

**Patterns of Plant Community Development in a Created and a Natural
Salt Marsh on the Gulf Coast of Louisiana, USA**

**Final Report Submitted to:
Garden Club of America
&
Virginia Institute of Marine Sciences**

By

**Tracy Elsey*
Masters Program
Ecology and Environmental Science
Biology Department
University of Louisiana Lafayette
&
National Wetlands Research Center
700 Cajundome Blvd
Lafayette, Louisiana 70506**

***Current address: College of Marine Studies
University of Delaware
700 Pilottown Road
Lewes, DE 19958**

CHAPTER 1

Seed Dispersal in a Created and Natural Salt Marsh Along the Gulf Coast of Louisiana, USA

INTRODUCTION

Seed dispersal is critical to the establishment and to the ultimate distribution patterns of species in created salt marshes. Similarly, in natural salt marshes, the availability of seeds influences plant distribution patterns in the wetland (Aguiar and Sala 1997, Rand 2000). Species distributions and zonation patterns in salt marshes are largely influenced by physical factors such as tidal inundation in the low marsh and biotic interactions such as interspecific facilitation and competition in the high marsh (Bertness and Ellison 1987, Bertness 1991). In a created marsh, which is developing its zonation patterns of plant communities, the dispersal of seeds may also influence species diversity and the succession processes that determine successful restoration. Therefore, studying the availability and distribution of seeds within a created salt marsh can allow for predictions about potential and future plant communities, depending on the environment of the wetland, and its ability to support those species dispersing to the site (Primack and Miao 1992, van der Valk 1992, Rand 2000).

In salt marshes, there are many factors influencing the distribution of seeds, including elevation, tidal currents (Huiskies et al. 1995), and the presence of adult plants (Rand 2000). While these dynamics have not been well studied on the northern Gulf of Mexico coast, understanding seed dispersal and distribution patterns in gulf coast marshes is important for enhancing coastal restoration efforts there. Along the northern gulf coast, wetlands are being lost at catastrophic rates because of hurricane damage,

subsidence, reduced sediment load from the Mississippi River, canal construction for gas and oil development (Turner et al. 1997), and sea-level-rise related to global climate change (Salinas et al. 1986). While northern gulf coast wetlands cover approximately 3.2 million hectares, representing 41% of the United States' coastal wetlands (Salinas et al. 1986), approximately 1,900 square miles have been lost since 1930 (Louisiana Department of Natural Resources 2003); much of this loss was coastal marsh habitat.

The loss of coastal marshes potentially can be offset by creating salt marshes using dredged sediments from shipping channels (Proffitt and Young 1998). Created salt marshes on the gulf coast can be large and the colonization of vegetation may be limited by lack of long distance seed dispersal. For example, a marsh created in 1993 in Calcasieu Lake Estuary in southwest Louisiana is approximately 200 ha in size (Proffitt and Young 1998). Large areas of dredge sediment are occasionally deposited at inappropriate elevations that may also hinder the movement of water-dispersed species (Connell & Keough 1985, Sousa 1985, Levin et al. 1996, Proffitt et al. 2003). In addition, the distribution of seeds at long distances from the edge may be limited by long distance dispersal if water movement is hindered (Middleton 1999). In the Netherlands, a majority of salt marsh seeds dispersing into a coastal salt marsh were concentrated at the edge of the marsh (Mineke & Bakker 2002). While deposition patterns such as this may be true for gulf coast marshes, the phenomenon has not been documented.

In many coastal salt marshes, the degree and frequency of tidal flooding decreases with increasing distance from the marsh edge and elevation (Brewer et al. 1997). In expansive gulf coast marshes, this relationship may not hold because a positive linear relationship between distance from the marsh edge and elevation does not always exist

(Edwards and Proffitt 2003). Therefore, the level of tidal flooding may not correlate with distance. In addition, gulf coast marshes have relatively minor tidal fluctuations where tides range approximately 1-2 feet from low to high tide (NOAA 2003). Elevation variability and low tidal flooding as distance increases from the marsh edge may influence the seed dispersal and distribution patterns in gulf coast salt marshes and may have important implications for appropriate salt marsh creation.

While tidal fluctuation is an important dispersal vector in salt marshes, seed dispersal by gravity, also known as seed rain, is important for localized dispersal (Rand 2000). Localized dispersal via gravity results in a strong correlation between the spatial distribution of seeds and adult plant populations in natural salt marshes (Bertness et al. 1992, Bertness and Yeh 1994, Rand 2000), but it is not known whether this positive relationship between adult plants and seed dispersal will also be true for created salt marshes, particularly since the opportunities for seed dispersal and establishment may be reduced in created marshes.

The objective of this study was to determine whether seed dispersal of species in a high and a low elevation area of a created salt marsh differed from a natural salt marsh. The hypothesis was tested that seed density of salt marsh species in a high elevation and low elevation area of a created marsh, and a natural reference salt marsh differed due to differences along a distance gradient from the marsh edge, in water levels, and in the proximity to adult plant populations.

METHODS

Study Site

This study was conducted on a large created dredge sediment marsh and a nearby natural reference marsh in Sabine National Wildlife Refuge in southwest Louisiana from August to January 2004. This area has expansive stretches of coastal marsh that have converted to open water in some areas due primarily to the role of the adjacent Calcasieu Ship Channel, which allows salt water intrusion from the Gulf of Mexico, 26 km south. To offset marsh loss, starting in 1983, the Army Corps of Engineers along with the Sabine National Wildlife Refuge have created marshes with dredge material from the maintenance dredging of the Calcasieu Ship Channel (Edwards and Proffitt 2003).

The dredge sediment marsh that was chosen for this study was created in 1999 and is located between a natural salt marsh to the north and a constructed water channel to the south. A non-continuous levee surrounds the created marsh and consequently, flooding may be more infrequent than in a natural tidal salt marsh and may occur primarily during storm events when the breaks in the levee allow for storm surge or wind driven flooding. The two breaks in the levee are located on the northern lower elevation area of the created marsh, allowing for more tidal flooding in the northern portion of the marsh. Also, the dredge sediment used to construct the marsh was deposited in such a way that the south end had a higher elevation than the north end, further allowing for more extensive tidal inundation in the north of the created marsh than in the south. The elevation difference between these two parts of the created marsh maintain distinct spatial and environmental differences so that the “low created” and “high created” marshes were designated as two different created marsh types for this study. A nearby natural reference

marsh was chosen for study that is bordered on the east by West Cove, a large brackish to salt water bay that opens to the Calcasieu Ship Channel, while the rest of the marsh is surrounded by contiguous salt marsh habitat (Figure 1.1).

Five years after marsh creation, the vegetation in the low-elevation area was predominantly *Spartina alterniflora*, while in the higher-elevation area, higher marsh species such as *Distichlis spicata*, *Baccharis halimifolia* and *Iva frutescens* had colonized. The reference marsh was historically a brackish sedge marsh dominated by *Schoenoplectus robustus* but has converted to salt marsh dominated by species such as *Spartina alterniflora*, *Distichlis spicata*, and *Spartina patens* with remnant patches of *Schoenoplectus robustus* (LDNR 1999). The edge of the natural marsh had predominantly higher marsh vegetation and as the distance into the marsh increased, the vegetation shifted to low marsh species as marsh elevation decreased and subsequently increased in water inundation (Figures 1.2).

Seed Dispersal

To determine whether seed dispersal was limited by distance from the marsh edge, ten transects were established in the created marsh, five from the northern low elevation edge and five from the southern high elevation edge. Along each transect, plots were established at four distances of 0, 10, 75, and 150 meters from the edge of the marsh and a set of seed traps were placed at each plot. Five replicate transects with sets of seed traps were established from the eastern edge of the natural marsh.

A set of seed traps consisted of an aquatic and a gravity seed trap made from portions of a 5 gallon plastic bucket (Middleton 1995). The aquatic trap was the top half of a bucket with a cloth liner that was attached by the rim of the lid to allow entry and

capture of seeds. The aquatic trap was placed on its side and had two 2 liter plastic bottles attached to the sides for flotation. The horizontal trapping surface of the aquatic seed trap had an area of 27 cm². The gravity trap was the bottom half of the bucket attached to Styrofoam © for flotation and weighted down with scrap metal attached with fishing line. Gravity traps were set upright for the capture of seed dispersing via wind or seed rain. Seeds that fell into the gravity trap attached to aluminum foil coated with Tanglefoot Pest Barrier™. Gravity traps had a 27 cm diameter (see Middleton 1995 for complete description and diagram).

Seed traps were placed in the marsh in mid-August, prior to seed set of any salt marsh species that had colonized the created marsh. The first seeds were collected on October 7, 2004 at the beginning of the seed fall season. Seeds were collected from traps once every other week thereafter until December 12, 2004 when there were too few seeds to warrant the effort of collection. All seed traps had equal sampling intensity throughout the sampling period.

Seeds were counted and sorted by species in the lab. Seed numbers greater than 200 per trap in gravity traps were estimated by counting seeds within a subsample area of the trapping surface and multiplying to estimate seed numbers. Aquatic traps were sampled by collecting contents in Ziplock© bags to be processed in the lab. Contents of Ziplock© bags were emptied into an 88 micron sieve (U.S. Standard Sieve Series No. 170). If seeds of any species were greater than 100 seeds per aquatic trap, then seeds were dried, ten replicate subsamples of 10 seeds were weighed and the total seed abundance was estimated by dividing the estimated weight of one seed by the total weight of the seed sample captured in the trap.

Aboveground Vegetation and Water Level Estimations

In the summer of 2004, the vegetation cover was estimated within a 1 m² quadrat at each seed trap to determine the influence of existing species on seeds caught in seed traps. For each species present in the plots, percent cover categories used were 0-5, 5-25, 25-50, 50-75, 75-95, 95-100 using a modified Daubemire method (Brower et al. 1998). In total, there were four replicate distances along five replicate transects within each of the three marsh sites surveyed for vegetative cover.

Water levels were recorded at each set of seed traps, along distance transects in each marsh type, during each biweekly seed collection. Water levels were recorded from the same location at each distance every sampling period using a meter stick. For comparison, water level data were also obtained from a nearby water level recorder NAVD88 Datum maintained by the Louisiana Department of Natural Resources (Ehab Meselhe, unpublished data).

STATISTICAL ANALYSES

Seed Dispersal

The number of seeds captured in seed traps was converted to seed density m⁻² by multiplying 17.5 for gravity traps and 13.7 for aquatic traps (Middleton 1995). All statistical analyses were conducted using SAS V8 (SAS Institute, Inc. 2003). Seeds in both trap types at each sample point were combined to determine spatial differences in seeds caught at distances into the different marsh types by the predominant mechanisms of dispersal in salt marshes (water, wind, and gravity). Only species that were captured more than once in more than one marsh were included in the analysis. Separate analyses

were conducted by species because each species was assumed to disperse their seeds independently of the other species. The main effect of marsh type (low created, high created, and natural reference) was tested as well as any interactions with covariates of distance from the marsh edge, percent cover of adult plants, and mean water level using analysis of covariance. Percent cover ranges were converted to the midpoint of each cover class, converted into proportions and arcsine square root transformed prior to statistical analysis. Log transformations on the number of seeds captured and distance were necessary to meet the assumptions of analysis of covariance. If distance, percent cover, or water level was not a significant covarying factor, it was dropped from the analysis and the analysis was performed again without insignificant terms in the model (Table 1). If a covariate had a significant affect on seed density, linear regression analyses was used to determine the percent of variation in seed density that the covariate explained (r^2 value).

RESULTS

Water level and elevation

Water level measurements revealed differences in water levels along a distance gradient over time among the three marsh types (Figures 1.2). The edge of the high created marsh was always inundated with water. As distance from the marsh edge increased, the elevation increased so that the water levels were lower in the south created marsh than in either of the other two marshes. In the low created marsh, water level was higher either the natural or high created marshes along the distance gradient. As the distance approached 150 meters from the edge of the low created marsh, the water level

declined so that at this distance it was lower than the natural marsh. The natural marsh was highest in elevation at the edge where there was constant erosion and deposition of sediments from the wave action of West Cove. As the distance into the natural marsh increased, the water level increased.

Water levels over time during the study period in each of the three marsh types also illustrated differences in water level fluctuation dynamics among the three marsh types (Figure 1.3).

Seed Dispersal

The seeds of eight species were collected in the seed traps, including *Aster subulatus*, *Amaranthus hybridus*, *Spartina alterniflora*, *Distichlis spicata*, *Iva frutescens*, *Baccharis halimifolia*, *Schoenoplectus robustus*, and *Spartina patens*. Three species were excluded from statistical analyses because of low seed numbers. For example, thirteen seeds of *Spartina patens* were collected in the low created marsh, but no seeds of this species were collected in other marshes. While 26 seeds of *Schoenoplectus robustus* were found in the natural marsh, only 1 seed was captured in the low created marsh. *Baccharis halmifolia* had a total of 10094 seeds captured in the high created marsh, while only 13 seeds were caught in one seed trap the natural marsh.

Of the five species included in the analyses, seed density varied among marshes along a distance gradient for one species, *Aster subulatus* (marsh*distance, $F_{2,53} = 7.21$, $P = 0.0017$). As distance from the edge of the marsh increased, seed density of *A. subulatus* varied depending on marsh type. For example, as distance increased from 0 to 10 meters from the edge, seed density increased in the high created marsh but decreased in both the low created and natural marshes (Figure 1.4). From 10 to 75 meters into the

marsh, seed density increased in all three marsh types and continued to increase from 75 to 150 meters in both the low created and natural marshes but declined from 75 to 150 meters in the high created marsh.

Aster subulatus had the greatest number of seeds m^{-2} of the five species, with over ninety-nine percent of the seeds captured in the high created marsh (Table 1.2). Across all three marsh types, the density of *A. subulatus* seeds increased with increasing percentage of adult *A. subulatus* plant cover ($F_{1,53} = 7.38$, $P = 0.0089$) (Figure 1.5). Plant cover explained 39% of the variation in *A. subulatus* seed density ($r^2 = 0.39$).

Spartina alterniflora seeds were the second most abundant, with approximately 130,575 seeds m^{-2} (Table 1.2). The only effect that influenced the variation in *S. alterniflora* seed density was marsh type ($F_{2,57} = 10.49$, $P = 0.0001$). The low created marsh had a significantly higher number of seeds than either the high created ($P = 0.0001$) or the natural ($P = 0.0045$) marsh types (Figure 1.6).

Seed density of *A. hybridus* also varied by marsh ($F_{2,55} = 8.03$, $P = 0.0009$) but was highest in the high created marsh, where 56.2% of the seeds were captured (high created vs. low created, $P = 0.0190$ and high created vs. natural, $P = 0.0007$) (Figure 1.6). *Amaranthus hybridus* seed density was also influenced by cover of adult plants ($F_{1,55} = 4.44$, $P = 0.0397$), as the seed density increased with cover of adult plants (Figure 1.5). Cover of adult plants explained 18% of the variation in seed density of *A. hybridus* ($r^2 = 0.1781$).

Another determinant of the variation in *A. hybridus* seed density was water level ($F_{1,55} = 6.22$, $P = 0.0156$), where the majority of seeds were found at water levels of less than 10 cm. Water level explained 10% of the variation in seed density of *A. hybridus*.

Seed density of *I. frutescens* varied by marsh ($F_{2,56} = 4.26$, $P = 0.0189$). Although ninety-nine percent of *I. frutescens* seeds were captured in the high created marsh, it did not differ from the north created marsh, but did vary in seed density from the natural marsh where no seeds were caught ($P = 0.0165$) (Figure 1.6). Seed density was largely influenced by the cover of adult *I. frutescens* plants ($F_{1,56} = 43.48$, $P < 0.0001$), whereby seed density increased with adult cover that explain 51% of the variation in seed density ($r^2 = 0.5100$) (Figure 1.5).

DISCUSSION

In a recently created salt marsh and a natural salt marsh, the most widespread determinant of seed density among the species was localized dispersal. Seeds of both annual and perennial species were found dispersing in both the created and natural salt marshes and for four out of five species in this study seed density increased with local cover of adult conspecifics.

The phenomenon of localized seed dispersal is also true for natural salt marshes in New England where seed deposition patterns paralleled the distribution patterns of adult individuals (Rand 2000), and this is also true for desert, forest and tundra ecosystems (Chambers and MacMahon 1994). Localized dispersal limited species distributions in a woodland in Massachusetts, where four annual plant species were limited in their range and distribution by localized dispersal (Primack and Miao 1991).

Differences among the marshes also determined seed density of species. The natural marsh had relatively low seed densities, which may be due to the older age of the plant populations that may have lower seed production. However, the relationship of

seed densities to adult plant abundance for the majority of species in the present study suggest that the differences in seed densities among marshes are related to the species that have established depending on specific in flooding dynamics. In natural salt marshes in New England, the distributions of many species are influenced by elevation and subsequent tidal dynamics (Brewer et al. 1997). For example, *S. alterniflora* is dominant in the low marsh where it can tolerate the stresses of tidal inundation and fluctuation. While other species are associated with the higher elevation zones with less tidal influence but higher interspecific competition, such as *D. spicata* and *I. frutescens* (Bertness and Ellison 1987, Bertness 1991, Bertness et al. 1992). Adult plants that have established in the created salt marsh on the gulf coast have distributions that were also associated with specific elevations and the regeneration dynamics of localized seed dispersal seemed to be reinforcing species distributions to certain elevation ranges. *Spartina alterniflora*, for example, had the highest seed densities in the lower elevations of the created marsh where there was more tidal flooding, while *Amaranthus hybridus* and *I. frutescens* had the highest seed densities in the high elevation, drier areas of the created and reference marshes. High marsh species' such as *Iva frutescens*, survival and regeneration in the high elevation areas of the created marsh may have been facilitated by its competitive abilities in the high marsh (Bertness et al. 1992), the availability of unoccupied habitat (Bertness and Yeh 1994) and also to the facilitation by species such as *D. spicata* and *S. alterniflora*, that alleviated high soil salinities (Egerova et al. 2003).

For successful restoration of ecosystems that are largely influenced by environmental gradients, the requirements of specific species to establish and regenerate need to be determined and met. Therefore, for this created salt marsh to have similar

species distributions and regeneration dynamics to a natural marsh, appropriate elevations and subsequent water level fluctuations must be similar so that species can establish in a landscape context that is appropriate and comparable to natural reference marshes.

Table 1.1. Analysis of covariance for significant effects of marsh type, distance from marsh edge, cover of vegetation, and water level on seed density of five salt marsh species in Calcasieu Estuary, Hackberry, Louisiana.

Species	Source of Variation	DF	Type III SS	MS	F Value	Pr>F
<i>Aster subulatus</i>	Marsh	2	7.32	3.66	0.69	0.5057
	Distance	1	24.37	24.37	4.6	0.0366
	Vegetation	1	39.1	39.1	7.38	0.0089
	Marsh*Distance	2	76.47	38.23	7.21	0.0017
<i>Amaranthus hybridus</i>	Marsh	2	114.97	57.48	8.03	0.0009
	Vegetation	1	31.78	31.78	4.44	0.0397
	Water level	1	44.58	44.58	6.22	0.0156
<i>Distichlis spicata</i>	Marsh	2	23.35	11.66	2.13	0.129
	Vegetation	1	54.14	54.14	9.86	0.0027
	Water level	1	32.45	32.45	5.91	0.0183
<i>Iva frutescens</i>	Marsh	2	33.08	16.53	4.26	0.0189
	Vegetation	1	168.64	168.64	43.48	<0.0001
<i>Spartina alterniflora</i>	Marsh	2	65.66	32.83	10.49	0.0001

Table 1.2. Total density of seeds of five salt marsh species per square meter in two created salt marsh types and a natural salt marsh in Calcasieu Estuary, Hackberry, Louisiana.

Species	Total seeds m ²	Percentage of seeds captured in each marsh		
		Low created	High created	Natural
<i>Amaranthus hybridus</i>	128666	14.3	56.2	29.5
<i>Aster subulatus</i>	589012	0.5	99.4	0.1
<i>Distichlis spicata</i>	16629	2.8	22	75
<i>Iva frutescens</i>	50284	0.7	99.3	0
<i>Spartina alterniflora</i>	130575	87.4	7.5	5

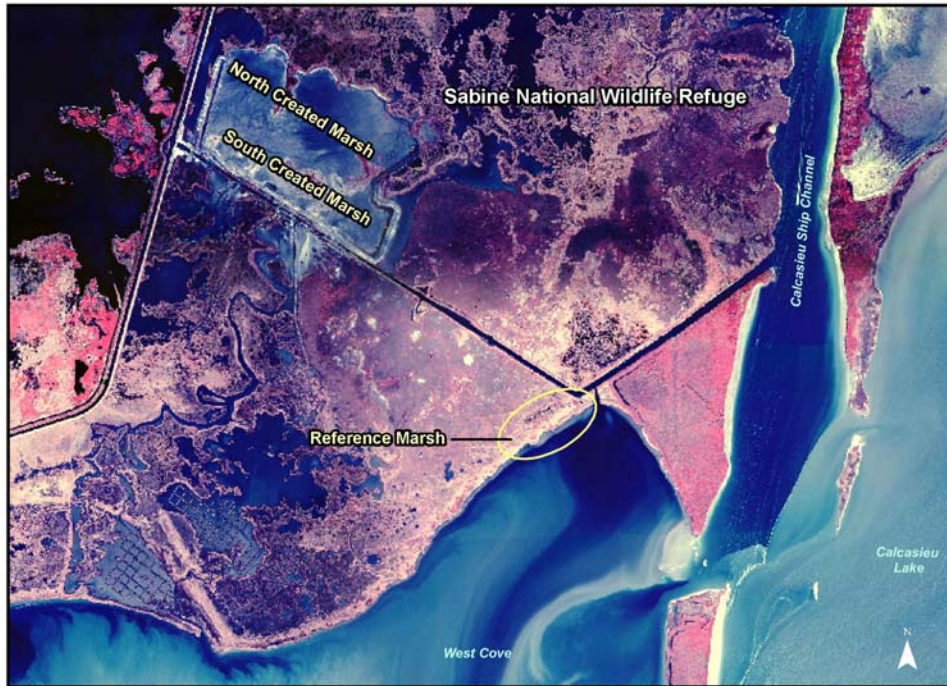


Figure 1.1. Map of the low created (“north created”), high created (“south created”) and natural (“reference”) marshes in Sabine National Wildlife Refuge in the Calcasieu Estuary on the Gulf Coast of Louisiana. Louisiana coastwide aerial photography, U. S. Geological Survey, National Wetlands Research Center, February 10, 2001.

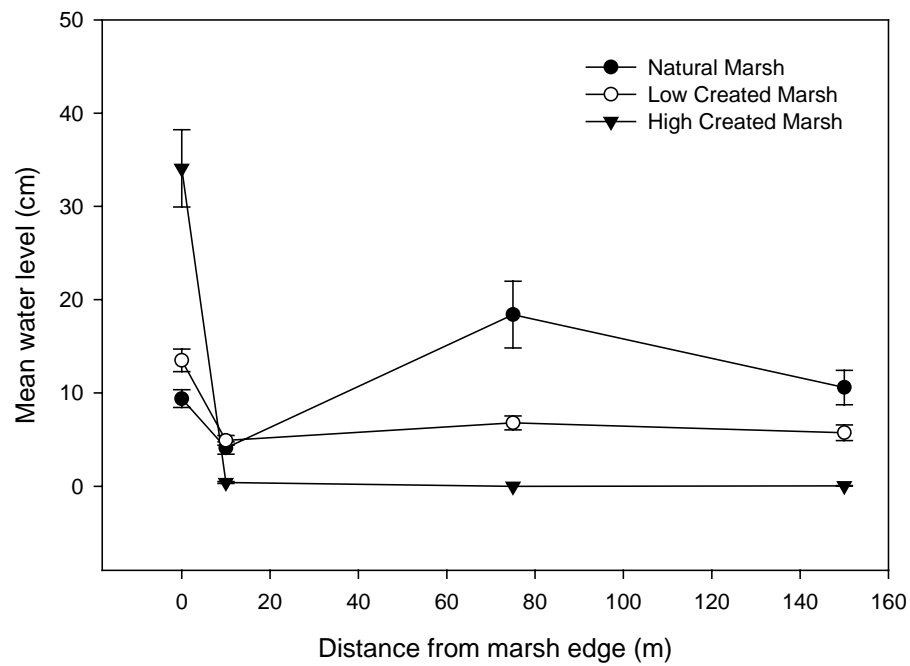


Figure 1.2. Mean water levels at increasing distance from the edge of three salt marsh types, Calcasieu Estuary, Hackberry, Louisiana (+/- SE, n=5).

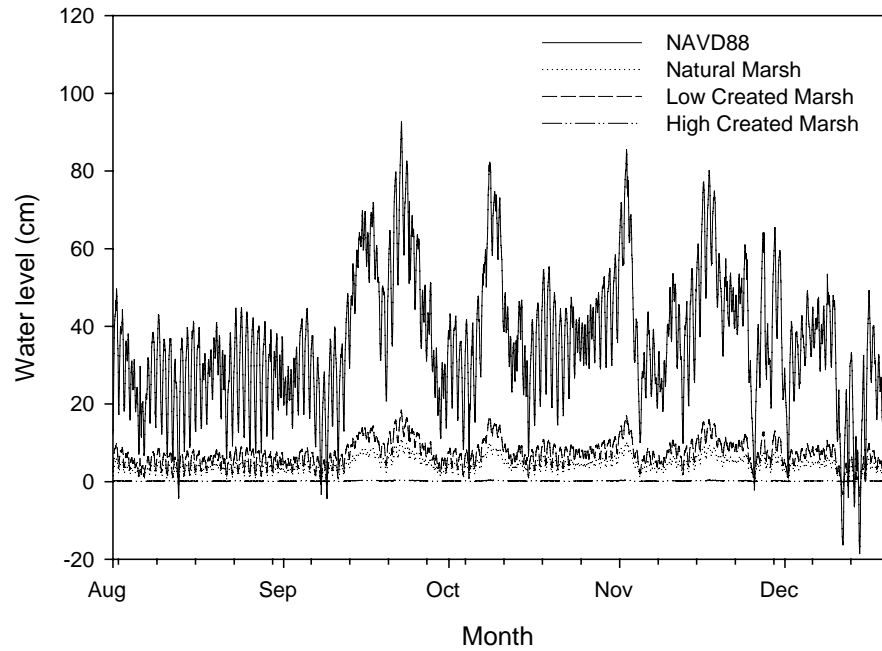


Figure 1.3. Water levels over time in each of the three marsh types based on recordings from a NAVD88 datum, Louisiana Department of Natural Resources 2004.

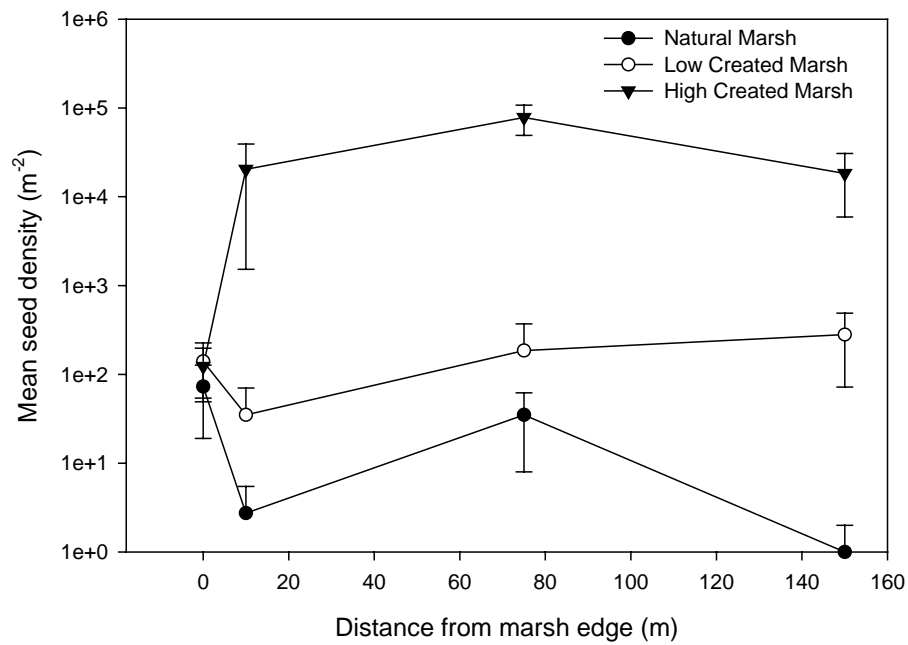


Figure 1.4. Mean density of seeds of *Aster subulatus* along a distance gradient into three different salt marsh types on a logarithmic scale (+/- SE, n=5), Calcasieu Estuary, Hackberry, Louisiana.

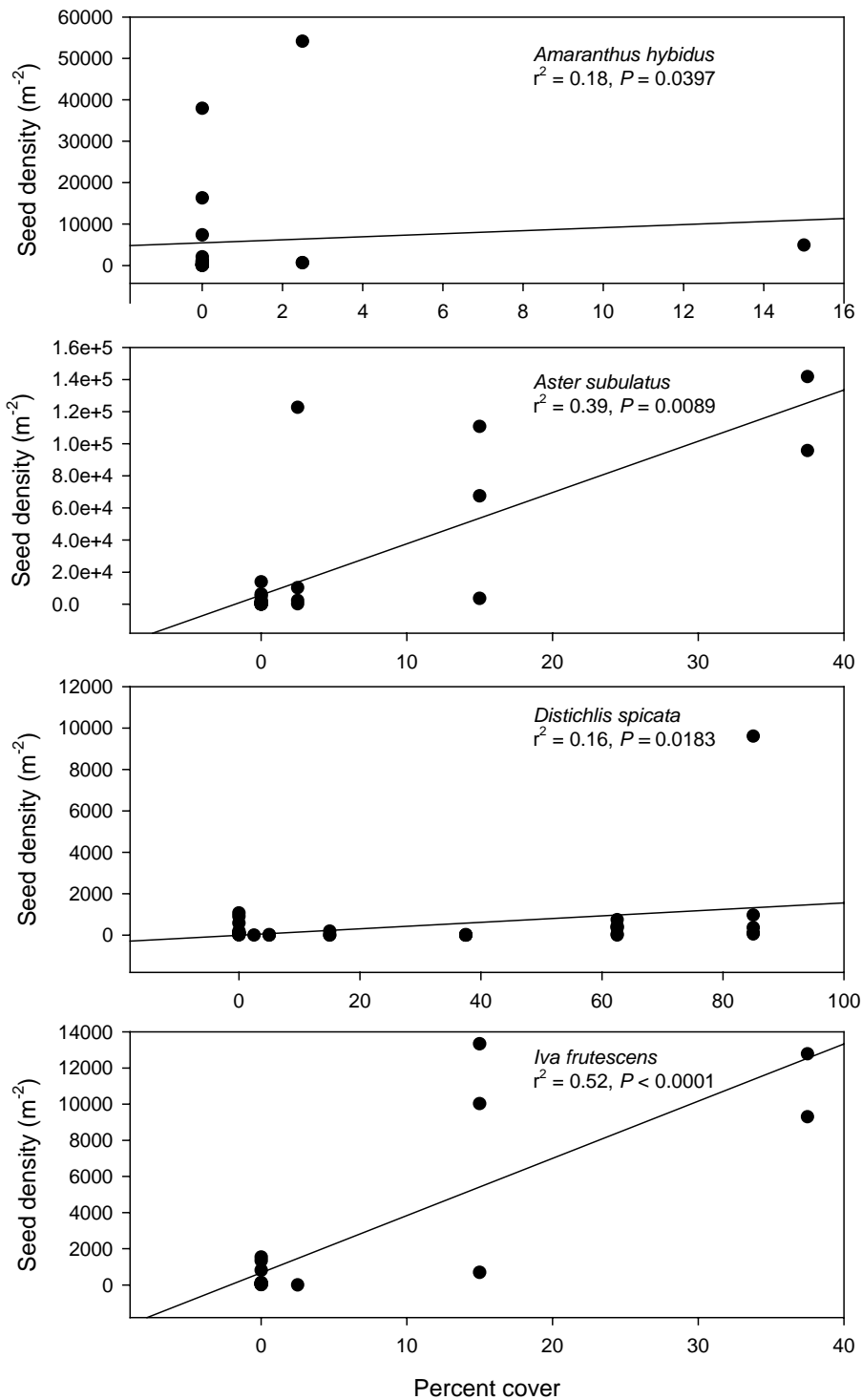


Figure 1.5. The relationship between seed density and the cover of adult plants and for four salt marsh plant species in Calcasieu Estuary, Hackberry, Louisiana.

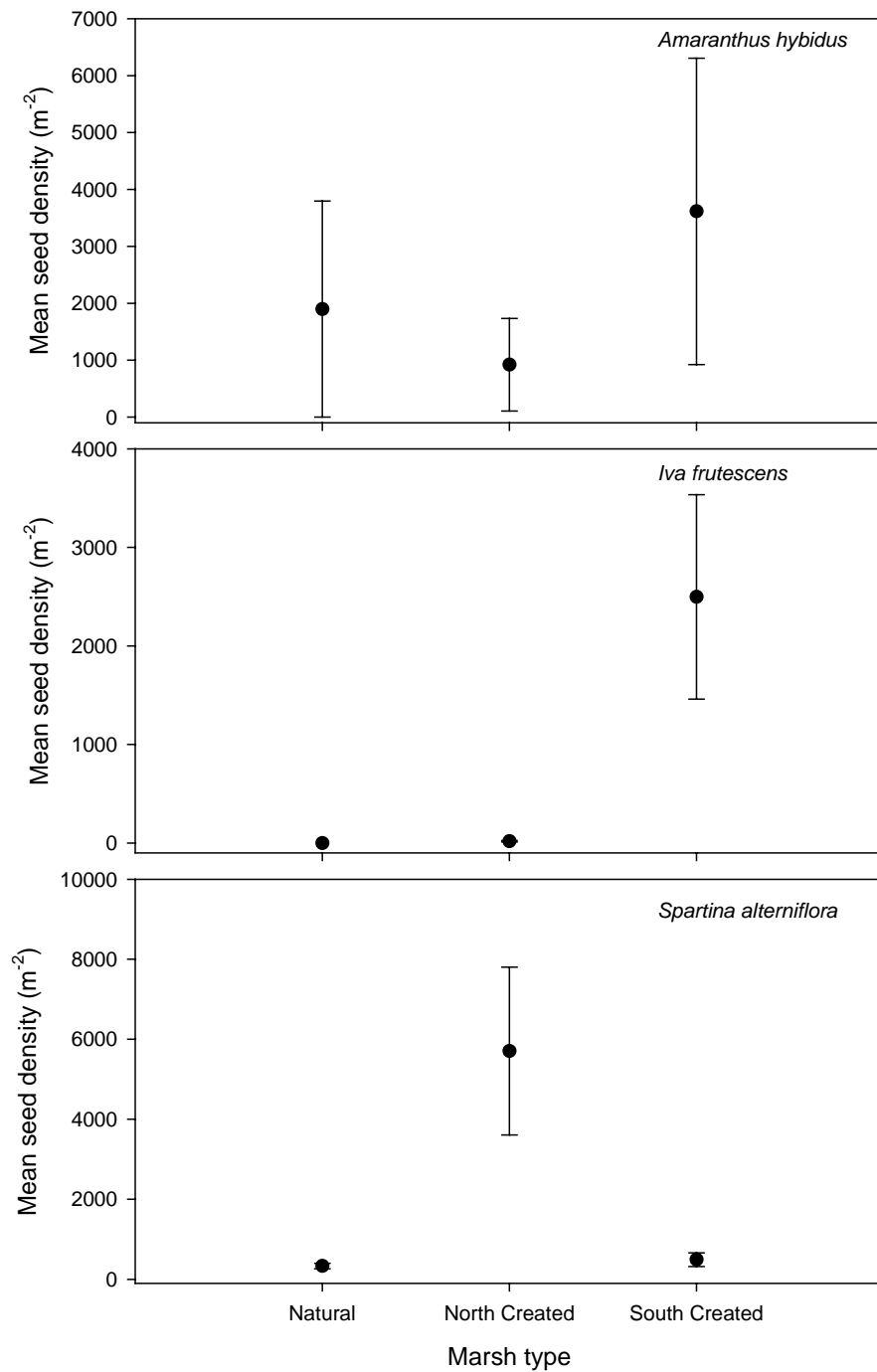


Figure 1.6. Seed density of three salt marsh species dispersing in low (“north”) and high (“south”) areas of a created marsh and in a natural marsh (+/- SE, n=20), Calcasieu Estuary, Hackberry, Louisiana.

CHAPTER 2

Seed Germination in a Created and Natural Salt Marsh Along the Gulf Coast of Louisiana, USA

INTRODUCTION

Seed germination is important for the natural colonization of created and restored wetlands and plays an important role in plant succession processes (van der Valk 1998). Germination of salt marsh seeds may vary depending on environmental conditions such as temperature, photoperiod (Khan and Ungar 1997; Baskin and Baskin 1998), salinity (Shumway and Bertness 1992; Baskin and Baskin 1998; Callaway and Zedler 1998), and soil moisture (Baldwin, McKee, and Mendelsohn 1996).

Depending on elevation and tidal regime, differences in soil salinity and soil moisture between created and natural marshes will have important effects on which species will germinate and ultimately establish (Baldwin et al. 1996, Brewer et al. 1997, Callaway and Zedler 1998). For example, some species such as *Spartina alterniflora* can tolerate high salinity levels and long durations of flooding (Hacker and Bertness 1995) and therefore, will be more likely to establish in the low marsh, whereas species such as *Iva frutescens*, a high marsh shrub is sensitive to salinity and moisture and may not germinate at low elevations (Hacker and Bertness 1995). Therefore, elevation differences between created and natural salt marshes as well as species-specific germination requirements could create differences in the vegetative composition of the plant communities between created and natural salt marshes.

The availability of open space may also differentially affect seedling emergence in created versus natural marshes depending on the abiotic conditions of the marsh types.

Small patches within natural salt marshes elevate salinity levels, which are eventually ameliorated by vegetation colonization (Bertness and Ellison 1987, Shumway and Bertness 1992). In created marshes where salinity levels depend upon elevation and the amount of vegetation, open patches may influence seed germination differently than in natural marshes. In addition, biotic interactions such as interspecific facilitation in the high marsh (Bertness and Ellison 1987, Bertness 1991, Bertness and Yeh 1994, Egergova et al. 2003, Proffitt et al. 2003) may increase the potential for seed germination for some species.

Seed germination in created marshes may also be limited by seed availability. In natural wetland communities seed availability is an important determinant of species richness (Xiong et al. 2003) and abundance (Rand 2000). Seed availability may be limited if there is a lack of a seed bank and species are not present or have no dispersal vectors to the created wetland (Middleton 1999, 2002). If seed availability is limited, species diversity and richness will be low (Lindig-Cisneros and Zedler 2002). Therefore, factors in natural marshes that influence plant distribution patterns including suitable environmental conditions for germination (Baldwin et al. 1996, Brewer et al. 1997, Calloway and Zedler 1998), species seed germination ability (Khan and Ungar 1997), and the availability of seeds (Rand 2000), and interactions between biotic and microhabitat factors (Proffitt et al. 2003) may also be important in created salt marshes.

The objective of this study was to determine whether seed germination patterns of five species in a created salt marsh differed from a natural salt marsh. I predicted that the number of seedlings in a created marsh would differ from a natural salt marsh due to

differences along a distance gradient from the marsh edge, seed availability, differences among species in seed germination ability, and the availability of open space.

METHODS

Germination in a Created and Natural Salt Marsh

Seed germination in clipped and unclipped plots was tested for five species including *Aster subulatus*, *D. spicata*, *I. frutescens*, *S. alterniflora*, and *S. robustus*; these species are present in both the created and natural salt marshes in southwest Louisiana (Edwards and Proffitt 2003, Egerova et al. 2003, Proffitt et al. 2005). To determine the seed germination potential of species in plots that were cleared vs. not cleared of vegetation, twelve 30 cm² plots were established at each of four distances (0, 10, 75, and 150 meters) from the edge of the natural and low elevation marshes (Figure 2). Two hundred and fifty seeds of each of five species were sown into both clipped and vegetated (unclipped) plots. Two unseeded control plots with both clipped and unclipped conditions were established to determine the effects of the seeding treatment. Plots had 50 cm spacing separating each plot and were established as a randomized block with distance.

Seeds were sown in January, which is the time of natural germination of salt marsh seeds in southwest Louisiana. These seeds were collected in Fall 2004 and were cold stratified at 6° C for two to three months depending on the timing of seed production. The seeds of each species were stratified according to their specific stratification requirements (Amen et al. 1970, Kantrud 1996). For example, *Spartina*

alterniflora and *D. spicata* were placed into distilled water during stratification (Mooring et al. 1971) while *A. subulatus*, *I. frutescens*, and *S. robustus* were stored dry (Table 1).

The existing aboveground vegetation was removed in clipped plots with shearing scissors and a trench cut was around the sides of the plot to sever rhizomes. The clipped treatment was maintained by re-clipping once every two weeks from January to March. Seedlings were identified, counted and removed from plots three times throughout the spring germination season in February, March, and May 2005.

Soil samples (0 - 5 cm) were collected in clipped and unclipped plots in each plot in April 2005 to measure soil salinity and soil moisture during the seed germination period. Soil salinity was measured by extracting water from soil samples by centrifugation and using a refractometer. Soil moisture was determined by measuring the weight of soil samples before and after drying at 60°C to a constant dry weight.

STATISTICAL ANALYSES

Germination in a Created and Natural Salt Marsh

Species with seeds that germinated in more than one treatment plot were included in the analyses. The number of seeds that germinated (seedlings) within a sample plot was converted to seedling density (m^{-2}) by multiplying by 3.33. The main effects of marsh, species, treatment and their interactions were tested using Poisson Regression with PROC GENMOD. Type III sums of squares was used and LS means multiple comparisons were made for any significant interactions. Analysis of Variance was used to determine seed germination differences between seeded and control plots for each

species and to determine spatial or treatment effects and any interactions on soil salinity and moisture using SAS V8 (SAS Institute, Inc. 2003).

RESULTS

Germination in a Created vs. Natural Salt Marsh

Five species were tested for seed germination in the low created and natural marsh types in both clipped and unclipped conditions. Seedlings of three species, *A. subulatus*, *I. frutescens*, and *S. alterniflora* emerged in more than one treatment plot. Depending on species and the availability of open habitat, seed germination differed between the natural and the low created marsh (marsh*species* vegetation treatment; $\chi^2_2 = 6.33$, $P = 0.0421$). The only species that was influenced by the availability of open habitat was *A. subulatus*. Open habitat increased *A. subulatus* seedling density in both the low created and natural marsh types, however, *A. subulatus* had significantly greater seed germination in the low created marsh with an open canopy than any other marsh/species/treatment combination (Fig. 5). An open canopy contributed more to seedling density of *A. subulatus* than marsh type suggested by greater seed germination in open areas of the natural marsh than closed canopy areas in the low created marsh ($\chi^2_1 = 3.91$, $P = 0.0481$). Under similar canopy conditions, *A. subulatus* seed germination was higher in the low created marsh, indicating that abiotic conditions may be more suitable for germination of *A. subulatus* in the low created marsh.

The low created marsh also had significantly higher *Spartina alterniflora* seed germination than in the natural marsh. However, open habitat did not affect seed germination of *S. alterniflora* in either marsh type. Neither clipping nor marsh type

influenced the relatively low seed germination of *I. frutescens*. Two *D. spicata* seeds and no *S. robustus* seeds germinated in the low created marsh and no *D. spicata* seeds and one *S. robustus* seed germinated in the natural marsh during the study period. These species were therefore not included in the analyses.

Seed Addition –Seed additions increased the number of germinated seeds of all three species. *Aster subulatus* increased mean seedling density from 5.7 m⁻² to 37.2 m⁻² with the addition of seeds ($F_{1,19} = 4.73, P = 0.0417$). *Iva frutescens* increased seedling density from an average of 2.2 seedlings m⁻² to 5.5 seedlings m⁻² ($F_{1,22} = 7.38, P = 0.0126$). *Spartina alterniflora* increased mean seedling density from 1.4 seedlings m⁻² to 16.3 seedlings m⁻² in seeded plots ($F_{1,34} = 11.70, P = 0.0016$).

DISCUSSION

When salt marshes are created at elevations that differ from natural marshes, the potential for seed germination of species not adapted to the specific abiotic conditions is limited. For example, in a restoration site in southern California, more salt tolerant species recruited at higher elevations (Lindig-Cisneros and Zedler 2002). Elevation of salt marshes has a profound effect on both salinity (Hacker and Bertness 1999) and tidal dynamics (Reed and Cahoon 1992), and both have major effects on species-specific seedling emergence (Rand 2000).

Despite the heterogeneity of abiotic conditions in all three marsh types in this study, the low elevation area of the created marsh was more conducive for seed germination than the natural marsh. Higher seed germination of both *A. subulatus* and *S. alterniflora* in the low created marsh may have been related to lower mean salinity level

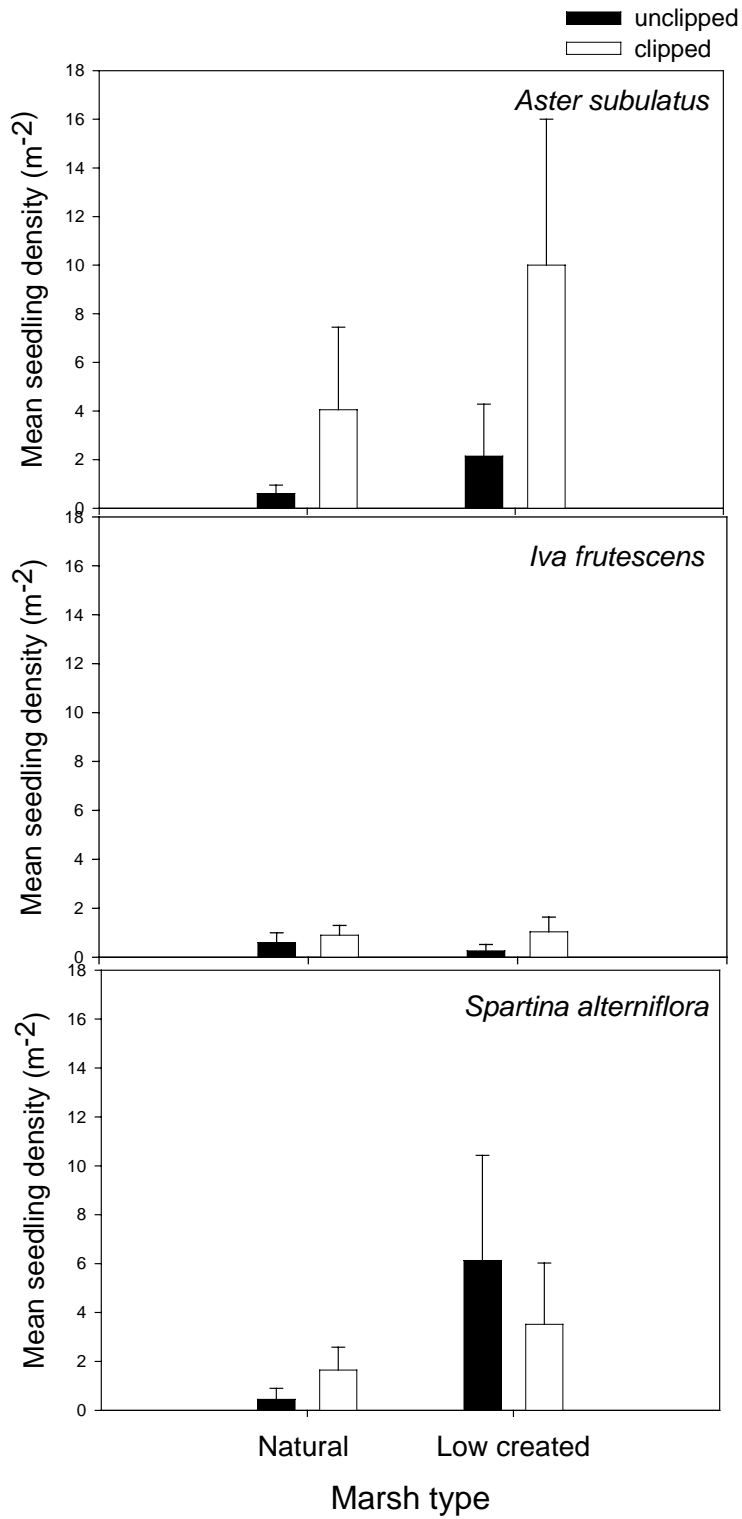
in the low created marsh (2.5 ppt) than in the natural marsh (4.2 ppt). The low seed germination of *I. frutescens* may have been related to the average soil moisture levels of 49% in the natural marsh and 39% in the low created marsh or unfavorable salinity levels in both marshes over the study period. Likewise, Noe and Zedler (2000) isolated soil salinity and moisture as contributing to differences among species in their germination.

The availability of open habitat influenced seed germination of only one species (*Aster subulatus*) in this study. Open habitat is also important to the survival of seedlings in San Francisco Bay where there was 70% seedling survival on bare substrate (Daehler 1999). For species that can germinate and recruit under canopies of vegetation, light level penetration differences among genotypes and species influence recruitment (Proffitt et al. 2005). Under similar canopy conditions, *A. subulatus* seed germination was higher in the low created marsh, indicating that abiotic conditions may be more suitable for germination of *A. subulatus* in the low created marsh.

Marsh type did not influence the seedling density of species with the addition of seeds suggesting that seed germination in both marshes is limited by seed availability. In this marsh system, recruitment of species such as *A. subulatus*, *I. frutescens* and *Atriplex patula* in newly created salt marshes were facilitated by the conditions in clone centers of *S. alterniflora*, where the characteristics of initial colonizing species such as clone size, center senescence, stem density, and height all influenced the recruitment and growth of other plant species (Proffitt et al. 2005).

Seed availability limited seedling emergence in both natural and created marshes for all species. Seed availability also limits recruitment in natural salt marshes in New England, where seedling density of annuals was increased by an order of magnitude with

seed additions (Rand 2000). Seed dispersal and seedling emergence were both high for *S. alterniflora* in the low elevations of the created marsh in this study.



LITERATURE CITED

- Aguiar M. R. and O. E. Sala. 1997. Seed distribution constrains the dynamics of the Patagonian Steppe. *Ecology* 78: 93-100.
- Amen, R. D., G. E. Carter, and R. J. Kelly. 1970. The nature of seed dormancy and germination in the salt marsh grass *Distichlis spicata*. *New Phytology* 69: 1005-1013.
- Baldwin, A. H., K. L. McKee, and I. A. Mendelssohn. 1996. The influence of vegetation, salinity, and inundation on seed banks of oligohaline coastal marshes. *American Journal of Botany* 83: 470-479.
- Baskin, C. C. and J. M. Baskin. 1998. Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego, California, USA.
- Bertness, M. D. and A. M. Ellison. 1987. Determinants of pattern in a New England salt marsh plant community. *Ecological Monographs* 57: 129-147.
- Bertness, M. D. 1991. Interspecific interactions among high marsh perennials in a New England salt marsh. *Ecology* 72:125-137.
- Bertness, M. D., L. Gough, and S. W. Shumway. 1992. Salt tolerances and the distribution of fugitive salt marsh plants. *Ecology* 73: 1842-1851.
- Bertness, M. D. and S. M. Yeh. 1994. Cooperative and competitive interactions in the recruitment of marsh elders. *Ecology* 75: 2415-2429.
- Brewer, J. S., J. M. Levine, and M. D. Bertness. 1997. Effects of biomass removal and elevation on species richness in a New England salt marsh. *Oikos* 80: 333-341.
- Brower, J. E., J. H. Zar, and C. N. von Ende. 1998. *Field and Laboratory Methods for General Ecology*. Fourth Edition. The McGraw-Hill Companies, Inc.
- Calloway, J. C. and J. B. Zedler. 1998. Interactions between a salt marsh native perennial (*Salicornia virginica*) and an exotic annual (*Polypogon monspeliensis*) under varied salinity and hydroperiod. *Wetlands Ecology and Management* 5: 179-194.
- Chambers, J. C. and J. A. MacMahon 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. *Annu. Rev. Ecol. Syst.* 25: 263-292.
- Daehler, C. C. 1999. Inbreeding depression in smooth cordgrass (*Spartina alterniflora* Poaceae) invading San Francisco Bay. *American Journal of Botany* 86: 131-139.

- Edwards, K. R. and C. E. Proffitt. 2003. Comparison of wetland structural characteristics between created and natural salt marshes in southwest Louisiana, USA. *Wetlands*, 23:2: 344-356.
- Egergova, J., C. E. Proffitt, and S. Travis. 2003. Facilitation of survival and growth of *Baccharis halimifolia* L. by *Spartina alterniflora* Loisel in a created Louisiana salt marsh. *Wetlands* 23: 250-256.
- Hacker, S. D., and M. D. Bertness. 1995. Morphological and Physiological Consequences of a Positive Plant Interaction. *Ecology* 76:2165-2175.
- Huiskes, A. H. L., Koutstaal, B. P., Herman, P. M., Beeftink, W.G., Markusse, M.M., Munck, W.D. 1995. Seed dispersal of halophytes in tidal salt marshes. *Journal of Ecology* 83: 559-567.
- Kantrund, H. A. 1996. The alkali (*Scirpus maritimus* L.) and saltmarsh (*S. robustus* Pursh) bulrushes: a literature review. U.S. Department of Interior, National Biological Service.
- Khan, M. A. and I. A. Ungar. 1997. Effects of light, salinity, and thermoperiod on the seed germination of halophytes. *Canadian Journal of Botany* 54: 1377-1385.
- Levin, L., A. D. Talley, and G. Thayer. 1996. Succession of macrobenthos in a created salt marsh. *Marine Ecology Progress Series* 141: 67-82.
- Lindig-Cisneros, R. and J. B. Zedler. 2002. Halophyte recruitment in a salt marsh restoration site. *Estuaries* 25:6A: 1174-1183.
- Louisiana Coastal Wetlands Conservation and Restoration Task Force and the Wetlands Conservation and Restoration Authority. 1999. *Coast 2050: Toward a Sustainable Coastal Louisiana, The Appendices. Appendix F- Region 4 Supplemental Information.* Louisiana Department of Natural Resources. Baton Rouge, La.
- Louisiana Department of Natural Resources. 2003. America's Wetland Fact Sheet. www.americaswetland.com.
- Middleton, B.A. 2002. Flood pulsing in the regeneration and maintenance of species in riverine forested wetlands of the southeastern United States. Pages 223-294 in B. Middleton, editor. *Flood pulsing in wetlands: restoring the natural hydrological balance.* John Wiley and Sons, New York.
- Middleton, B. A. 1999. *Wetland Restoration: Flood Pulsing and Disturbance Dynamics.* New York, John Wiley and Sons, Inc.
- Middleton, B.A. 1995. Sampling devices for the measurement of seed rain and

- hydrochory in rivers. *Bulletin of the Torrey Botanical Club* 122: 2: 152-155.
- Mineke, W. and J. P. Bakker. 2002. Soil seed bank and driftline composition along a successional gradient on a temperate salt marsh. *Applied Vegetation Science* 5: 55-62.
- Mooring, M. T., A. W. Cooper, and E. D. Seneca. 1971. Seed germination response and evidence for height ecophenes in *Spartina alterniflora* from North Carolina. *American Journal of Botany* 58:1: 48-55.
- Noe, G. B. and J. B. Zedler. 2000. Differential effects of four abiotic factors on the germination of salt marsh annuals. *American Journal of Botany* 87:11: 1679-1692.
- Primack, R. B. and S. I. Miao. 1992. Dispersal can limit local plant distribution. *Conservation Biology* 6: 513-519.
- Proffitt, C. E., and J. Young. 1998. Salt marsh plant colonization, growth, and dominance on large mudflats created using dredged sediments. *Recent Research in Coastal Louisiana: Natural System Function and Response to Human Influence, A Symposium*, pp.218-228.
- Proffitt C. E., S. E. Travis, and K. R. Edwards. 2003. Genotype and elevation influence *Spartina alterniflora* colonization and growth in a created salt marsh. *Ecological Applications* 13:180-192.
- Rand, T. A. 2000. Seed dispersal, habitat suitability and the distributions of halophytes across a salt marsh tidal gradient. *Journal of Ecology* 88:608-621.
- Reed, D. J. and D. R. Cahoon. 1992. The relationship between marsh surface topography, hydroperiod, and growth of *Spartina alterniflora* in a deteriorating Louisiana salt marsh. *Journal of Coastal Research* 8:77-81.
- Salinas, L. M., R. D. DeLaune, and W. H. Patrick, Jr. 1986. Changes occurring along a rapidly submerging coastal area: Louisiana, USA. *Journal of Coastal Research* 2: 269-284.
- Shumway, S. W., and M. D. Bertness. 1992. Salt stress limitation of seedling recruitment in a salt marsh plant community. *Oecologia* 92: 490-497.
- Turner, R.E. 1997. Wetland loss in the northern Gulf of Mexico: multiple working hypotheses. *Estuaries* 20: 1-13.
- van der Valk, A.G. 1992. Establishment, colonization, and persistence. Plant Succession: Theory and Prediction. Pages 60-102 in. D.C. Glenn-Lewin, R.K. Pect, and T.T. Veblin. Chapman and Hall, London, England.

van der Valk, A. G. 1998. Succession theory and restoration of wetland vegetation. Wetlands for the Future, Adelaide, Gleneagles.

Xiong, S. J., M. E. Johansson, F. M. R. Hughes, A. Hayes, K. S. Richards, and C. Nilsson. 2003. Interactive effects of soil moisture, vegetation canopy, plant litter, and seed addition on plant diversity in a wetland community. *Journal of Ecology* 91:976-986.