ECOGEOMORPHOLOGY AND VEGETATION DYNAMICS IN A SEDIMENT DIVERSION OF THE MISSISSIPPI RIVER

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TABLE OF CONTENTS

Acknowledgments…………………………………………………………………...ii

List of Tables……………………………………………………………………..vi

List of Figures…………………………………………………………………...vii

Introduction……………………………………………………………………....1

Chapter 1: Temporal trends in the seed bank of a deltaic freshwater wetland seed bank: fluvial and within-system influences……………………………………………...8

- Introduction……………………………………………………………………..9
- Methods………………………………………………………………….......14
- Results…………………………………………………………………………19
- Discussion……………………………………………………………………..27
- List of References……………………………………………………………..31

Chapter 2: Vegetation and shear strength in a delta-splay mouth bar…………………...35

- Introduction…………………………………………………………………...36
- Methods……………………………………………………………………….40
- Results………………………………………………………………………...49

Discussion……………………………………………………………………..55

List of References…………………………………………………………..58

Chapter 3: Competition eclipses abiotic factors in limiting two monoculture-forming wetland plants……………………………………………………………………………63

Introduction…………………………………………………………………...64

Methods………………………………………………………………………67

Results…………………………………………………………………………...73

Discussion……………………………………………………………………80

List of References……………………………………………………………84

Appendix 1: Supplementary figures and tables for Chapter 1…….…………………….…...89

Appendix 2: Supplementary tables for Chapter 2…………………………….……………...93

List of Tables

2.1: Definitions of community types……………………………………………………45

3.1: Principal components computed for *Schoenoplectus* morphological data…………74

3.2: Principal components computed for *Phragmites* morphological data………………75

A1.1: Abundance data for all genera collected/observed………………………………..89

A2.1: Relative abundance of all plant species observed, bay-wide survey……………...93

A2.2: Relative abundance of all plant species observed, emergent island survey………94

List of Figures

1.1: Hydrograph of the Mississippi River measured at Venice, LA between 1987 and 2011. ………………………………………………………………………………….13

1.2: Sampling locations in West Bay, December 2014 and May 2015. ………………...15

1.3: Geotechnical profile of cores 9 and 22. ……………………………………………….20

1.4: Shannon and Simpson diversity scores of seed banks collected from the flood and emergent layers……………………………………………………………………………..22

1.5: Shannon and Simpson diversity scores of seed banks collected from all layers and assessments of aboveground vegetation……………………………………………….....23

1.6: Mean similarity between the surface-layer seed bank and standing vegetation assessed in December 2014 and May 2015……………………………………………..25

1.7: Mean similarity between the standing vegetation assessed in 2015 and the seed banks of the surface, emergent, and flood layers………………………………………………26

2.1: The West Bay Sediment Diversion and receiving basin…………………………...41

2.2: Sampling locations in West Bay………………………………………………….....43

2.3: Relationship between belowground biomass and shear strength measured at emergent island stations…………………………………………………………………...50

2.4: Mean shear strength values across communities, bay-wide stations………………52

2.5: Mean shear strength values across communities, emergent island stations……….53

2.6: Mean inundation frequencies across communities, water year 2014, all stations…54

3.1: Interaction between the competition and organic content treatments on the first principal component (Productivity) for *Schoenoplectus*………………………………..76

3.2: Interaction between the salinity, nitrogen, and organic content treatments on the second principal component (Reproductive Potential) for *Schoenoplectus* ……………76

3.3: Interaction between the salinity and organic content treatments on the root-to-shoot ratio of *Schoenoplectus* ……………………………………………………………77

3.4: Interaction between the competition, nitrogen, and organic content treatments on the root-to-shoot ratio of *Schoenoplectus*…………………………………………………...77

3.5: Interaction between the competition and nitrogen treatments on the first principal component (Productivity) for *Phragmites*……………………………………………78

3.6: Interaction between the competition and nitrogen treatments on the root-to-shoot ratio for *Phragmites*…………………………………………………………………..79

3.7: Interaction between the competition, nitrogen, and salinity treatments on the root-to-shoot ratio for *Phragmites*…………………………………………………………79

A1.1: Geotechnical profiles of all cores ………………………………………………..91

Introduction

The biosphere of a region can be defined by, but also exert influence on, its physical surface processes (Coombes 2016). The science dealing with these complex interactions and feedbacks is known as ecogeomorphology; combining biogeomorphology, biomorphodynamics, and ecohydrology (Wheaton et al 2011). Ecogeomorphology was first described as a distinct field in the 1990's (Wheaton et al 2011), and the publication rate of studies pertaining to ecogeomorphology has increased sharply since 2008 (Kirwan and Murray 2007, Coombes 2016).

Studies pertaining to ecogeomorphology range across ecosystem types and taxonomic groups. In some cases, the interaction is framed as a physical control on biological processes. For example, the grain size distribution of sediments deposited in streams has been found to affect the biodiversity of benthic bacterial communities (Santmire and Leff 2007); in other wetlands, the flood frequency and its associated availability of oxygen affects microbial decomposition of soil organic matter such that its elemental byproducts exist in different ionic forms, which affects bioavailability of nutrients and soil toxicity (Mitsch and Gosselink 1993). In other cases, the interactions are described as biological modification of physical processes, which in turn affect the biosphere. For example, the activity of burrowing animals in aquatic and marine environments can modify biogeochemical processes within the sediment, which in turn control the amount of bioavailable nutrients available to the ecosystem (Meysman et al

2006). In another example, the impacts of riparian vegetation (that which grows on the banks of streams and rivers) on bank stabilization and regulation of water temperature, as well as the corresponding influence of hydrology and sediment deposition on plant succession, have been well documented (Corenblit et al 2007). In both riparian and wetland situations, the presence of plant stems creates friction that attenuates water flow, which in turn promotes deposition of fine-grained sediments and inhibits erosion (Gurnell 2013).

A gap in knowledge exists in the ecogeomorphology of actively growing river deltas and their associated wetlands; although these systems have been studied extensively, their ecological and geological aspects have been considered in a largely compartmentalized manner (Nyman 2014). This gap is of special consequence to coastal Louisiana, which have experienced 4900 km^2 of wetland loss since 1932 due to sediment starvation, subsidence, saltwater intrusion, and sea level rise associated with climate change (Day et al 2007, Blum and Roberts 2009). To offset this land loss, the State of Louisiana has developed a Master Plan which relies heavily on diversion of the Mississippi River in order to replicate the natural delta cycle (Roberts 1997, LACPRA 2017). The projects to be included in the Master Plan are designed and assessed using a suite of predictive models which simulate distinct ecological, geological, hydrological, and economic processes, but also account for interactions among different processes (LACPRA 2017). The ecogeomorphological interactions between the depositional development of deltaic land and the wetland vegetation community are an important consideration in predicting the landscape that will result from a sediment diversion.

The West Bay Sediment Diversion is an uncontrolled levee breach near the mouth of the Mississippi River which can serve as a model system for future projects (Yuill et al 2016). Located at Pilottown, LA, approximately 8 km upstream from the mouth of the Mississippi River, the diversion was originally constructed in 2003 (US Army Corps of Engineers 2004). Following the extreme Mississippi River flood year of 2011, sufficient sediment was delivered to the receiving basin such that a subaerial delta splay had developed and subsequently supported a community of emergent wetland vegetation (Xu et al 2016). The recent development of this land provides an opportunity to assess ecogeomorphology in the earliest stages of deltaic wetland development. The research in this dissertation addresses ecogeomorphological interactions associated with the developing subdelta marsh of West Bay in three contexts.

The first chapter focuses on the Mississippi River high water event of 2011 that created the marsh, examining the seed bank contained in sedimentary layers deposited before and after the 2011 flood. I also compared the most recently deposited seed bank at the surface with the aboveground vegetation in two growing seasons. I found that before and after the marsh formed, the composition of the seed bank was significantly different with respect to common taxa. The most common seed in both layers belonged to the genus *Heliotropium* which did not grow aboveground in West Bay. Its seeds exhibited high levels of physical degradation, and decreased in abundance after the flood, making *Heliotropium* a likely marker of Mississippi River flooding. The seed bank contained in the emergent marsh was composed of a significantly higher proportion of seeds belonging to locally occurring taxa. The aboveground vegetation became significantly more similar to the surface layer seed bank in 2015 compared to 2014, and the standing vegetation was more similar to the surface layer seed bank than to that of the deeper layers. These findings are consistent with a pattern of development by which initial propagules are deposited almost entirely by the Mississippi River, some of which are able to grow once the sub-delta breaches the water surface, and the seed bank is modified over time by the increasing contribution of local plants to the seed rain.

Once a subset of the seed bank is able to germinate and colonize the subdelta, the emergent plants provide additional cohesion to the sediment supporting the marsh. In the second chapter, I examined the relationship between belowground plant biomass and soil shear strength, and the relationship between vegetation community and soil shear strength throughout the bay. I found that shear strength significantly increased with belowground biomass, and that locations dominated by sedges, grasses, and woody species were associated with higher shear strength than those dominated by aquatic vegetation, forbs, common reed, or no vegetation at all. Since shear strength describes the land's resilience to erosion, these results suggest that the establishment of vegetation may reduce erosion in this system as in others, and that land colonized by some types of vegetation may persist longer than others, which could define future patterns of water flow and sediment deposition.

In the third chapter, I tested the effects of salinity, nitrogen loading, and soil organic content – all factors which can be affected by changes in the geophysical environment of a river diversion sub-delta – on *Schoenoplectus deltarum* and *Phragmites australis* grown in competition and monoculture. I found in the second chapter that *Schoenoplectus* was associated with higher shear strength than *Phragmites*, so competition between these two plants could in turn modulate future geomorphology. I had expected that certain combinations of treatment levels would favor one species over the other. Instead, I found that competition suppressed growth of both species more than any abiotic factor, and that both species were approximately equal competitors under all treatment regimes. However, certain treatments affected the monocultures. Excess nitrogen inhibited the productivity and root-to-shoot ratio of *Phragmites* in monoculture, and brackish water inhibited flowering in *Schoenoplectus* although it also increased root-to-shoot ratio when soil organic matter was high. I concluded that competitive exclusion in the field between *Schoenoplectus* and *Phragmites* would be unlikely given the range of conditions and densities tested here, and that Louisiana's proposed operation strategy for future sediment diversions is consistent with conditions that maximized belowground productivity, and therefore soil shear strength, of both species.

The three studies described above all exemplify the role of vegetation as an autogenic (within-system) modifier of other biotic and abiotic wetland processes. In the first chapter, the vegetation community was shown to modify the seed bank. An initial bank of propagules was deposited by the river during the 2011 flood, some of which were able to recruit given the environmental circumstances and contribute their own seeds in addition to the annual river deposition. In this way, as the marsh gets older, a higher proportion of the seed bank is represented by seeds produced within the system, and the composition of the seed bank becomes more similar to the aboveground plant community. In the second chapter, the implication of the observed result is that without vegetation, the pattern of sediment deposition and erosion would be largely controlled by outside factors: the type and amount of sediment delivered, and the hydrology of the river water moving through the system, while the existing geomorphology is a within-system control. The presence of vegetation, however, affects the erodibility of the sediment to different degrees depending on community type. In this way, vegetation acts in addition to geomorphology to increase the relative influence of within-system factors on the physical development of the wetland. Finally, in the third chapter the vegetation served as an autogenic control on *itself:* productivity in both species under competition did not change based on physical treatment levels, and was consistently lower than under the monoculture treatments. The results of these studies provide numerous avenues for future research in both theoretical ecology and practical applications in wetland restoration.

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Chapter 1: Temporal trends in the seed bank of a deltaic freshwater wetland seed bank: fluvial and within-system influences

Abstract

The community of ungerminated seeds contained in the soil (the seed bank) will determine which plant species will initially colonize a new area of land as well as which species will repopulate the land following a disturbance. Additionally, environmental restoration projects often reference the seed bank of a nearby or similar ecosystem in order to re-introduce native vegetation to the target region. A primary successional wetland environment on the Mississippi River Delta provides an opportunity to discern the relative contributions of allochthonous and autochthonous seeds, and the similarity of seeds deposited at various points in time to the standing vegetation. We found that the community composition of the seed bank differed significantly before and after the formation of the wetland, and the differences were primarily driven by a decrease in the proportion of seeds delivered from outside the system. Following the formation of the wetland, the seed bank contained a higher proportion of seeds belonging to locally growing taxa. Additionally, we found that more recently deposited seed banks were more similar to standing vegetation than seeds in older sediment layers, and that similarity between the surface seed bank and standing vegetation increased between growing seasons. These findings are consistent with a pattern of decreasing fluvial (allogenic) influence and increasing autogenic contribution to the seed bank over the trajectory of a

developing marsh. In a noteworthy aside, we found that two common invasive species in the area (*Phragmites australis* and *Alternanthera philoxeroides*) were well-represented aboveground, but very rare or absent in the case of *A. philoxeroides* in the seed bank. This suggests a decoupling of these two species from the described pattern.

Introduction

The seed bank of an ecosystem is defined as the collection of dormant seeds buried in soil and represents all plants that could potentially grow in that location (Harper 1977). The seed bank provides a reserve of propagules that allow a habitat to quickly be recolonized following a disturbance (Brock et al 2003). The population and community dynamics of the standing vegetation are subject to control by and exert influence on the seed bank (Harper 1977) so characterizing an area’s seed bank may be necessary for understanding its environmental history, including both ecological succession and geomorphological changes.

The seed bank also plays an important role in restoration ecology. Success of a restoration project is largely defined by the presence of a suite of target species ranging from dominant keystone species to rare species (Bakker et al 1996). While a seed bank can still be found at most restoration sites, it is often unable to produce all target species, especially rare ones, by natural germination alone (Bossuyt and Honnay 2008). Establishing these target species may require enhancement of natural seed dispersal to the project area, or even direct manual incorporation into the seed bank (Bakker et al 1996). The presence of propagules from aggressive colonizers, both native and exotic, may also hinder the establishment of the intended biodiversity (Zedler 2000). It is therefore also important to study the seed banks of reference ecosystems for future application by restoration managers.

The applications to both succession and restoration are confounded by the disparity between the species which occur in the seed bank and the composition of the aboveground standing vegetation. Seeds in the seed bank can suffer mortality from predation and senescence and many seeds will only germinate under favorable conditions, which may be defined on an individual species basis by photoperiod, temperature, inundation, nutrient or oxygen availability, or external chemical triggers (Harper 1977). The abiotic conditions of a habitat can be thought of as a variable “environmental sieve” which, for a given state, would only permit the recruitment of plant species with a compatible life history (Harper 1977, van der Valk 1981).

Those species whose seeds pass through the environmental sieve to the seedling stage have the opportunity to contribute their own seeds to the seed bank via seed rain (Harper 1977), although as the abiotic factors change it is possible for established aboveground species to be extirpated from the system (van der Valk 1981). The similarity of the aboveground vegetation to the seed bank is thus determined by the environmental sieve, and varies across ecosystem types. Two separate meta-analyses of seed bank studies concluded that grassland vegetation is most similar to its seed bank, while forest vegetation is least similar, with wetlands exhibiting intermediate similarity (Hopfensperger 2007, Bossuyt and Honnay 2008). Bossuyt and Honnay (2008) argued that high levels of stress, and to a lesser degree successional stability, lead to dissimilarity between the seed bank and the standing vegetation.

The stressors associated with wetland environments can be unpredictable in timing and severity, and the particular suite of possible stressors is highly variable among different environments characterized as “wetlands” (Bossuyt and Honnay 2008). The similarity in fluvially-dominated marshes can be further confounded by the hydrologic transport of seeds into the system from elsewhere in the watershed (Goodson et al 2001). Depositional settings such as the Mississippi River Delta (MRD) are characterized by relatively dramatic changes in hydrology associated with the accretion of mineral sediment and the attenuation of stream velocity over a short period of time (Roberts 1997). As a marsh develops, a subset of the species whose seeds are delivered by the river will rapidly colonize the new land and contribute their own seeds, while those that do not germinate remain dormant in the seed bank (Cahoon et al 2011, Harper 1977). A comparison of seed banks before and after wetland formation with the standing vegetation can indicate which species are delivered by the river and which are contributed from within the system.

The MRD is a relevant study system for restoration ecology as the region is characterized by land loss driven by the compound effects of sediment starvation, subsidence, and sea level rise (Day et al 2007, Blum and Roberts 2009). The State of Louisiana has proposed a coastwide restoration effort, which relies heavily on diversion of the Mississippi River into its floodplain in order to build new land in the manner of the natural delta cycle (LACPRA 2017). The lack of research on wetland seed banks in Louisiana is cited as a significant knowledge gap in the prediction of vegetation composition in the resulting wetlands (Visser et al 2016). The West Bay Sediment Diversion, located on the MRD, has been cited as a model system for planning future diversions (Kolker et al 2012, Yuill et al 2016). It was originally engineered to deliver river sediment to an outside wetland, unlike smaller freshwater diversions on the Mississippi which have nonetheless built land (USACE 2004). This system provides an opportunity to characterize the development of the seed bank that may occur in a river diversion, as it transitioned from a shallow-water bay to a subaerial delta splay following the 2011 Mississippi River Flood, and has since been colonized by freshwater wetland vegetation (Xu et al 2016). The 2011 flood was a historic high-water event rivaling the catastrophic Mississippi River floods of 1927 and 1973 in discharge, but due to diversion of flood waters through the Morganza and Bonnet Carre spillways, the river stage downstream of New Orleans (Figure 1.1) was comparable to that of 7 other flood events since 1986 (Kolker et al 2014).

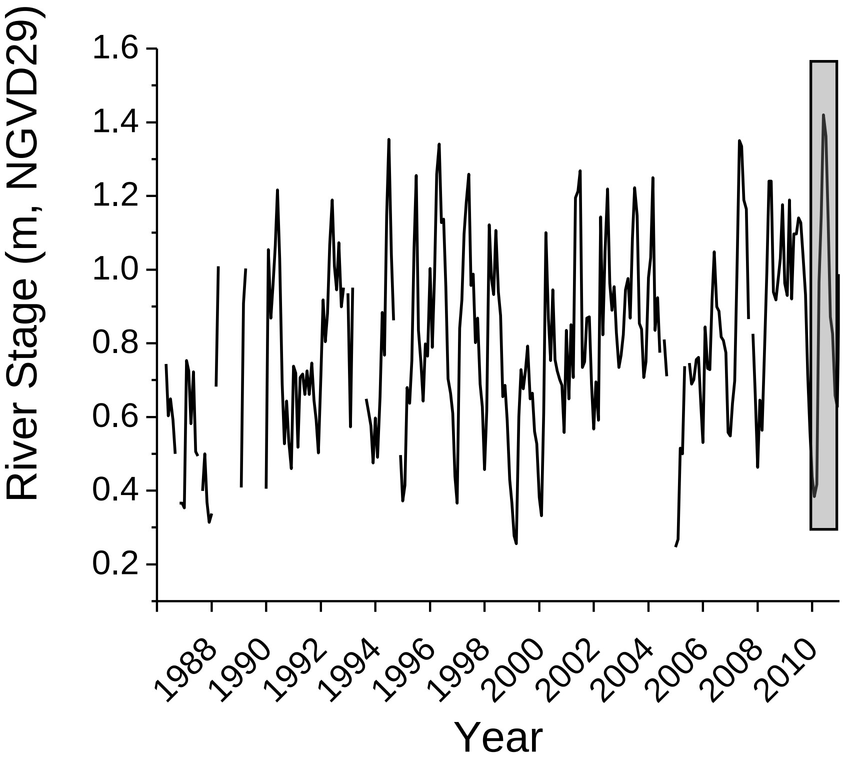

Figure 1.1: Hydrograph of the Mississippi River measured at Venice, LA between 1987 and 2011. The 2011 flood peak is denoted by the shaded box. Data courtesy of the US Army Corps of Engineers, http://rivergages.mvr.usace.army.mil/WaterControl/stationinfo2.cfm?sid=01480&fid=&dt=S

By analyzing geotechnical properties of cores taken in the West Bay Diversion and extracting the seeds, we identified the signature of the 2011 flood and characterized the seed bank before and after the wetland formed. We also characterized the newest standing vegetation in depositional areas of the splay, and tested a series of hypotheses related to the temporal evolution of the seed bank. First, we hypothesized that the seed bank deposited during the flood would differ in community structure from that of the subsequent wetland. Second, we hypothesized that the standing vegetation would become more similar to the most recently deposited seed bank in a subsequent growing season. Third, we hypothesized that the standing vegetation would be most similar to the most recently deposited seed bank and least similar to the seed bank deposited during the flood.

Methods

Seed banks and emergent vegetation communities were characterized on two occasions in the receiving basin of the West Bay Sediment Diversion, near the mouth of the Mississippi River at Pilottown, LA. On December 12, 2014, we sampled at 22 locations on two actively prograding sub-delta splay islands which became subaerial following the 2011 flood. Stations were located at the outer margin of emergent vegetation. At each station we collected duplicate samples of surface sediment from the top 1 cm, and estimated the percent cover of all vegetation species within 9 m^2. On May 28, 2015, we reassessed the vegetation cover at all 22 stations (Figure 1.2). Ten of the stations were randomly selected for coring. We collected cores of 10 cm depth and 10.2 cm diameter which were subsequently extruded and partitioned at 2 cm depth intervals and bagged in the field.

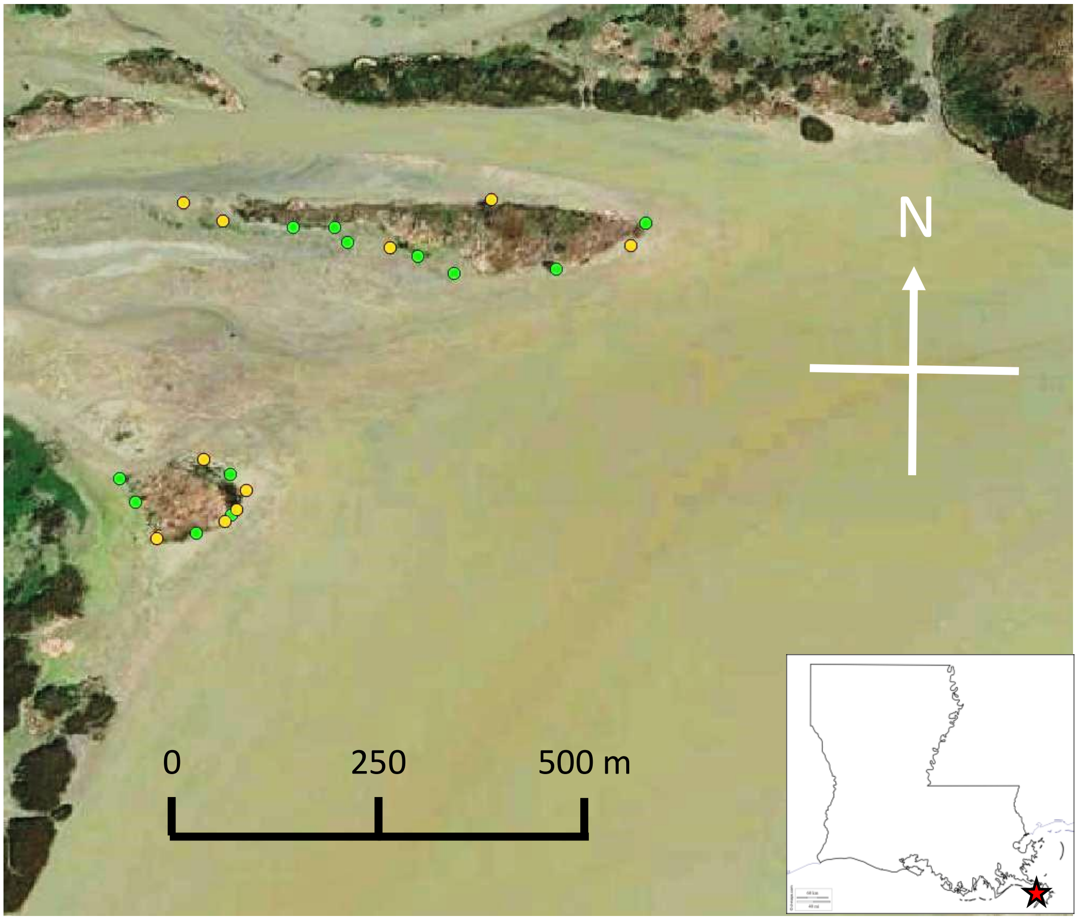

Figure 1.2: Sampling locations in West Bay. Diversion mouth and Mississippi River are located to the east. Standing vegetation was assessed at all stations in both December 2014 and May 2015; cores were also collected in May 2015 at stations marked in orange.

Flood events are associated with the deposition of mineral-rich, low-organic river sand and thus can be identified in the sedimentary record by the presence of large grain size and high bulk density (Coleman and Gagliano 1964, Roberts 1997). A subsample from each core section was weighed before and after drying at 60°C for 24 hours to obtain water content, and weighed again before and after burning at 400°C for 6 hours to obtain organic content. Another subsample was analyzed for particle size distribution using a laser diffraction particle size analyzer (Malvern Instruments, Malvern, UK). Bulk density was calculated from water content and organic content following Kolker et al (2012). A large increase in both median grain size and calculated bulk density in the vertical core profile was interpreted as the boundary between the 2001 flood deposit (hereafter “flood layer”) and the subsequent subaerial wetland (hereafter “emergent layer”).

The surface samples from 2014 and the core sections from 2015 were treated overnight with a saturated solution of baking soda to deflocculate clay particles in 1.5% hydrogen peroxide (to degrade organic detritus). Samples were sieved at 1 mm and 500 µm and air dried. Seeds were manually separated from the remaining detritus under a binocular microscope and identified by comparison against specimens from the Louisiana State University Herbarium, analysis with dichotomous keys, and consultation with experts (K DiMarco, JA Nyman, *personal communication*).

The seed bank communities in the flood and emergent layers were compared using a multiplicity-adjusted bootstrap analysis based on Hill’s generalized diversity index

$$ {}^{q}D = \left(\sum_{s=1}^{S} \pi_s^q\right)^{1/(1-q)} \tag{1}$$

where S is the total number of taxa, π is the relative frequency of taxon s, and q is the order of the diversity index (Hill 1973). ${}^{q}D$ is equivalent to richness when q=0, is equivalent to the exponential of Shannon’s diversity when q is very close to 1, and is equivalent to the inverse of Simpson's diversity when q=2 (Pallmann et al 2012). This statistical method is desirable for the following reasons. Differences in species composition between two groups can manifest in either rare or common species, to which each diversity index is differentially sensitive (Hill 1973). Testing all indices simultaneously requires a sacrifice in statistical power, but the bootstrapping approach used here is less conservative than a Bonferroni correction (Pallmann et al 2012). Distributions of diversity measures often do not satisfy the normality requirements associated with analysis of variance (Pallmann et al 2012). Most importantly, this approach exploits the "doubling property" associated with the generalized diversity number. The diversity number of a given distribution of species is doubled if a second set of new species with the same distribution is added (Hill 1973). In a practical example, a t-test on Simpson diversity scores of two groups with the same evenness and number of species but no species in common would not indicate a significant difference, but this approach would detect the difference as it accounts for commonality of species as well as richness and evenness (Pallmann et al 2012).

The two communities were compared on integer values of q ranging from -1 to 3 using 5000 bootstrap steps (as recommended in Pallmann et al 2012). Seed community data from sections corresponding to the same layer within a core were pooled to avoid pseudoreplication, resulting in sample sizes of n=9 for the flood layer and n=10 for the emergent layer. Initial observation suggested that one genus (*Heliotropium*) contributed an overwhelming majority of the total collected seeds, possibly masking any differences in the remaining community composition. Therefore, the test was repeated with the same initial parameters, but with *Heliotropium* excluded from the dataset. These analyses were performed using the R function “mcpHill” within the package “simboot” (refs for R and packages needed). Genera observed within the seed bank of each layer were classified based on their observed presence or absence in West Bay since 2011. The frequencies of counted seeds that had and had not been observed aboveground in the area were compared with a chi-square test.

Seed communities and aboveground communities were compared using Sorenson’s similarity index, given by

$$M = \frac{2w}{A+B} \tag{2}$$

where A is the total number of taxa aboveground, B is the total number of taxa in the seed bank, and w is the number of taxa that appear in both communities (Hopfensperger 2007). Sorenson’s similarity index can be interpreted as the proportion of species in common between two groups, and is especially useful in assessing groups measured in different ways (Hopfensperger 2007). To test whether aboveground vegetation became more similar to the surface seed bank between growing seasons, a Wilcoxon paired non-parametric test was performed between the similarities of the surface seed banks to the aboveground community in 2014 and the aboveground community in 2015. To test whether the seed bank became more similar to the aboveground community over the lifetime of the marsh, the similarities of the aboveground community to the surface, emergent, and flood layers were compared using a Kruskal-Wallis nonparametric analysis of variance, followed by a Dunn-Sidak nonparametric multiple comparison test.

Separate analyses were performed with respect to the 2014 and 2015 aboveground communities.

Results

The boundary between the flood and emergent layers was found at a mean depth of 6.2 cm (± 1.2 cm; standard deviation). The core taken at station 4 did not include a boundary and so all five slices were classified as “emergent”; for the remainder of the cores the boundary occurred between 4 and 8 cm. The flood layer was characterized by a mean median grain size of 91.2 µm (± 42.7 µm) and a mean bulk density of 1.3 g cm^{-3} (± 0.2 g cm^{-3}), while the emergent layer was characterized by a mean median grain size of 28.0 µm (± 14.3 µm) and a mean bulk density of 0.9 g cm^{-3} (± 0.2 g cm^{-3}). Both the median grain size ($t_{47} = 4.87$, $p < .01$) and bulk density ($t_{47} = 6.73$, $p < .01$) were significantly greater in the flood layer. Geotechnical properties and boundary locations of two example cores are plotted in Figure 1.3; plots of all cores are available in Figure A1.1 of Appendix 1.

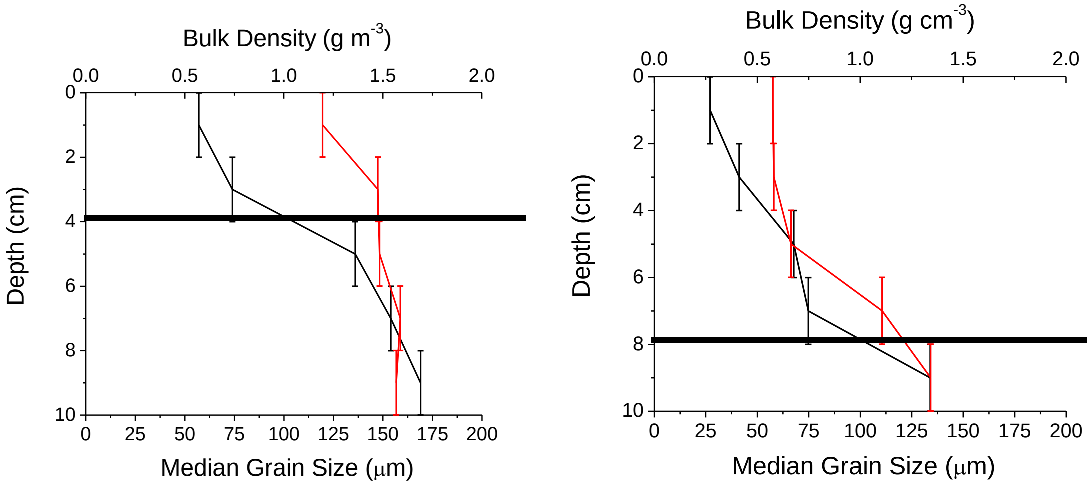

Figure 1.3: Geotechnical profiles of cores 9 (left) and 22 (right). Median grain size (µm) is denoted in black, bulk density (g cm^{-3}) is denoted in red. The horizontal line denotes the boundary between the flood (below) and emergent (above) layers.

The five most abundant genera in the seed bank of the flood layer were *Heliotropium* (70.5%), *Schoenoplectus* (13.9%), *Amaranthus* (3.6%), *Juncus* (2.0%), and *Potamogeton* (1.8%), with 23 genera present altogether. 24.7% of the seeds counted in the flood layer belonged to a genus that has been observed growing aboveground in West Bay. The five most abundant genera in the emergent layer were *Heliotropium* (52.3%), *Amaranthus* (10.9%), *Schoenoplectus* (6.7%), *Typha* (4.8%), and *Potamogeton* (4.7%), with 31 genera present altogether. The seeds of *Heliotropium* and *Juncus* exhibited high physical deterioration, while those of the other genera were relatively similar in appearance to herbarium specimens. 41.7% of the seeds counted in the emergent layer belonged to genera that have been observed growing aboveground in West Bay. Table A1.1 in Appendix 1 includes the relative abundances of all genera observed in this study.

The simultaneous test of Hill diversities yielded significant differences between the diversities of the seed banks in the flood and emergent layers for ${}^{1}D$ ($p = .04$), ${}^{2}D$ ($p = .04$), and ${}^{3}D$ ($p = .04$), while the difference was not significant for ${}^{-1}D$ ($p = .75$) or ${}^{0}D$ ($p = .83$). The differences in normalized Shannon and Simpson diversities between the flood and emergent layer seed banks, as calculated from ${}^{1}D$ and ${}^{2}D$ respectively, are plotted in Figure 1.4. Shannon's diversity is equivalent to the natural logarithm of ${}^{1}D$, and is normalized between 0 and 1 by dividing by the natural logarithm of the total number of taxa. Simpson's diversity is equivalent to one minus the reciprocal of ${}^{2}D$ (Pallmann et al 2012). The normalized Shannon and Simpson diversities for all groups (flood, emergent, surface, aboveground 2014, and aboveground 2015) are plotted in Figure 1.5, but no test was performed comparing all five groups.

When *Heliotropium*, which was the most common genus in both layers, was excluded from the dataset, the diversities of the remaining seed communities were not significantly different between layers for any value of q. The emergent layer contained a significantly greater proportion than the flood layer of seeds belonging to genera that have been observed growing aboveground in West Bay ($\chi^2 = 74.29$, df = 1, $p < .01$).

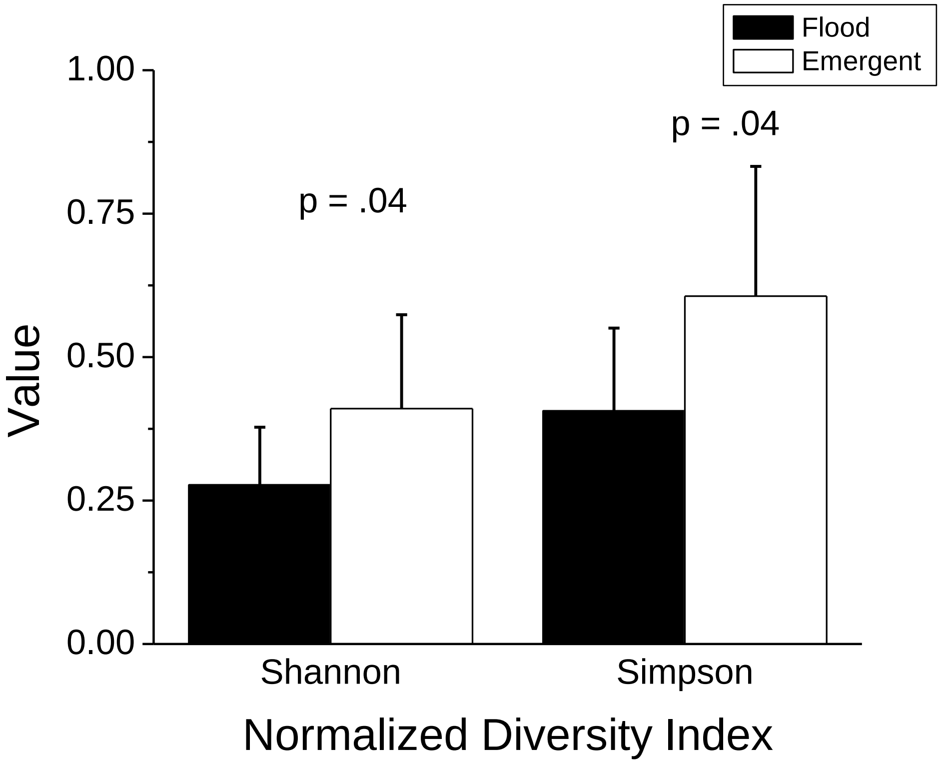

Figure 1.4: Shannon (^{1}D) and Simpson (^{2}D) diversity scores of seed banks collected from the flood and emergent layers. Both indices are normalized to a scale of 0 (total dominance by one species) to 1 (complete evenness). Error bars indicate standard deviation.

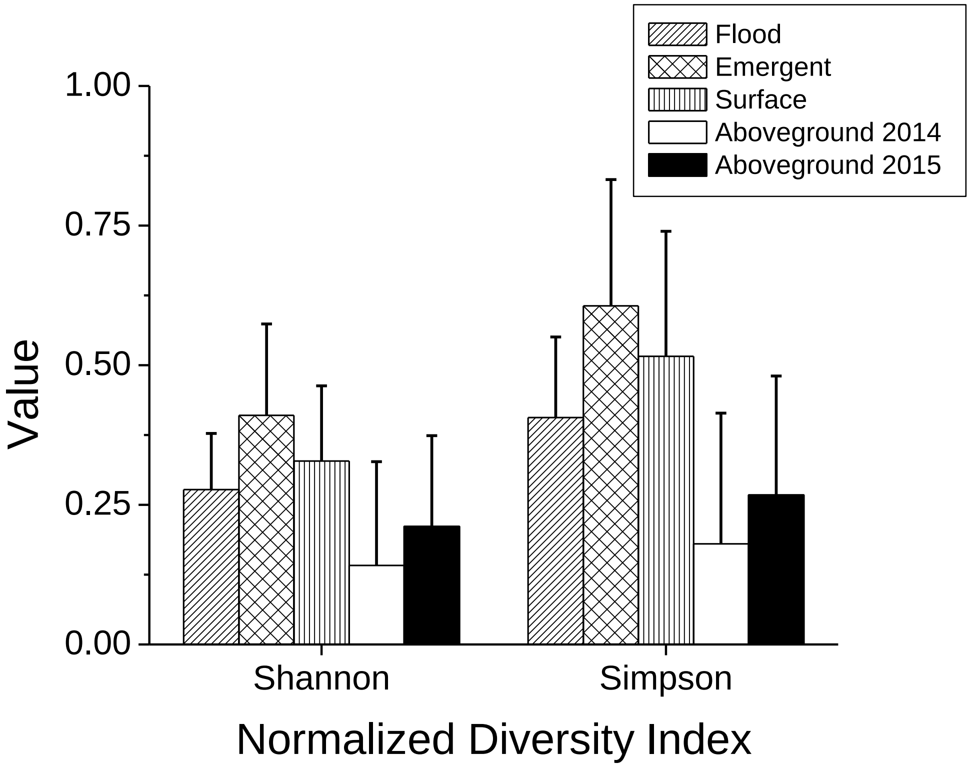

Figure 1.5: Shannon (^{1}D) and Simpson (^{2}D) diversity scores of seed banks collected from all layers and assessments of aboveground vegetation. Both indices are normalized to a scale of 0 (total dominance by one species) to 1 (complete evenness). Error bars indicate standard deviation. Note that the surface layer is a subset of the emergent layer, and that aboveground biomass was assessed using percent cover while seed banks were assessed by raw counts.

The five most abundant genera in the seed bank of the surface layer were *Heliotropium* (49.2%), *Amaranthus* (35.6%), *Potamogeton* (3.6%), *Schoenoplectus* (2.4%), and *Phragmites* (1.9%), with 26 genera present altogether. The aboveground community assessed in 2014 contained 7 genera: *Schoenoplectus* (55.6%), *Sagittaria* (15.7%), *Typha* (12.1%), *Phragmites* (11.0%), *Alternanthera* (4.7%), *Zizaniopsis* (0.8%), and *Cyperus* (0.2%). The aboveground community assessed in 2015 contained 8 genera: *Schoenoplectus* (49.8%), *Potamogeton* (24.8%), *Alternanthera* (7.5%), *Phragmites* (7.1%), *Typha* (5.7%), *Ruppia* (3.1%), *Zizaniopsis* (1.5%), and *Sagittaria* (0.4%).

The surface seed bank was significantly more similar to the aboveground community in 2015 than in 2014 (T^* = 2.640, n = 22, p = .008, Figure 1.6). In 2014, the aboveground community did not significantly differ in similarity between the seed banks of the surface, emergent, and flood layers (H = 3.159, df = 2, n = 41, p = .206); however there was a significant difference with respect to the 2015 aboveground community (H = 12.657, df = 2, n = 41, p = .002, Figure 1.7). Specifically, the aboveground community in 2015 was more similar to the surface layer seed bank than to either the emergent (p = .021) or flood (p = .007) layer seed banks.

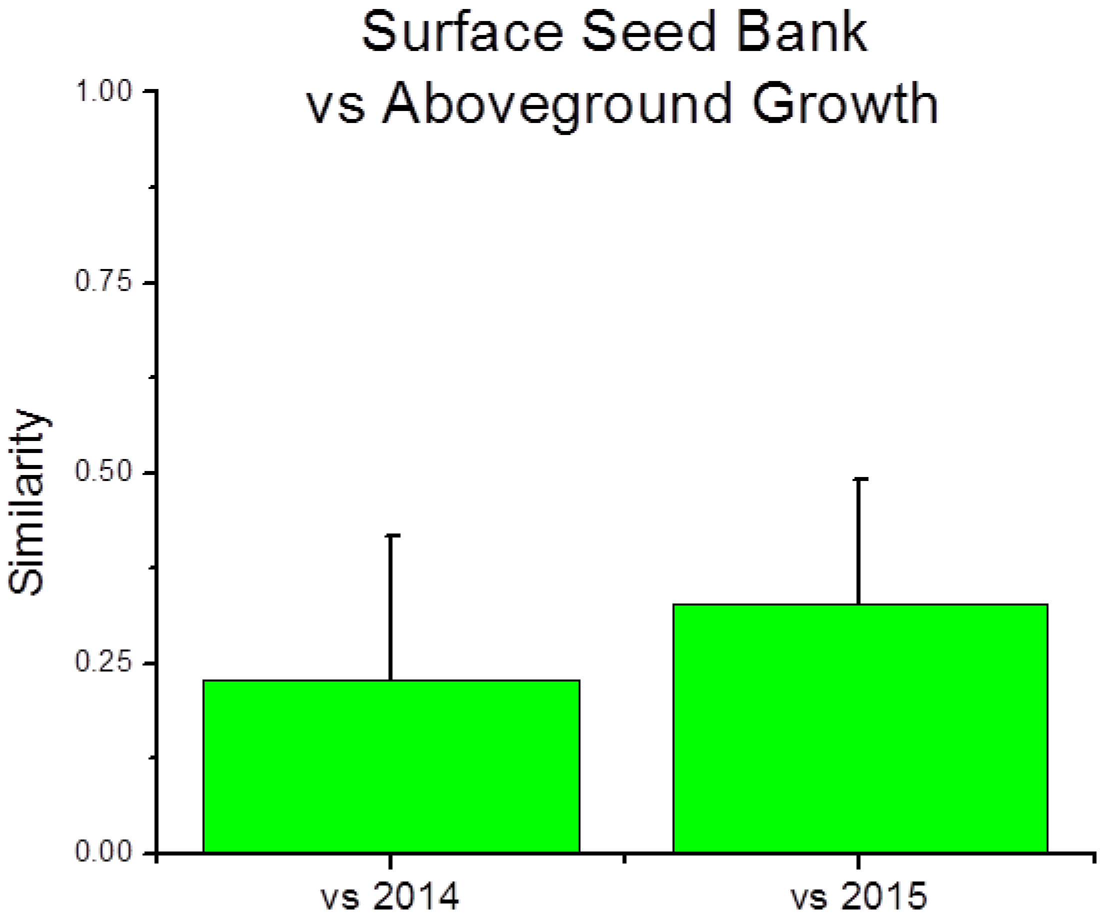

Figure 1.6: Mean value of Sorenson’s similarity between the surface-layer seed bank and standing vegetation assessed in December 2014 and May 2015. Error bars indicate standard deviation.

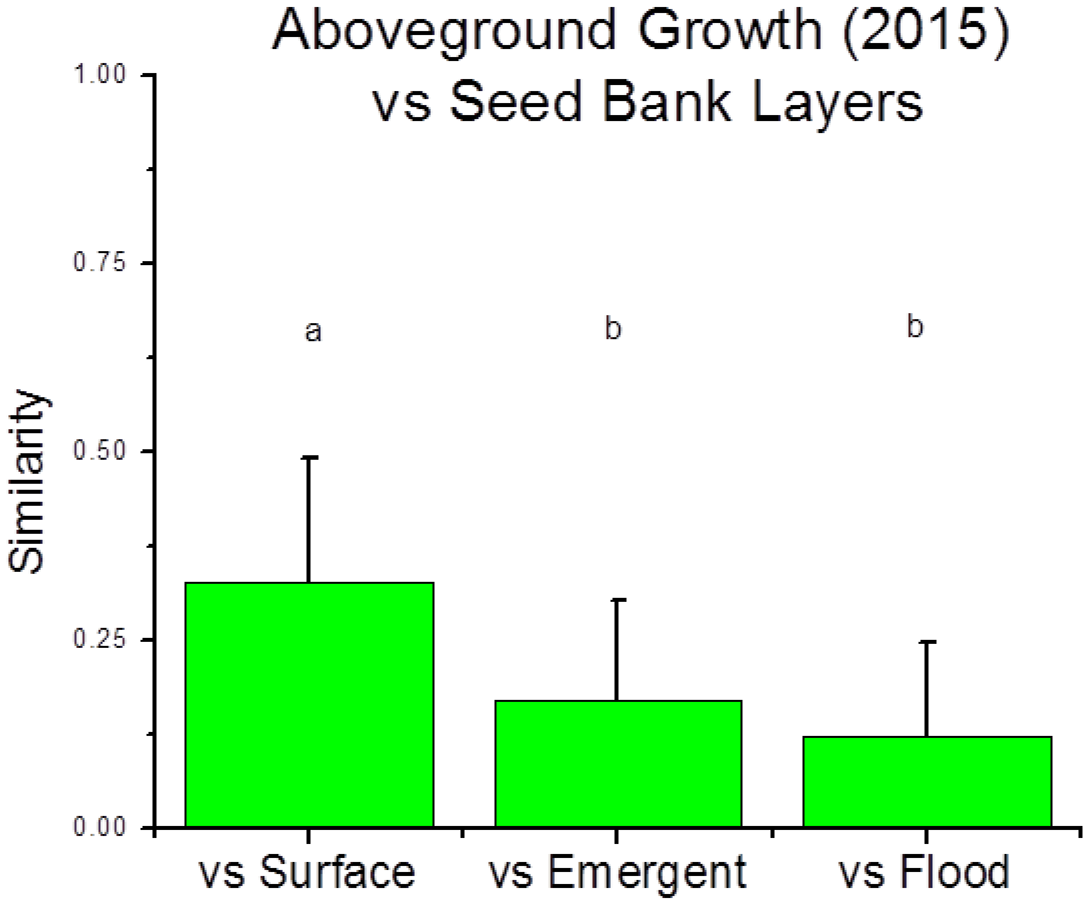

Figure 1.7: Mean value of Sorenson's similarity between the standing vegetation assessed in 2015 and the seed banks of the surface, emergent, and flood layers. Error bars indicate standard deviation. Bars denoted by different letters were significantly different.

Discussion

We observed significant changes in the seed bank over time, and increasing similarity between the standing vegetation and the most recently deposited seed bank. Our results are consistent with a pattern of seed deposition from outside the system during the 2011 flood and recruitment through an environmental sieve, leading to a temporal increase in similarity between the seed bank and the standing vegetation. The composition of the seed banks in the flood and emergent layers differed significantly with respect to more dominant species (Pallmann et al 2012). It is likely that this trend was strongly or entirely driven by the decrease in abundance in the emergent layer of *Heliotropium* seeds, which is a genus not represented in the aboveground vegetation. The significant increase in the emergent layer in the abundance of genera which do appear aboveground is also consistent with theoretical descriptions of selective recruitment of the initial seed bank and subsequent contribution of new seeds from the standing vegetation, altering the seed composition in favor of those taxa (Harper 1977, van der Valk 1981).

Previous studies have suggested that increasing similarity over time of the aboveground community to the seed bank, as we observed between December 2014 and May 2015, can be attributed to recruitment from the seed bank (Leck and Simpson 1987, 1995), although a longer study period would be needed to assess whether this is the case in West Bay. However, our ability to identify the seed bank deposited in 2011 coupled with the significantly higher similarity of the standing vegetation to the 2014 seed bank compared to the 2011 seed bank contributes further support to our hypothesis that the seed bank and aboveground community contribute to each other and become more similar each growing season.

A number of genera observed in this study provide additional insights. *Heliotropium* seeds are likely associated with delivery from the Mississippi River, as it is the most abundant genus in the flood layer yet it has not been observed in West Bay, and decreased in relative abundance once the marsh formed and began to receive seed rain from within the system. The USGS BISON database include 141 records of four species of *Heliotropium* in Louisiana, 93% of which are *H. curassavicum* (seaside heliotrope) and *H. indicum* (Indian heliotrope). Both are monocarpic weeds with cosmopolitan distributions which produce large numbers of seeds per plant (Hegazy 1994, Chauhan and Johnson 2008). It is unclear whether the degraded state of the seeds found in all seed bank layers is a result of the hydrogen peroxide treatment used in the separation procedure, or if the seeds decomposed naturally. Since *Heliotropium* seeds are considered persistent in their ability to remain dormant (Chauhan and Johnson 2008), further evidence of natural decomposition would strengthen the argument that these seeds originated far from the point of deposition. In future research, it may be interesting to examine the temporal trends in the seeds of non-local species (not necessarily *Heliotropium*) in freshwater marshes associated with smaller fluvial influences. In this case, *Heliotropium* seed abundance can serve as a biological indicator for high-discharge river events. This could allow geologists to discern flood events in a coastal environment like West Bay which is subject to both river and marine influence. For example, both sediment reworking by a hurricane and downstream transport during a river flood can result in the deposition of coarsely-grained sand particles (Wallace and Anderson 2010), but only the river event would exhibit a spike in *Heliotropium* seed abundance.

Schoenoplectus seeds were also more abundant in the flood layer than in the emergent layer, yet *Schoenoplectus* is well-represented in the standing vegetation throughout West Bay in two species, *S. validus* (softstem bulrush) and *S. deltarum* (delta bulrush). A study on two closely related species to *S. validus* and *S. deltarum* – *S. acutus* and *S. americanus* respectively (Shiels et al 2014) – indicated that germination of both species' seeds are enhanced under inundated circumstances (Wagner and Oplinger 2017). Once established, *S. deltarum* ramets propagate clonally for three growing seasons before reaching a sufficient density to become dominant (White 1993). This suggests that the initial propagules of *Schoenoplectus* in West Bay were deposited during the 2011 flood, and that the local plants are contributing few seeds to the system. As *Schoenoplectus* seeds are a major food source for ducks (Hohman et al 1990), the relative contribution of allocthonous versus autochthonous seeds may be of interest to wildlife managers.

Phragmites australis (common reed, Roseau cane) and *Alternanthera philoxeroides* (alligator weed) are two common invasive plants in West Bay. While the native lineage of *Phragmites* does exist on the MRD, the dominant haplotypes are introduced (Hauber et al 2011). While a small number of *Phragmites* seeds were found in all layers of the seed bank, no *Alternanthera* seeds were found in the sediment despite being present at aboveground locations. *Phragmites* seed germination is prevented by flooding, but it can propagate aggressively by clonal spreading and fragmentation (Chambers et al 2003); however recruitment from the seed bank can also be high under appropriate conditions (Saltonstall & Stevenson 2007). *Phragmites* is at least partially self-incompatible, and so seed production may decline with the clonal expansion of genets as pollination of genetically identical flowers becomes more likely (Ishii and Kadono 2002). *Alternanthera* generally spreads by clonal fragmentation and transportation of floating plants, and does not produce viable seeds in its introduced range (Bassett 2008). It is likely, then, that the population dynamics of these two species are decoupled from the seed bank.

This study identified temporal changes in the deposition of seeds (the seed rain) as well as the similarity between seed banks and standing vegetation. However, we did not directly test the effects of the environmental sieve. Because seeds were separated using a partially destructive method, it is not possible to determine viability of the seeds collected in this study. Viability of seeds can be assessed by sieving and germinating seeds (Ter Heerdt et al 1996), and replicate samples could be germinated under varying conditions associated with a wetland environmental sieve, such as flood regime (van der Valk 1981). Understanding these germination requirements – especially of species which contribute to similarity with the standing vegetation – could allow for more effective management of target restoration species, as well as fill an existing knowledge gap in the prediction of vegetation establishment from seed (Visser et al 2016).

The West Bay receiving basin experienced one previous high-water event (2008) since its construction in 2003 (Figure 1.1), and again in 2016 after this study was performed. This reoccurrence rate of 4-5 years is consistent with Kolker et al (2014)'s longer-term description of 7 (8 including 2016) comparable events since 1986. Therefore, diversion basins on the lower Mississippi may be subjected to an influx of allochthonous seeds approximately every five years, in addition to the annual deposition associated with spring flooding. Depending on the interplay between the deposited seeds and the environmental sieve, the community composition of the existing marsh could be altered by the introduction of new seeds. The balance between allochthonous inputs of seeds and sediments from river floods and storm surge driven events, coupled with autochthonous production of seeds and biomass (see Chapter 2) provides the driving forces that govern both the ecology and landscape progression of West Bay, and likely other river-dominated coastal wetlands.

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Chapter 2: Vegetation and shear strength in a delta-splay mouth bar

Abstract

The mechanism by which new deltaic wetlands form is a complex suite of biological and physical processes that can modify one another. Understanding these processes and their interactions is imperative to successful coastal restoration. This study investigated the relationship between belowground plant biomass and sediment cohesion. We hypothesized that greater root densities increase shear strength variably across plant communities, and that these communities are associated with distinct inundation regimes. A significant relationship was found between belowground biomass and surface shear strength when accounting for sediment grain size, water content, and loss on ignition. Sites dominated by native graminoids or woody species had significantly higher shear strengths than unvegetated areas. However, sites dominated by *Phragmites australis* or forbs did not differ significantly in shear strength from unvegetated sites. Sites dominated by *Phragmites australis* were also subject to significantly higher inundation rates during the previous water year than any other vegetation type. These results suggest that vegetation community differences lead to differences in shear strength that result in locally differential erosion rates, in turn modifying future geomorphology, hydrology, sedimentation, and vegetation distribution. This feedback implies that certain vegetation

communities in wetland restoration projects could not only impart immediate erosion resistance to the substrate but affect the long-term potential for land creation.

Introduction

Human development in southern Louisiana has interrupted the natural delta cycle and is responsible for a large proportion of the state's coastal wetland loss, an estimated 4900 km^2 since 1900 (Day et al 2007, Couvillion et al 2011). The state is planning a large-scale restoration plan which will divert Mississippi River water to its delta to promote deposition of suspended sediment (Louisiana Coastal Protection and Restoration Authority 2017). The interaction between sediment transport, vegetation and the emergence of land in such systems is an emerging area of research (Nyman et al 2006, Esposito et al 2013, Fagherazzi et al 2015). However, disregarding the interactions between physical and biological processes could result in inaccurate conclusions, poorly informed decision making, and ultimately ineffective restoration projects. Furthermore, we can build upon our current understanding of both geology and ecology by explicitly considering feedback effects between the two.

The processes associated with delta building are complex and interdependent. Deltaic wetlands are formed from the deposition of suspended sediments that experience a loss in velocity when the river's flow enters a receiving basin. Crevasse splays experience periods of aggradation before and during the time at which the system becomes subaerial, followed by periods of reduced sedimentation as the bar top becomes hydrodynamically isolated (Roberts 1997, Esposito et al 2013). The delta increases in area as sediment is deposited further offshore, and gains elevation as sediment continues to be delivered to the sub-aerial land during periodic river floods. In order for the delta to persist over time, the depositional growth must outpace the land loss processes of erosion by wave action and subsidence by the belowground compaction of sediment (Roberts 1997).

As the delta gains elevation, it eventually supports a community of emergent plants (Johnson et al 1985, Cahoon et al 2011). Flooded soils exclude most plant species due to inhibition of gas exchange and hydraulic conductivity at the roots, as well as toxicity from ions associated with reduced soil conditions (Teal and Kanwisher 1961, Colmer and Voesenek 2009). Wetland species achieve flood tolerance through a variety of metabolic and morphological adaptations, most of which involve either pumping atmospheric oxygen through the shoots to the rhizosphere, or by storing excess carbohydrates which can support the plant during periods of inundation (Vartapetian and Jackson 1997). Different adaptations to flood tolerance are optimized for floods of varying depth and duration (Colmer and Voesenek 2009), so the most flood-tolerant species are found in locations subject to the most frequent inundation. Because the flood regime is determined by the elevation and wetland substrates, the geomorphology of the wetland exerts a high degree of control over plant community distribution (Mitsch and Gosselink 1993).

Once vegetation is established, it is capable of further altering the hydrology and geomorphology of the new land (Tal and Paola 2007). Water velocity over vegetated land or submerged aquatic vegetation is attenuated by friction from the stems, promoting sediment deposition (Gurnell 2013, Manners et al 2015, Luhar et al 2017). Plant biomass contributes to the organic portion of the soil, adding bulk and contributing to vertical growth (Nyman et al 2006). A positive feedback loop then develops by which emergent vegetation presence promotes deposition and eventually growth of subaerial land, which in turn supports more vegetation (Johnson et al 1985, Esposito et al 2013). Theoretically, a plant community could alter the surrounding elevation to such a degree that it becomes a more suitable habitat either for itself or a different species (Connell and Slatyer 1977).

Another important mechanism associated with wetland vegetation is the increase in soil cohesion, which results from plant roots physically binding together sediment grains, resisting erosion to a greater degree than would bare sediment. Vegetated deltas are characterized by high ground and lower rates of channel avulsion, while unvegetated deltas exhibit numerous braided channels subject to frequent overwash and avulsion (Edmonds and Slingerland 2010). Laboratory flume experiments have replicated this pattern using alfalfa sprouts as model vegetation (Tal and Paola 2007). *Spartina alterniflora* belowground biomass decreased when exposed to excessive nitrogen (Darby and Turner 2008), and other stations at the same study site exhibited decreased shear strength associated with the same nitrogen treatment (Turner 2011). Howes et al (2010) demonstrated that subsurface shear strength decreases significantly below the root zone, but no root samples were collected.

Sediment is eroded when the force associated with moving water exceeds the critical shear stress (Shi et al 2015), so areas with higher surface shear strength values will be more difficult to erode. By simultaneously measuring vegetation cover, belowground biomass, and surface shear strength, it is possible to determine which plant species most effectively hold wave-exposed sediments in place. Physical characteristics of sediment such as water content, grain size, and soil density can also affect shear strength (Shi et al 2015), and are easily measured from field samples, so they can be used as covariates in a statistical analysis, further isolating the biological strengthening effect.

The complexity of the interactions between wetland processes and the variability in sources which drive these processes illustrate the challenges of successfully engineering new sustainable wetlands, but also present an opportunity for interdisciplinary research that can lead to better understanding of both the geology and ecology of wetlands throughout the world. The field of ecogeomorphology investigates the interactions between the biosphere and lithosphere. Wetland ecogeomorphology is poorly understood but necessary in order to restore and maintain deteriorating systems (Paola et al 2009, Nyman 2014).

Field surveys are an important first step in understanding whether vegetation modifies the geomorphology of a system. Since wetland vegetation can be very heterogeneous, it is important to identify the degree to which different species are associated with such changes. Here we tested the following three hypotheses concerning wetland ecogeomorphology at a restoration site in Southeast Louisiana: ***(1)*** *on newly formed mudflats, shear strength will increase with belowground biomass due to sediment cohesion from plant roots independent of grain size, water content, and organic content of the sediment;* ***(2)*** *the degree of shear strength conferred to the soil will differ across plant communities due to differences in functional morphology of the dominant species;* ***(3)*** *communities will differ in the frequency of inundation experienced as calculated from elevation.*

Methods

Study Site

The West Bay Sediment Diversion is an uncontrolled artificial crevasse in the west bank of the Mississippi River located at 29.211169° N, 89.292289° W, approximately 8 km upstream from Head of Passes (Figure 2.1). The diversion was constructed by the Army Corps of Engineers in 2003 in order to deliver riverine sediment to the shallow receiving basin and construct approximately 40 km^2 of new marsh (US Army Corps of Engineers 2004). The system was originally about 8 m deep and carried approximately 710 m^3 s^{-1} of water, but has since expanded to about 25 m deep and carries about 1500 m^3 s^{-1} (Kolker et al 2012, Yuill et al 2016). Following the high water event on the Mississippi in 2011, two teardrop-shaped islands supporting a small amount of emergent vegetation were observed to the west of the diversion (Kolker et al 2012, Yuill et al 2016). The larger island, referred to as Remi's Island, is 400 m in length and 90 m across at its widest and is located 1 km west of the diversion opening. The smaller island, referred to as Walter's Island, is 180 m long, 30 m across, and is located 500 m northwest from the center of Remi's Island. The morphology of the islands was reworked following a direct hit by Hurricane Isaac in 2012, and has continued to evolve into a larger subdelta complex.

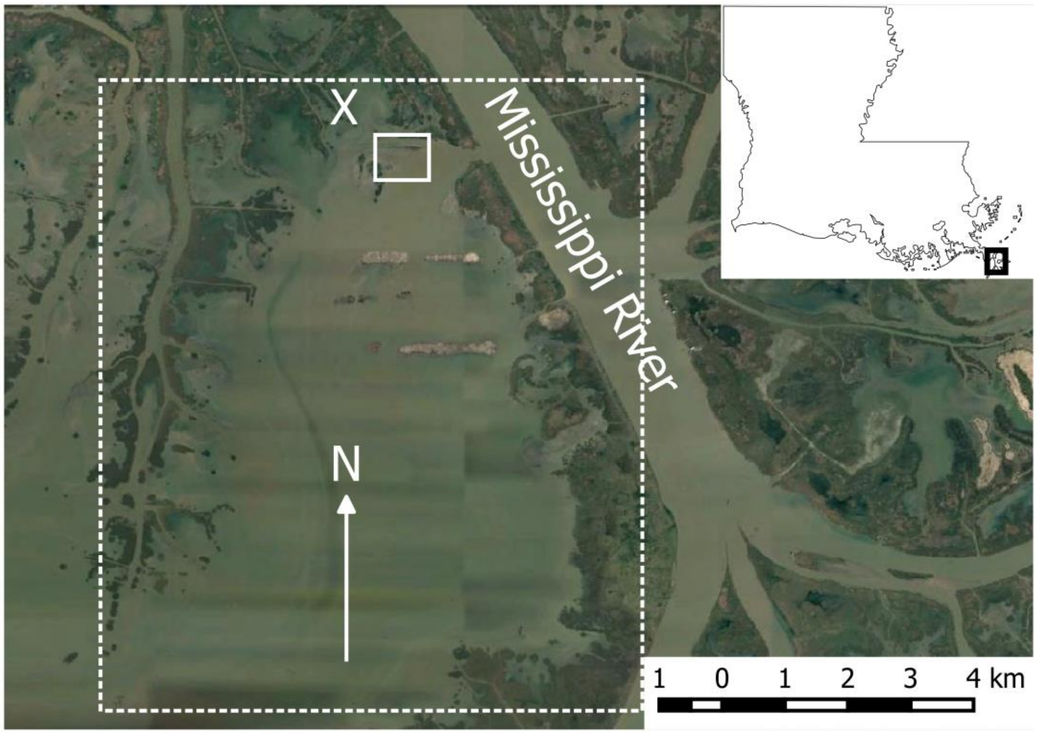

Figure 2.1: The West Bay Sediment Diversion and receiving basin. The area enclosed by the dotted line contains all stations assessed during the bay-wide survey, while the area enclosed in the solid line represents the spatial extent of the emergent island survey. The location of the US Army Corps of Engineers river gauge in West Bay is denoted by a white "X," and the inset map at the top right denotes the location of West Bay within the state of Louisiana

The vegetation community on the new islands is characteristic of Louisiana freshwater marsh. The most common emergent species observed in the area include *Typha* spp., *Sagittaria lancifolia, Schoenoplectus validus, Schoenoplectus deltarum, Phragmites australis, Zizaniopsis miliacea, Salix nigra, Polygonum punctatus,* and

Amaranthus australis. Aquatic vegetation includes *Potamogeton epihydrous, Nelumbo lutea, Eicchornia crassipes,* and *Alternathera philoxeroides.*

Field Surveys

A spatially extensive vegetation survey was conducted in West Bay during June of 2014 at 118 shoreline and shallow-water stations (0-1.24 m water depth, mean 44 cm) throughout the bay (Figure 2.2a). Stations included both newly formed and persistent habitat throughout the bay. The percent cover of each species was visually estimated in a 1 m^2 area. Latitude, longitude, and elevation were measured using a Real Time Kinematic (RTK) survey-grade GPS system (Trimble Navigation Ltd., Sunnyvale, CA, US; model R6). A 2 cm by 4 cm shear vane (Seiken, Tokyo, Japan; model DO-1018) was used to measure the torque required to break the surface layer of sediment in the most densely vegetated area of the quadrat. Torque measurements were not performed when water depths exceeded approximately 1 m, at which the instrument would be submerged and damaged.

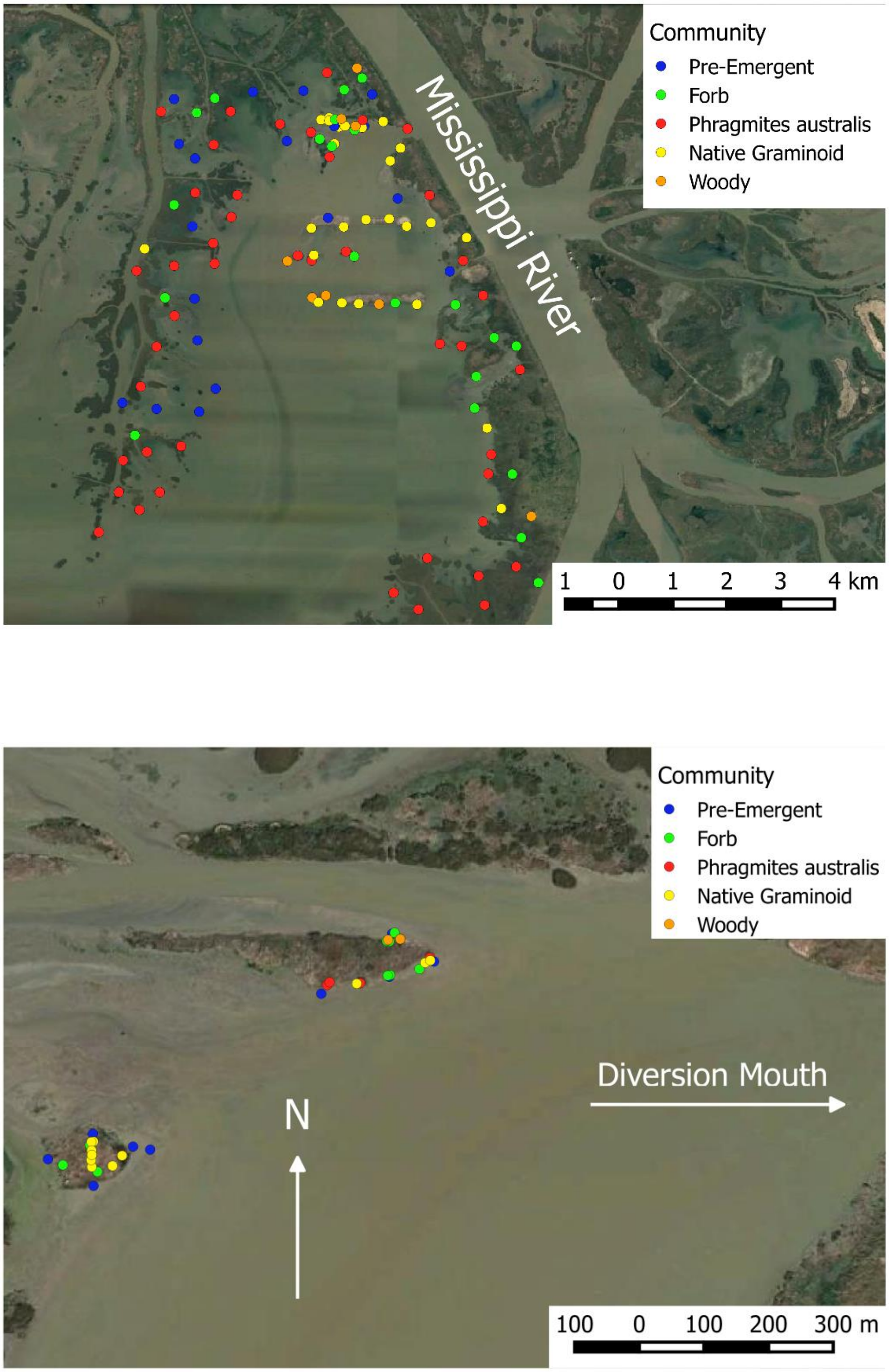

Figure 2.2: Sampling locations in West Bay for the bay-wide (above) and emergent island (below) surveys, color-coded according to the community type

A second survey was performed in West Bay in August 2014, at 35 sampling locations restricted to vegetated and unvegetated areas on two islands that became subaerial following the Mississippi River flood of 2011. Sampling locations are mapped in Figure 2.2b. Latitude, longitude, and elevation of each location were measured the RTK. All aboveground vegetation species were recorded, and all biomass within a .5 m^2 quadrat was clip-harvested at ground level and stored in 50-gallon leaf-litter bags for laboratory analysis. Belowground biomass was sampled by extracting a core using a peat auger from the center of the sampling quadrat (Eijkelkamp, Giesbeek, Netherlands; model 040903C). The auger had a maximum depth of 50 cm, a diameter of 5 cm, and a volume of 0.5 L; cores were taken to the depth of maximum penetration and had a mean depth of 11.0 cm with a standard deviation of 4.8 cm. The depth of the core was recorded at the time of sampling, after which all material was bagged and homogenized. A surface sample comprised of approximately the top 2 cm of sediment was collected with a hand trowel. Finally, after all biomass had been harvested, critical breaking strength of the surface sediment was measured with the 2 cm by 4 cm shear vane at the center of the most densely vegetated area within the quadrat. All samples were stored at 2°C prior to analysis.

Vegetation was characterized as one of five communities (Table 2.1). These communities consisted of 1) a pre-emergent community, characterized by bare land, open water, or aquatic vegetation such as *Nelumbo lutea* or *Potamogeton* spp.; 2) a community dominated by the forbs *Sagittaria lancifolia*, *Typha* spp., or *Colocasia esculenta*; 3) dense monoculture of invasive Eurasian or cryptic Gulf Coast haplotypes of *Phragmites australis* (Saltonstall 2002); 4) a community dominated by native graminoids

(*Zizaniopsis miliacea, Schoenoplectus validus,* or *Schoenoplectus deltarum*); 5) a woody community dominated by a combination of *Salix nigra* and aggressive early successional woody species such as *Sesbania* spp., *Amaranthus australis,* and *Pluchea camphorata*. Community assignment was determined by percent cover in the June survey and aboveground biomass in the August survey.

Community	**Dominant Species**
Pre-emergent	*Potamogeton epihydrous, Nelumbo lutea*, or no vegetation
Forbs	*Sagittaria lancifolia, Sagittaria latifolia, Colocasia esculenta, Typha* spp.
Non-native Graminoids	*Phragmites australis,* haplotypes M and I
Native Graminoids	*Schoenoplectus deltarum, Schoenoplectus validus, Zizaniopsis miliacea*
Woody	*Salix nigra, Amaranthus australis, Sesbania* spp.

Table 2.1: Definitions of community types, based on characteristic dominant vegetation species

Laboratory analysis

Each aboveground biomass sample was separated by species and dried at 80°C for 24-48 hours. Dry biomass of each plant species was recorded for each plot. Belowground biomass samples were treated with 500 mL of warm tap water and 100 mL of industrial-strength Windex (2-butoxyethanol and ammonium hydroxide solution) and allowed to soak for 24 hours in order to deflocculate the sediment particles from each other and from the biomass. Each sample was then agitated for approximately 30 seconds and poured through a #10 (2 mm) and #35 (.5 mm) sieve. All rootlike organic matter (roots, rhizomes, and stolons) trapped by the sieves was collected using forceps and transferred to a weighing dish. No effort was made to separate the roots of different species or to differentiate live from dead biomass. Collected root material was dried at 80°C for 24 hours and dry belowground biomass was subsequently weighed. Belowground biomass is presented in milligrams of total root material in the core, divided by the volume of the core containing the roots.

Subsamples weighing between 200 and 500 mg were collected from each wet surface sediment sample for particle size analysis. Each subsample was treated with 2 mL of 30% hydrogen peroxide solution (2 hours) and 10 mL of .5M sodium hexametaphosphate solution (12-24 hours) in order to remove organic matter and deflocculate the sediment grains, respectively. The remaining sediment was run through a laser diffraction particle size analyzer (Beckman-Coulter Inc, Brea, CA; model LS 13-320) to generate a particle size distribution. The remainder of each wet sample was transferred to an aluminum, weighing dish and dried at 60°C for 18-24 hours, weighing before and after drying to calculate percent water content. Approximately 1 g of the dried sample was pulverized with a mortar and pestle and burned in a 400°C muffle oven for 6 hours, again weighing before and after to calculate percent loss on ignition as a proxy for organic content. Finally, the torque τ (N m^{-2}) measured at each field location was converted to shearing strength using the formula

$$\tau = \frac{M_{max}}{\pi\left(\frac{D^2 H}{2} + \frac{D^3}{6}\right)} \quad (1),$$

where M_{max} is the torque required to break the soil (N m), D is the diameter of the vane (m), and H is the height of the vane (m) (Seiken “Model No. DO-1018”).

RTK elevations ranged in vertical accuracy from 1.3 cm to 48.9 cm. The June data had a mean accuracy of 3.4 cm with a standard deviation of 4.6 cm; the August data had a mean accuracy of 2.1 cm and a standard deviation of 0.5 cm. Eleven outliers in accuracy were identified and removed from the June dataset based on the boxplot method. Values falling 1.5 interquartile ranges either above the third quartile or below the first quartile were deemed outliers, where the interquartile range is the difference between the data points representing the 75th and 25th percentile (Tukey 1977). All of our eleven elevation measurements were excluded from the June dataset for exceeding 4.75 cm in accuracy. Following the removal of these outliers, the June elevation data had a mean accuracy of 2.5 cm and a standard deviation of 0.7 cm.

Elevation was converted to inundation frequency using the US Army Corps of Engineers tide gauge located within the West Bay Diversion receiving area (Station 01516). A correction factor between the RTK elevation and the hourly gauge height relative to NAVD88 was calculated using control points taken along shorelines (consistent with the water level) at known times throughout the day. The daily tide gauge dataset was downloaded for the entirety of water year 2014 (October 1, 2013 – September 30, 2014), and the inundation frequency was calculated as the percentage of daily data points with a gauge height above a given elevation. See Online Resource 1 for hourly and daily gauge heights, and see Online Resources 2 (June) and 3 (August) for the converted elevations.

Statistical Analysis

To test the hypothesis that belowground biomass is positively correlated with shear strength, the August 2014 data were analyzed using a multiple linear regression model with shear strength as the dependent variable. Shear strength values were natural-log transformed to better satisfy the homogeneity of variance and normality assumptions associated with general linear models (Sokal and Rohlf 1995). The predictor of greatest interest was belowground biomass. Median grain size, water content, and loss on ignition were included as covariates, as were the second-order interaction terms between biomass and each covariate. The interaction effect between water content and grain size on shear strength was included as well, as it has been observed in other studies (Shi et al 2015).

To test the hypothesis that shear strength varied across vegetation communities, analysis of variance was conducted with shear strength as the dependent variable and community as the predictor. Separate analyses were performed for each survey, because of differences in spatial extent and site selection criteria between the two field campaigns. The June survey was conducted throughout West Bay and included stations on both recently formed islands and older marshes, while the August survey was restricted to the recently formed Walter’s and Remi’s Islands. In each case significant differences were further investigated using Tukey’s Honest Significant Difference test for all pairwise comparisons.

To test the hypothesis that different communities experience different inundation regimes, we performed a nonparametric Kruskal-Wallis test on the pooled June and August elevation data, with inundation frequency as the dependent variable and community as the predictor. Significant differences were further investigated using Gao's nonparametric multiple comparison procedure (Gao et al 2008).

Results

Vegetation Communities

Of the 118 stations sampled in June, 44 were dominated by *Phragmites*, 25 by native graminoids, 22 by forbs, 8 by woody species, while 19 were pre-emergent. Of the 35 stations sampled in August, 11 were dominated by native graminoids, 9 by forbs, 4 by *Phragmites,* 2 by woody species, while 9 were pre-emergent. Full species abundance data are available in Appendix 2.

Shear Strength, Belowground Biomass and Sediment Properties

Median surface grain sizes collected on the emergent islands ranged from 9.8 μm to 160.5 μm, with a mean of 42.8 μm and a standard deviation of 40.9 μm. The island margins most proximal to the diversion mouth included both large and small grain sizes, while the more distal and interior stations were strictly fine-grained. Sediment water content ranged between 23.1% and 59.6%, with a mean of 38.8% and a standard deviation of 9.6%. LOI ranged between 1.7% and 9.7%, with a mean of 5.2% and a standard deviation of 1.8%. No clear spatial patterns were observed for either water content or LOI.

A significant positive correlation was identified between shear strength and belowground biomass ($F_{1,24}$=17.6175, p = .0003, Figure 2.3), and a significant negative correlation was found between shear strength and percent water content ($F_{1,24}$=16.9161, p = .0004). The interaction between water content and grain size was also significant ($F_{1,24}$=5.4233, p = .0286). No other covariates or interaction effects were significant.

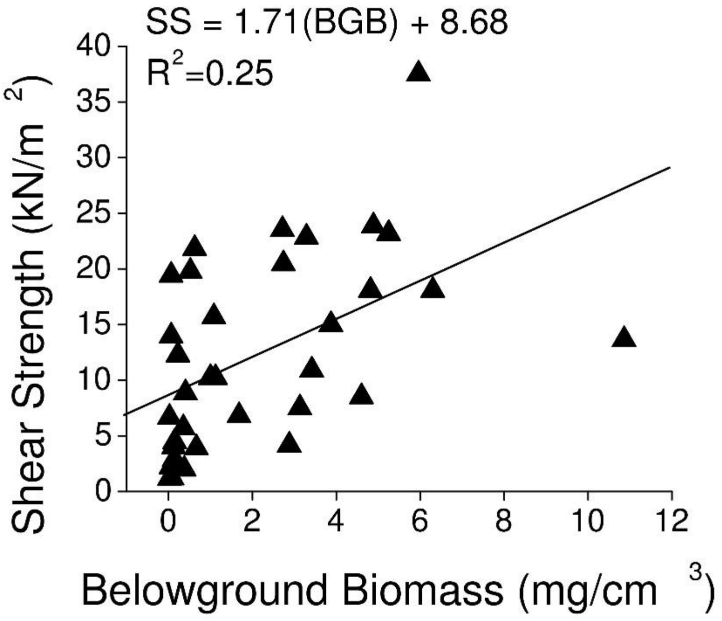

Figure 2.3: Relationship between belowground biomass and shear strength measured at emergent island stations, superimposed by a linear regression

Shear Strength, Biomass and Community

In the June year survey of bay-wide stations, shear strength varied significantly across communities ($F_{4,84}$=6.7158, p = .0001, Figure 2.4). The post-hoc multiple comparison test indicated that the native graminoid community had significantly higher shear strength than the pre-emergent (p = .0108), forb (p = .0083), and *Phragmites* (p = .0021) communities. The woody community also had higher shear strengths than each of the three aforementioned communities (p = .0296, .0451, and .0259, respectively).

In the August survey of emergent island stations, shear strength varied significantly across communities ($F_{4,30}$=4.4191, p = .0063, Figure 2.5). The post-hoc multiple comparison test indicated a significant difference between shear strengths of the native graminoid and pre-emergent communities (p = .0029). No other comparisons were significant.

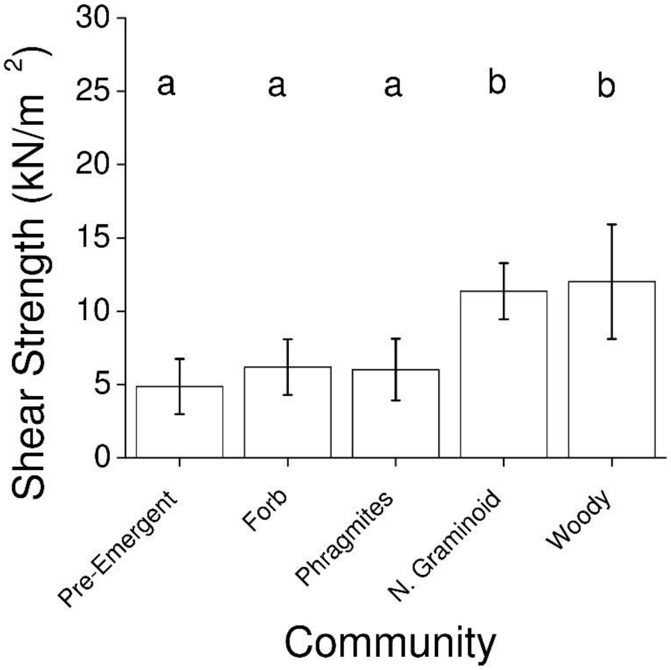

Figure 2.4: Mean shear strength values across communities measured at bay-wide stations. Error bars represent 95% confidence intervals; groups sharing no letters in common are significantly different

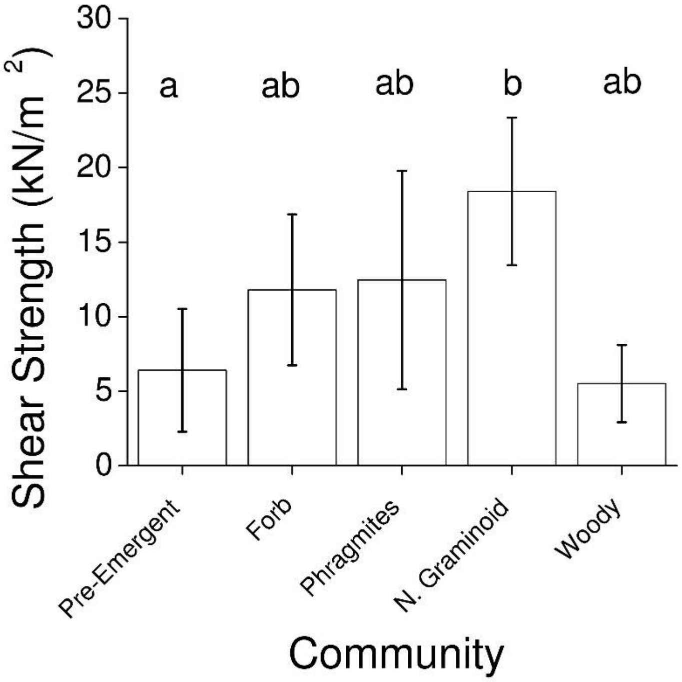

Figure 2.5: Mean shear strength values across communities measured at emergent island stations. Error bars represent 95% confidence intervals; groups sharing no letters in common are significantly different

Inundation and Community

There was a significant difference across communities in the percentage of time flooded during water year 2014 (Kruskal-Wallis $\chi^2 = 41.172$, df = 4, p < .0001, Figure 2.6). The post-hoc multiple comparison test indicated that the pre-emergent and *Phragmites* communities were inundated significantly more during water year 2014 than either the native graminoid (p = .0060, p < .0001 respectively) or woody (p = .0189, p <

.0001 respectively) communities. Additionally, the *Phragmites* community was inundated significantly more than the forb community (p < .0001).

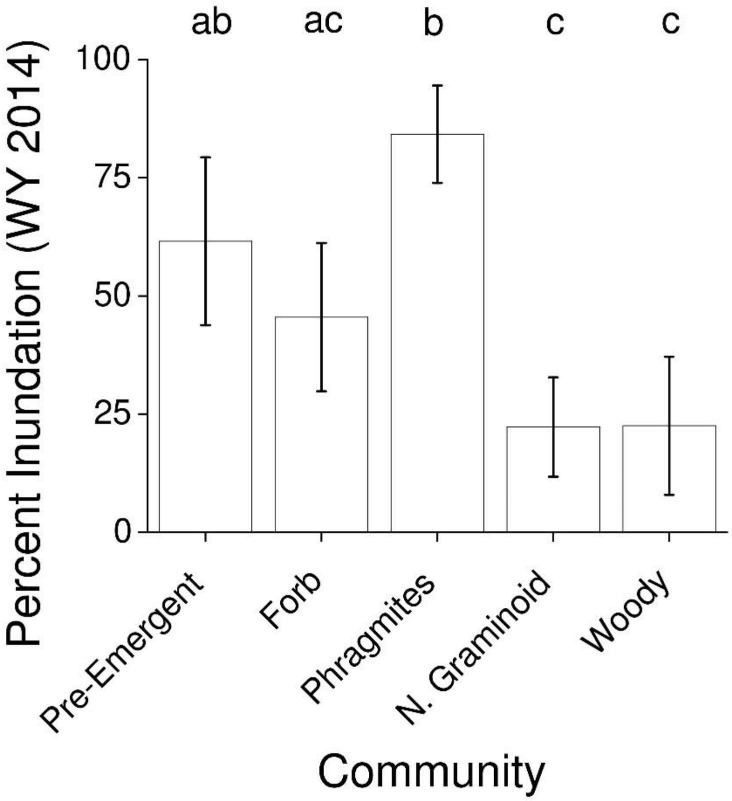

Figure 2.6: Mean inundation frequencies, as calculated from elevation measurements relative to the gauge height in the West Bay Diversion outfall during water year 2014, across communities for both bay-wide and emergent island stations. Groups sharing no letters in common are significantly different

Discussion

The importance of belowground biomass to the sustainability of a wetland is usually cited in terms of its contribution of organic matter to mineral soil, as a source of nutrients to plants and microbes as well as a driver of vertical accretion to a marsh by virtue of the space it takes up (Nyman 2014). The results of this study indicate an additional benefit of plant roots to the health of a marsh, by which the biomass provides cohesion to the soil in addition to the previously cited contribution of bulk material, increasing shear strength and therefore erosion resistance (Figure 2.3). This is a separate mechanism from the more commonly cited effect of aboveground biomass protecting against erosion by attenuating wind and wave action (Gurnell 2013, Manners et al 2015). These studies describe a reduction in the amount of energy introduced to the system, while the results of this study represent an increase in the amount of energy the system can withstand before erosion begins. In both cases, the presence of vegetation inhibits erosion as a driver of land change and increases the influence of elevation gain by sediment deposition. In a separate effect from that of vegetation, the shear strength was controlled by water content and grain size, where the lowest shear strengths were associated with high water content and small grain size, consistent with prior observations (Shi et al 2005). Theoretically, the modulatory effect of vegetation represents a trend by which the system, over time, is influenced by increasingly autogenic processes.

The results demonstrated some differences in shear strength across communities, as expected. Communities represented by *Salix nigra, Zizaniopsis miliacea, Schoenoplectus deltarum,* and *Schoenoplectus validus,* which invest heavily in belowground productivity, were associated with higher shear strengths than all other communities (Figure 2.4). The association of *Phragmites australis* with lower shear strengths counters a claim by Rooth and Stevenson (2000) that *Phragmites* is very effective at soil stabilization. Mozdzer et al (2016) found that *Phragmites* roots are found significantly deeper in the rhizosphere than other species, which would not cause increased sediment cohesion at the surface, where erosive forces would actually impact sediment.

Among the vegetated stations, those dominated by *Phragmites* experienced significantly more inundation throughout water year 2014 as compared to all other community types (Figure 2.6), indicating a characteristic association with lower elevations. *Phragmites* has been reported to thrive in water depths up to 2 m, due to its ability to pump large amounts of oxygen from its aboveground culms through its roots and into the surrounding anoxic soil (Gries et al 1990). However, this capability develops over the plant's lifetime, and *Phragmites* seedlings require periods of little to no inundation in order to establish (Mauchamp et al 2001). The stands of *Phragmites* found in West Bay may have established on land that subsequently eroded or subsided, or at a lower initial elevation during a period of unusually low river discharge. Conversely, the native graminoid and woody communities which were associated with the least frequent inundation may have either established based on elevation (Cahoon et al 2011), or persisted despite positive or negative changes in elevation (Shaffer et al 1992). Regardless, more frequent inundation and greater water depth increase the height and erosive energy of waves (Le Hir et al 2000). Therefore, the association of *Phragmites* with both lower shear strengths and more frequent inundation suggest that *Phragmites* stands may be subject to higher erosion rates than other vegetation types. Since *Phragmites* is the dominant vegetation in approximately two-thirds of the Mississippi River Delta (Hauber et al 2011), this conjecture should be further investigated in a long-term study of community-specific erosion rates.

The role of vegetation in soil stabilization has been well-documented in settings such as riverbanks (Abernethy and Rutherford 2001), hillsides (Stokes et al 2009), and sand dunes (Tsoar 2005). The discussion of plant roots providing erosion resistance, in the context of Louisiana coastal restoration, has largely been confined to hurricane resilience (Howes et al 2010). Kearny et al (2011) argued that marshes in St. Bernard Parish, LA suffered disproportionate land loss during Hurricane Katrina in 2005, due to inhibition of belowground productivity by excess nutrient loading. However, smaller-scale erosion occurs across the coast on a daily basis as a result of wind-driven wave action and marsh over-wash during high river stages (Day et al 2007). The association of shear strength differences with vegetation type implies that erosion rates can vary on a very small spatial scale, influencing the geomorphology of individual deltaic islands. This could in turn modify the hydrology, future sediment deposition, and the ensuing plant community. Hypothetically, the initial vegetation distribution could determine the overall amount of marsh created via a series of ecogeomorphological feedbacks, representing an increase over time of the proportional influence of autogenic factors. The sampling design of this study specifically targeted the most densely vegetated 3.1 cm^2 within 25 cm^2 quadrats, so these values may not be representative of larger spatial areas where vegetation density is often heterogeneous. However, higher-resolution sampling of shear strength, belowground biomass, and sediment properties within individual vegetation types could be useful in the parameterization of land-building models.

Diversions and restoration projects are often designed to promote specific grain size classes and elevations (Craft et al 2002, Kenney et al 2013). This strategy could be expanded to include the promotion of native species associated with higher shear strength values, in order to increase the lifetime of the new marsh. Further study would be required to determine the niche requirements of the species in question. Determining establishment and recruitment rates would indicate whether each species could be propagated by the local seed bank, or if planting of seedlings would be required to ensure colonization. Additionally, it is important to understand the nature and degree of competitive interactions between the species that dominate the various communities. Synthesizing these ecological and geological processes could lead to more effective planning and management of deltaic wetland restoration projects.

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Chapter 3: Competition eclipses abiotic factors in limiting two monoculture-forming wetland plants

Abstract

Community composition can be understood as the spatial manifestation of individual species' niche requirements along one or more environmental gradients. It can also be interpreted as differential competitive outcomes along an environmental gradient that changes either spatially or temporally. Here we investigate the relative roles of competition and environmental stressors in two wetland plants important for coastal restoration, in the context of both multidimensional niche space and limiting resource ratios. *Schoenoplectus deltarum* and *Phragmites australis* were grown in both monoculture and competition, and subjected to two levels each of nitrogen, salinity, and soil organic matter in a factorial greenhouse experiment. Productivity in both species was consistently suppressed under competition, to a greater degree than, and regardless of, the abiotic treatments. In monoculture, *Schoenoplectus* productivity responded negatively to low organic matter and reproduction responded negatively to brackish water; *Phragmites* productivity responded negatively to increased nitrogen. *Schoenoplectus* root-to-shoot ratio responded positively to brackish water given high organic matter, and *Phragmites* root-to-shoot ratio responded negatively to increased nitrogen. *Phragmites* and *Schoenoplectus* are ubiquitous in tidal freshwater marshes along the US Gulf Coast, including those targeted for large-scale restoration activities in south Louisiana. These results suggest that the proposed strategy for sediment diversion operations is consistent

with species coexistence and increased root production, which are respectively associated with increased ecosystem services and soil stability. The physically dynamic nature of an early-successional freshwater deltaic wetland and its influence on community composition can be understood through a synthesis of multidimensional niche theory, competition as a limiting factor, and changing resource ratios.

Introduction

Coexistence between species within a community requires both environmental variation and differential exploitation of this variation by each species. Gause (1934) argued that without these factors, one species will eventually outcompete and exclude all other species. Since niche space is multidimensional, two species may occupy distinct regions of one niche dimension while overlapping with respect to other dimensions (Silvertown 2004).

Community composition can be drastically altered when environmental change replaces one niche dimension with another as the most important limiting factor. In Glacier Bay, Alaska, short-growing early dominant plants are replaced by taller-growing species over the course of primary succession. The initial environment is limited by soil nitrogen and only the best competitors can survive. As these plants senesce and contribute more nitrogen to the soil, nitrogen is no longer limiting and new species are able to establish. Those that grow taller shade out the initial species; the tall species is now dominant and light is now the limiting niche dimension (Tilman 1986). Plant species in freshwater marshes are often restricted to characteristic elevations as a response to differing degrees of inundation tolerance (Mitsch and Gosselink 1993). Restoration-based studies of wetland plant niche requirements often test flood regime as a primary or sole controlling factor (e.g. Frazer and Karnezis 2005, Alleman and Hester 2011, Sloey et al 2016). However, in primary successional environments on the Mississippi River Delta, the highest species diversity was found at the lowest elevations in the first two growing seasons (White 1993). It is therefore possible that in the earliest phases of wetland building, the niches of wetland plant species are defined by axes other than elevation.

Understanding niche requirements and competitive interactions associated with wetland plant species is important to the planning of successful and sustainable wetland restoration. The Mississippi River Delta in southern Louisiana is an example of a dynamic system whose community composition is likely subject to the successional patterns described by Tilman (1986). The MRD has occupied six distinct lobes over the past 7500 years, each characterized by a predictable cycle of rapid elevation and aerial gain due to sediment deposition, geomorphic stability during the period when sediment supply and subsidence balance, and deterioration due to wave erosion and subsidence in the later years (Roberts 1997). While the lifespans of these major delta lobes are approximately 1000-2000 years, smaller sub-deltas within the major lobes exhibit the same pattern within 150-200 years (Roberts 1997). Coastal Louisiana sub-deltas currently experiencing the depositional phase can gain between 1.5 and 5.6 cm yr^{-1} in elevation from sediment accumulation, although the net increase in elevation is often reduced due to natural subsidence (Kolker et al 2012, Esposito et al 2013, Rosen and Xu 2015). As a result, even if the river stage were identical in two consecutive years, vegetation at the same location on a sub-delta would experience less flooding stress in the second year if the elevation gain from sediment deposition is greater than the elevation loss from subsidence. Under such conditions, the role of flood regime as a limiting factor on vegetation would slowly but consistently diminish as the marsh develops. The State of Louisiana's Comprehensive Master Plan for a Sustainable Coast relies heavily on diverting the Mississippi River through gate-controlled structures (LACPRA 2017). This will restart the sub-delta cycle in its floodplain, which has been starved of sediment throughout the 20th century as a result of flood control levees (LACPRA 2017). Because the resulting wetlands will experience annual elevation gain, it would be of interest to assess vegetation dynamics as flooding stress is relaxed.

Here we examine three abiotic factors that could influence wetland plant community composition in the MRD in the absence of flooding stress. First, excess nitrogen loading has been found to promote different patterns in biomass allocation between C3 and C4 species (White et al 2012) and favor C4 species in competition (Langley and Megonigal 2010). Second, tidal freshwater marshes may experience episodes of saltwater intrusion if the influence of wind- or tidal-driven seawater is greater than that of the river's freshwater input (Anderson and Lockaby 2012). Salt tolerance differs among plant species, and community composition can shift over a salinity gradient (La Peyre et al 2001). Third, the organic matter content of marsh soils can vary based on sediment input, the amount of plant litter entering the soil, the rate of decomposition, and the age of the marsh (Nyman et al 1990). The amount of organic material in soil can affect plant growth in non-flooded environments by changing the physical density or porosity of the soil, modifying the water retention of the system as well as the ability of plants to produce belowground biomass (Mitsch and Gosselink 1993).

We hypothesized that dynamic changes in nitrogen, salinity, and suspended sediment would be important in determining freshwater wetland plant community structure. First, we predicted that C4 plants would be superior competitors compared to C3 plants such that under elevated nitrogen conditions, root-to-shoot ratios of C3 plants would decrease. Second, we predicted that salt-tolerant species would be superior competitors compared to freshwater species such that under brackish conditions, freshwater species would exhibit greater senescence. Third, we predicted that disturbance-adapted species would be superior competitors to less opportunistic species such that under low-organic conditions, the disturbance-adapted species would have more biomass although both groups would have lower root-to-shoot ratios.

We tested these predictions under greenhouse conditions using the disturbance-adapted (Zedler and Kercher 2004), salt-tolerant (Meyerson et al 2000), C4-capable (Srivastava et al 2014) grass *Phragmites australis* (common reed) and the less opportunistic (White 1993), less salt-tolerant (Howard and Mendelssohn 1999), C3 (Bruhl and Wilson 2007) sedge *Schoenoplectus deltarum* (delta bulrush). Both species are ubiquitous in the MRD, form dense monospecific stands, and propagate vegetatively (White 1993, Hauber et al 2011). This study tests the roles of nitrogen, salinity, and soil organic matter in limiting these important freshwater marsh species, and discusses the implications of our findings for restoration in the MRD.

Methods

We designed a blocked additive pairwise competition experiment to test the effects of environmental factors on *Phragmites australis* (hereafter *Phragmites*) and

Schoenoplectus deltarum (hereafter *Schoenoplectus*). We replicated the experiment across three blocks, each of which contained a randomly assigned factorial array of a competition (3 levels), salinity (2 levels), nitrogen (2 levels), and organic content (2 levels).

Collection and Propagation

Following the flood year of 2011, a sub-delta complex has emerged in the receiving basin of the West Bay Sediment Diversion, approximately 8 km upstream from the mouth of the Mississippi River, and continues to grow in area (Yuill et al 2016). Young (1 m or shorter) shoots of *Phragmites* and *Schoenoplectus* were harvested on August 23, 2014 from one monospecific stand of each species in West Bay (SCDE: 29.21206N, 89.30127W. PHAU: 29.21207N, 89.30280W), and transported to the Tulane University greenhouse in New Orleans, LA. Upon arrival, the shoots were transplanted across 36 pots for each species, at a density of 5 stems per pot. The plants were allowed to grow in the greenhouse until July 2015. Pots were watered for one hour every six hours at a rate of 12.1 L hr^{-1} pot^{-1}, and weeded on a weekly basis. In January 2015, greenhouse whiteflies (*Trialeurodes vaporariorum*) were observed feeding on *Phragmites* leaves. All pots of both species were treated with acephate-based insecticide (Bonide Products Inc., Oriskany, NY) once a week for four weeks until the insects were no longer observed. No negative effects were observed on the health of either species.

Treatment Applications

Experimental units were planted between July 20 and July 31, 2015, each receiving one of three species mixtures, one of two water sources, and one of four soil mixtures. All stems were cut to 100cm at time of transplanting to account for initial size bias (Gibson et al 1999). Pots were topped with cypress mulch beginning July 22, 2015.

Additive pairwise competition experiments include experimental units containing the two species in competition, as well as each species in monoculture (Gibson et al 1999). Densities were determined by averaging stem counts taken within 1m^2 quadrats throughout West Bay in June 2014. Initial planting densities were either 8 stems per pot (*Phragmites* monoculture), 26 stems per pot (*Schoenoplectus* monoculture), or 4 *Phragmites* plus 13 *Schoenoplectus* stems (competition treatment).

All pots received tap water controlled by a timer to deliver 1 hour of watering every six hours at a rate of 12.1 L hr^{-1} pot^{-1}. The water line was split after the timer in order to apply the salinity treatment. One line continued unadulterated to the freshwater treatment pots. The brackish treatment pots received tap water, mixed with brine from an external reservoir with an inline suction injector (Jain Irrigation, Jalgaon, India). The brine was a mixture of tap water which also passed through the timer unit and Instant Ocean (Spectrum Brands Holdings Inc., Madison, WI), mixed to between 130 and 160 parts per thousand. New brine was mixed approximately every 7 days. The injector could be controlled to vary the amount of brine drawn from the reservoir and salinity could remain relatively constant despite different brine salinities. Salinity of water received by plants was measured from a randomly chosen pot on fourteen occasions throughout the study period. The mean salinity was 5.11 ppt with a standard deviation of .35. All salinity measurements fell between 4.46 and 5.65 ppt, and July 31 was the first day any plants were treated with brackish water.

The high-organic soil used was HapiGro Potting Soil (Hope Agri Products, Hope, AR), which contains sand, pine bark mulch, ash, and perlite. The organic content was estimated by calculating loss on ignition (LOI), which is the percent difference in mass when a dried, pulverized sample is burned at 400°C for six hours. The high organic soil had an LOI of 29.6%. The low organic soil was achieved by mixing the same HapiGro soil with Quikrete Play Sand (Quikrete Companies, Atlanta, GA), which had a nearly-negligible LOI of 0.05%. Based on the densities of the two products, a mixture of 2 parts sand to one part potting soil was calculated to yield an LOI of approximately 5%, which is typical of young mudflat sediment within West Bay where the plants were collected.

The low-nitrogen treatment was determined by the total nitrogen content of the HapiGro Soil. The high-nitrogen treatment was set at four times the low concentration. Elevated nitrogen levels were achieved by adding Vigoro Lawn Fertilizer (Vigoro Corporation, Lake Forest, IL), a time-release product which contained a NKP ratio of 29:0:4 and delivered nitrogen in the form of urea. Four varying levels of fertilizer were added to samples of each organic treatment soil, and duplicate samples of each mixture were analyzed for total nitrogen by the Coordinated Instrument Facility (CIF) at Tulane University. The low nitrogen treatment, based on the total nitrogen content of the potting soil, was 0.113%. The amount of fertilizer required to achieve a concentration of 0.113% in the low-organic treatment, as well as a high-N concentration of 0.451% in both organic treatments, was calculated by performing linear regressions of total N on fertilizer addition for the CIF results. Separate regressions were run for the two soil types.

Quality Control

Mulch was added to the pots beginning on July 22, 2015, in response to an ammonia smell in the water draining from the plants. Urea-based fertilizer can convert to ammonia when soil temperature is high, as was the case in the greenhouse during July in New Orleans. The entirety of Block 1 and pots 1-12 in Block 2 had been transplanted before mulch was added to lower soil temperatures and retain water. The ammonia smell was absent following mulch application. All pots were manually watered upon transplanting, and periodic manual watering was performed throughout the day until July 24. There were only two such waterings on July 20, when pots 1-18 were planted. Significant plant stress to both species was noted on July 21, and watering was increased to four times a day. The plants transplanted on subsequent days did not exhibit such stress. Therefore, the first 18-36 pots to be transplanted may have been affected by stress from ammonia, drought, or both. Since this stress was not distributed evenly across blocks, any resulting physiological effects were expected to manifest as block effects rather than treatment effects.

Harvest

Experimental units were subjected to the four treatments from July 31, 2015 to November 2, 2015. Aboveground biomass was harvested between November 3 and 6, 2015. All stems in each pot were counted, clipped, and bagged by species. Belowground biomass was harvested between November 17 and 24, 2015. Each pot was emptied of soil and the root ball extracted. Trapped sediment was removed from the root ball by soaking in a mixture of water and dish soap, manual agitation in the water/soap mixture, and rinsing with a hose over a 1 mm sieve. The roots were then separated by species and bagged.

Laboratory analysis

Before assessing biomass, the height and base diameter of 10 randomly selected stems were measured for each sample. For pots containing *Schoenoplectus*, the number of stems producing flowers was also recorded for each sample. No *Phragmites* stem produced a flower during the experiment or pre-experimental propagation. All aboveground and belowground biomass samples were dried at 70°C for 48 hours and subsequently weighed.

Statistical analyses

Biomass and morphological variables for each species were condensed using principal components analysis with Varimax rotation (Denis 2016). The number of components for each species was determined by examining a Scree plot (Denis 2016). The loadings of the original variables on each component were examined to assign a biological interpretation to each component. The root-to-shoot ratio of each experimental unit was calculated as the quotient of the total belowground dry biomass over the total aboveground dry biomass.

Treatment effects were assessed for each species by performing a factorial mixed-model ANOVA for each principal component. Competition, nitrogen, salinity, and organic matter treatments, as well as all higher-order interactions, were included as fixed effects, and block was the random factor. To test for treatment effects on biomass allocation, the same mixed-model ANOVAs were performed using the natural logarithm of the root-to-shoot ratio of each species as a dependent variable. The root-to-shoot ratios were natural-log-transformed in order to satisfy the normality and homogeneity of variance assumptions of ANOVA (Sokal and Rohlf 1995).

Results

PCA analysis and interpretation:

The variables measured for *Schoenoplectus* were reduced to three principal components, which together accounted for 87.2% of the original dataset's variance (Table 3.1). The first principal component was associated with high values of stem count, aboveground biomass, and belowground biomass, and was therefore interpreted as "Productivity." The second principal component was associated with high values of mean stem height and percentage of stems with flowers. *Schoenoplectus* is a wind-pollinated plant, so in order to successfully produce seeds the plant must produce many flowers and grow to a height at which pollen can be distributed by the wind. Based on this reasoning, the second component was interpreted as "Reproductive Potential." Finally, the third component was associated with high values of mean stem width alone, and was interpreted as "Stem Morphology."

	1 – Productivity	2 – Reproductive Potential	3 – Stem Morphology
Variance Explained	54.2%	17.6%	15.4%
Loadings			
Stem Count	0.896*	0.261	-0.068
Mean Stem Height	0.180	0.817*	0.309
Mean Stem Diameter	0.075	0.047	0.964*
Aboveground Biomass	0.840*	0.465	0.115
Belowground Biomass	0.928*	0.074	0.142
Percent Flowering	0.266	0.834*	-0.189

Table 3.1: Principal components computed for *Schoenoplectus* morphological data. Starred loading scores indicate the variables interpreted to contribute significantly to the overall component score.

The variables measured for *Phragmites* were reduced to two principal components, which together accounted for 92.6% of the original dataset's variance (Table 3.2). Once again, the first principal component was associated with high values of stem count, aboveground biomass, and belowground biomass, and was interpreted as "Productivity." The second component was associated with high values of mean stem height and mean stem diameter, and was interpreted as "Stem Morphology."

	1 – Productivity	2 – Stem Morphology
Variance Explained	70.2%	22.4%
Loadings		
Stem Count	0.909*	0.274
Mean Stem Height	0.251	0.939*
Mean Stem Diameter	0.231	0.944*
Aboveground Biomass	0.900*	0.369
Belowground Biomass	0.936*	0.126

Table 3.2: Principal components computed for *Phragmites* morphological data. Starred loading scores indicate the variables interpreted to contribute significantly to the overall component score.

Treatment effects:

Schoenoplectus: Productivity (Principal Component 1) was significantly affected by the competition treatment ($F_{1,32}$ = 32.995, p<.001), as well as an interaction effect between competition and organic content ($F_{1,32}$ = 5.235, p=.029, Figure 3.1). Reproductive Potential (PC2) was significantly affected by salinity ($F_{1,30}$ = 11.257, p=.002), as well as a three-way interaction between salinity, nitrogen, and organic content ($F_{1,30}$ = 4.799, p=.036, Figure 3.2). No significant effects on Stem Morphology (PC3) were associated with any main effect. The Reproductive Potential component was significantly different across blocks (χ^2 = 5.39, df = 1, p = .020). The root-to-shoot ratio of *Schoenoplectus* was significantly impacted by the organic treatment ($F_{1,30}$ = 17.289, p<.001), the interaction between organic content and salinity ($F_{1,30}$ = 4.769, p=.037, Figure 3.3), and the three-way interaction between competition, organic content, and nitrogen ($F_{1,30}$ = 4.543, p=.041, Figure 3.4).

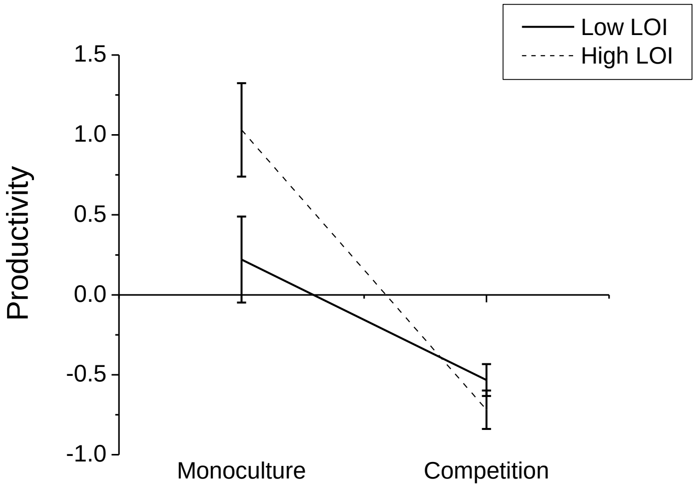

Figure 3.1: Interaction between the competition and organic content treatments on the first principal component (Productivity) for *Schoenoplectus*. Error bars indicate 95% confidence intervals.

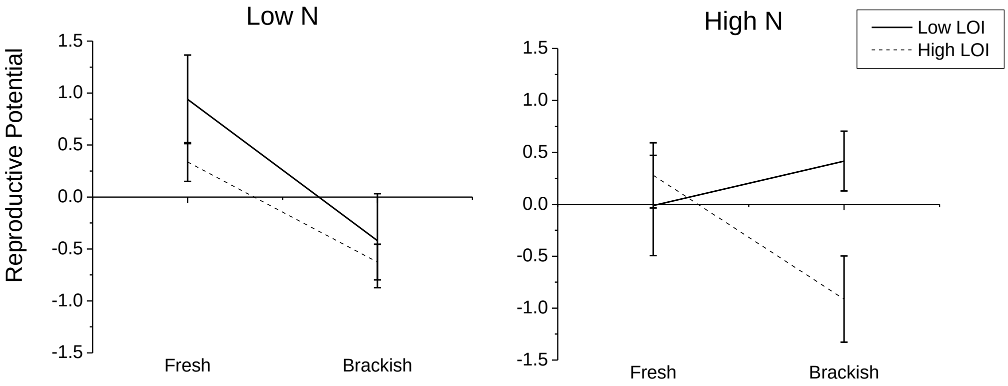

Figure 3.2: Interaction between the salinity, nitrogen, and organic content treatments on the second principal component (Reproductive Potential) for *Schoenoplectus*. Error bars indicate 95% confidence intervals.

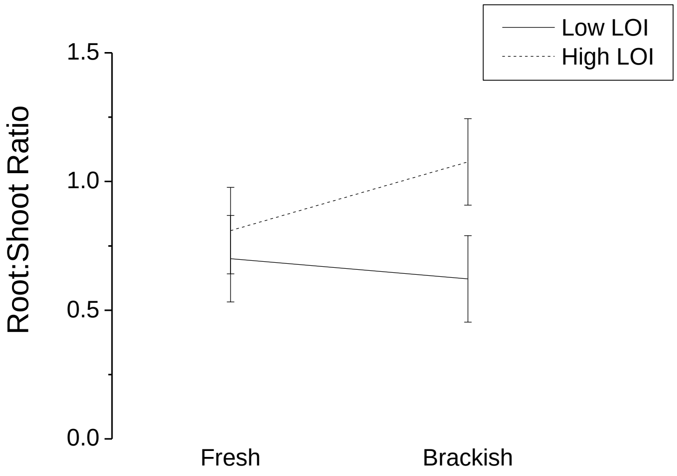

Figure 3.3: Interaction between the salinity and organic content treatments on the root-to-shoot ratio of *Schoenoplectus*. Error bars indicate 95% confidence intervals.

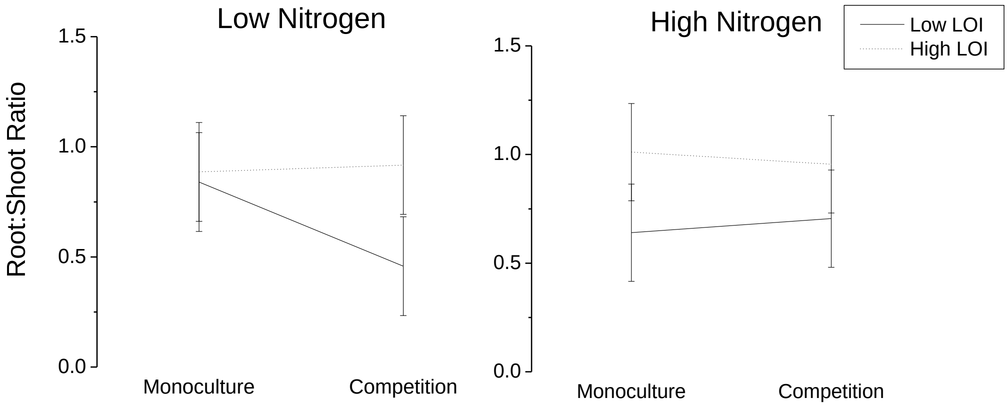

Figure 3.4: Interaction between the competition, nitrogen, and organic content treatments on the root-to-shoot ratio of *Schoenoplectus*.

Phragmites: Productivity (PC1) was significantly affected by the main effects of competition ($F_{1,28.121}$ = 62.374, p<.001) and nitrogen ($F_{1,27.814}$ = 20.036, p<.001). The interaction between competition and nitrogen significantly affected Productivity ($F_{1,27.814}$ = 16.410, p<.001, Figure 3.5), as did the four-way interaction between competition, nitrogen, salinity, and organic content ($F_{1,27.814}$ = 5.542, p=.026). No significant effects on Stem Morphology (PC2) were associated with any main effect, but this parameter did significantly differ across blocks (χ^2 = 13.40, df = 1, p < .001). The root-to-shoot ratio of *Phragmites* was significantly affected by competition ($F_{1,32}$ = 4.322, p=.046), nitrogen (F1,32 = .012), the interaction between competition and nitrogen ($F_{1,32}$ = 5.564, p=.025, Figure 3.6), and the three-way interaction between competition, nitrogen, and salinity ($F_{1,32}$ = 6.632, p=.015, Figure 3.7).

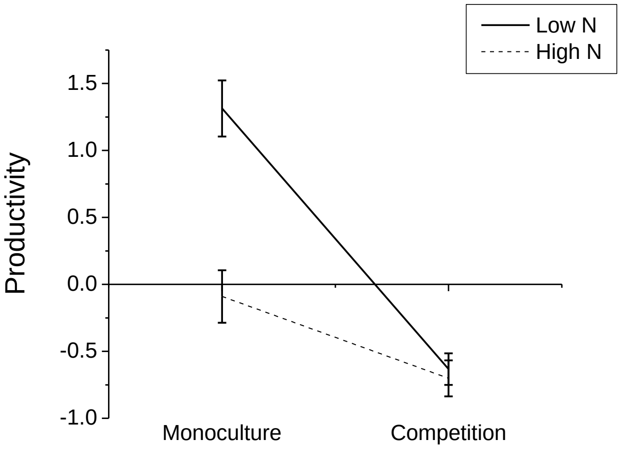

Figure 3.5: Interaction between the competition and nitrogen treatments on the first principal component (Productivity) for *Phragmites*. Error bars indicate 95% confidence intervals.

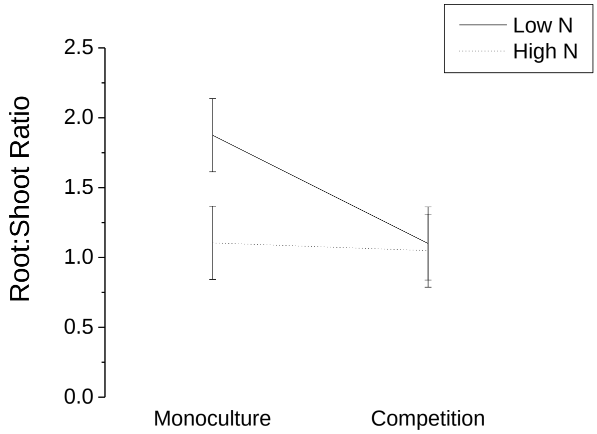

Figure 3.6: Interaction between the competition and nitrogen treatments on the root-to-shoot ratio for *Phragmites.* Error bars indicate 95% confidence intervals.

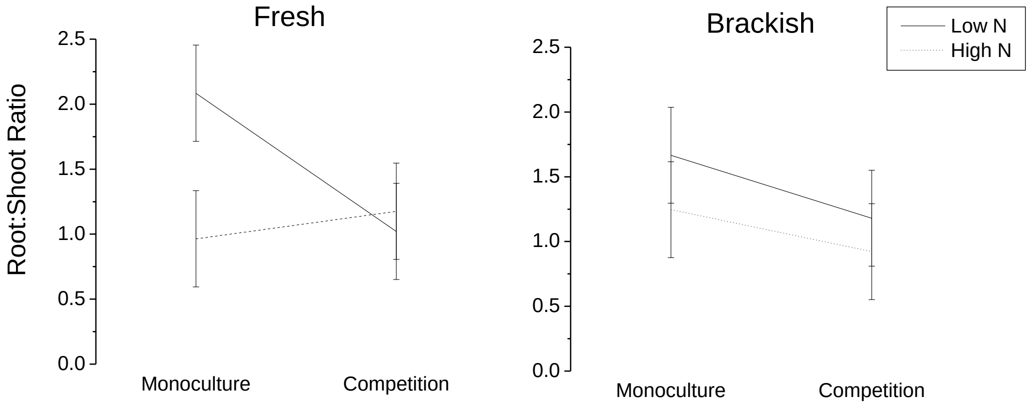

Figure 3.7: Interaction between the competition, nitrogen, and salinity treatments on the root-to-shoot ratio for *Phragmites.* Error bars indicate 95% confidence intervals.

Discussion

Our initial hypotheses predicted that the nitrogen, salinity, and organic matter treatments would affect the competitive abilities of each species. Instead, we observed significant treatment effects when plants were grown in monoculture, but not under competition. Additionally, there were no cases of complete competitive exclusion. The main result of this study, therefore, is that competition was generally a more important factor than the abiotic stressors in limiting both species. While plant performance scores were decreased by stressors in monoculture, the competition treatment consistently produced lower scores than monoculture regardless of other treatment levels. This is not an unprecedented outcome. In a greenhouse experiment that subjected either monocultures or mixtures of three freshwater marsh species to four salinity levels, the monocultures responded strongly to salinity as a function of each species' salt tolerance (La Peyre et al 2001). However, while the community composition of the mixture shifted towards the most salt-tolerant species at higher salinities, the suppressive effect of competition was greater than – and independent of – the salinity gradient (La Peyre et al 2001).

Contrary to the nitrogen hypothesis, excess nitrogen negatively affected *Phragmites* productivity, although it did reduce root-to-shoot ratio as expected (Figure 3.6). We suspect the detrimental effect of nitrogen on *Phragmites* productivity to be a consequence of nitrogen overdose. Urea-based fertilizer delivers organic nitrogen to the soil where it must be mineralized and nitrified before the nutrient can be assimilated by vegetation, hence its marketing as a time-release formula. However, *Phragmites* has been shown to directly uptake organic nitrogen molecules, including urea (Mozdzer et al

2010), while no studies have reported this phenomenon in any species of *Schoenoplectus*. Under such eutrophic conditions, *Phragmites* has been reported to exhibit stem loss, decreased sclerenchyma production resulting in structural weakening of tissue, and decreased root-to-shoot ratio (Engloner 2009).

As expected, *Schoenoplectus* was negatively affected by salinity in terms of its ability to produce flowers and grow tall, but it unexpectedly increased its root-to-shoot ratio in brackish water. In accordance with the organic soil hypothesis, *Schoenoplectus* was inhibited in low-organic soils while *Phragmites* did not differ based on soil organic content. Many of these effects were conditional on other treatment levels. For example, *Schoenoplectus* reproduction was sensitive to brackish water only when nitrogen and organic content were high. *Schoenoplectus* was able to allocate biomass belowground only when organic matter was high and thus soil density was low. The nitrogen effect on *Phragmites* root-to-shoot ratio was only significant in freshwater – in brackish water the ratio was low regardless of nitrogen level.

Wetland restoration projects should provide ecosystem services comparable to a naturally formed wetland (LACPRA 2017), and should remain sustainable after construction (Young et al 2005). While our study of a single mixture of two species does not necessarily reflect the dynamics of every possible competitive scenario in a species-rich marsh, the competitive “stalemate” observed between *Schoenoplectus* and *Phragmites* implies that at the densities tested here, one species cannot fully eliminate the other under any of the abiotic conditions tested here. Important ecosystem services are associated with both species. *Schoenoplectus* seeds and rhizomes are a high-quality food source for birds (Hohman et al 1990). *Phragmites* can provide habitat and food for herbivores, and is capable of removing toxic heavy metals from the environment (Kiviat 2013). Both species produce dense networks of belowground biomass that can contribute both bulk material and physical cohesion to marsh soils (Nyman et al 2006, Tal and Paola 2007). However, it is possible that *Phragmites* could quickly establish in a new marsh and prevent colonization by *Schoenoplectus. Phragmites* can quickly establish and become dominant following a canopy-gap disturbance (Zedler and Kercher 2004), while *Schoenoplectus* requires three growing seasons of belowground proliferation before it becomes dominant (White 1993). Additionally, the detrimental effect of low organic content on *Schoenoplectus* and not *Phragmites* could affect the relative abundance of each species in areas of the delta exposed to higher-velocity currents. In such a situation, the lighter organic material and fine-grained sediments would be exported while leaving behind heavy mineral sand particles. While this did not affect competitive outcome, it is plausible that under these conditions a *Phragmites* monoculture could colonize a greater area than a *Schoenoplectus* monoculture in a given growing season.

Because plant roots increase soil cohesion and resist erosion (Tal and Paola 2007), our results concerning root-to-shoot ratios are relevant to the sustainability of a wetland restoration project. As was the case with *Phragmites* in this experiment, excessive nitrogen inputs have been reported to decrease root-to-shoot ratios in wetland vegetation (Darby and Turner 2008). The introduction of nitrogen-polluted Mississippi River water into the marshes of Breton Sound, LA has been argued to be responsible for the weakening of grass roots, creating a marsh platform with less cohesion and increased vulnerability to the erosive forces of Hurricane Katrina in 2005 (Howes et al 2010, Kearney et al 2011).

In the West Bay area of the MRD, wetland soils dominated by *Phragmites* had lower shear strengths – and thus greater susceptibility to erosion – than those dominated by *Schoenoplectus* (see Chapter 2). *Schoenoplectus* root production, therefore, may be of particular interest to restoration efforts of systems vulnerable to erosion-driven land loss. The observed increase in root-to-shoot ratio of *Schoenoplectus* under brackish conditions is concurrent with previous research. The salt-tolerant sedge *Schoenoplectus triqueter* responds to salinity stress by thickening root epidermis, cortex, and vascular tissue to conserve water, as well as increasing aerenchyma area to increase gas exchange and ion sequestration (Batool & Hameed 2013). *Schoenoplectus americanus*, a close relative of *S. deltarum* capable of hybridization (Shiels et al 2014), increases the belowground production at the expense of aboveground biomass under brackish conditions (Cherry et al 2009). It is possible that *Schoenoplectus deltarum* reallocates biomass in a similar fashion at the expense of flower production. However, the brackish root-to-shoot increase was only observed when organic content was high. Productivity of *Schoenoplectus californicus* has been shown to be suppressed in soils with high bulk densities (Hester et al 2016), as would be the case when organic content is very low.

The proposed operation strategy involves opening the diversions during winter high-water events and the rising limb of the spring flood (Peyronnin et al 2017). This would effectively capture enough mineral sediment to build new marshes while restricting nutrient input from the river and freshwater flushing of obligate saltwater species such as oysters and shrimp (Peyronnin et al 2017). In the context of this study's results, this strategy would minimize the loss of *Phragmites* root-to-shoot ratio resulting from eutrophication, while exploiting the increased belowground allocation of *Schoenoplectus* in response to brackish water exposure.

The relationship between competition and abiotic stress has been argued as being either inverse (Grime 1973) or positive (Wiens 1977). This study closely parallels La Peyre et al's (2001) observation that competition can be independent and more influential on plant growth under the range of conditions tested. The significant interactions among abiotic treatment levels suggest that a variation in one environmental parameter could cause another to become the limiting factor. This supports the theories of multidimensional niche space (Silvertown 2004) and the dependence of community dynamics on limiting resource ratios (Tilman 1986). Factorial additive pairwise studies can complement the modeling of physical environmental conditions to predict trends in community compositions in dynamic environments.

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Appendix 1: Supplementary Tables and Figures for Chapter 1

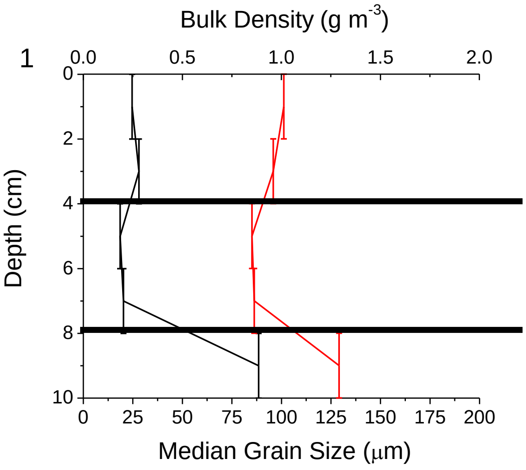
Vegetation Type			**Relative Abundance (%)**				
			Seed Bank Layers			Aboveground	
Genus	Common Name	Present in WB	Flood	Emergent	Surface	2014	2015
Heliotropium	Heliotrope	No	70.5	52.3	49.2	0	0
Schoenoplectus	Bulrush	Yes	13.9	6.7	2.4	49.8	55.6
Amaranthus	Amaranth	Yes	3.6	10.9	35.6	0	0
Juncus	Rush	No	2.0	2.4	0.2	0	0
Potamogeton	Pondweed	Yes	1.8	4.7	3.6	24.8	0
Echinodorus	Burhead	No	1.7	1.1	0.3	0	0
Phragmites	Common reed	Yes	1.4	4.4	1.9	7.2	11.0
Polygonum	Knotweed	Yes	0.8	1.6	0.2	0	0
Typha	Cattail	Yes	0.7	4.8	0	5.7	12.1
Hydrocotyle	Marshpennywort	Yes	0.5	0.4	0.2	0	0
Ludwigia	Primrose-willow	Yes	0.5	2.0	0.6	0	0
Paspalum	Crowngrass	Yes	0.5	2.2	0.6	0	0
Sagittaria	Arrowhead	Yes	0.5	0.8	1.1	0.4	15.7
Panicum	Maidencane	No	0.4	0.5	0	0	0
Cyperus	Flatsedge	Yes	0.3	1.3	0.2	0	0.2
Najas	Waternymph	No	0.2	0.1	0	0	0
Portulaca	Purslane	No	0.2	0.1	0	0	0
Rumex	Dock	No	0.2	0.3	0.1	0	0
Ipomoea	Morning-glory	Yes	0.1	0.3	0.1	0	0
Lonicera	Honeysuckle	No	0.1	0.1	0	0	0
Morella	Waxmyrtle	No	0.1	0	0	0	0
Myriophyllum	Watermilfoil	Yes	0.1	0.4	0.2	0	0
Rhynchospora	Beaksedge	Yes	0.1	0.1	0.1	0	0
Alternathera	Alligator weed	Yes	0	0	0	7.5	4.7
Aster	Aster	No	0	0.1	1.5	0	0
Bidens	Beggartick	No	0	0.1	0.9	0	0
Brasenia	Watershield	Yes	0	0.1	0.4	0	0
Centella	Centella	No	0	0.5	0.2	0	0
Chenopodium	Goosefoot	No	0	0	0.2	0	0
Cladium	Sawgrass	No	0	0.3	0.1	0	0

(Table continues from previous page)

Vegetation Type			**Relative Abundance (%)**				
			Seed Bank Layers			Aboveground	
Genus	Common Name	Present in WB	Flood	Emergent	Surface	2014	2015
Eichhornia	Water hyacinth	Yes	0	0	0.1	0	0
Eleocharis	Spikerush	Yes	0	0.1	0	0	0
Fimbristylis	Fimbry	No	0	0.3	0	0	0
Iva	Marsh elder	Yes	0	0	0.1	0	0
Ruppia	Widgeonweed	Yes	0	0.4	0.1	3.1	0
Zizaniopsis	Cutgrass	Yes	0	0.5	0	1.5	0.8

Table A1.1: Abundance data for all genera collected/observed in this study, both belowground and aboveground, sorted by relative abundance in the flood layer

1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Median Grain Size (µm)

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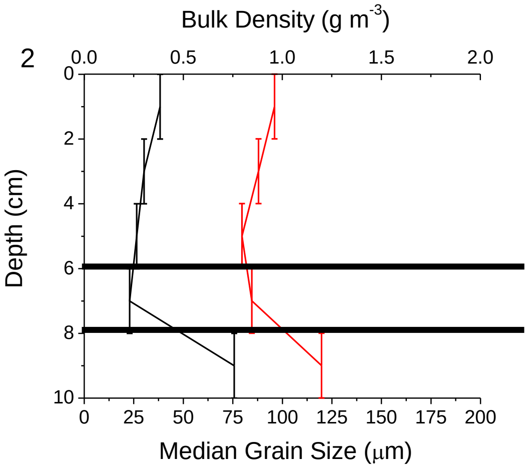
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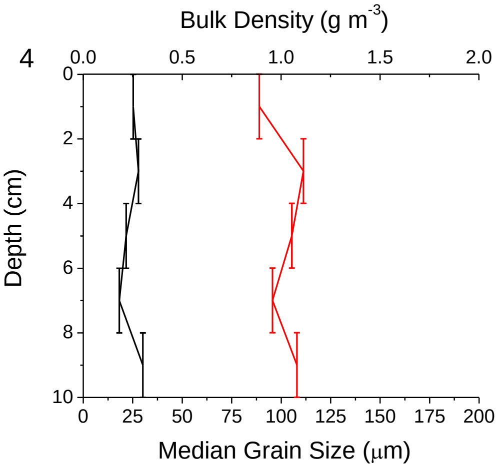
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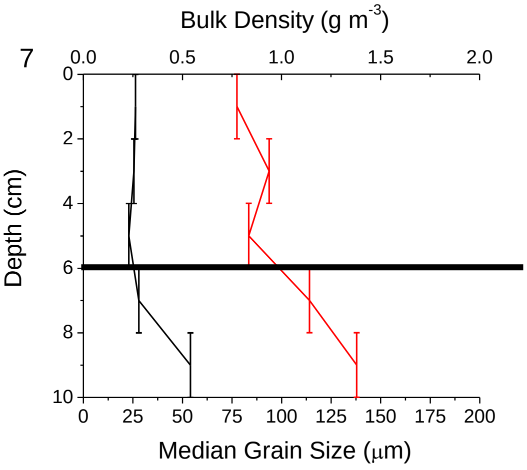
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Median Grain Size (µm)

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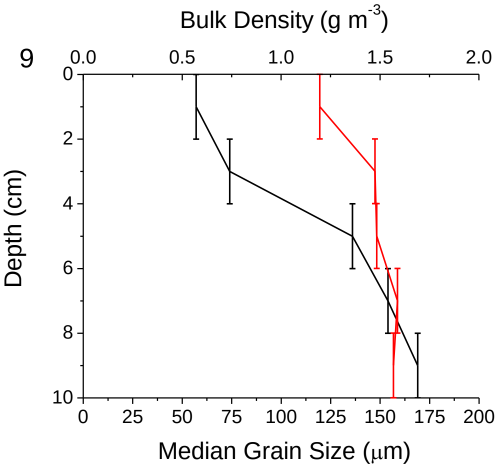
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Median Grain Size (µm)

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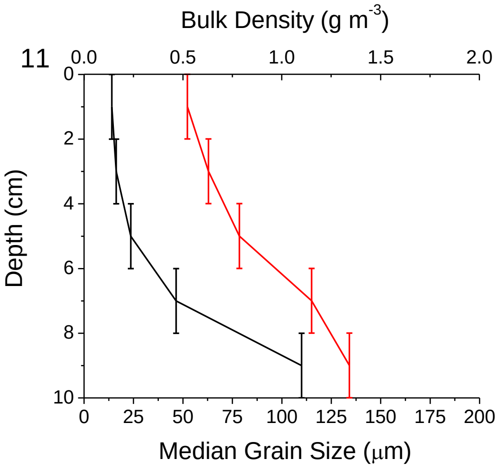
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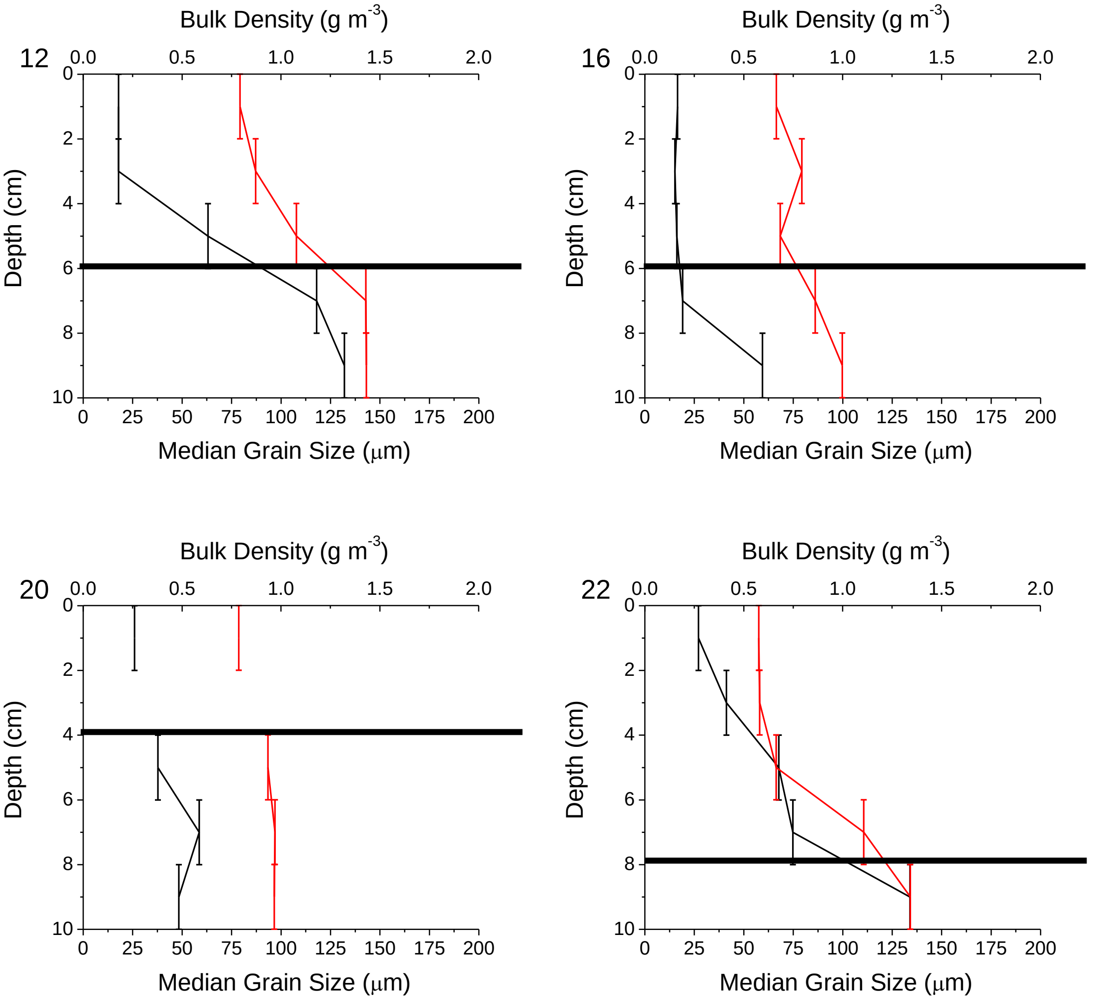

Figure A1.1: Geotechnical profiles of all cores; core ID is noted in the upper left corner of each graph. Median grain size (μm) is denoted in black, bulk density (g cm^{-3}) is denoted in red. The horizontal line denotes the boundary between the flood (below) and emergent (above) layers. Note that the flood layer is not captured in core 4.

Appendix 2: Supplementary Tables for Chapter 2

Species	**Common name**	**Growth Habit**	**Relative Abundance (%)**
Phragmites australis	Common reed	Graminoid	33.70
Schoenoplectus validus	Softstem bulrush	Graminoid	10.02
Nelumbo lutea	American lotus	Aquatic	8.82
Typha spp.	Cattail	Forb	8.55
Schoenoplectus deltarum	Delta bulrush	Graminoid	5.95
Potamogeton epihydrous	Ribbonleaf pondweed	Aquatic	5.26
Distichlis spicata	Saltgrass	Graminoid	5.12
Sagittaria lancifolia	Bulltongue	Forb	4.41
Zizaniopsis miliacea	Giant cutgrass	Graminoid	4.07
Spartina alterniflora	Smooth cordgrass	Graminoid	3.22
Salix nigra	Black willow	Woody	2.56
Digitaria spp.	Crabgrass	Graminoid	2.56
Eleocharis spp.	Spikerush	Graminoid	1.93
Colocasia esculenta	Elephant ear	Forb	1.14
Polygonum punctatum	Dotted smartweed	Forb	0.80
Alternanthera philoxeroides	Alligator weed	Forb	0.57
Amaranthus australis	Southern amaranth	Woody	0.51
Cyperus spp.	Flatsedge	Graminoid	0.26
Symphyotrichum subulatum	Saltmarsh aster	Forb	0.17
Sesbania spp.	Sesbania	Woody	0.14
Ludwigia leptocarpa	Primrose willow	Forb	0.14
Pluchea camphorata	Camphor weed	Forb	0.09
Hydrocotyle spp.	Pennywort	Forb	0.01

Table A2.1: Relative abundance of all plant species observed during the bay-wide survey, calculated as the proportion of total plant cover represented by each species

Species	**Common name**	**Growth Habit**	**Relative Abundance (%)**
Schoenoplectus validus	Softstem bulrush	Graminoid	29.97
Phragmites australis	Common reed	Graminoid	23.56
Salix nigra	Black willow	Woody	21.29
Typha spp.	Cattail	Forb	15.64
Sagittaria lancifolia	Bulltongue	Forb	4.35
Schoenoplectus deltarum	Delta bulrush	Graminoid	4.02
Cyperus spp.	Flatsedge	Graminoid	0.49
Zizaniopsis miliacea	Giant cutgrass	Graminoid	0.37
Ammania coccinea	Valley redstem	Woody	0.29
Alternanthera philoxeroides	Alligator weed	Forb	0.03

Table A2.2: Relative abundance of all plant species observed during the emergent island survey, calculated as the proportion of total aboveground dry biomass represented by each species

Biography

Alexander Ameen was born and raised in Wanaque, NJ and attended Lakeland Regional High School. He received a Bachelor of Science in Environmental Sciences from the University of Virginia in 2010. He then moved to Cocodrie, LA to work for the Louisiana Universities Marine Consortium, where he became aware of the wetland loss crisis facing the state's coast. In order to further pursue this topic, he enrolled in Tulane University's Ph.D. program in Ecology and Evolutionary Biology, where he studied under Caz Taylor and Alexander Kolker. He received his Ph.D. in 2017 and plans to continue a career in the conservation and restoration of South Louisiana's wetland resources.