopy cover of *S. alterniflora* was measured using a visual estimation method. I measured canopy cover at each STL and reference block three times during the *L. irrorata* experiment (6/07, 7/07, and 9/07) in 0.25 m^2 plots near the enclosures. Live and dead canopy cover was measured separately, and the mean values from June 2007 to September 2007 were used in statistical tests.

4.2.5 Soil Physico-chemical Measurements

Several soil physical and chemical properties were measured in November of 2006. A core (5 cm diameter x 10 cm long) was taken at each STL and reference block to measure soil bulk density, organic matter content, percent moisture and electrical conductivity. After collection, the cores were analyzed for wet weight, dried at 65°C , and weighed again to determine bulk density and percent moisture. A portion of the dried soil was also used to measure electrical conductivity and organic matter content. To determine electrical conductivity,

5 g of dried soil was mixed vigorously with 30 ml of distilled water for one hour. The mixture was then centrifuged at 2817 g for five minutes, and the supernatant was analyzed for electrical conductivity on a Cole Parmer 19820-00 meter. To determine organic matter content, approximately 2-3 grams of dry soil was treated with 1N HCl until all inorganic carbonates were volatilized. The soil was then analyzed for percent organic matter through loss on ignition at 550 °C in a Fisher Isotherm combustion oven (Programmable Forced Draft Furnaces, model 10-750-126) (Nelson and Sommers, 1996).

A second soil core (5 cm diameter x 15 cm long) was simultaneously taken at each STL and reference block to measure soil pH, soil extractable nutrients and other elements (NH₄-N, NO₃-N, P, Fe, K, Mg, Mn, Na, and S). The soil cores were immediately placed on ice in the field and transported back to the laboratory at Louisiana State University, where they were homogenized. After homogenization, several soil aliquots were collected to perform the following extractions: NH₄-N and NO₃-N (2 M KCl (Bremner and Kenney, 1966)); P (Bray-2 (Byrnside and Sturgis, 1958)); Ca, K, Mg and Na (ammonium acetate (Thomas, 1982)); and Fe and Mn (DTPA (Lindsay and Norvell, 1978)). Following extraction, NH₄-N and NO₃-N samples were filtered through a 0.45 µm filter and measured on a segmented flow AutoAnalyzer (Flow Solution IV AutoAnalyzer, O-I Analytical, USA). The remaining extracts were measured with an inductively coupled argon plasma emission spectrometer (ICP) (Spectro Ciros CCE, Spectro Analytical Instruments, Germany).

Redox potential was also measured during the same sampling event using bright platinum electrodes, a calomel reference electrode and a portable Cole-Parmer digital pH-mV meter. Three platinum electrodes were placed 15 cm below the soil surface at each STL and reference replicate, and the average of the three readings was used in statistical analysis.

A third soil core was taken in February 2007 to measure soil sulfide concentrations. The cores (5 cm diameter x 10 cm long) were taken from each STL and reference block and immediately placed in a centrifuge tube (500 ml) containing air-tight septa. The core was purged with nitrogen gas for two minutes to maintain an anoxic environment and then stored on ice. Once the cores were returned to the laboratory, they were centrifuged at 2817 g for 20 minutes to extract porewater from the soil. The supernatant was decanted, stabilized with an anti-oxidant buffer and analyzed for total soluble sulfides (Lazar Model IS-146 sulfide electrode, Lazar Research Laboratories, Los Angeles, CA).

4.2.6 Statistical Analyses

Sediment addition treatments were applied in a randomized incomplete block design (6 treatment levels, n=2-4) (Figure 4.1). The incomplete designation arises from the fact that not all treatment levels are found in every replicate block. For example, the four blocks containing the sediment addition treatments do not contain reference treatments, and the reference blocks do not contain sediment addition treatments.

Separate one-way mixed model ANOVAs, with sediment treatment level as the fixed effect and block as the random effect, were used to test for differences in each biological response (*L. irrorata* growth rate, survival rate, production rate and *S. alterniflora* canopy cover) across sediment treatment levels.

Soil physical and chemical analytes were consolidated into composite variables using principle component analysis (PCA). Only principle components (PCs) with eigenvalues > 1 were used for subsequent analyses. To determine the effect of sediment addition on the rotated factor scores, I used a one-way mixed model ANOVA, with sediment subsidy as the fixed effect and block as the random effect.

To determine which environmental factors most influenced growth, survival and production, I conducted multiple regression analyses, which included principle component factor scores, elevation and live and dead canopy cover as the independent variables. Significant slope parameters were selected with the step-wise selection method ($p < 0.05$). Separate multiple regression analyses were performed for *L. irrorata* growth rate, survival rate and production. Additionally, correlation analyses were performed for all response variables relating soil variables and canopy cover estimates to growth, survival and production rates.

For all statistical tests, normality and homogeneity of variance were determined by using the Shapiro-Wilks test, and box-plots. Natural log and square root transformations were used to improve normality only in the PCA. Pairwise comparisons were made using Fisher's Protected LSD tests. All statistical tests were performed using the MIXED, FACTOR, REG or CORR procedures of SAS 9.1.2 unless otherwise noted (SAS Institute Inc., 2004).

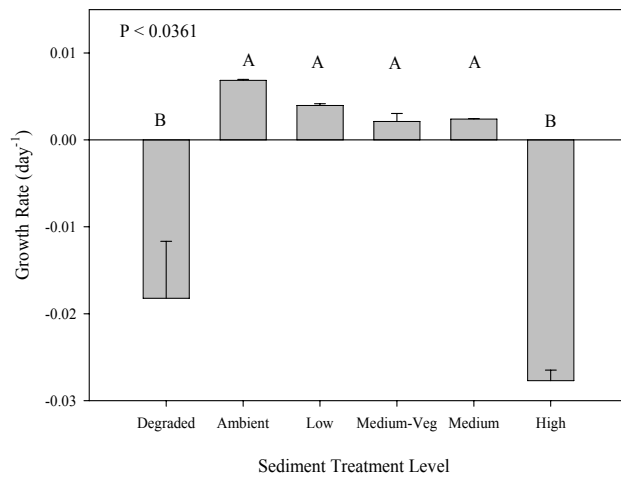
4.3 Results

4.3.1 *Littoraria irrorata*

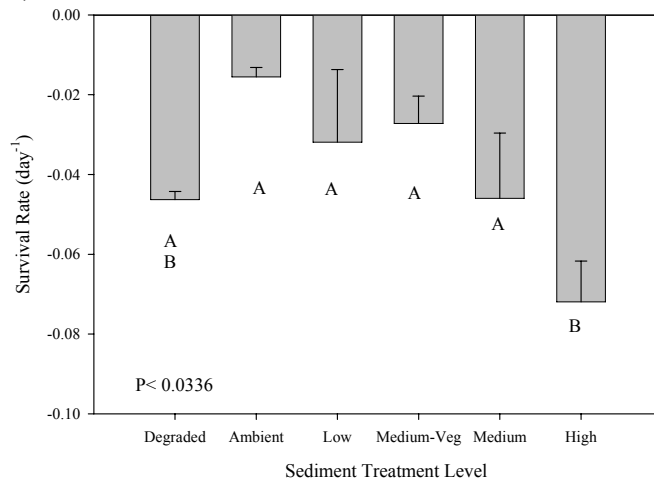
Sediment addition had a significant effect on *L. irrorata* growth rate (Figure 4.3.1), which was lower in the degraded reference compared to the moderately subsidized zones and the ambient reference. However, *L. irrorata* growth rate also decreased in areas that received large amounts of sediment (High STL); thus growth rate was maximal in areas of moderate elevation and decreased in either direction of elevation change. Furthermore, the minimal growth rates observed at extremely high and low elevations were negative; indicating, not only that no net growth occurred here, but also that there was a decrease in the mean biomass over time.

Survival rates were also low in the degraded marsh, which accounts for the decrease in biomass over time (Figure 4.3.2). Additionally, survival rates were lowest in the High STL and

1)



2)



3)

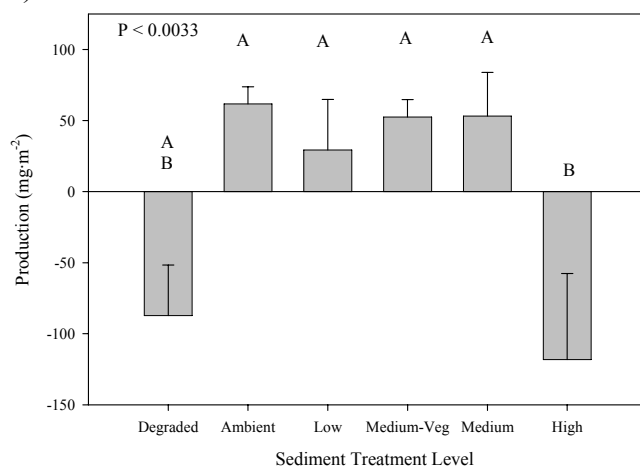


Figure 4.3. Effect of sediment subsidy on *L. irrorata* 1) Growth rate, 2) Survival rate and 3) Production. Error bars represent standard errors, and different letters represent significantly different means (Fisher's Protected LSD, $p < 0.05$).

were two to four times lower than survival rates in the moderately subsidized areas and the ambient reference, respectively. Similarly, *L. irrorata* production was lowest in the High STL and degraded reference, compared to areas of moderate elevation (Figure 4.3.3). Therefore, these results demonstrate that areas restored with moderate amounts of sediment addition are equally conducive to *L. irrorata* growth, survival and production compared to the natural reference marsh. However, the degraded areas, which exhibited negative growth and production rates, and low survival rates, are not able to support *L. irrorata*. Areas of extreme high elevation are also inhospitable to *L. irrorata*, as the High STL exhibits the lowest growth and survival rates and production compared to all other STLs. Thus, an elevation threshold exists with elevations above or below this threshold negatively impacting *L. irrorata* growth; moderate elevation (5-20 cm) are optimal for production, but areas of extreme low and extreme high elevation do not provide a suitable habitat for these organisms.

4.3.2 *Spartina alterniflora*

Sediment subsidy also had a significant effect on canopy cover (Figure 4.4). *S. alterniflora* canopy cover was greatest in the ambient reference marsh, and in the moderately subsidized STLs (Low and Medium-Veg). Conversely, *S. alterniflora* cover was significantly lower in areas of extreme low elevation (degraded reference) and in STLs with elevations greater than 20 cm above ambient marsh (High and Medium STLs). Similar to *L. irrorata*, it appears that canopy cover also responded to a sediment subsidy threshold. Thus, moderate intensities of sediment subsidy restore canopy cover to values equivalent to the ambient reference marsh, but high levels of subsidy result in elevations that are out of the optimum intertidal range of *S. alterniflora*. Additionally, *S. alterniflora* cover and *L. irrorata* growth and survival trends were similar with respect to increasing sediment addition (Figures 4.3-4.4). These similarities suggest

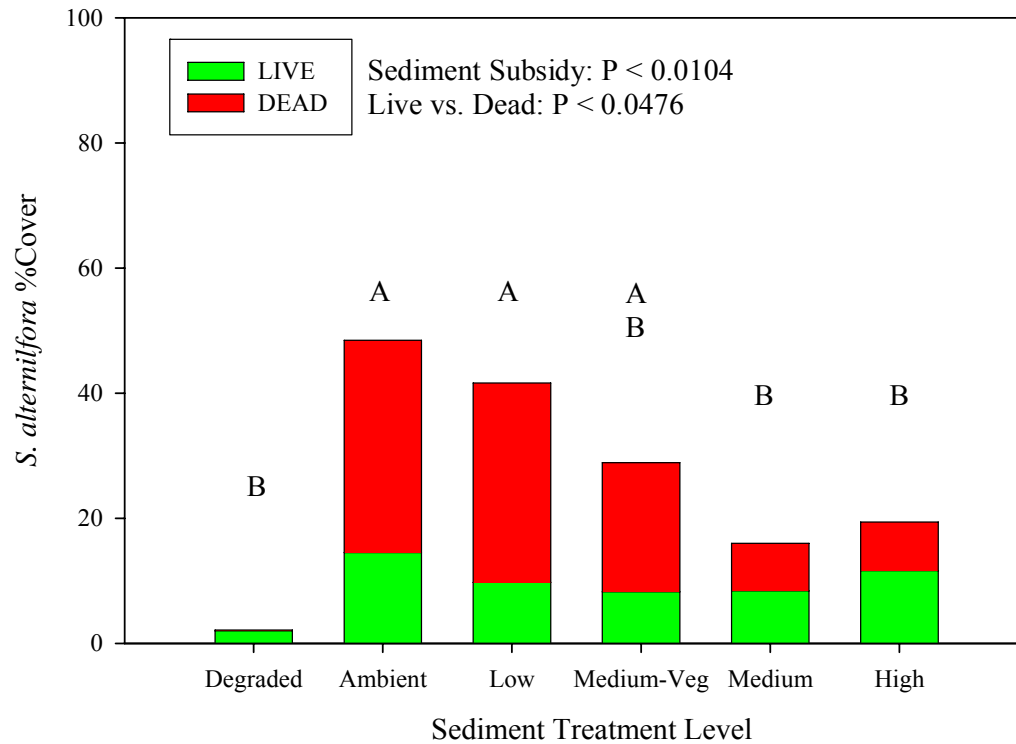


Figure 4.4. *Spartina alterniflora* canopy cover at different levels of sediment addition. Error bars represent standard errors, and different letters represent significantly different means, with respect to the effect of sediment addition on total cover (live+dead) ($p < 0.0104$) (Fisher's Protected LSD $p < 0.05$). Shading denotes live or dead cover, which was significantly different at all STLs ($p < 0.0476$).

that vegetation cover and snail production are positively correlated, such that areas of moderate elevation support both *S. alterniflora* growth and *L. irrorata* growth and survival.

4.3.3 Soil Conditions

The physico-chemical parameters characterizing the marsh soil were highly intercorrelated (Table 4.1). Principle component analysis of soil variables resulted in three principal components (PCs) accounting for 87 % of the variability in the dataset.

The three PCs associated with the soil variables included a soil moisture/salinity component, an iron/phosphorus component and an oxidation/nitrate component.

PC1 (Soil Moisture/Salinity), which accounted for 65 % of variability in the dataset, was defined by variables associated with flooded soils such as increasing sulfide ammonium, percent

Table 4.1. Correlations between indicator variables and principal components (PCs) for soil characteristics. Eigen values and percent variation explained are included for each PC. Bolded loadings indicate variables that define the PC. Symbols ^{ln} and ^{-1/2} denote natural log transformation and square root transformation of the data, respectively.

Indicator Variables	PC1: Soil Moisture/ Salinity	PC2: Fe/ P	PC3: Oxidation/ NO ₃
Ammonium ^{ln}	0.83247	-0.18516	-0.16489
Conductivity ^{ln}	0.85505	0.10384	-0.38157
Iron ^{-1/2}	0.18504	0.83739	-0.37063
Magnesium ^{ln}	0.93832	0.12132	-0.14653
Manganese ^{ln}	-0.80179	0.43504	-0.19053
Nitrate ^{ln}	0.16883	-0.31325	0.88821
Phosphorous ^{ln}	0.16739	0.84666	-0.06506
Potassium ^{ln}	0.89373	0.33703	-0.14348
Sodium ^{ln}	0.95166	0.09397	-0.13701
Sulfur ^{ln}	0.94849	0.18008	-0.13968
Sulfide ^{ln}	0.7437	-0.08587	-0.42412
Redox potential	-0.52481	-0.13647	0.71007
Bulk density	-0.94743	-0.27017	0.03441
Ph	-0.8529	-0.19624	-0.09858
% Moisture ^{ln}	0.93261	0.30102	-0.04564
% Organic Matter ^{ln}	0.93754	0.19977	0.03306
Eigenvalue	10.38	2.43	1.14
% Variance Explained	65 %	15 %	7 %
Cumulative % Variance Explained	87 %		

moisture, percent organic matter and decreasing bulk density. Additionally, PC1 was also defined by variables associated with salinity such as conductivity, sodium, potassium and magnesium. PC2 (Fe/P) was positively loaded with iron and phosphorus and accounted for 15 % of the variance associated with the dataset. PC3 (Oxidation/NO₃) was defined by reduction-oxidation potential and nitrate concentrations and explained only 7 % of the variance in the soil dataset.

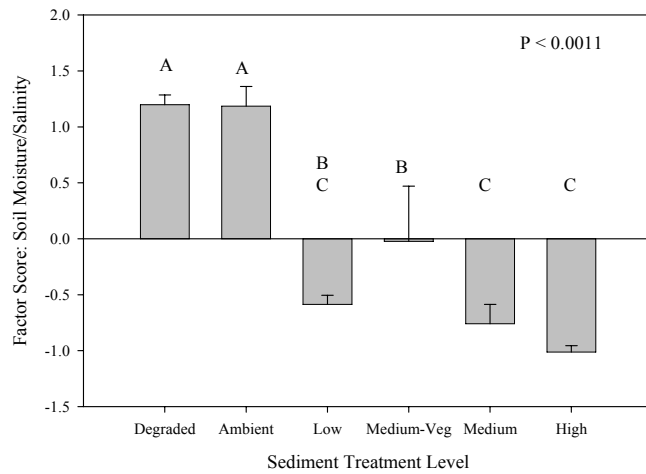
Sediment subsidy significantly affected soil characteristics as evidenced by the observed decrease in PC1 (Soil Moisture/Salinity) at the High, Medium, Medium-Veg and Low STLs compared to the reference areas (Figure 4.5.1). Iron and phosphorus concentrations (PC2) were equivalent between the reference sites and the Low and Medium-Veg STLs and significantly lower at the High and Medium STLs (Figure 4.5.2). In contrast no discernable trend was observed for PC3 (Oxidation/NO₃) (data not shown). However, sediment subsidy significantly affected redox potential, *per se*, with Eh values higher in areas receiving sediment addition compared to the reference sites (Figure 4.5.3).

4.3.4 Determinants of *L. irrorata* Growth, Survival and Production

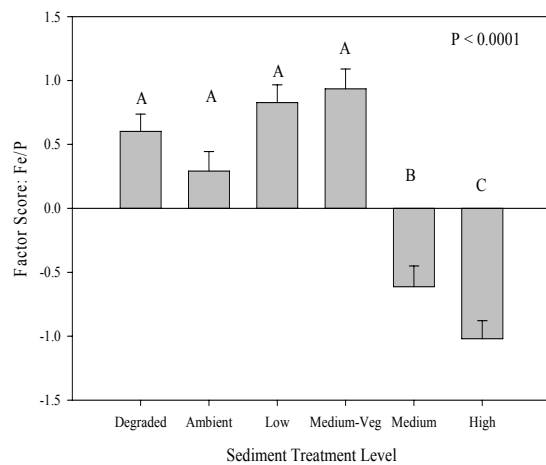
All *L. irrorata* responses were positively correlated with increasing *S. alterniflora* canopy cover (Table 4.2). I observed similar trends in the effects of sediment subsidy on both *S. alterniflora* and *L. irrorata*, such that moderate elevations resulted in higher canopy cover and *L. irrorata* production and survival compared to areas of extreme low elevation (degraded reference) or extreme high elevation (High and Medium STLs) (Figures 4.2-4.5). Furthermore, canopy cover explained the majority of the variance associated with *L. irrorata* growth rate, survival rate and production (49 %, 35 % and 50 % respectively) (Table 4.2). However, live and dead cover are not equally influential across growth rate, survival rate and production. Specifically, live cover is the main explanatory parameter for survival rate (33 %); whereas dead cover explains the greatest variability in growth rate and production (49 % and 45 %, respectively).

In addition to canopy cover, soil moisture and salinity significantly influenced growth rate. As soil moisture and salinity (PC1) increased (with decreasing elevation), growth rate declined. However, increasing elevation, or sediment addition, had a negative impact on both

1)



2)



3)

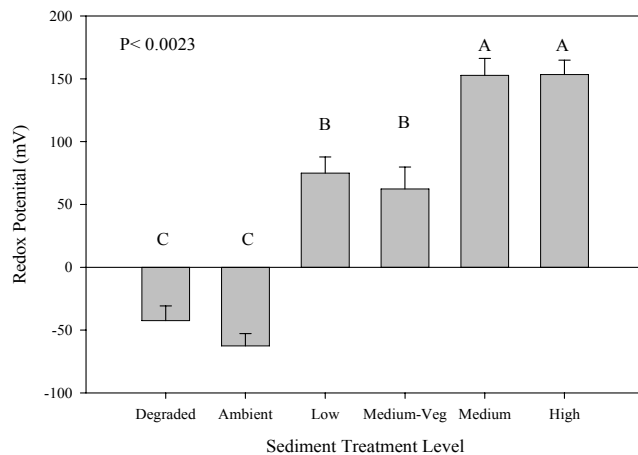


Figure 4.5. Effect of sediment subsidy on 1) Soil moisture and salinity (PC1), 2) Iron and phosphorus (PC2) and 3) Redox Potential. Error bars represent standard errors, and different letters denote significant differences among means (Fisher's Protected LSD, $p < 0.05$).

Table 4.2. Multiple regression analyses describing relationships between *L. irrorata* responses and environmental characteristics.

Response Variable	Independent Variable	Parameter Estimate	Partial R ²	R ²	P-value
Growth Rate	Sediment Addition	-6.16E-03	0.0829	0.7138	0.0145
	PC1(Soil Moisture/Salinity)	-8.59E-03	0.1446		
	Dead Cover	4.50E-04	0.4863		
Survival Rate	Elevation	-7.61E-03	0.2017	0.5534	0.0041
	Live Cover	1.43E-03	0.3322		
	Dead Cover	0.000272	0.0196		
Production	PC2 (Fe/P)	25.0198	0.0798	0.5801	0.0285
	Live Cover	3.76074	0.0545		
	Dead Cover	1.413	0.4457		

growth and survival rate. Accordingly, survival rate was negatively correlated with redox potential and bulk density, which increased with elevation (Table 4.3). Further, calcium was also positively correlated with growth and survival, and was also lowest at the High STL (data not shown). Additionally, both iron and phosphorus (PC2) significantly influenced production (Table 2), but only iron concentrations were positively associated with growth and survival (Table 4.3).

4.4 Discussion

Restoration of degraded salt marshes with moderate levels of sediment addition provided a suitable habitat for *L. irrorata*, such that growth, survival and production were equivalent to natural marshes. Elevations 5-20 cm above ambient marsh resulted in the highest growth rates, survival rates and production; however, elevations outside of this range did not support *L. irrorata*. Degraded marshes, which were characterized by low elevation (-0.5 to -2.5 cm), and

Table 4.3. Correlations between *L. irrorata* biological responses and environmental variables. Bolded values indicate significant correlation (Pearson correlation coefficient, $p < 0.05$). Symbol $^{-1/2}$ indicates variable that was square root transformed to improve normality.

Environmental Variable	Response Variable		
	Growth Rate	Survival Rate	Production
Live Cover	0.58	0.53	0.58
Dead Cover	0.70	0.65	0.67
Elevation	-0.41	-0.48	-0.34
% Moisture	0.30	0.44	0.32
Redox Potential	-0.39	-0.52	-0.36
Bulk Density	-0.31	-0.43	-0.32
Iron $^{-1/2}$	0.66	0.63	0.51
Calcium	0.35	0.35	0.14

sediment subsidized zones above 20 cm (High and Medium STLs) had the lowest growth, survival and production rates. Distribution trends of *L. irrorata* in natural marshes appear to follow a similar pattern with elevation, such that densities of sub-adult snails are highest in the low marsh and decline as elevation increases or decreases from this optimal elevation (Hamilton, 1978; Rader, 1984; Schindler *et al.*, 1994). As a primary regulator of tidal inundation, the elevation of the marsh surface impacts soil physico-chemical properties, vegetation zonation and consumer distributions. Thus, elevation change associated with sediment addition may influence *L. irrorata* production through the interaction of several factors, including physical tolerances to abiotic stimuli, biotic interactions and resource availability.

The presence of *S. alterniflora* is directly linked to increased abundance, growth and survival of *L. irrorata* in natural marshes (Bingham, 1979b; Stiven and Hunter, 1976; Rader, 1984). Accordingly, my results indicate that canopy cover of *S. alterniflora* is the most powerful explanatory variable describing *L. irrorata* production, which parallels changes in canopy cover

along the elevation gradient in the sediment subsidized marsh. Therefore, the restoration of *S. alterniflora* is crucial in providing optimal conditions for *L. irrorata* growth and survival.

The interaction between *L. irrorata* and *S. alterniflora* may be important on several levels. As the primary food source for *L. irrorata* (Haines, 1976; Alexander, 1979; Stiven and Kuenzler, 1979; Kemp *et al.*, 1990; Barlocher and Newell, 1994), *S. alterniflora* may act as a resource limiter on *L. irrorata* growth, survival and production.

However, recent evidence suggests that *L. irrorata* does not graze in the traditional sense, but “farms” fungal biomass along the wounds of *S. alterniflora* leaves for subsequent ingestion (Newell and Barlocher, 1993; Silliman and Newell, 2003). Nevertheless, *S. alterniflora* is still an important component of *L. irrorata*’s diet. Growth rates of *L. irrorata* are significantly higher when fed a diet of standing dead *S. alterniflora* leaves, compared to diets consisting of pure fungal biomass, or sterilized *S. alterniflora* leaves that are artificially inoculated with mycelia (Barlocher and Newell, 1994). Additionally, the protein content, phenolics and lipids of all *S. alterniflora* leaves (naturally colonized and inoculated) are similar (Barlocher and Newell, 1994), suggesting that naturally standing dead *S. alterniflora* leaves possess unique characteristics that support *L. irrorata* growth. Further, it has been documented that *L. irrorata* prefers dead to live *S. alterniflora* (Alexander, 1976; Bebout, 1988; Kemp *et al.*, 1990), and that growth rates of *L. irrorata* fed dead leaves are higher than *L. irrorata* fed live leaves (Barlocher and Newell, 1994), which supports my finding that dead cover is more influential than live cover in *L. irrorata* growth and production.

In addition to providing essential nutrition to *L. irrorata*, *S. alterniflora* may also grant refuge from both predators and physical stressors (Hamilton, 1976; Warren, 1985; Vaughn and Fisher, 1988; McBride, 1989; William and Appel, 1989; Henry *et al.*, 1993). For example, *S.*

alterniflora acts as a physical barrier to impede predator foraging efficiency and also provides a vertical climbing substrate for the avoidance of natant predators (Hamilton, 1976; Warren, 1985) and high temperatures (McBride, 1989; Henry *et al.*, 1993).

Predator exclusion experiments have demonstrated that when *L. irrorata* is allowed to climb above the water surface, predation significantly decreases (Warren, 1985; Vaughn and Fisher, 1988). Predation frequency may also be a function of elevation, or tidal inundation. For instance, predation intensity of natant predators, such as *Callinectes. sapidus* (Stiven and Hunter, 1976; Hamilton, 1978; Stanhope *et al.*, 1982), is limited in the upper reaches of the marsh, where flood duration, and thus foraging time, is shortest (Kneib, 1984; Schindler *et al.*, 1994). Consequently, I observed low survival rates in the degraded reference, where *S. alterniflora* cover is minimal (2.1 ± 5.4 %), and flood duration is high (71 % time flooded; Materne and Mendelssohn, 2006). Although predation was not quantified in this experiment, the enclosures were not constructed to exclude predators, i.e. predation was still possible. Therefore, low survival rates at the degraded reference may be a result of several factors associated with low elevation and excessive inundation. For example, increased flood duration at low elevations leads to 1) the inhibited growth of *S. alterniflora* (Mendelssohn and Seneca, 1980), which acts as a predator refuge and food source for *L. irrorata* (Hamilton, 1976; Alexander, 1979), and 2) greater foraging time for predators (Schindler *et al.*, 1994), all contributing to the demise of *L. irrorata*. However, if predation were the primary control on mortality, I would expect to see increased survival rates at the high elevations, where flood duration and subsequent predation is low (Schindler *et al.*, 1994). Given that mortality is greatest at the High STL; other factors aside from predation must be influencing *L. irrorata* survival at high elevations.

In addition to predator avoidance, the circumtidal climbing behavior of *L. irrorata* functions as a mechanism for thermoregulation (McBride, 1989). Vertical migration of *L. irrorata* is positively correlated with substratum temperatures and increases as sediment and water temperatures rise above 29 °C (McBride, 1989). Furthermore, Warren (1985) found that mortality rates increased when snails were not allowed to climb, even though predators were absent, indicating that *L. irrorata* primarily climbs *S. alterniflora* stalks to thermoregulate and secondarily avoids predation (McBride, 1989). Therefore, the absence of vegetation may have disrupted the thermoregulation of *L. irrorata*, resulting in higher mortality rates not only at the High STL, but also at the degraded reference. Water temperatures, which should be similar to substrate temperatures (McBride, 1987; McBride, 1989), ranged from 24.0 to 34.7 °C for the duration of the experiment (June 2007-September 2007; <http://www.tidesandcurrents.noaa.gov/> NOAA, 2009). Consequently, these temperatures were sufficient to stimulate climbing (≥ 29.6 °C; McBride, 1989), but because these areas were devoid of vegetation, the snails were forced to remain on the sediment surface, potentially resulting in metabolic stress and mortality (Baxter, 1983).

Additionally, high water temperatures may exacerbate metabolic stress in *L. irrorata* through a decrease in dissolved oxygen (Henry *et al.*, 1993). The increased demand for oxygen as temperatures and metabolic rates increase is a primary regulator of circumtidal climbing, as *L. irrorata* seeks refuge from oxygen-poor waters (Henry *et al.*, 1993). Thus, without the ability to climb above the water surface, where temperatures are lower (McBride, 1989) and oxygen is more available, these animals may face both direct thermal stress as well as a shortage of oxygen when submerged by flood waters at the degraded reference site (Henry *et al.*, 1993).

However, in areas devoid of vegetation (High STL and degraded reference), I observed snails climbing PVC poles framing the enclosures, indicating that the impedance of vertical migration was not solely responsible for high mortality rates. Nonetheless, *S. alterniflora* may still play a role in moderating temperature stress by providing shade and cover (Baxter, 1983; Lasaik and Dye, 1986; Vaughn and Fisher, 1992;). *L. irrorata* juveniles and sub-adults are more commonly found near the base of *S. alterniflora* culms and under leaves compared to open substrate (Baxter, 1983; Vaughn and Fisher, 1992), which may function as a mechanism to avoid heat and desiccation stress. Although Henry *et al.* (1993) concluded that *L. irrorata* are tolerant to high degrees of desiccation, snail size was not specified, and other juvenile and sub-adult gastropods, such as *Melampus bidentatus* and *Nodilittorina unifasciata*, are more susceptible to desiccation stress than adults (Kneib, 1984; Chen and Richardson, 1987). Additionally, I observed a significant positive correlation between soil moisture and *L. irrorata* survival, suggesting that the dry conditions at the High STL may be responsible for increased mortality rates.

Several other environmental factors were also highly correlated with *L. irrorata* growth, survival and production including redox potential, bulk density, iron and calcium. While it is likely that iron, redox potential and bulk density are indirectly influencing survival through their ameliorating impacts on *S. alterniflora* cover (Stagg, 2009); calcium may have a direct impact on *L. irrorata* growth. Rates of calcium deposition for shell growth have been shown to limit growth rates of *Littorina littorea* and other prosobranch gastropods (Palmer, 1981; Kemp and Bertness, 1984). Therefore, it may be possible that low calcium concentrations limited shell growth and consequently growth rates of *L. irrorata* in upper elevations in the marsh.

4.5 Conclusions

In summary, moderate sediment addition to this degraded salt marsh restored the growth, productivity and survival of *L. irrorata* to that of the natural reference marshes. However, excessive sediment addition (High STL) had a negative impact on *L. irrorata* with growth and survival similar to that in the degraded sites. The decline of *L. irrorata* production and survival at both extreme high and low elevation are directly linked to the decrease in *S. alterniflora* cover. *S. alterniflora* provides both refuge and nutrition, so that, at both the degraded and High STL, declines in *L. irrorata* survival may be due to decreased resource availability or increased thermal and metabolic stress. Additionally, at the degraded reference, high mortality rates may be linked to increased predation through two mechanisms: 1) increased flood duration, and increased predator foraging time, and 2) decreased refuge (*S. alterniflora*), and increased predation efficiency.

I conclude that the production of *L. irrorata* is dependent on an elevation gradient where abiotic and biotic factors interact to provide essential habitat requirements at moderate elevations. Addition of sediment, and subsequent changes in elevation and flood regime, results in concomitant increases in *L. irrorata* production and *S. alterniflora* cover. Sediment addition at moderate levels (13-20 cm above ambient marsh, 42-50 cm NAVD 88) sufficiently alleviates flooding and salinity stress, resulting in maximal *S. alterniflora* production and cover (Stagg, 2009). Additionally, moderate sediment addition restored *L. irrorata* function, in terms of growth, survival and production, to natural marsh equivalency. *S. alterniflora* is not only the primary food source of *L. irrorata*, but also provides refuge from predation and physical stressors. I propose that *S. alterniflora* is a keystone species that mediates biotic and abiotic stressors, which is emphasized by the precipitous decline in *L. irrorata* production and survival

in *S. alterniflora*'s absence. Therefore, as the primary regulator of *L. irrorata* production and survival, restoration of *S. alterniflora* production is imperative for the successful restoration of *L. irrorata* function.

4.6 Literature Cited

- Alber, M., Swenson, E.M., Adamowicz, S.C. and Mendelssohn, I.A. 2008. Salt marsh dieback: an overview of recent events in the US. *Estuarine, Coastal and Shelf Science*, 80: 1–11.
- Alexander, S.K. 1976. Relationship of macrophyte detritus to the salt marsh periwinkle, *Littorina irrorata* (Say). Ph. D. dissertation, Louisiana State University, Baton Rouge, LA.
- Alexander, S.K. 1979. Diet of the periwinkle *Littorina irrorata* in a Louisiana salt marsh. *Gulf research report*, 6: 293-295.
- Barlocher, F., Newell, S.Y. 1994. Growth of the salt marsh periwinkle *Littorina irrorata* on fungal and cordgrass diets. *Marine Biology*, 118: 109-114.
- Baxter, D.A. 1983. the influence of habitat heterogeneity on the population ecology of *Littorina irrorata* Say, the salt marsh periwinkle. Ph. D. dissertation, Duke University, Durham, NC.
- Bebout, B.M. 1988. The role of marine fungi in the food selection and nutrition of the salt marsh periwinkle *Littorina irrorata* Say (Gastropoda). Master's thesis, University of North Carolina, Chapel Hill, NC.
- Bingham, F.O. 1972a. Shell growth in the gastropod *Littorina irrorata*. *Nautilus*, 85: 136-141.
- Bingham, F.O. 1972b. Influence of environmental stimuli on the direction of movement of the supralittoral gastropod *Littorina irrorata*, with notes on additional biological aspects of the species. Master's Thesis. Florida State University, Tallahassee, FL.
- Bremner, J. M. and Kenney, D.R. 1966. Determination and isotope-ratio analysis of different forms of nitrogen in soils: 3. Exchangeable ammonium, nitrate, and nitrite by extraction-distillation methods. *Soil Science Society of America Proceedings*, 30: 577-582.
- Byrnside, D.S. Jr. and Sturgis, M.B. 1958. Soil phosphorus and its fractions as related to response of sugar cane to fertilizer phosphorus. Bull No. 513, Louisiana State University Agriculture Experiment Station, Baton Rouge, Louisiana, USA.
- Chen, Y.S. and Richardson, M.M. 1987. Factors affecting the size structure of two populations of the intertidal periwinkle, *Nodilittorina unifasciata* (Gray, 1839), in the Derwent River, Tasmania. *Journal of Molluscan Studies*, 53: 69-78.

- Crisp, D.J. 1984. Energy flow measurements. In Holme, N.A. and McIntyre, A.D., editors. *Methods for the Study of Marine Benthos*. Blackwell Scientific Publications: Boston, U.S.A. pp. 284-372.
- Haines, E.B. 1976. Stable carbon isotope ratios in the biota, soils and tidal water of a Georgia salt marsh. *Estuarine and Coastal Marine Science*, 4: 609-616.
- Hamilton, P.V. 1976. Predation on *Littorina irrorata* (Mollusca: Gastropoda) by *Callinectes sapidus* (Crustacea: Portunidae). *Bulletin of Marine Science*, 26: 403-409.
- Hamilton, P.V. 1978. Intertidal distribution and long-term movements of *Littorina irrorata* (Mollusca: Gastropoda). *Marine Biology*, 46: 49-58.
- Henry, R.P., McBride, C.J. and Williams, A.H. 1993. Responses of the salt marsh periwinkle, *Littoraria (Littorina) irrorata* to temperature, salinity and desiccation, and the potential physiological relationship to climbing behavior. *Marine Behaviour and Physiology*, 24: 45-54.
- Kemp, P. and Bertness, M.D. 1984. Snail shape and growth rates: evidence for plastic shell allometry in *Littorina littorea*. *Proceedings of the National Academy of Sciences, U.S.A.*, 81: 811-813.
- Kemp, P.F., Newell, S.Y. and Hopkinson, C.S. 1990. Importance of grazing on the salt marsh grass *Spartina alterniflora* to nitrogen turnover in a macrofaunal consumer, *Littorina irrorata* and to decomposition of standing-dead *Spartina*. *Marine Biology*, 104: 311-319.
- Kneib, R.T. 1984. Patterns of invertebrate distribution and abundance in the intertidal salt marsh: causes and questions. *Estuaries*, 7: 392-412.
- Knott, D.M., Wenner, E.L. and Wendt, P.H. 1997. Effects of pipeline construction on the vegetation and macrofauna of two South Carolina, USA salt marshes. *Wetlands*, 17: 65-81.
- Lasaik, T. and Dye, A. H. 1986. Behavioral adaptations of the mangrove whelk *Telescopium* (L.) to life in a semi-terrestrial environment. *Journal of Molluscan Studies*, 52: 174-179.
- Lindsay, W. L., and Norvell, W.A. 1978. Development of a DTPA soil test for zinc, iron, manganese, and copper. *Soil Science Society of America* 42: 421-428.
- Lindstedt, D.M., Swenson, E.M., Reed, D., Twilley, R. and Mendelssohn, I.A. 2006. Marsh dieback technical synthesis report. Technical Report, Coastal Restoration Division, Louisiana Department of Natural Resources.
- Materne, M.D. and Mendelssohn, I.A. 2006. Beneficial use of hydraulically dredged sediment-slurries for wetland restoration: II. Spatial, hydrologic and vegetative assessment. Governor's Applied Coastal Research and Development Program.

- McBride, C. J. 1987. Biological and physical factors affecting the behavior of *Littorina irrorata*. Thesis, Auburn University, Auburn AL.
- McBride, C.J. 1989. Effects of temperature on climbing behavior of *Littorina irrorata*- on avoiding a hot foot. *Marine Behaviour and Physiology*, 14: 93-100.
- McKee, K.L., Mendelssohn, I.A. and Materne, MD. 2004. Acute salt marsh dieback in the Mississippi River Deltaic Plain: a drought-induced phenomenon? *Global Ecology and Biogeography*, 13:67–73.
- Mendelssohn, I. A. and Seneca, E. D. 1980. The influence of soil drainage on the growth of salt marsh cordgrass *Spartina alterniflora* in North Carolina. *Estuarine and Coastal Marine Science*, 11: 27-40.
- Mendelssohn, I.A. and Kuhn, N.L. 2003. Sediment subsidy: effects on soil-plant responses in a rapidly submerging coastal salt marsh. *Ecological Engineering*, 21: 115-128.
- Nelson, D.W. and Sommers, L.E. 1996. Carbon and organic matter: loss on ignition method. *In* Methods of Soil Analysis, Part 3, Chemical Methods, Soil Science Society of America, Inc., American Society of Agronomy, Inc., Madison, WI. pp. 1001-1010.
- Newell, S.Y. and Barlocher, F. 1993. Removal of total organic matter from decaying cordgrass leaves by shredder snails. *Journal of Experimental Marine Biology and Ecology*, 171: 39-49.
- NOAA, 2009. Meteorological observations, station 8761724 Grand Isle, Louisiana. www.tidesandcurrents.noaa.gov
- Odum, E.P. and Smalley, A.E. 1959. Comparison of population energy flow of a herbivorous and deposit-feeding invertebrate in a salt marsh ecosystem. *Proceedings of the National Academy of Sciences, U.S.A.*, 45: 617-622.
- Palmer, A.R. 1981. Do carbonate skeletons limit the rate of body growth? *Nature*, 292: 150-152.
- Rader, D.N. 1984. Salt marsh benthic invertebrates: small scale patterns of distribution and abundance. *Estuaries*, 7: 413-420.
- SAS Institute Inc., 2004. SAS® 9.1.2. *Qualification Tools User's Guide*, Cary, NC.
- Schindler, D.E., Johnson, B.M., MacKay, N.A., Bouwes, N. and Kitchell, J.F. 1994. Crab: snail size-structured interactions and salt marsh predation gradients. *Oecologia*, 97: 49-61.
- Schrift, A.M., Mendelssohn, I.A. and Materne, M.D. 2008. Salt marsh restoration with sediment-slurry amendments following a drought-induced large-scale disturbance. *Wetlands*, 28: 1071-1085.

- Silliman, B.R. and Zieman, J.C. 2001. Top-down control of *Spartina alterniflora* production by periwinkle grazing in a Virginia salt marsh. *Ecology*, 82: 2830-2845.
- Silliman, B.R. and Bertness, M.D. 2002. A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Science, U.S.A.*, 99: 10500-10505.
- Silliman, B.R. and Newell, S.Y. 2003. Fungal farming in a snail. *Proceedings of the National Academy of Science, U.S.A.*, 100: 15643-15648.
- Slocum, M.G., Mendelssohn, I.A. and Kuhn, N.L. 2005. Effects of sediment slurry enrichment on salt marsh rehabilitation: plant and soil responses over seven years. *Estuaries*, 28: 519-528.
- Stagg, C.L. 2009. Remediating impacts of global climate change-induced submergence on salt marsh ecosystem functions. Ph.D. dissertation. Louisiana State University, Baton Rouge, LA.
- Stanhope, H.S., Banta, W.C. and Temkin, M.H. 1982. Size-specific emergence of the marsh snail, *Littorina irrorata*: effect of predation by blue crabs in a Virginia salt marsh. *Gulf Research Reports*, 7: 179-182.
- Stiven, A.E. and Hunter, J.T. 1976. Growth and mortality of *Littorina irrorata* Say in three North Carolina marshes. *Chesapeake Science*, 17: 168-176.
- Stiven, A. E. and Kuenzler, E.J. 1979. The response of two salt marsh molluscs, *Littorina irrorata* and *Geukensia demissa*, to field manipulations of density and *Spartina* litter. *Ecological Monographs*, 49: 151-171.
- Teal, J.M. 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology*, 43: 614-624.
- Vaughn, C.C. and Fisher, F.M. 1988. Vertical migration as a refuge from predation in intertidal marsh snails: a field test. *Journal of Experimental Marine Biology and Ecology*, 123: 163-176.
- Vaughn, C. C. and Fisher, F.M. 1992. Dispersion of the salt marsh periwinkle *Littoraria irrorata*: effect of water level, size, and season. *Estuaries*, 15: 246-250.
- Warren, J.H. 1985. Climbing as an avoidance behavior in the salt marsh periwinkle, *Littorina irrorata* (Say). *Journal of Experimental Marine Biology and Ecology*, 89: 11-28.
- Williams, A.H. and Appel, A.G. 1989. Behavioral thermoregulation in *Littorina irrorata* by climbing. *Marine Behaviour and Physiology*, 16: 31-41.

CHAPTER 5

CONTROLS ON RESILIENCE AND STABILITY IN A SEDIMENT SUBSIDIZED SALT MARSH AND DETERMINATION OF LONG-TERM SUSTAINABILITY

5.1 Introduction

Extensive alteration of Louisiana's coastal landscape, through canal dredging and levee construction, has distorted hydrological and sediment deposition regimes, resulting in substantial degradation of coastal wetlands (Turner, 1997, Day *et al.*, 2000). Additionally, geological subsidence and climate change-induced eustatic sea level rise and severe drought, have further contributed to submergence and subsequent land loss (Boesch *et al.*, 1994; Jelgersma, 1996; McKee *et al.*, 2004).

An average land loss rate of $77 \text{ km}^2 \cdot \text{year}^{-1}$ (Barras *et al.*, 2003) has instigated numerous restoration efforts in the region (Louisiana Department of Natural Resources, Office of Coastal Restoration and Management, 2009). One relatively new method of salt marsh restoration, sediment-slurry addition, aims to ameliorate the effects of submergence by increasing the elevation of the marsh surface. This approach is based on the understanding that excessive inundation can lead to inhibited growth, or even mortality, of *S. alterniflora* (Mendelssohn and McKee, 1988), whereas increasing soil drainage can improve plant production (Mendelssohn and Seneca, 1980; Wilsey *et al.*, 1992). The addition of hydraulically dredged materials to degraded salt marshes increases the elevation of the salt marsh, and has been shown to increase mineral content, soil aeration, nutrient availability and restore vegetative structure and function (Mendelssohn and Kuhn, 2003; Slocum *et al.*, 2005; Schrifft *et al.*, 2008; Stagg, 2009).

However, because sediment-slurry addition is a relatively new restoration technique, little research has been conducted on the long-term sustainability of sediment subsidized marshes.

Slocum *et al.* (2005) found that seven years after restoration, areas of moderate sediment-slurry addition (~ 12 cm above ambient marsh) had the highest plant cover compared to areas receiving more or less sediment or no sediment subsidy. However, with this exception (Slocum *et al.*, 2005), investigations considering the effects of sediment addition to salt marshes have been short-term, 2 years or less (Reimold *et al.*, 1978; DeLaune *et al.* 1990; Ford *et al.* 1999; Mendelssohn and Kuhn, 2003; Schrifft and Mendelssohn, 2008). Therefore, I sought to increase the understanding of long-term effects of sediment subsidy by comparing the vegetation resilience of two marshes that were restored at different times; a marsh restored 15 years ago and a newly restored marsh that received sediment subsidy 5 years prior to this study.

Resilience (rate of recovery after disturbance) and stability (ability to recover to steady state after disturbance) (Grimm and Wissel, 1997) have been proposed as indicators of ecosystem health (in addition to organization and vigor) (Costanza, 1992; Costanza *et al.*, 1998; Rapport *et al.*, 1998). As an emergent property of ecosystems, resilience is influenced by the interaction of multiple factors and processes, thus providing an integrated measure of ecological status (Gunderson, 2000). The use of experimental disturbances to measure resilience and stability has recently been shown to accurately reflect underlying stress in salt marsh systems (Slocum and Mendelssohn, 2008). Additionally, experimental disturbance applications provide the opportunity to measure recovery after different intensities of disturbance. Thus, because vegetation responds differently to varying intensities of disturbance (Slocum and Mendelssohn, 2008), the use of both mild (non-lethal) and intense (lethal) experimental disturbances provides a more sensitive measure of resilience and stability. Additionally, this method provides insight into not only the present ecological status of the salt marsh, but also potential responses to future natural and anthropogenic disturbances before they occur (Underwood, 1989). Because sediment

subsidy is an increasingly popular wetland remediation technique, there is a growing number of newly restored sediment subsidized marshes (Louisiana Coastal Area Beneficial Use of Dredged Material Program, 2006). Therefore, it is important to determine not only if resilience is maintained in older marshes, but also how the increasing number of newly restored marshes will respond to relatively common disturbances such as oil spills and hurricanes.

In addition to comparisons across restoration sites of differing age, resilience was measured at varying levels of sediment subsidy within each marsh. Therefore, I was able to determine at which elevation resilience is maximized, as well as whether or not salt marshes restored using sediment subsidy are sustainable over time.

I asked the following questions: 1) How does sediment subsidy affect resilience and stability compared to natural, unsubsidized marshes? 2) At what relative elevation, or level of sediment subsidy, are resilience and stability maximized? 3) What factors influence resilience and stability at each site? 4) Do older restored marshes maintain their resilience compared to recently restored marshes?

Based on the results of Slocum and Mendelssohn (2008), I hypothesized that sediment subsidy would enhance resilience and stability at both the old and newly restored marshes. I also postulated that a sediment subsidy threshold would limit vegetation resilience and stability at extreme high elevations. However, because the older site has subsided and compacted over time, I hypothesized that a sediment subsidy threshold would limit stability and resilience only at the newly restored site, but over time, this threshold effect would disappear (in the old site).

5.2 Materials and Methods

5.2.1 Site Description and Experimental Design

The sites of interest include two submerging salt marshes that were restored using sediment-slurry addition (Figure 5.1). The two sites were restored at different times, providing the opportunity to study an older sediment subsidized marsh (Venice, 15 years old) and a newly restored marsh (Fourchon, 5 years old). Although the cause for restoration and the method for sediment slurry application were different at the two sites, the resulting elevation change after sediment subsidy was similar and allowed for a qualitative comparison of ecological responses to the restoration effort. The characteristic natural marsh surrounding both restored sites was dominated by *Spartina alterniflora* Loisel.

The Venice site (29°12.31'N, 89°26.23'W) was located within the Modern (Bird foot) Delta of the Mississippi River Delta Complex (Figure 5.1.2). High rates of relative sea level rise ($1.25 \text{ cm}\cdot\text{yr}^{-1}$; Penland and Ramsey, 1990), extensive canal dredging and restricted sediment deposition resulted in the submergence and degradation of the salt marshes in this area (Dunbar *et al.*, 1992).

In 1992, an adjacent canal filled with sediment slurry accidentally overflowed into the salt marsh, depositing differential amounts of sediment over 43 ha of marsh. The spill created a depositional elevation gradient ranging from 0-40 cm above the original marsh surface. However, over time these sediments compacted, and by 1998 the relative elevation of the sediment enhanced salt marsh ranged from 0-22 cm above the ambient marsh surface (Mendelssohn and Kuhn, 2003). Additional measurements were taken again in 2008, and most recent elevations at the restored site ranged from 0-26 cm above ambient marsh.

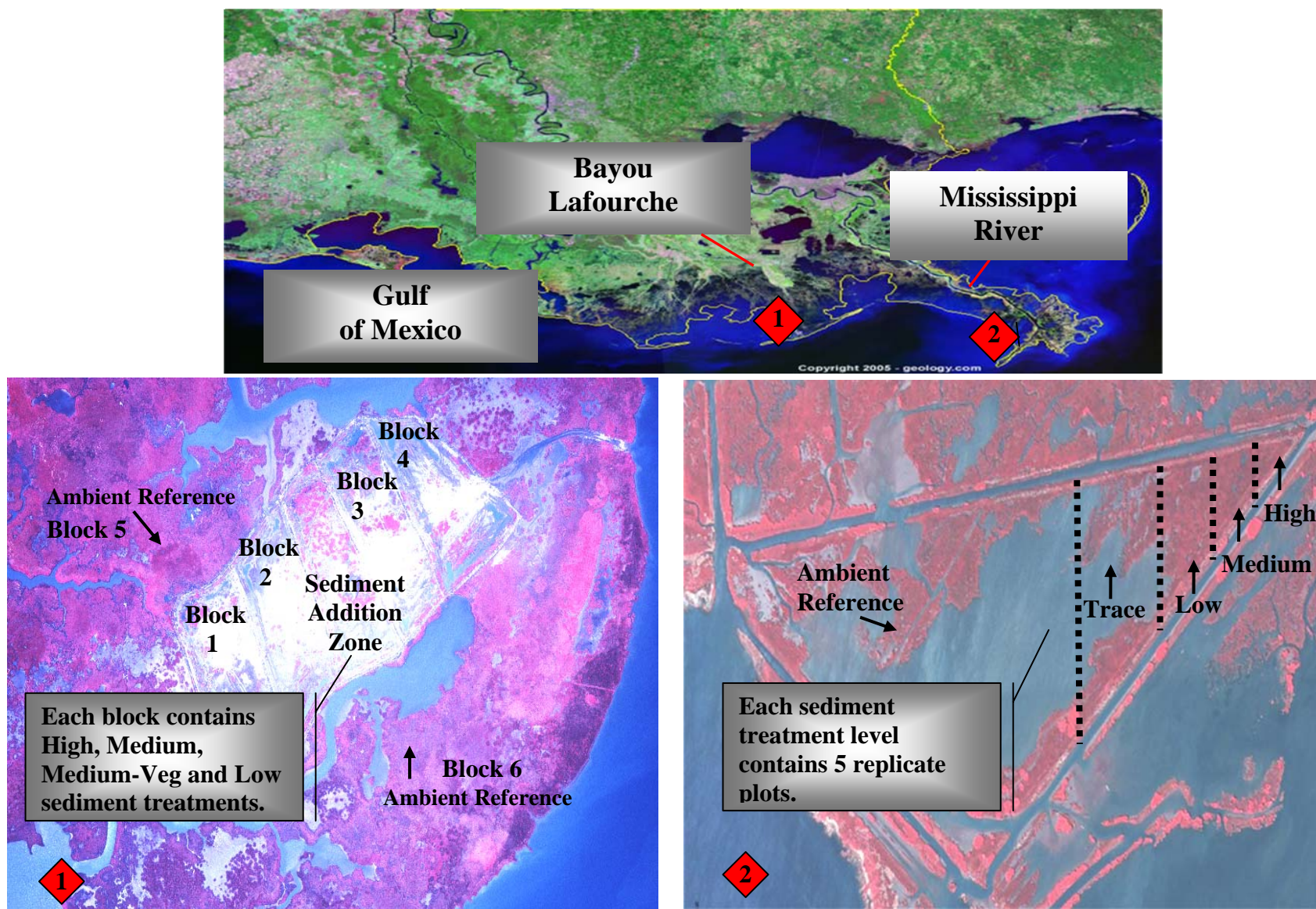


Figure 5.1. Sediment addition at 1) Fourchon (sediment addition: 2002) and 2) Venice (sediment addition: 1992) restoration sites.

The sediment subsidy gradient was divided into 5 elevational regions (Mendelssohn and Kuhn, 2003) that included a no deposition zone (Reference) and four sediment treatment levels (STLs): 1) Reference: received no sediment, -12 cm below to 8 cm above ambient marsh, 2) Trace STL: received very little sediment, 0-7 cm above ambient marsh, 3) Low STL: 12-19 cm above ambient marsh, 4) Medium STL: 17-20 cm above ambient marsh, 5) High STL: 19-26 cm above ambient marsh. Experimental stations were set up in each of the 5 deposition zones (n=5) (Figure 5.1.2). These elevations can be related to the North American vertical datum of 1988 (NAVD 88) by adding 33.22 cm to the marsh surface elevations.

The Fourchon site (29° 10.58'N and 90° 14. 23'W) was located in the Terrebonne Basin, a part of the Mississippi River Deltaic Plain (Figure 5.1.1). The specific area of interest was a submerging, degraded salt marsh located on the west bank of Bayou Lafourche near Leeville, LA. This area was affected by a sudden marsh dieback (SMD) event, which was linked to extreme drought conditions during the summer of 2000 (McKee *et al.*, 2004; Alber *et al.*, 2008). Thousands of acres of *S. alterniflora* dominated salt marshes died and subsequently submerged (Lindstedt *et al.*, 2006; Materne and Mendelssohn, 2006). To restore the degraded area, sediment-slurries were applied to the site in 2002.

The degraded salt marsh was divided into four cells through the construction of small earthen dikes. The cells were hydraulically connected through culverts and breaks in the levees that allowed for tidal exchange. Hydraulically dredged sediments from adjacent Bayou Lafourche were pumped into each cell resulting in four separate sediment subsidy treatment blocks (Figure 5.1.1). The sediment-slurries were comprised of approximately 20-30 % solids and 70-80 % water by volume. Addition of these sediment slurries at differential volumes within each replicate block resulted in four separate sediment subsidy treatment levels (STLs): 1) Low

STL: 13-18 cm above ambient marsh, 2) Medium-Vegetated (Medium-Veg) STL: areas with 100 % vegetative cover in the fall of 2003 and an average elevation of 20 cm above ambient marsh, 3) Medium STL: 20-25 cm above ambient marsh and 4) High STL: 28-36 cm above ambient marsh. In addition to the sediment treatment areas, a reference area, which neither died back nor received sediment, was also included in the experimental design (Figure 5.1.1). The reference marsh was 2-5 cm above the ambient benchmark. These elevations can be related to the North American vertical datum of 1988 (NAVD 88) by adding 29.78 cm to the marsh surface elevations.

5.2.2 Resilience and Stability

I assessed the resilience and stability of both sediment subsidized salt marshes by measuring the response of *S. alterniflora* to two intensities of experimental disturbances (Slocum and Mendelssohn, 2008). Experimental disturbances included: 1) Non-lethal disturbance- aboveground vegetation was removed at the soil surface using a gasoline-powered hand-held trimmer at both sites in the summer of 2006. 2) Lethal disturbance – herbicide (Aquamaster Pro®-active ingredient N-(phosphonomethyl) glycine, Monsanto Industrial, St. Louis, MO) was applied in a water/detergent solution at recommended levels to aboveground vegetation in the summer of 2006. Two herbicide applications were conducted at each site to ensure complete mortality. Standing dead vegetation was removed from experimental plots using a hand-held gasoline powered trimmer. The resulting impact of these experimental disturbances was similar to natural disturbances that occur frequently in these systems; for example, the non-lethal disturbance mimics herbivory and the lethal disturbance mimics hurricane wrack deposition. At each sediment treatment level (STL), experimental disturbances were randomly applied to three plots (1x1 m²), one for each disturbance intensity, and one control (no disturbance).

Although resilience has been defined in multiple ways in the literature (Grimm and Wissel, 1997), I followed Holling's (1996) protocol, where resilience is defined as the rate of recovery after disturbance (engineering resilience; Holling, 1996). To measure recovery, canopy cover (% cover) of the disturbed plots was related to canopy cover of the control plots through a % recovery value which was calculated as:

$$\% \text{ recovery} = (\% \text{ cover disturbed} / \% \text{ cover control}) \cdot 100 \quad (5.1)$$

Canopy cover was measured 5 times after experimental disturbances, from September 2006 to October 2007, using visual estimation (Slocum and Mendelssohn, 2008). Percent recovery was then calculated for each sampling event. The rate of recovery (% recovery \cdot month⁻¹) was derived using a regression analysis with a natural log model:

$$Y = a \cdot \ln(t) \quad (5.2)$$

where y = % recovery, t = time (months) and a = slope (rate of recovery).

Stability was defined as the ability of the vegetation to recover to within 95% of the disturbance control within one year. The odds of stability were used to describe the likelihood of success (stability) in the sediment subsidized areas compared to the likelihood of stability in the reference area. Percent cover values from the last sampling period (1 year after disturbance), in disturbed and control plots, were used to determine if a plot was stable or not stable, based on whether they recovered to within 95 % confidence intervals of the control plots. A binary model was then used to determine odds ratios (odds of stable/odds of not stable) for disturbed plots at each STL, which were then compared to the reference area (no sediment subsidy). Although the range of odds ratios can be very large, this method of determining likelihood of occurrence provides a relative scale by which one can judge statistical differences between multiplicative comparisons that would otherwise exceed 100 % probability. Additionally, odds of stability were

also calculated for each disturbance intensity, relating odds of stability after non-lethal disturbance to odds of stability after lethal disturbance. The binary model was derived using the GENMOD procedure of SAS 9.1.2 (SAS Institute Inc., 2004).

5.2.3 Soil Physico-chemical Parameters

Several soil physical and chemical properties were measured on February 12, 2007 in Venice and February 23, 2007 in Fourchon. A core (5 cm diameter x 10 cm long) was taken at each STL and reference replicate to measure soil bulk density, organic matter content, percent moisture and electrical conductivity. After collection, the cores were analyzed for wet weight, dried at 65 °C, and weighed again to determine bulk density and percent moisture. A portion of the dried soil was also used to measure electrical conductivity and organic matter content. To determine electrical conductivity, 5 g of dried soil was mixed vigorously with 30 ml of distilled water for 1 hour. The mixture was then centrifuged at 2817 g for 5 minutes, and the supernatant was analyzed for electrical conductivity on a Cole Parmer 19820-00 meter. To determine organic matter content, approximately 2-3 grams of dry soil was treated with 1N HCl until all inorganic carbonates were volatilized. The soil was then analyzed for percent organic matter through loss on ignition at 550 °C in a Fisher Isotherm combustion oven (Programmable Forced Draft Furnaces, model 10-750-126) (Nelson and Sommers, 1996).

A second soil core (5 cm diameter x 15 cm long) was simultaneously taken at each STL and reference replicate to measure soil pH (moist sediment), soil extractable nutrients and other elements (NH₄-N, NO₃-N, P, Fe, K, Mg, Mn, Na, and S). The soil cores were immediately placed on ice in the field and transported back to the laboratory at Louisiana State University, where they were homogenized. After homogenization, several soil aliquots were collected to perform the following extractions: NH₄-N and NO₃-N (2 M KCl (Bremner and Kenney, 1966));

P (Bray-2 (Byrnside and Sturgis, 1958)); Ca, K, Mg and Na (ammonium acetate (Thomas, 1982)); and Fe and Mn (DTPA (Lindsay and Norvell, 1978)). Following extraction, $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ samples were filtered through a $0.45\ \mu\text{m}$ filter and measured on a segmented flow AutoAnalyzer (Flow Solution IV AutoAnalyzer, O-I Analytical, USA). The remaining extracts were measured with an inductively coupled argon plasma emission spectrometer (ICP) (Spectro Ciros CCE, Spectro Analytical Instruments, Germany).

Redox potential was measured simultaneously using bright platinum electrodes, a calomel reference electrode and a portable Cole-Parmer digital pH-mV meter. Three platinum electrodes were placed 15 cm below the soil surface at each STL replicate, and the average of the three readings was used in statistical analysis.

Additionally, a third soil core was taken to measure soil sulfide concentrations. The cores (5 cm diameter x 10 cm long) were taken from each treatment replicate and immediately placed in a centrifuge tube (500 ml) containing air-tight septa. The cores were purged with nitrogen gas for 2 minutes to maintain an anoxic environment and then stored on ice. Once the cores were returned to the laboratory, they were centrifuged at 2817 g for 20 minutes to extract porewater from the soil. The supernatant was decanted, stabilized with an anti-oxidant buffer and analyzed for total soluble sulfides (Lazar Model IS-146 sulfide electrode, Lazar Research Laboratories, Los Angeles, CA).

5.2.4 Statistical Analyses

The sediment addition treatments at the Venice study site were applied in a completely randomized block design (CRD, $n=5$), and a randomized incomplete block design (RICBD, $n=2-4$) was used at the Fourchon study site (Figure 5.1.1-2). The incomplete designation arises from the fact that not all treatment levels occurred in every replicate block. For example, the four

blocks containing the sediment subsidy treatments did not contain reference treatments, and the reference blocks did not contain sediment subsidy treatments. The disturbance treatments were nested at each STL and reference resplicate, resulting in a split plot design, where level of sediment subsidy was the whole plot and disturbance intensity was the split plot (Venice n=5, Fourchon n= 2-4).

I determined how sediment subsidy and disturbance intensity affected recovery rate at Venice using a split-plot mixed model ANOVA, with sediment treatment level (whole plot) and disturbance (split plot) as the fixed effects and block (nested in sediment treatment level) as the random effect. The mixed model ANOVA used for Fourchon recovery rates was similar; however, the random effect was the block and the block x STL interaction.

Soil variables were consolidated into composite variables using principle component analysis (PCA). Only principle components (PCs) with eigenvalues > 1 were used for subsequent analyses. To determine the effect of sediment subsidy on the factor scores, I used a one-way mixed model ANOVA, with sediment treatment level as the fixed effect and block as the random effect (as specified above).

To determine which factors most influenced recovery rate, I conducted both a correlation analysis and a multiple regression analysis. The correlation analysis was conducted by comparing several environmental indicator variables such as sediment treatment level, and the soil PCs to the response variable, recovery rate. The models used in the multiple regression analyses were derived by performing the stepwise selection method to include only those independent variables in the models that significantly influenced the response variables ($p < 0.15$).

For all statistical tests, normality and homogeneity of variance were determined by using the Shapiro-Wilks test, and box-plots. Natural log transformations were used to improve normality only in the PCA. Pairwise comparisons were made using Fisher's Protected LSD tests. All statistical tests were performed using the MIXED, FACTOR, CORR, or REG procedures of SAS 9.1.2 unless otherwise noted (SAS Institute Inc., 2004).

5.3 Results

5.3.1 Total Cover

One year after applying disturbances, total *S. alterniflora* canopy cover significantly varied with sediment subsidy at both Venice and Fourchon restoration sites (Figure 5.2.1-3). At Venice, sediment subsidy and disturbance intensity had a significant interactive effect on total cover (Figure 5.2.1). In the reference marsh, which did not receive sediment addition, disturbance reduced vegetation cover. In contrast, in sediment subsidized marshes disturbance had no significant effect. The effect of disturbance on total cover was dependent on relative elevation, or sediment subsidy. In the sediment subsidized areas, total cover after disturbance was equivalent to the disturbance controls, with the exception of the Medium STL, where total cover increased after lethal disturbance. However, in the reference area, which did not receive sediment subsidy, total cover was significantly lower after disturbance compared to the control. These results indicate that recovery in the sediment subsidized areas at Venice is greater than recovery in the reference zone.

At Fourchon, there was no significant interaction between sediment subsidy and disturbance intensity; however, both main effects were significant (Figure 5.2.2-3). *S. alterniflora* cover in the Low and Medium-Veg STLs was equivalent to total cover in the reference area. In contrast, cover at the High and Medium STLs was significantly lower than

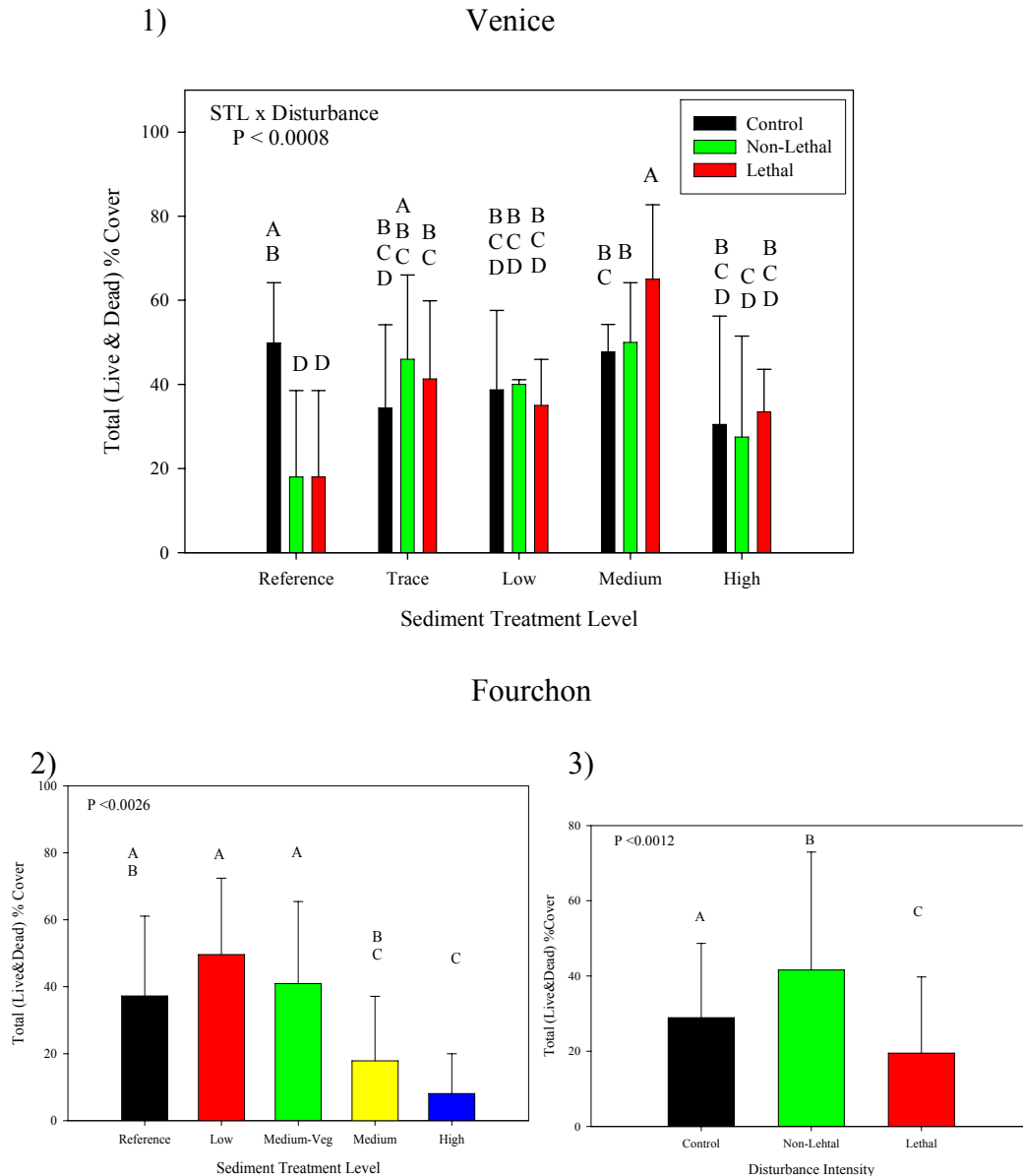


Figure 5.2. The effect of sediment subsidy and disturbance intensity on total (live and dead) *S. alterniflora* cover one year after applied disturbances. 1) Interaction of sediment subsidy and disturbance intensity on total cover at Venice. Main effects of 2) sediment subsidy and 3) disturbance intensity on total cover at Fourchon. Error bars represent standard errors, and different letters denote significantly different means (Fisher's Protected LSD, $p < 0.05$).

cover in the reference area and other lower elevation STLs (Figure 5.2.2). These results indicate that a sediment subsidy threshold limits resilience of *S. alterniflora* cover. Sediment addition resulting in moderate elevations (e.g., Medium-Veg and Low STLs) promoted recovery of *S.*

alterniflora cover. However, higher elevations were not conducive to the recovery of *S. alterniflora* cover.

Additionally, disturbance intensity significantly affected *S. alterniflora* cover (Figure 5.2.3). One year after applying the disturbances, canopy cover in the lethally disturbed plots was significantly lower than cover in the disturbance control plots, indicating a lack of complete recovery. Conversely, canopy cover in the non-lethally disturbed plots was not only greater than cover in the lethally disturbed plots, but was also significantly greater than cover in the disturbance controls. Hence, as expected, lethal disturbances prevent the recovery of vegetative cover, more than non-lethal disturbances.

5.3.2 Recovery Rate

At Venice, sediment subsidy resulted in significantly higher rates of recovery ($33-39 \pm 4$ % recovery \cdot month $^{-1}$) compared to the reference area, which did not receive sediment (17 ± 4 % recovery \cdot month $^{-1}$) (Figure 5.3.1). Recovery rates in all areas receiving sediment were significantly higher than recovery rates in the reference areas, demonstrating that sediment subsidy enhances resilience. In contrast, at Fourchon, because of high variation, the effect of sediment subsidy on recovery rate was not statistically significant at $p < 0.05$, although it was significant at 0.10 (Figure 5.3.2). Hence, there was a tendency for recovery rates to be higher in areas of moderate sediment subsidy (Low and Medium-Veg STLs) compared to areas of more intense sediment subsidy and higher elevation (Medium and High STLs) and compared to the reference area. This trend is similar to the pattern observed for total *S. alterniflora* cover reported previously (Figure 5.2.1). As mentioned above, these trends support the existence of a sediment subsidy threshold, where sediment subsidy resulting in elevations above 20 cm lead to decreased resilience.

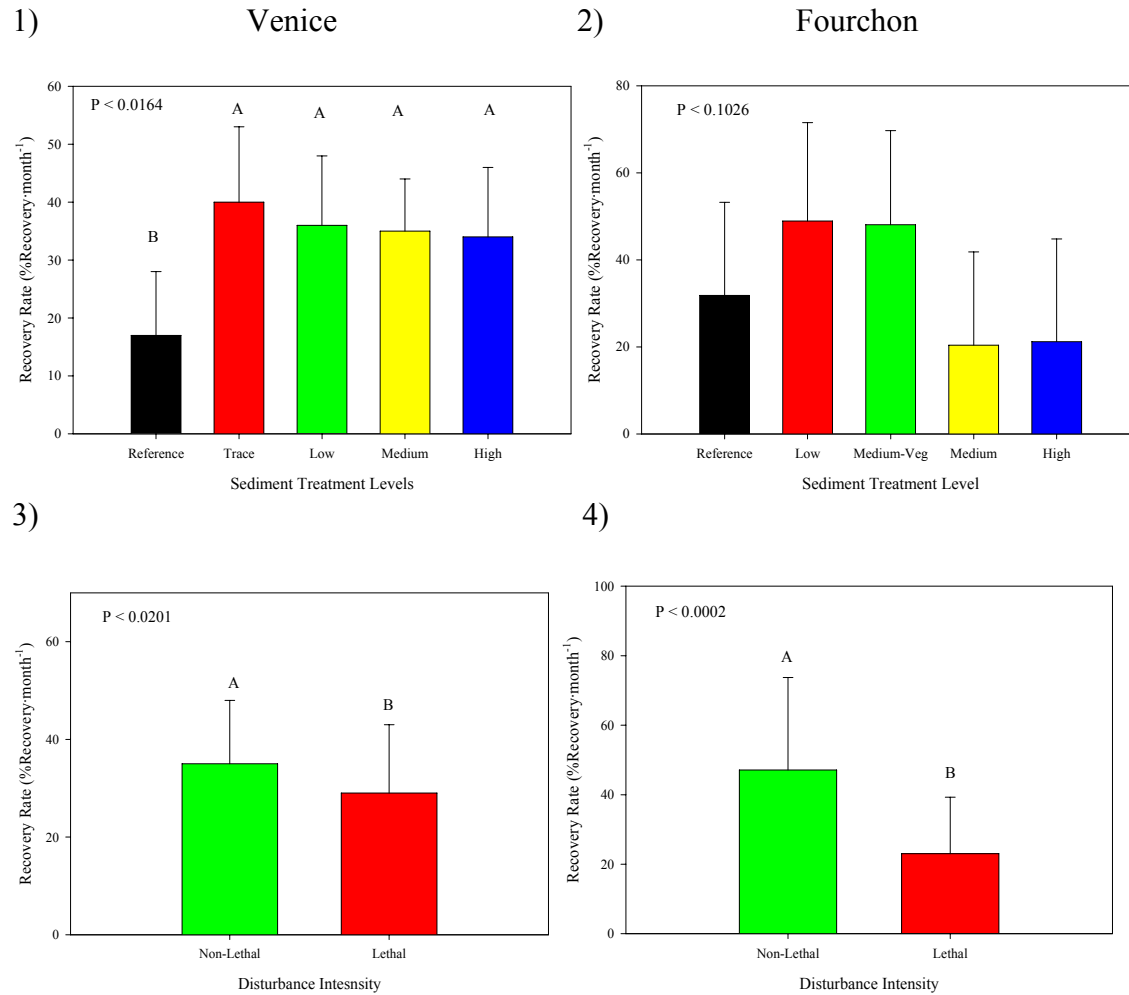


Figure 5.3. Effect of sediment subsidy on recovery rate at 1) Venice and 2) Fourchon. Effect of disturbance intensity on recovery rate at 3) Venice and 4) Fourchon. Recovery rate is measured as the rate of recovery of total cover after disturbance (% control). Error bars represent standard errors, and different letters denote significantly different means (Fisher's Protected LSD, $p < 0.05$).

Similar to total cover, at both Venice and Fourchon restoration sites, disturbance intensity significantly affected recovery rates (Figures 5.3.3-4). More intense, lethal, disturbances resulted in significantly lower recovery rates compared to recovery of non-lethally disturbed vegetation. However, the effect of sediment treatment on recovery did not vary with disturbance intensity.

5.3.3 Stability

At the Venice and Fourchon restoration sites, sediment subsidy had a positive effect on *S. alterniflora* stability (Figures 5.4 & 5.5.1-2), with greater odds of stability occurring in areas receiving sediment compared to the reference area.

At Venice, all areas that received sediment subsidy had better odds of recovering to 95% of the control within 1 year after disturbance (becoming stable) compared to the reference area. Odds of stability increased with increasing relative elevation up to the Medium STL, which were 7×10^{11} times greater than the odds of stability in the reference zone. However, at the highest elevation (High STL) the odds of stability decreased to values equivalent to the Trace STL (Figure 5.4). This trend is suggestive of a sediment subsidy threshold, where stability increases with increasing elevation up to a point, above which benefits of higher elevation decrease. Although this threshold effect was observed for both total cover and recovery rate at the Fourchon study site, stability was the only measured ecological response that exhibited this threshold pattern at Venice, although a tendency for a recovery threshold at Venice was apparent.

Although disturbance intensity did not significantly affect stability at Venice (data not shown), vegetation at Fourchon was nine times more likely to become stable after a non-lethal disturbance compared to a lethal disturbance (Figure 5.5.1). Because there was a significant difference in stability between non-lethal and lethal disturbances, I conducted separate odds ratio tests for non-lethally and lethally disturbed vegetation (Figure 5.5.2-3). After non-lethal disturbance, the odds of a full recovery (stability) were equivalent in reference plots and moderately subsidized zones (Medium-Veg and Low STLs) (Figure 5.5.2). These results indicate that, in the subsidized marsh, vegetation recovering from a relatively mild disturbance will reach a stable state with the same frequency as the natural or reference marsh. However, odds of

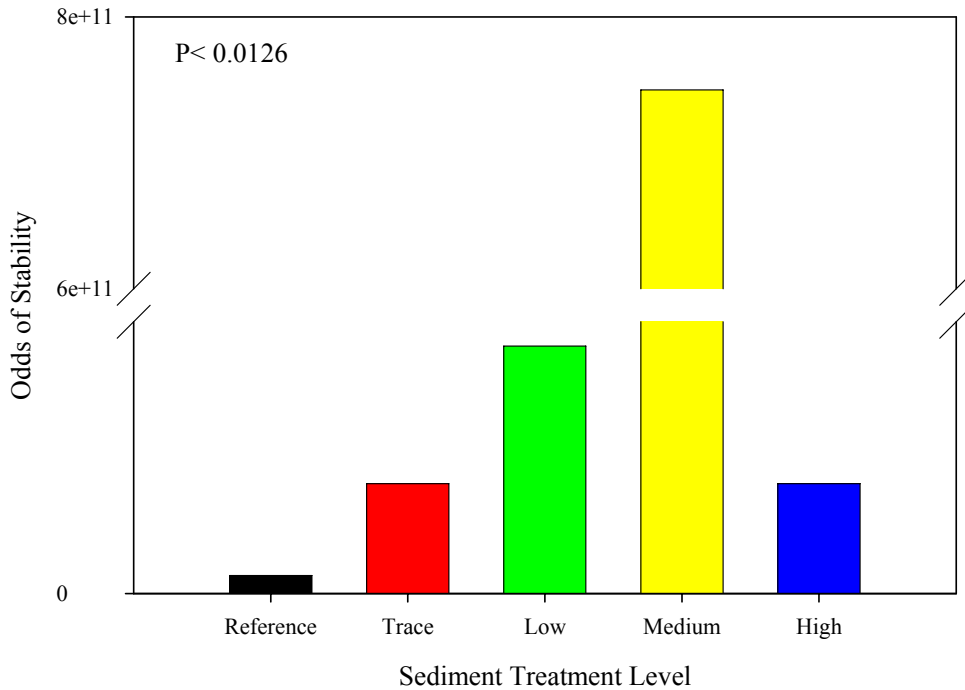
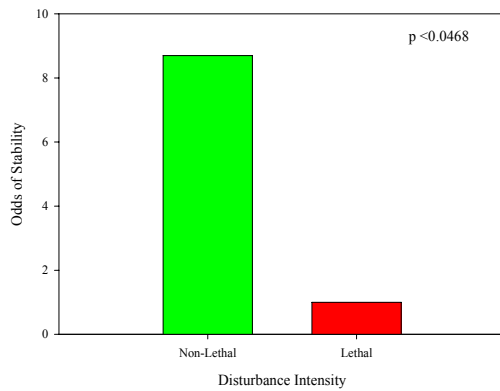


Figure 5.4. Effect of sediment subsidy on odds of stability at Venice (Type 3 Likelihood Ratio test, $p < 0.05$). There was no significant effect of disturbance intensity on stability at Venice. Stability is measured as the odds of vegetation recovering to 95% of the control within 1 year. Odds of stability in areas that received sediment are all compared to the reference area, which is set to 1.

stability in areas of higher elevation, High and Medium STLs, were 9×10^{12} to 10×10^{11} times less likely to reach stability than the reference, Medium-Veg and Low STLs. These results suggest that elevations above 20 cm limit stability, and further support the existence of a sediment subsidy threshold.

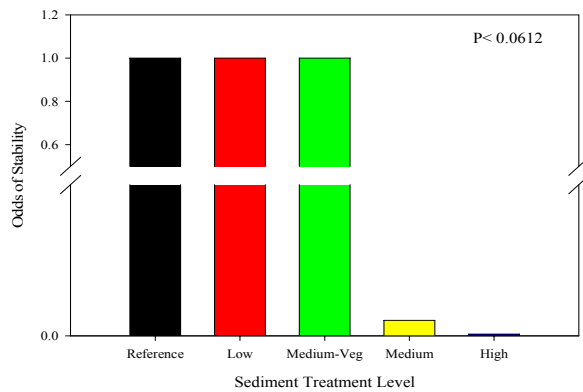
Similarly, after lethal disturbance, odds of stability were higher in the reference, Medium-Veg and Low STLs compared to the High STL. The High STL was 1×10^{12} times less likely to reach stability compared to the reference area. Again, the decrease in stability at high elevations suggests a sediment subsidy threshold effect. However, in contrast to the non-lethally disturbed plots, lethally disturbed vegetation in the Medium-Veg and Low STLs had greater odds of stability than the reference area. The odds of stability in the Medium-Veg and Low STLs were

1)



2)

Non-Lethal



3)

Lethal

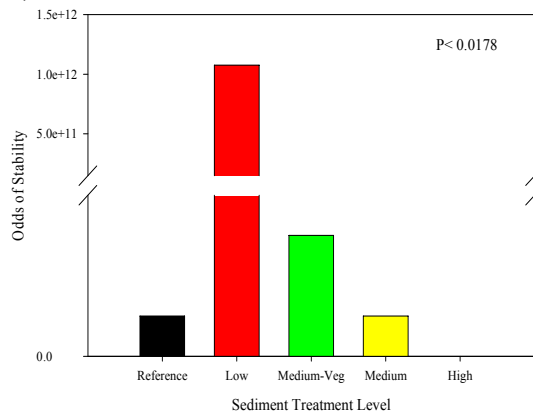


Figure 5.5. 1) Effect of disturbance intensity on stability at Fourchon. Effect of sediment subsidy on stability after 2) non-lethal and 3) lethal disturbances at Fourchon (Type 3 Likelihood Ratio test, $p < 0.05$). Stability is measured as the odds of vegetation recovering to 95% of the control within 1 year. Odds of stability after non-lethal disturbance are compared to the lethal disturbance, which is set to 1. Odds of stability in areas that received sediment are all compared to the reference area, which is set to 1.

3 to 1×10^{12} times the odds of stability in the reference area, respectively. Therefore, after lethal disturbance, the reference area is less likely to fully recover compared to areas of moderate elevation, whereas after a non-lethal disturbance it is equally likely that the unsubsidized and moderately subsidized marshes will fully recover.

5.3.4 Soil Physico-Chemical Characteristics

The physico-chemical parameters characterizing the marsh soil were highly intercorrelated at both Venice and Fourchon restoration sites (Table 5.1). At Venice, PCA of soil variables resulted in two principal components (PCs) accounting for 66 % of the variability in the dataset. The two PCs associated with the soil variables included a salinity component (PC1) and a reduction component (PC2). PC1 (Salinity) was defined by variables such as sodium, potassium, magnesium, calcium and boron, and explained 38 % of the variation. In addition to salinity variables, other elements such as iron, phosphorous and manganese were positively loaded onto PC1. The second PC (Reduction) was positively associated with % organic matter, % moisture, and negatively associated with redox potential and bulk density. Additionally interstitial ammonium was also negatively loaded onto the PC2 (Reduction), illustrating that as soils became more reduced, ammonium concentrations decreased compared to more weakly reduced conditions. PC2 accounted for 28 % of the variance associated with the soil dataset.

At Fourchon, three principal components were derived from the soil data, and these factors account for 87 % of the variation in the dataset (Table 5.1). Principle components included a soil moisture/salinity component (PC1), an iron/phosphorus component (PC2) and an oxidation component (PC3). PC1 (Soil moisture/Salinity), which accounted for 65 % of variability in the dataset, was defined by variables associated with flooded soils such as sulfide, ammonium, % moisture, % organic matter and low bulk density. Additionally, PC1 was also

defined by variables associated with salinity such as conductivity, sodium, potassium and magnesium. PC2 (Fe/P) was associated with iron and phosphorus and accounted for 15 % of the variance associated with the dataset. PC3 (Oxidation/NO₃) was defined by reduction-oxidation potential and nitrate and explained only 7 % of the variance in the soil dataset.

Table 5.1. Correlations between indicator variables and principal components (PCs) for soil characteristics at Venice and Fourchon restoration sites. Eigen-values and percent variation explained are included for each PC. Bolded loadings indicate variables that define the PC. Symbols ^{ln} and ^{-1/2} denote natural log transformation and square root transformation of the data, respectively. The symbol · denotes missing value, variable was not highly correlated and not included in the final PCA.

Indicator Variables	Principle Components				
	Venice		Fourchon		
	PC1 Salinity	PC2 Reduction	PC1 Soil Moisture/ Salinity	PC2 Fe/P	PC3 Oxidation/ NO ₃
Ammonium	-0.18164 ^{ln}	-0.54008^{ln}	0.83247^{ln}	-0.18516 ^{ln}	-0.16489 ^{ln}
Boron	0.84152	-0.04917	·	·	·
Calcium	0.61676	-0.0396	·	·	·
Conductivity	·	·	0.85505^{ln}	0.10384 ^{ln}	-0.38157 ^{ln}
Iron	0.87223^{ln}	-0.11585 ^{ln}	0.18504 ^{-1/2}	0.83739^{-1/2}	-0.37063 ^{-1/2}
Magnesium	0.82895	-0.09634	0.93832^{ln}	0.12132 ^{ln}	-0.14653 ^{ln}
Manganese	0.78387	-0.31062	-0.80179^{ln}	0.43504 ^{ln}	-0.19053 ^{ln}
Nitrate	·	·	0.16883 ^{ln}	-0.31325 ^{ln}	0.88821^{ln}
pH	·	·	-0.8529	-0.19624	-0.09858
Phosphorus	0.75234	0.0818	0.16739 ^{ln}	0.84666^{ln}	-0.06506 ^{ln}
Potassium	0.84934	0.35013	0.89373^{ln}	0.33703 ^{ln}	-0.14348 ^{ln}
Sodium	0.90467	0.14322	0.95166^{ln}	0.09397 ^{ln}	-0.13701 ^{ln}
Sulfur	-0.06944 ^{ln}	0.56553 ^{ln}	0.94849^{ln}	0.18008 ^{ln}	-0.13968 ^{ln}
Sulfide	0.23822	0.2842	0.7437^{ln}	-0.08587 ^{ln}	-0.42412 ^{ln}
Eh	-0.35988	-0.64156	-0.52481	-0.13647	0.71007
Bulk Density	0.1089	-0.94553	-0.94743	-0.27017	0.03441
% Moisture	-0.06638	0.95438	0.93261^{ln}	0.30102 ^{ln}	-0.04564 ^{ln}
% Organic Matter	-0.21428	0.90573	0.93754^{ln}	0.19977 ^{ln}	0.03306 ^{ln}
Eigenvalue	5.7	4.1	10.4	2.4	1.1
% Variance Explained	38 %	28 %	65 %	15 %	7 %
Cumulative % Variance Explained	66 %		87 %		

At Venice, soil salinity (PC1) significantly increased with increasing elevation up to the Medium STL, after which soil salinity decreased at the High STL (Figure 5.6.1). Soil reduction status also increased with increasing sediment subsidy, with the lowest factor scores for PC2 (Reduction) occurring in the reference zone and the Trace STL, and the highest factor scores occurring in the Medium and High STLs (Figure 5.6.3).

At Fourchon, characteristics of soil inundation (PC1 Soil Moisture/Salinity) significantly decreased in all areas receiving sediment subsidy compared to the reference site (Figure 5.6.2). In contrast, iron and phosphorus concentrations (PC2 Fe/P) were equivalent between the reference sites and the Low and Medium-Veg STLs and significantly lower at the High and Medium STLs (Figure 5.6.4). There was no significant effect of sediment subsidy on PC3 (Oxidation/NO₃) (data not shown).

5.3.5 Determinants of Resilience

Based on the multiple regression model, total cover at Venice was influenced by redox potential, sulfide concentration and soil potassium concentration (Table 5.2.1). These soil characteristics explain approximately 44 % of the variance in *S. alterniflora* cover. Additionally, redox potential and potassium are positively associated with total cover, indicating that increasing total cover is dependent on aerobic soil conditions and relatively higher potassium concentrations. On the other hand, as sulfide concentrations increase, total cover values decrease. In addition to these soil parameters, PC1 (Salinity) also had a significant positive correlation with total cover (Pearson's coefficient: 0.79262, $p < 0.1098$), indicating that PC1 (Salinity) increased, total cover also increased. Additionally, potassium, a parameter that positively influenced total cover (Table 5.2.1), is included in PC1 (Salinity) further supporting observations that salinity has a positive effect on *S. alterniflora* cover.

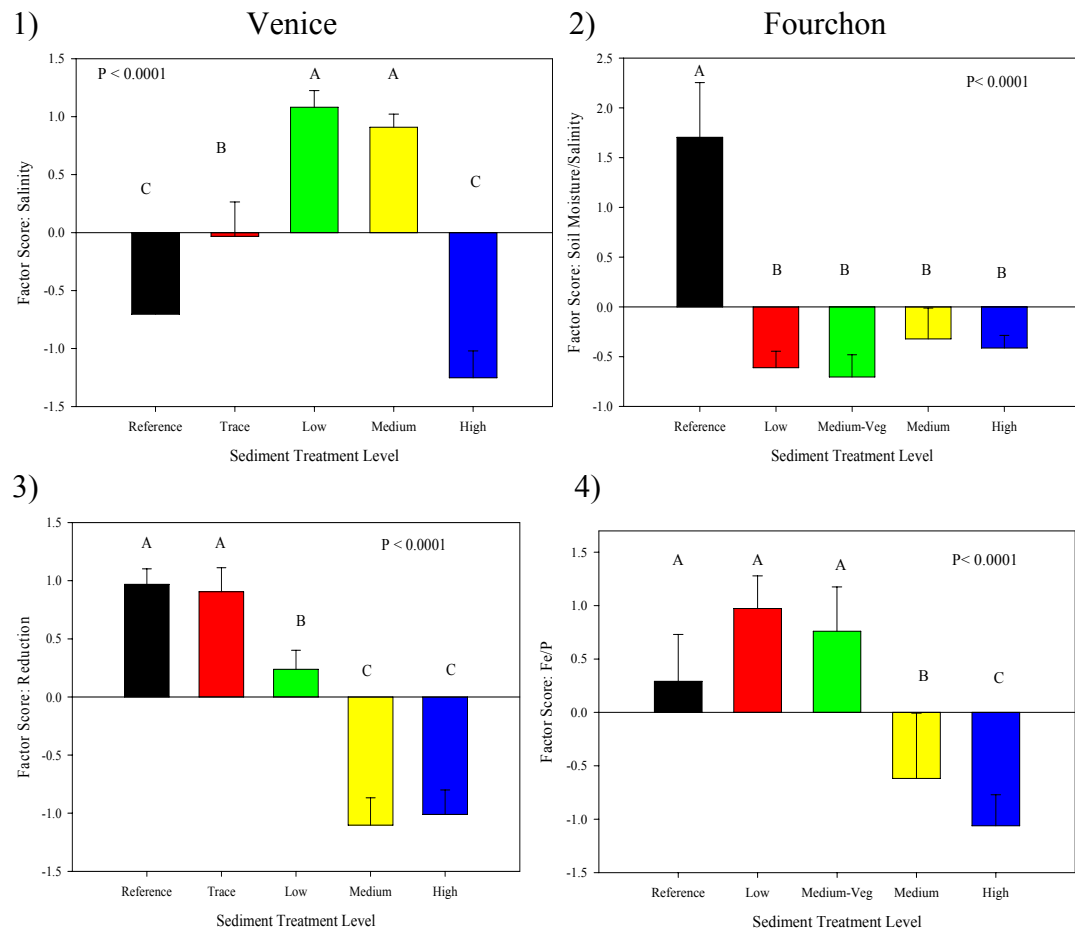


Figure 5.6. Effect of sediment subsidy on PC1s at 1) Venice: PC1 (Salinity), and 2) Fourchon: PC1 (Soil Moisture/Salinity). Effect of sediment subsidy on PC2s at 3) Venice: PC2 (Reduction), and 4) Fourchon: PC2 (Fe/P). Error bars represent standard errors, and different letters denote significantly different means (Fisher's Protected LSD, $p < 0.05$).

PC2 (Reduction) and bulk density had a significant influence on recovery rate (Table 5.2.1). PC2 (Reduction) accounted for approximately 14 % of the variation associated with recovery rate. PC2 (Reduction), containing variables associated with reduced soils, was negatively correlated with recovery rate, implying that as soils become more reduced, recovery rate of *S. alterniflora* decreases.

At Fourchon, that total cover was influenced by sediment subsidy (42 % variance explained), and recovery rate was dependent upon both redox potential and PC1 (Soil Moisture/Salinity) (40 % variance explained) (Table 5.2.2). Based on the negative association

between elevation and total cover, it appears that as sediment subsidy increases, total cover decreases. However, I observed a significant increase in total cover at moderate levels of sediment subsidy, followed by a sharp decrease in cover at the High and Medium STLs (Figure 5.2.2). The relationship between relative elevation and total cover does not appear to be linear, and the results of the multiple regression are likely weighted by the very low cover values found at the High and Medium STLs.

Table 5.2. Multiple regression parameters that explain variance associated with response variables, total cover and recovery rate, at each of the two restoration sites 1) Venice and 2) Fourchon. Parameters included in multiple regression models were derived using the stepwise selection method, which took into account all environmental parameters ($p < 0.15$).

Restoration Site	Response Variable	Independent Variable	Parameter Estimate	Partial R^2	Overall R^2	Overall P-value
1) Venice	Total Cover	Redox	0.13976	0.1108	0.4411	0.0059
		Sulfide	-48.646	0.0769		
		Potassium	0.58223	0.0702		
	Recovery Rate	Reduction (PC2)	-0.28754	·	0.1440	0.0549
2) Fourchon	Total Cover	Sediment Addition	-9.5363	·	0.4223	0.0035
	Recovery Rate	Oxidation	-0.21	0.2656	0.4013	0.0213
		Soil Moisture /Salinity(PC2)	-11.529	0.1357		

Recovery rate was dependent on both redox potential and PC1 (Soil Moisture/Salinity) (Table 5.2.2). Recovery rate was negatively associated with redox potential (27 % variance explained) suggesting that recovery rate is limited in aerated soils. However, the negative relationship between recovery rate and PC1 (Soil Moisture/Salinity) (14 % variance explained) indicates that increased inundation limits recovery rate. Furthermore, more frequently flooded

soils are typically more reduced. This apparent contradiction is reflective of the fact that recovery rates are lowest in areas of very high elevation, which contain more aerated soils, and also in areas of extreme low elevation, which are inundated more frequently. This pattern is supported by previous results which suggest the existence of the sediment subsidy threshold.

In addition to these variables, PC2 (Fe/P) was significantly correlated with both total cover (Pearson coefficient: 0.96787, $p < 0.0069$) and recovery rate (Pearson coefficient: 0.93697, $p < 0.0188$). Both correlations were positive, indicating that iron and phosphorus stimulate canopy cover and the rate of recovery.

5.4 Discussion

The results from this study support my hypothesis that sediment subsidy has a beneficial effect on resilience and stability. At both Venice and Fourchon, total cover, resilience and stability all increased with some level of sediment subsidy compared to the reference areas that did not receive sediment. My results indicate that sediment subsidy promotes resilience and stability through ameliorating the impacts of excessive inundation by increasing the elevation of the marsh surface.

5.4.1 Venice Total Cover and Resilience

At Venice, total cover was significantly higher in sediment subsidized areas, which were characterized by higher elevations, increased redox potentials and decreased sulfide. Several studies have shown that redox potential increases with increasing elevation (Mendelssohn and Kuhn, 2003; Slocum *et al.*, 2005; Schrifft and Mendelssohn, 2008), and that more aerated soils promote *S. alterniflora* growth (Linthurst, 1980; Howes *et al.*, 1981). In contrast, low-lying and frequently flooded soils characteristically display low redox potentials, resulting in the reduction of sulfate to sulfide (Postgate, 1959). It has been well documented that excessive inundation

results in sulfide accumulation (Linthurst, 1980; Patrick and DeLaune, 1972; Mendelssohn and McKee, 1988), which is directly linked to inhibited growth and potential mortality of *S. alterniflora* (Mendelssohn and Seneca, 1980; Linthurst, 1980; Mendelssohn *et al.*, 1981; Ingold and Havill, 1984; Mendelssohn and McKee, 1988; Bradley and Dunn, 1989; Koch and Mendelssohn, 1989; Webb *et al.*, 1995). I also found that *S. alterniflora* cover was minimal in the reference areas, which were characterized by low elevation and redox potential and high sulfide concentrations. In contrast, total cover was highest in sediment subsidized areas. Therefore, I conclude that sediment subsidy effectively reduces inundation stress on *S. alterniflora* through increasing the elevation of the marsh and subsequently increasing redox potential and decreasing sulfide concentrations.

Interestingly, my results also indicate that, as the elevation of the marsh increases, salinity and *S. alterniflora* cover increase. Although it is well documented that salinity limits *S. alterniflora* growth (Gosselink, 1970; Mooring *et al.*, 1971; Broome *et al.*, 1975; Nestler, 1977; Parrondo *et al.*, 1978; Naidoo *et al.*, 1992; Brown and Pezeshki, 2007), both potassium and salinity (PC1) were positively correlated with increasing canopy cover. I found significantly higher potassium concentrations (data not shown) and PC1 (Salinity) factor scores in the STLs that supported the highest canopy cover. However, I do not believe that salinity is directly stimulating *S. alterniflora* recovery. Alternatively, it is more likely that increased elevation in the sediment subsidized zones change the hydro-edaphic character of the soil to promote *S. alterniflora* growth (i.e. increased aeration, decreased sulfides), but concurrently results in higher soil salinity. For example, as marsh elevation increases, tidal inundation is less frequent. Finer sediment particles drain poorly, resulting in accumulation of salt ions in the soil (Weigert and

Freeman, 1990). Although soil salinities increased, *S. alterniflora* cover also increased, suggesting that these salinities were within the range of tolerance for *S. alterniflora*.

Therefore, it is more likely that other factors associated with decreased inundation, such as improved aeration, are influencing recovery. Additionally, as sediment subsidy and elevation increased, bulk density also increased, potentially changing the ionic character of the soil. Higher bulk density can promote *S. alterniflora* growth (Wiegert *et al.*, 1983) and change the cation exchange capacity (CEC) of the soil. Specifically, highly organic soils exhibit a high CEC dominated by hydrogen ions, whereas mineral soils have a lower CEC dominated by major metal cations such as K^+ , Mg^{2+} , Ca^{2+} and Na^+ (Gorham, 1967), which are included in the salinity component (PC1). PC1 (Salinity) also includes phosphorus, iron and manganese, which are associated with high bulk density mineral soils (Mendelssohn and Kuhn, 2003). Phosphorus is commonly found in high concentrations in mineral soils, because of the high retention capacity of the mineral fraction for this nutrient (Syers *et al.*, 1969; Brady and Weil, 1996). Mendelssohn and Kuhn (2003) also observed significantly higher exchangeable phosphorus concentrations in areas of increasing sediment subsidy and high *S. alterniflora* biomass, suggesting that this nutrient stimulated plant growth. Furthermore, Fe and Mn precipitate hydrogen sulfide, thereby decreasing its toxicity and promoting the growth of *S. alterniflora* (Gambrell and Patrick, 1978; King *et al.*, 1982). Therefore, the results from this study reflect the response of *S. alterniflora* cover to an interaction of factors related to increasing marsh surface elevation with the addition of mineral sediments.

Similarly, recovery rate at Venice also increased with sediment subsidy, and was also associated with a decrease in soil reduction status (PC2). PC2 (Reduction) is characterized by factors associated with reduced soils such as high soil organic matter, high % moisture, low bulk

densities and low redox potential, which are all factors that have been associated with decreased *S. alterniflora* growth (DeLaune *et al.*, 1979; King *et al.*, 1982; Morris and Dacey, 1984; Mendelssohn and Kuhn, 2003). As was seen with total cover, resilience is greater in those areas where an increase in elevation decreases the stress of prolonged inundation, which is reflected by the decrease in PC2 (Reduction). Mendelssohn and Kuhn (2003) also reported a significant increase in *S. alterniflora* cover, height and biomass with increasing sediment subsidy. In agreement with my results, they concluded that sediment subsidy resulting in increased elevation and mineral matter lead to better drainage and aeration and decreased sulfide stress, which all contribute to a more favorable environment for *S. alterniflora* growth.

5.4.2 Fourchon Total Cover and Resilience

Likewise, sediment subsidy significantly increased total cover and resilience at Fourchon. However, unlike total cover and resilience at Venice, these vegetation responses were limited at the highest STLs at Fourchon, providing evidence for a sediment subsidy threshold. These results indicate that, at the newly restored site, the effect of sediment subsidy on total cover is non-linear; and, at moderate levels of sediment subsidy, canopy cover is maximal. However, elevations above 20 cm can have an unfavorable effect on *S. alterniflora* recovery. Similarly, in a study by Slocum *et al.* (2005), *S. alterniflora* biomass and canopy cover were significantly lower at elevations above 20 cm (above ambient marsh surface) compared to areas of intermediate elevation. These authors, who investigated the effects of sediment subsidy on *S. alterniflora* vigor over a 7 year period, cited decreased nutrient content and high soil salinity as potential negative influences on the low vigor observed at high levels of sediment subsidy. As elevation increases, flooding becomes intermittent, promoting leaching of nutrients (Patrick and Wyatt, 1964) and concentrating salts through evaporation (Wiegert and Freeman, 1990). Although soil

salinity did not increase at the High STL, I did observe a decrease in $\text{NH}_4\text{-N}$, which may have contributed to lower cover values at the highest elevation.

Resilience at Fourchon also showed a sediment subsidy threshold, characterized by low recovery rates at extreme low and high elevations (reference and High STL, respectively). Additionally, increased flooding (associated with low elevation) and increased redox potential (associated with high elevation) have a negative influence on resilience (Table 5.2.2). However, while excessive flooding has been shown to limit productivity in salt marshes (Mendelssohn and Seneca, 1980; Mendelssohn and McKee, 1988; Webb *et al.*, 1995), increased redox potentials typically indicate more favorable conditions for *S. alterniflora* growth (Linthurst, 1980; Mendelssohn and Seneca, 1980; Howes *et al.*, 1981). Although there is a negative correlation between redox potential and resilience, the observed increase in redox potential is not necessarily causing slower recovery of *S. alterniflora*. High redox potentials are reflective of the dry conditions in the High STL, which are possibly limiting *S. alterniflora* resilience.

A study conducted by Naidoo *et al.*, (1992) concluded that *S. alterniflora* is more tolerant of flooded than drained conditions. This conclusion was supported by observations of greater leaf elongation in flooded versus drained conditions, even under high salinity regimes. Furthermore, a study by Brown and Pezeshki (2007) illustrated the effects of drought conditions on *S. alterniflora*, concluding that, even in low salinity soils, osmotic stress can have a negative effect on *S. alterniflora* growth, gas exchange and survival. Accordingly, I observed minimal resilience in the High STL which is flooded less than 5 % of the time (Materne and Mendelssohn, 2006). Therefore, at Fourchon, the primary controls on *S. alterniflora* total cover and resilience are a result of increasing elevation, with negative influences at either elevation

extreme, i.e. in excessively inundated or extremely dry conditions, whereas optimal resilience occurs at a moderate level of sediment subsidy, which results in flooding 10-20 % of the time.

5.4.3 Venice and Fourchon Stability

Stability at both Venice and Fourchon also increased with sediment subsidy. The relationship between sediment subsidy and stability is not linear, however, and both sites show an elevation threshold. At Fourchon, the threshold effect on stability agrees with the pattern observed for total cover and resilience; therefore, stability is likely influenced by the same parameters that limit resilience at high elevations: insufficient flooding and soil nutrient availability. However, the sediment subsidy threshold effect on stability at Venice is interesting for two reasons: 1) Slocum and Mendelssohn (2008) measured stability at Venice and did not observe a sediment subsidy threshold effect, and 2) neither total cover nor resilience was affected by a sediment subsidy threshold at Venice in the present study. These two discrepancies indicate that 1) stability has changed at the Venice site within the last 6 years and 2) stability is more sensitive to changes in elevation than total cover and resilience.

Although Slocum and Mendelssohn (2008) ultimately concluded that stability was not limited by an elevation threshold at Venice, they originally hypothesized that resilience and stability would be lower at the high deposition zone compared to the moderate deposition zone. This *a priori* prediction was based on results from Slocum *et al.* (2005), who found that, 9 years after sediment addition, *S. alterniflora* cover and biomass decreased in the high deposition zone compared to the moderate deposition zone. Restricted flooding, resulting in leaching of nutrients and accumulation of salt ions, were cited as potential causes for the decreased vigor at the high elevation. However, Slocum and Mendelssohn (2008) found that stability in the high deposition zone was greater than stability in the moderate deposition zone. They concluded that the initial

deposition of nutrient rich sediment, which caused a pulse of growth in the high deposition zone (Mendelssohn and Kuhn, 2003), was sufficient to maintain high levels of stability 9 years later.

In contrast, I found that stability was lower at the High STL, indicating that the effect of this nutrient pulse was no longer present. Therefore, 15 years after sediment subsidy, stability at the High STL is primarily controlled by elevation, such that decreased flooding at high elevations has a negative effect on stability. Thus, at both the new (Fourchon) and old (Venice) sites, vegetation is less likely to become stable within one year after a disturbance in areas of extreme high elevation. Furthermore, the change in stability from 2001 (9 years after restoration) to 2007 (15 years after restoration) at Venice, underlines the importance of conducting long-term studies of these dynamic systems.

Additionally, stability (likelihood of a full recovery) appears to be more sensitive to changes in elevation than resilience (rate of recovery). This trend may be due to the effects of varying intensities of disturbance on soil nutrient content. Although resilience is generally higher after non-lethal disturbances compared to lethal disturbances; at the High STL, recovery rates are equivalent between non-lethal and lethal plots (data not shown). This indicates that recovery rates after lethal disturbance are enhanced, which is likely due to a nutrient release after plant mortality (Slocum and Mendelssohn, 2008). Therefore, recovery rates at the High STL may have been enhanced by a nutrient pulse resulting in equivalent resilience values between the High STL and other sediment subsidized areas.

Furthermore, although there is no significant difference between the odds of stability in non-lethal and lethal plots; at the High STL, lethal plots stabilized 100 % of the time, and non-lethal plots stabilized only 60 % of the time. Again, the increased stability in the lethally disturbed plots is likely due to the nutrient pulse that was released after original plant mortality.

On the other hand, non-lethally disturbed plots did not receive this nutrient pulse, indicating that decreased stability at the High STL is primarily influenced by elevation, or a sediment subsidy threshold. Therefore, it is probable that high recovery rates observed at the High STL are elevated by a nutrient pulse following plant mortality in the lethally disturbed plots, potentially masking the effects of a sediment subsidy threshold on resilience. However, the low odds of stability after non-lethal disturbance are sufficient to illustrate the effect of a sediment subsidy threshold, emphasizing the importance of using varying intensities of disturbances.

At Fourchon, vegetation was more likely to recover after a non-lethal disturbance compared to a more intense, lethal, disturbance. Additionally, I observed that after a mild disturbance, the unsubsidized marsh is just as likely to recover as the moderately subsidized marsh. However, after a severe disturbance, stability in the reference zone is much lower than stability in the moderately subsidized zones. These results are supported by Slocum and Mendelssohn (2008), who found that excessively inundated vegetation did not recover as quickly or with the same frequency as less stressed vegetation. Additionally, a study by Whitford *et al.* (1999) also concluded that recovery was slower in vegetation growing in stressful conditions. Thus, those areas that are already stressed by excessive flooding are less likely to recover after a severe disturbance compared to subsidized areas where the stress of prolonged inundation has been ameliorated. Therefore, I conclude that sediment subsidy effectively minimizes the stress of prolonged inundation such that stability is maximized at moderate elevations, regardless of disturbance intensity.

5.4.4 Venice vs. Fourchon

Comparisons among the old (Venice) and new (Fourchon) restoration sites illustrated that resilience and stability are higher in areas of sediment subsidy compared to the reference zones

at both sites, with optimal resilience and stability occurring at moderate elevations. At Venice (older site), maximum resilience ($35\% \text{ recovery} \cdot \text{month}^{-1}$) was observed at the Low STL (45-52 cm NAVD88). Similarly, at Fourchon, the highest resilience ($49\% \text{ recovery} \cdot \text{month}^{-1}$) was observed at the Low STL (42-47 cm NAVD88). Additionally, odds of stability at Venice were highest ($7.5e^{11}$) at the Medium STL (50-53 cm NAVD88); and, at Fourchon odds of stability were highest ($3.5e^{11}$) at the Medium-Veg STL (47-49 cm). Therefore, resilience and stability are similar between the two sites, and recovery is optimal at similar elevations (42-53 cm NAVD88).

However, there is a clear sediment subsidy threshold effect on both resilience and stability at Fourchon; whereas, at Venice, this pattern is not as dominant. This difference illustrates how sediment subsidized sites can change over time. At Venice, for example, the High STL elevation ranges from 19-26 cm above ambient marsh; however, in the period immediately following sediment subsidy, elevation at the High STL was greater than 40 cm above the ambient marsh surface (Mendelssohn and Kuhn, 2003; Slocum *et al.*, 2005). Thus, over time this restored marsh has compacted and subsided, resulting in a marsh with relative elevations that are comparable to the moderately subsidized zones of the new (Fourchon) site. Additionally, even though resilience and stability are not significantly lower in the High STL at Venice, maximum values are still observed in areas of moderate elevation (12-20 cm above ambient marsh, 45-53 cm NAVD88). Therefore, I conclude that in a newly restored marsh, resilience and stability will be optimal in areas of moderate elevation (Fourchon, 42-50 cm NAVD88). Furthermore, over time, these moderately subsidized zones will still have high resilience and stability (Venice, 45-53 cm NAVD88) indicating that sediment subsidy at moderate elevations (42-53 cm NAVD88) is sustainable over time.

5.5 Conclusions

These results support my hypothesis that sediment subsidy increases total cover, resilience and stability compared to natural unsubsidized marshes. However, addition of too much sediment can result in decreased resilience and stability. The sediment subsidy threshold appears to occur at elevations greater than 20 cm above ambient marsh (53 cm NAVD88), thereby surpassing the intertidal position of *S. alterniflora* and negating the benefits of increased elevation. The use of sediment subsidy to increase the relative elevation of the marsh to moderate elevations (42-53 cm NAVD88) effectively reduced the stress of prolonged inundation and optimized resilience and stability through increasing soil aeration, and decreasing phytotoxic sulfide concentrations. Additionally, the 15-year old site had similar resilience and stability to the 4-year old site, suggesting that sediment subsidy at moderate elevations is a sustainable restoration technique.

5.6 Literature Cited

- Barras, J., Beville, S., Britsch, D., Hartley, S., Hawes, S., Johnston, J., Kemp, P., Kinler, Q., Martucci, A., Porthouse, J., Reed, D., Roy, K., Sapkota, S. and Suhayda, J. 2003. Historical and projected coastal Louisiana land changes: 1978-2050. USGS Open File Report 03-334.
- Boesch, D.F., Josselyn, M.N., Mehta, A.J., Morris, J.T., Nuttle, W.K., Simenstach, C. A. and Swift, D.J.P. 1994. Scientific assessment of coastal wetland loss, restoration and management in Louisiana. *Journal of Coastal Research: Special Issue*, 20: 1–103.
- Brady, N.C. and Weil, R.R. 1996. *The nature and properties of soils*, 11th edition. Prentice-Hall, Upper Saddle River, NJ, USA.
- Bradley, P.M. and Dunn, E.L. 1989. Effects of sulfide on the growth of 3 salt marsh halophytes of the southeastern United States. *American Journal of Botany*, 76: 1707-1713.
- Bremner, J. M. and Kenney, D.R. 1966. Determination and isotope-ratio analysis of different forms of nitrogen in soils: 3. Exchangeable ammonium, nitrate, and nitrite by extraction-distillation methods. *Soil Science Society of America Proceedings*, 30: 577-582.

- Broome, S. W., Woodhouse, W. W. Jr. and Seneca, E. D. 1975. The relationship of mineral nutrients to growth of *Spartina alterniflora* in North Carolina: II. The effects of N, P and Fe fertilizers. *Soil Science Society of America*, 39: 295-301.
- Brown, C.E. and Pezeshki, S.R. 2007. Threshold for recovery in the marsh halophyte *Spartina alterniflora* grown under the combined effects of salinity and soil drying. *Journal of Plant Physiology*, 164: 274-282.
- Byrnside, D.S. Jr. and Sturgis, M.B. 1958. Soil phosphorus and its fractions as related to response of sugar cane to fertilizer phosphorus. Bull No. 513, Louisiana State University Agriculture Experiment Station, Baton Rouge, Louisiana, USA.
- Costanza, R., 1992. Toward an operational definition of health. In Costanza, R., Norton, B., Haskell, B., editors. *Ecosystem Health, New Goals for Environmental Management*. Island Press, Washington, DC, USA, pp. 239–256.
- Costanza, R., R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V. O'Neill, J. Paruelo, R. J. Raskin, P. Sutton and M. van den Belt. 1998. The value of the world's ecosystem services and natural capital. *Ecological Economics*, 25: 3-15.
- Day, J. W., Shaffer, G.P., Britsch, L.D., Reed, D.J., Hawes, S.R., and Cahoon, D.R. 2000. Pattern and process of land loss in the Mississippi Delta: a spatial and temporal analysis of wetland habitat change. *Estuaries*, 23: 425-438.
- DeLaune, R.D., Buresh, R.J. and Patrick, W.H. Jr. 1979. Relationship of soil properties to standing crop biomass of *Spartina alterniflora* in a Louisiana marsh. *Estuarine and Coastal Marine Science*, 8: 477–487.
- DeLaune, R. D., Pezeshki, S. R., Pardue, J. H., Whitcomb, J. H. and Patrick, W. H. Jr. 1990. Some influences of sediment addition to a deteriorating salt marsh in the Mississippi River deltaic plain: A pilot study. *Journal of Coastal Research*, 6: 181-188.
- Dunbar, J.B., Britsch, L.D. and Kemp, E.B. III. 1992. Land loss rates. Report 3: Louisiana coastal plain. US Army Corps of Engineers Waterways Experiment Station, Vicksburg, MS, USA. Technical Report GL-90-2.
- Ford, M.A., Cahoon, D.D. and Lynch, J.C. 1999. Restoring marsh elevation in a rapidly subsiding salt marsh by thin layer deposition of dredged material. *Ecological Engineering*, 12: 189–205.
- Gambrell, R. P. and Patrick, W. H. Jr. 1978. Chemical and microbiological properties of anaerobic soils and sediments. In Hook, D. D. and Crawford, R. M. M., editors. *Plant Life in Anaerobic Environments*. Ann Arbor Scientific Publishing, Inc., Ann Arbor, MI, USA, pp. 375-423.

- Gorham, E. 1967. Some chemical aspects of wetland ecology. Technical memorandum 90, Committee on geotechnical research, National Research Council of Canada. pp. 2-38.
- Gosselink, J. G. 1970. Growth of *Spartina patens* and *S. alterniflora* as influenced by salinity and source of nitrogen. Louisiana State University, *Coastal Studies Bulletin*, 5: 97-110.
- Grimm, V. and Wissel, C. 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia*, 109: 323–334.
- Gunderson, L. 2000. Ecological resilience – in theory and application. *Annual Review of Ecology and Systematics*, 31: 425–39.
- Howes, B.L., Howarth, R.W., Teal, J.M. and Valiela, I. 1981. Oxidation-reduction potentials in a salt marsh: spatial patterns and interactions with primary production. *Limnology and Oceanography*, 26: 350-360.
- Ingold, A. and Havill, D.C. 1984. The influence of sulphide on the distribution of higher plants in salt marshes. *Journal of Ecology*, 72: 1043-1054.
- Jelgersma, S. 1996. In Milliman, J.D. and Haq, B.U., editors. *Sea Level and coastal subsidence. Causes, consequences, and strategies*. Kluwer, Dordrecht. pp. 47-62.
- King, G.M., Klug, M.J., Wiegert, R.G. and Chalmers, A.G. 1982. Relation of soil water movement and sulfide concentration to *Spartina alterniflora* production in a Georgia salt marsh. *Science*, 218: 61-63.
- Koch, M.S. and Mendelssohn, I.A. 1989. Sulphide as a soil phytotoxin: differential responses in two marsh species. *Journal of Ecology*, 77: 565-578.
- Lindsay, W. L. and Norvell, W.A. 1978. Development of a DTPA soil test for zinc, iron, manganese, and copper. *Soil Science Society of America* 42: 421-428.
- Lindstedt, D.M., Swenson, E.M., Reed, D., Twilley, R. and Mendelssohn, I.A. 2006. Marsh dieback technical synthesis report. Technical Report, Coastal Restoration Division, Louisiana Department of Natural Resources.
- Linthurst, R.A. 1980. A growth comparison of *Spartina alterniflora* Loisel. Ecophenes under aerobic and anaerobic conditions. *American Journal of Botany*, 67: 883-887.
- Louisiana Coastal Area-Beneficial Use of Dredged Material Program, 2006. Supplemental environmental impact statement scoping program. United States Army Core of Engineers, Louisiana Department of Natural Resources.
- Louisiana Department of Natural Resources, Office of Coastal Restoration and Management, 2009. <http://dnr.louisiana.gov/crm>

- McKee, K.L., Mendelssohn, I.A. and Materne, MD. 2004. Acute salt marsh dieback in the Mississippi River Deltaic Plain: a drought-induced phenomenon? *Global Ecology and Biogeography*, 13: 67–73.
- Mendelssohn, I. A. and Seneca, E. D. 1980. The influence of soil drainage on the growth of salt marsh cordgrass *Spartina alterniflora* in North Carolina. *Estuarine and Coastal Marine Science*, 11: 27-40.
- Mendelssohn, I. A., McKee, K. L. and Patrick, W. H. Jr. 1981. Oxygen deficiency in *Spartina alterniflora* roots: Metabolic adaptation to anoxia. *Science*, 214: 439-441.
- Mendelssohn, I. A., McKee, K. L. 1988. *Spartina alterniflora* die-back in Louisiana: Time-course investigation of soil waterlogging effects. *Journal of Ecology*, 76: 509-521.
- Mendelssohn, I.A. and Kuhn, N.L. 2003. Sediment subsidy: effects on soil-plant responses in a rapidly submerging coastal salt marsh. *Ecological Engineering*, 21: 115-128.
- Mooring, M. T., Cooper, A.W. and Seneca, E.D. 1971. Seed germination response and evidence for height ecophenes in *Spartina alterniflora* from North Carolina. *American Journal of Botany*, 58: 48-55
- Morris, J.T. and Dacey, J.W.H. 1984. Effects of O₂ on ammonium uptake and root respiration by *Spartina alterniflora*. *American Journal of Botany*, 71: 979-985.
- Naidoo, G., McKee, K.L. and Mendelssohn, I.A. 1992. Anatomical and metabolic responses to waterlogging and salinity in *Spartina alterniflora* and *S. patens* (Poaceae). *American Journal of Botany*, 79: 765-770.
- Nelson, D. W. and Sommers, L.E. 1996. Total carbon, organic carbon, and organic matter. In Bartels, J. M. and Bigham, J. M., editors. *Methods of Soil Analysis. Part 3. Chemical Methods*. Soil Science Society of America and American Society of Agronomy, Madison, WI 53711, USA. pp. 961-1010.
- Nestler, J. 1977. Interstitial salinity as a cause of ecophenic variation in *Spartina alterniflora*. *Estuarine and Coastal Marine Science*, 3: 707- 14.
- Parrondo, R. T., Gosselink, J.G. and Hopkinson, C.S. 1978. Effects of salinity and drainage on the growth of three salt marsh grasses. *Botanical Gazette*, 139: 102-107.
- Patrick, W.H. Jr. and Wyatt, R.1964. Soil nitrogen loss as a result of alternate submergence and drying. *Proceedings of the Soil Science Society of America*, 28: 647–653.
- Patrick, W.H. Jr. and DeLaune, R.D.1972. Characterization of the oxidized and reduced zones in flooded soil. *Proceedings of the Soil Science Society of America*, 36: 573-576.

- Penland, S. and Ramsey, K.E. 1990. Relative sea level rise in Louisiana and the Gulf of Mexico 1908-1988. *Journal of Coastal Research*, 6: 323-342.
- Postgate, J. 1959. Sulphate reduction by bacteria. *Annual Reviews in Microbiology*, 13: 505-520.
- Rapport, D.J., Costanza, R. and McMichael, A.J. 1998. Assessing ecosystem health. *TREE*, 13: 397-402.
- Reimold, R.J., Hardisky, M.A. and Adams, P.C. 1978. The effects of smothering a *Spartina alterniflora* salt marsh with dredged material. US Army Corps of Engineers, Washington, DC. Technical Report D-78-38.
- SAS Institute Inc., 2004. SAS® 9.1.2. *Qualification Tools User's Guide*, Cary, NC.
- Schrift, A.M., Mendelssohn, I.A. and Materne, M.D. 2008. Salt marsh restoration with sediment-slurry amendments following a drought-induced large-scale disturbance. *Wetlands*, 28: 1071-1085.
- Slocum, M.G., Mendelssohn, I.A. and Kuhn, N.L. 2005. Effects of sediment slurry enrichment on salt marsh rehabilitation: plant and soil responses over seven years. *Estuaries*, 28: 519-528.
- Slocum, M.G. and Mendelssohn, I.A. 2008. Use of experimental disturbances to assess resilience along a known stress gradient. *Ecological Indicators*, 8: 181-190.
- Stagg, C.L. 2009. Remediating impacts of global climate change-induced submergence on salt marsh ecosystem functions. Ph.D. dissertation. Louisiana State University, Baton Rouge, LA.
- Syers, J.K., Shaw, R. and Walker, T.W. 1969. Fractionation of phosphorus in two alluvial soils and particle-size separates. *Soil Science*, 108: 283-289.
- Thomas, G. W. 1982. Exchangeable cations. In Page, A. L., Miller, R. H., and Keeney, D. R., editors. *Methods of soil analysis: Part 2--chemical and microbiological properties*, second edition. American Society of Agronomy, Inc. and Soil Science Society of America, Inc., Madison, WI. pp.159-165.
- Turner, R. E. 1997. Wetland loss in the Northern Gulf of Mexico: multiple working hypotheses. *Estuaries*, 20:1-13. Thomas, 1982
- Underwood, A.J. 1989. The analysis of stress in natural populations. *Biological Journal of the Linnean Society* 37: 51-78.
- Webb, E. C., Mendelssohn, I. A. and Wilsey B. J., 1995. Causes for the vegetation dieback in a Louisiana salt marsh: A bioassay approach. *Aquatic Botany*, 51: 281-289.

- Wiegert, R.G., Chalmers, A.G. and Randerson, P.F. 1983. Productivity gradients in salt marshes – the response of *Spartina alterniflora* to experimentally manipulated soil-water movement. *Oikos*, 41: 1-6.
- Weigert, R.G. and Freeman, B.J. 1990. Tidal salt marshes of the Atlantic coast: A community profile. Biological Report 85(7.29), U.S. Fish and Wildlife Service. Washington, D.C., U.S.A.
- Whitford, W.G., Rapport, D.J. and deSoyza, A.G. 1999. Using resistance and resilience measurements for ‘fitness’ tests in ecosystem health. *Journal of Environmental Management*, 57: 21–29.
- Wilsey, B. J., McKee, K. L. and Mendelssohn, I. A. 1992. Effects of increased elevation and macro- and micronutrient additions on *Spartina alterniflora* transplant success in salt-marsh dieback areas in Louisiana. *Environmental Management*, 16: 505-511.

CHAPTER 6

CONCLUSION

6.1 Conclusions

In summary, I found that moderate intensities of sediment addition resulting in elevations 12-20 cm above ambient marsh (42-50 cm NAVD 88) successfully restored ecosystem function to degraded salt marshes. Both primary and secondary production significantly increased with intermediate levels of sediment addition (12-20 cm above ambient marsh) compared to the degraded marsh. Furthermore, production at these intermediate elevations was functionally equivalent to the natural marsh. Similarly, sediment addition resulting in 12-20 cm above ambient marsh significantly increased resilience and stability of *Spartina alterniflora*. Decomposition was also optimized at this elevation, indicating that decay rates would support nutrient availability without detracting from positive elevation change.

In general, areas of intermediate sediment addition (12-20 cm) were functionally equivalent to natural marshes, and in some cases functionally superior to natural marshes. However, all ecological functions were affected by a sediment addition threshold that was characterized by a decline in production and resilience and accelerated decomposition in areas of intense sediment addition (i.e., high elevation [> 20 cm above ambient marsh]). The primary regulator of enhanced ecological function in the restored marshes was the alleviation of flooding stress observed in the degraded reference marshes. Declines in ecological function above the sediment addition threshold were primarily influenced by dry conditions that resulted from insufficient and infrequent flooding at the high elevations.

Above- and belowground primary production in the moderately subsidized marsh (12-20 cm above ambient marsh, 42-50 cm NAVD 88) increased due to a decrease in flooding and

salinity stress. However, at elevations above 20 cm (50 cm NAVD 88), both above- and belowground production significantly decreased due to insufficient flooding resulting in low soil moisture. Belowground production was greater than aboveground production at all elevations, emphasizing the relatively greater importance of belowground production in contributing organic matter for accretion. Belowground production significantly increased from 2005 to 2007, which was attributed to changes in the soil nutrient content as the system matured. Additionally, although the moderately subsidized marsh was functionally equivalent to the ambient natural marsh, I propose that the restored marsh will exceed the natural marsh in primary production over time. Functional trajectories of sediment subsidized marshes show that belowground production continues to increase exponentially over time in the first few years after sediment addition (Edwards and Mills, 2005). Based on these observations and the high flood duration and sulfide concentrations in the natural marsh, I predict that primary production in the natural marsh will decline, and both above- and belowground production in the restored marsh will surpass natural marsh production.

Like primary productivity, decomposition of roots and rhizomes also increased with sediment addition. However, unlike production, which declined at high elevations, roots and rhizomes decomposed faster with greater sediment subsidy and were principally influenced by redox potential. Moreover, at extremely high levels of sediment addition, rhizomes decomposed at a disproportionately higher rate than roots and rhizomes at other STLs, which may result in negative elevation change over time. Therefore I suggest that intermediate sediment subsidy, resulting in an elevation of 42-50 cm above NAVD 88 (12-20 cm above the ambient marsh surface at this study site) be applied to achieve optimum mineralization and still allow for organic matter accumulation.

In comparison to root and rhizome tissue, cellulose decomposition was not primarily influenced by redox potential, but was accelerated by higher ammonium concentrations, greater soil moisture, and the interaction of these flood-related factors with plant presence. Cellulose decomposition was greatest in areas of high primary production, with peaks in decomposition occurring in the root zone, indicating that plant presence significantly influenced decomposition. Therefore, the use of sediment subsidy at moderate intensities (12-20 cm above marsh surface) can restore hydrologic conditions necessary to achieve appropriate soil moisture, nutrient availability and plant-soil interactions that optimize decomposition.

Like primary production, growth, survival and production of *Littoraria irrorata* increased with intermediate additions of sediment, but then declined at high elevations. *L. irrorata* production was principally controlled by changes in *S. alterniflora* canopy cover, which not only served as the primary food source for *L. irrorata*, but also provided refuge from predation and physical stressors. The decline of *L. irrorata* production and survival at both extreme high and low elevation were directly linked to the decrease in *S. alterniflora* cover, which likely resulted in decreased resource availability and potentially increased thermal and metabolic stress. Additionally, at the degraded reference, high mortality rates may be linked to increased predation through two mechanisms: 1) increased flood duration, and increased predator foraging time, and 2) decreased refuge (*S. alterniflora*), and increased predation efficiency. Therefore, the restoration of *S. alterniflora* production is crucial in providing a suitable habitat for *L. irrorata*. This was achieved with intermediate additions of sediment (12-20 cm above ambient marsh), where *L. irrorata* growth, survival and production were equivalent to natural marshes.

As an emergent property of ecosystems, I expected resilience and stability to follow the same trends as the measured ecological functions, which when integrated would support positive

elevation change and marsh sustainability. Accordingly, resilience at the primary study site (Fourchon) increased with sediment addition up to the elevation threshold, then decreased to levels equivalent to the degraded and natural reference. However, in contrast to primary and secondary production, resilience and stability in moderately subsidized marshes was not equivalent to the natural marsh, but greater than the natural marsh, further supporting my prior conclusion that these sediment restored marshes are functionally superior to natural marshes in this area.

Additionally, comparisons among the old (Venice) and new (Fourchon) restoration sites illustrated that resilience and stability are maintained over time in marshes receiving intermediate sediment addition, with the greatest resilience and stability occurring at intermediate elevations (12-20 cm above ambient marsh; 42-53 cm NAVD 88). Although a sediment subsidy threshold was evident in the younger marsh (Fourchon), this pattern was less pronounced in the older restoration site (Venice). At Venice, the High STL elevation ranged from 19-26 cm above ambient marsh surface; however, in the period immediately following sediment subsidy, elevation at the High STL was greater than 40 cm above the ambient marsh surface (Mendelssohn and Kuhn, 2003; Slocum *et al.*, 2005). Thus, over time this restored marsh compacted and subsided, resulting in comparable elevations between areas of greatest sediment addition in the older site and areas of intermediate sediment addition in the young site. Although resilience was high in the High STL 15 years after sediment addition, resilience and stability in areas of intermediate sediment addition are still greatest in both the new and older restoration site, indicating that sediment subsidy at intermediate elevations (42-53 cm NAVD 88) is optimum and sustainable over time.

In summary, sediment-slurries applied at intermediate levels restored ecological functions that are important drivers of organic matter accumulation, a key process controlling marsh elevation change and sustainability during periods of sea level rise. Moderately subsidized marshes with elevations within the intertidal zone (12-20 cm above ambient marsh), had functionally equivalent primary production, decomposition and secondary production relative to the ambient natural marsh. Although processes governing organic matter accumulation may be equivalent between restored and natural marshes, the greater elevation of the sediment subsidized marshes will provide an advantage over natural marshes during periods of sea level rise. Additionally, greater resilience and stability in the restored versus natural marshes further suggests that sediment subsidized salt marshes may be better equipped to recover from disturbances, such as hurricanes, which may increase in frequency and intensity with global climate change. In conclusion, this research provided a comprehensive examination of the effects of sediment addition on key ecological functions, and illustrated that sediment addition is a viable technique that can successfully restore ecological function to degraded marshes and provide resilience that is sustainable over time.

Presently, the state of Louisiana and federal research agencies are evaluating different approaches to restore coastal Louisiana, including marsh terracing, freshwater diversions, and plantings. Although all of these methods have value under certain conditions, the methodology of sediment-slurry addition has the benefit of directly restoring land that, at appropriate elevations, revegetates and, as shown in this study, restores many ecological functions to natural marsh equivalence. Therefore, this methodology has an advantage over many other restoration techniques, because it results in rapid land building and functional restoration, in contrast to freshwater diversions which may take many years to significantly influence marsh elevation, if at

all. However, sediment-slurry addition is costly, and care must be taken to collect uncontaminated sediments. Nonetheless, sediment-slurry methodology competes favorably with other restoration techniques, which have their own set of problems. It must also be emphasized that any of our coastal restoration approaches have to be planned in the context of global climate change and subsequent increases in sea level that will be observed in the future. At extreme rates of sea level rise (up to 1.5 m; Mitrovica *et al.*, 2009) this method along with others will be seriously challenged.

6.2 Literature Cited

- Edwards, K.R. and Mills, K.P. 2005. Aboveground and belowground productivity of *Spartina alterniflora* (Smooth Cordgrass) in natural and created Louisiana salt marshes. *Estuaries*, 28: 252-265.
- Mendelssohn, I.A. and Kuhn, N.L. 2003. Sediment subsidy: effects on soil-plant responses in a rapidly submerging coastal salt marsh. *Ecological Engineering*, 21: 115-128.
- Mitrovica, J.X., Gornex, N. and Clark, P.U. 2009. The sea-level fingerprint of West Antarctic collapse. *Science*, 323: 753.
- Slocum, M.G., Mendelssohn, I.A. and Kuhn, N.L. 2005. Effects of sediment slurry enrichment on salt marsh rehabilitation: plant and soil responses over seven years. *Estuaries*, 28: 519-528.

VITA

Camille LaFosse Stagg was born in March 1979, in Baton Rouge, Louisiana, and spent her childhood in Lafayette, Louisiana. She enrolled in Christian Brothers University and earned a Bachelor of Science in biology in 2002. She entered the graduate program at Clemson University, where her research focused on toxicity characterization of oilfield produced waters and the use of constructed wetland treatment systems to remediate toxicity and provide water for beneficial reuse applications. Her work with wetland systems in South Carolina directed her interests toward coastal wetlands in her home state, Louisiana. After earning her Master of Science in environmental toxicology, she began her doctoral research at Louisiana State University in 2004, where she obtained a doctorate in oceanography and coastal sciences in 2009. Presently, she is continuing her study of the impacts of global climate change on coastal wetland systems as a contractor for the United States Geological Survey, National Wetlands Research Center, in Lafayette, Louisiana.