Journal of Coastal Research	15	4	872–883	Royal Palm Beach, Florida	Fall 1999

Recovery of a Louisiana Barrier Island Marsh Plant Community Following Extensive Hurricane-Induced Overwash

Richard P. Courtemanche Jr.†, Mark W. Hester‡, and Irving A. Mendelssohn§

†Wetland Biogeochemistry Institute
Center for Coastal, Energy, and Environmental Resources
Louisiana State University
Baton Rouge, LA 70803, U.S.A.

‡Southeastern Louisiana State University
Department of Biological Sciences
Hammond, LA 70402, U.S.A.

§Wetland Biogeochemistry Institute
Center for Coastal, Energy, and Environmental Resources
Louisiana State University
Baton Rouge, LA 70803, U.S.A.

ABSTRACT

COURTEMANCHE, R.P., JR.; HESTER, M.W., and MENDELSSOHN, I.A., 1999. Recovery of a Louisiana Barrier Island Marsh Plant Community Following Extensive Hurricane-Induced Overwash. *Journal of Coastal Research*, 15(4), 872–883. Royal Palm Beach (Florida), ISSN 0749-0208.

The Isles Dernieres barrier island chain provides the front line of protection for the Lower Terrebonne Estuary, Louisiana. Landfall of Hurricane Andrew on August 26, 1992 resulted in overwash of most of this island chain, thereby accelerating the erosional processes and altering the plant communities of the islands. Four zones were identified by the depth of overwash sands received (from >50 cm to <10 cm) to examine the factors affecting the colonization of vegetation following overwash. Within each zone a permanent transect and thirty permanent plots were established and sampled four times over two years for biotic and abiotic variables. A total of 32 plant species was identified, 30 of which were located in the zone with the highest loadings of sand. Over time this zone also had the greatest increases in species richness. The most important survivor and early colonizer of the high zone overwash was *Spartina alterniflora*. However, over time *Spartina patens* became dominant. The other zones, receiving moderate to no sand deposits, differed greatly. The few species present in these zones (<7) were indicative of high salt marsh and salt pan habitats and were dominated by *Spartina alterniflora* throughout the study. Using multivariate analyses, biotic and abiotic variables were correlated. The soil variables representative of topographical elevation and soil salinity influenced plant community zonations on the Isles Dernieres. Soil fertility and herbivory were not dominant factors affecting vegetation establishment. Backbarrier marsh areas that received the greatest sand loadings are now characterized by dune and swale plant species, while areas that received low sand loadings are returning to a marsh community.

ADDITIONAL INDEX WORDS: *Plant distribution, vegetative changes, natural disturbance, backbarrier marsh, overwash*

INTRODUCTION

On August 26, 1992, Hurricane Andrew made landfall on the Louisiana coast just west of the Isles Dernieres. The impact of this class four hurricane on the western barrier islands of Louisiana was severe. The maximum storm surge associated with Hurricane Andrew was estimated at 1.9 m and inundated most of the Isles Dernieres. Coastline erosion resulted in a loss of >40 m of coastline on Trinity Island, the main island in the Isles Dernieres chain. Raccoon Island, at the western end, experienced land losses of 30 to 40 percent (STONE *et al.*, 1993).

Sand overwashed by the storm surge was deposited behind the dune onto the existing marsh surface, altering the topography. The degree of overwash burial was greatest immediately behind the former dune line, where sand deposits greater than 100 cm were recorded. Sand deposition gradually decreased toward the rear of the backbarrier marsh.

Plant community recovery after hurricane overwash on backbarrier marshes is not well understood. Although several studies have examined vegetative recruitment of barrier island plant species after overwash disturbance, these studies focussed more on the role of interspecific competition on plant zonation (WATKINSON and DAVY, 1985; CORDAZZO and SEELIGER, 1993; FAHRIG *et al.*, 1993) and life history characteristics of barrier island species (WATKINSON, 1978; VAN DER MEIJDEN and VAN DER WAALS-KOOI, 1979; HESTER and MENDELSSOHN, 1991).

Abiotic conditions (*e.g.* elevation and edaphic variables such as soil conductivity, moisture content, and fertility) can also greatly influence plant establishment and success. For example, soil elevation can be a major determinant of plant establishment. Differences in species' flood tolerances often result in species zonation patterns along elevational gradients (OOSTING and BILLINGS, 1942; VAN DER VALK, 1975;

97133 received 21 October 1997; accepted in revision 30 December 1998.

WILSEY *et al.*, 1992; BERTNESS, 1991). Moreover, the effects of flooding duration and frequency along elevational gradients largely dictate soil conductivities, which may further affect species recruitment and zonation (MAUN, 1994; PATTERSON and MENDELSSOHN, 1991; BERTNESS and ELLISON, 1987). In addition to the stressors associated with the marine environment, soil fertility limitations of overwash sands may be an additional modifying factor that affects species establishment and distribution (ROBERTSON, 1982; HESTER and MENDELSSOHN, 1991; HESTER and MENDELSSOHN, 1992; OLFF *et al.*, 1993).

Although it is obvious that both biotic and abiotic factors interact to control species recruitment and succession after overwash events, relatively few studies have incorporated both types of variables together (COSTA *et al.*, 1996; BARBOUR *et al.*, 1987). This study was designed to investigate the recovery of the backbarrier marsh plant community on Trinity Island as the function of a combination of biotic and abiotic factors that may affect species recruitment. Specifically, we examined the abiotic environment (*e.g.* elevation, depth of sand burial, soil macro- and micronutrients, pH, organic matter and soil conductivities) as they relate to successful species recruitment and establishment. Biotic factors, such as the effect of herbivory and the presence of existing vegetation, were also evaluated as potential determinants of species recruitment and success.

MATERIALS AND METHODS

Field Design and Sampling

To assess the aerial extent of overwash onto the backbarrier marsh plant community and the degree of shoreline erosion at the study site on Trinity Island, low altitude vertical aerial photographs were examined. Photographs taken prior to Hurricane Andrew (1988) were examined and compared with photographs taken three months after the storm (November 1992) and two years after the storm (December 1994).

Site investigations during the summer of 1993 revealed extensive overwash deposits of marine sands onto the original backbarrier marsh surface (Figure 1). The depth of sand burial of the original marsh surface was assessed by numerous excavations throughout the site and was observed to decrease with distance from the beach. Four shore-parallel zones of overwash burial were then delineated at an extensive marsh overwash site. The high zone was characterized by greater than 50 cm of sand burial. The medium zone had between 25 and 35 cm of sand burial. A zone of less than 10 cm of overwash sand was identified as the low zone. A reference zone, where no noticeable sand accumulation occurred, was established further bayward (Figure 2).

Within each zone, 20 potential sampling location sites were identified where colonizing vegetation had become established adjacent to areas devoid of plants. This collection of 20 possible sites was randomly reduced to 10 per zone. Three permanent 1 m^2 plots were established at each site. One plot contained no vegetation. The two vegetated plots had similar plant species and density, one enclosed with a 0.9 m tall mesh fence to prevent entry of herbivores such as nutria (*Myocaster coypus*) and swamp rabbits (*Sylvilagus aquaticus*) and the other left unfenced. In the reference zone, non-vegetated plots could not be established because there were no areas devoid of vegetation. Plots within a site were separated by no more than five meters to maintain similar microenvironments.

A benchmark was installed at the site, and permanent plot elevations were related to the elevation of the lowest plot in the reference zone using an EAGL-2 laser level.

Permanent plots were sampled for both biotic and abiotic variables in October of 1993, in April and October of 1994, and in April of 1995. At each plot, percentage live and dead vegetative cover by species was determined by ocular estimation in 5% intervals by the same two researchers.

A modified species importance value was calculated for each species across treatments within a zone and date by adding the relative species frequency and the relative species percentage cover. Relative species frequency is the frequency of a species in the zone (based on a maximum of 10 occurrences out of 10 quadrats in each treatment) divided by the summed frequencies of all species occurring in the zone. Relative species percentage cover is the total percentage cover of a species in a treatment within a zone divided by the summed total percentage cover of all species in the treatment.

Based on these definitions, the sum of all species importance values in a zone is always 200. Therefore, the maximum importance value for any one species is 200, which would only occur in a monospecific stand. Relative density was not included as a component of the importance value because of the difficulty of determining the density of plants with a prostrate or a clonal growth form, which are common for many coastal plant species (*e.g. Ipomoea stolonifera, Sesuvium portulacastrum, S. patens,* and *S. alterniflora*).

In order to further assess species recruitment, a permanent 300 m transect was established within each zone. Every five meters along each transect, species presence or absence was determined in 1 m^2 quadrats placed 1 m from both sides of the transect line (*i.e.* a total of 122 plots sampled per transect). Transect sampling was conducted during each permanent plot sampling.

Soil Analyses

During each field site sampling, two soil cores were obtained from the outer edges of each permanent plot to a depth of 15 cm using a stainless steel trowel. Soil samples were combined, sealed in plastic bags devoid of air space, kept cool, and processed within 48 hours. Soil inorganic nitrogen was determined by extracting 20 g of wet soil with 20 ml of 2 N KCl. EPA Method 353.2 (Colorimetric, Automated Cadmium Reduction) was employed for nitrate-nitrite determination, and ammonium was determined using EPA Method 350.1 (Colorimetric, Automated Phenate; U.S. ENVIRONMENTAL PROTECTION AGENCY, 1979).

The Louisiana State Soil Testing Laboratory of the LSU Department of Agronomy analyzed soil samples for P, K, Na, As, Ca, Cd, Cu, Fe, Mg, Mn, Ni, Pb, Zn, soil organic-matter content, and soil pH. All soil nutrient extractions were conducted with soils at their field moisture. Phosphorus was ex-

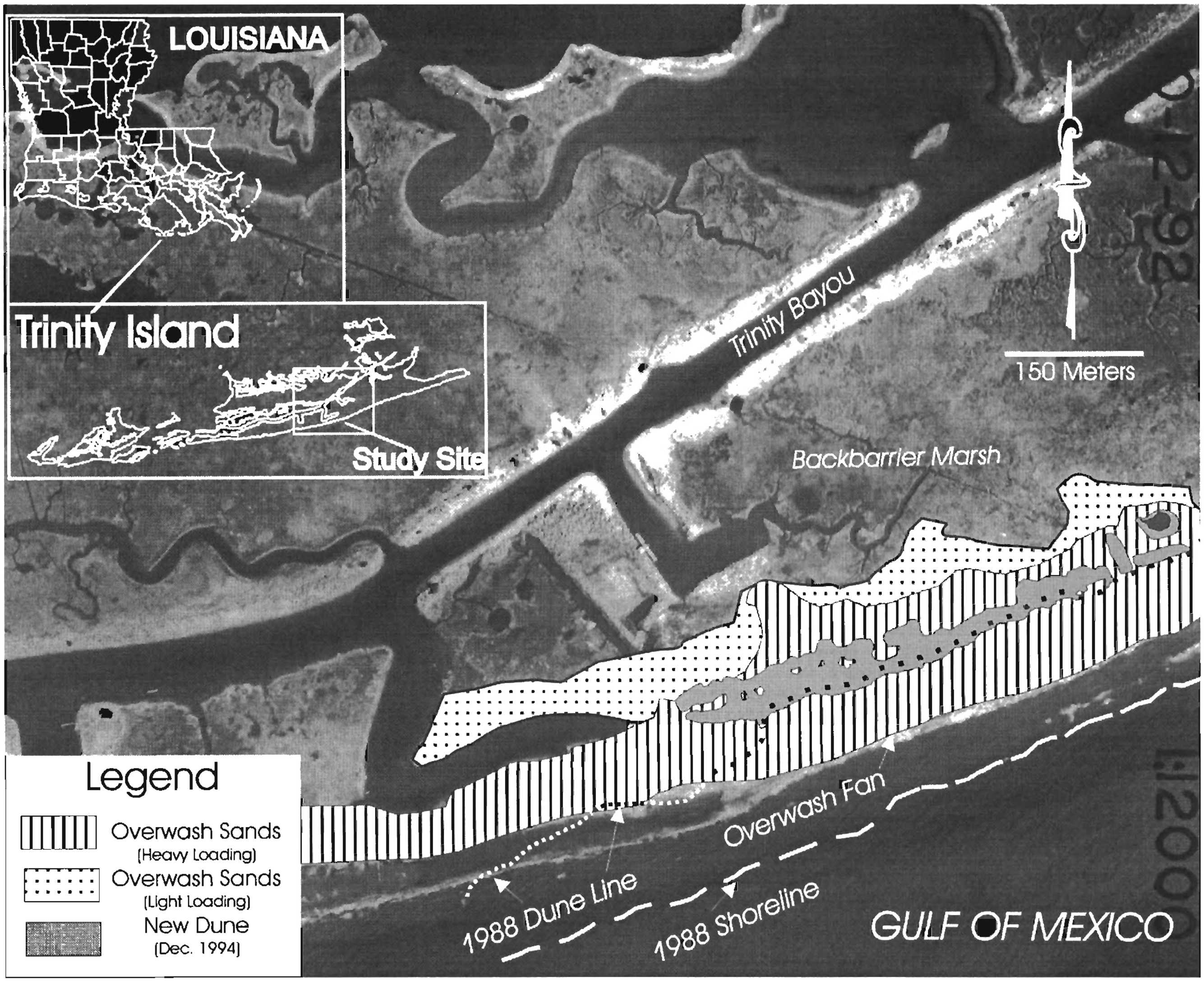

Figure 1. Location of experimental site on the overwash fan created by Hurricane Andrew, August 26, 1992, on Trinity Island of the Isles Dernieres based on vertical aerial photography acquired in October, 1992. Erosional patterns created by superimposing aerial photographs before, two months after, and two years after the storm.

tracted with Bray #2 (0.1 N HCl + 0.03 N NH_4F); potassium, sodium, calcium, and magnesium were extracted using a 1 N, pH 7 ammonium acetate solution; and trace and heavy metals were extracted with 0.1 N HCl. Elemental concentrations were determined with an inductively coupled argon plasma-optical emission spectrophotometer and were expressed on a microgram element per gram dry weight soil basis.

Percent organic matter was determined by the modified Wakley-Black method (USEPA, 1979). Soil pH was analyzed by combining deionized water with an equal measure of soil, allowed to stabilize for two hours, and then measured by combination electrode.

Soil moisture was determined gravimetrically after oven drying at 80°C for 72 hours, until a constant weight was achieved. Percentage moisture was calculated on a per dry weight basis (100 × (wet wt. − dry wt.)/(dry wt.)). Soil conductivities were determined on a 1:5 ratio of dry soil to deionized water that was shaken for one hour and measured with a Fischer Conductivity Meter, Model 152.

Statistical Analyses

The biotic and abiotic response variables were first analyzed as a repeated measures split plot analysis of variance (ANOVA) with the main plot effect being sand burial depth (zone). Nested within zones were the subplot effects of vegetated, vegetated fenced, and non-vegetated treatments. Time was the repeated measure.

Analysis of the data was conducted using the General Linear Model (GLM) procedure of SAS (Statistical Analysis Systems, 1985). The effect of herbivory on species recruit-

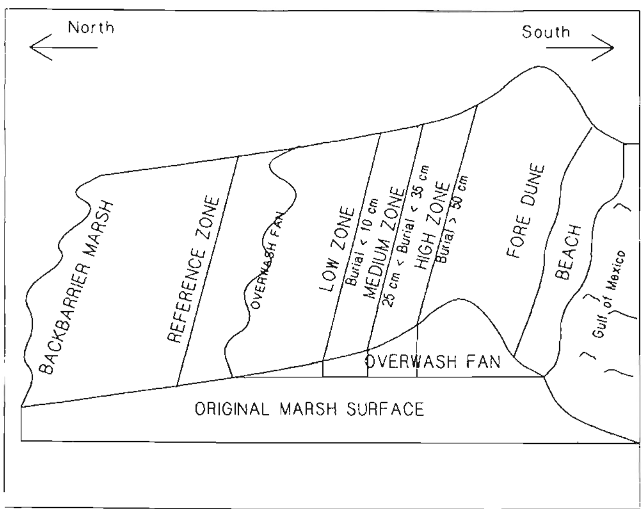

Figure 2. Cross-sectional diagram depicting transect placement in relationship to the depth of sand burial on the original backbarrier marsh.

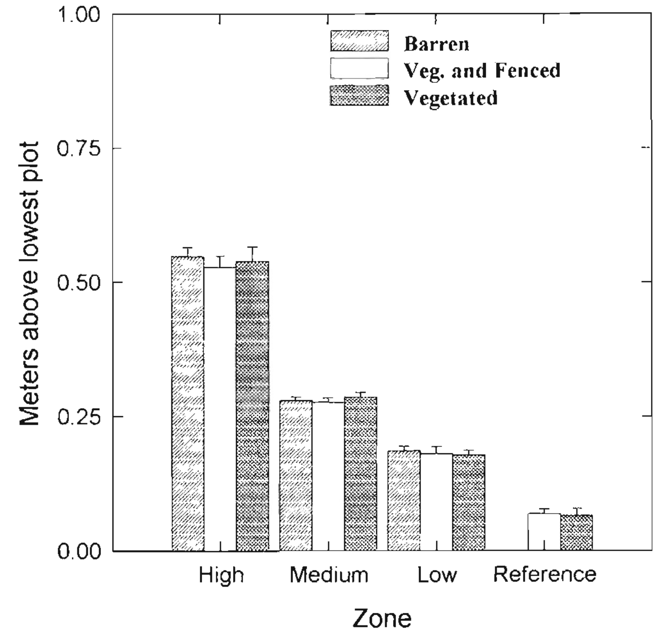

Figure 3. Mean relative elevation by strata and plot type as determined by a laser level and related to the lowest plot in the reference stratum.

ment was tested by comparing the fenced and unfenced plots. The effect of pre-established vegetation on species recruitment was evaluated by comparing the vegetated and barren plots. Contrasts were determined using the Repeated Measures statement, to adjust the results of all contrasts to meet Tukey's assumptions of maintaining a significance level of 0.05 for all conducted contrasts. Canonical correlations were conducted using the CANCORR procedure (SAS, 1985) to assess the relationships between abiotic and biotic factors and to reduce the edaphic and elevational data set to those variables which significantly influenced vegetative responses.

RESULTS

Extent of Overwash Impact

Comparisons between aerial photographs revealed the size and extent of overwash impact to the study site. In 1988, the study area on Trinity Island (Figure 1) measured 11.2 ha. Of this total, 5.6 ha were delineated as beach/dune and 5.6 ha as vegetated backbarrier marsh. November, 1992 photography revealed that following the hurricane the total study area decreased to 7.8 ha, indicating a 30 percent loss. The storm deposited an overwash fan measuring 6.8 ha that covered much of the beach and backbarrier marsh.

Within the overwash fan, an area of 6.0 ha was delineated that received heavy overwash deposits (as much as 100 cm), essentially burying all existing vegetation. Another zone, measuring 0.9 ha, received light loadings of sand (<10 cm) and left much of the vegetative communities unburied. The remainder of the study site received no noticeable sand accumulation.

Areas that accumulated the greatest depths of sand quickly developed into a new dune system during the spring of 1993. By comparing aerial photographs with fixed landmarks, shoreline erosion was estimated at approximately 68 m.

Results from laser elevational surveys confirmed distinct elevational differences between our delineated overwash zones ($P<0.01$; Figure 3), but not between plots within zone ($P=0.82$).

Transect Data

Thirty-two species were found in the 488 plots (Table 1). The number of species present and the frequency of occurrence of individual species within each sand burial zone increased over time. However, *Avicennia germinans,* a dominant species in the prehurricane marsh, was present in high numbers during the first sampling and then decreased greatly by the second sampling when many partially buried plants failed to recover from the overwash. In April 1995, new *A. germinans* contributed to the increased frequency of this species.

The high zone contained the highest species richness with 30 species (94% of species found in all zones) present (Table 1). Sixteen plant species (50% of the total species) were found exclusively within the high zone. Fewer species (5) were recorded in the medium zone during the first year comprising only 16% of the total species at the site.

The low and reference zones were fairly consistent in species composition during the four sampling dates (Table 1). Both zones were dominated by *S. alterniflora* with a consistent presence of *A. germinans*. However, in the low zone seven species were initially present. Of these, *Distichlis spicata* and the two *Salicornia* species displayed substantial increases in frequency throughout the study (Table 1). In the reference zone, *S. alterniflora* was present in 98% of all plots. The only areas that did not contain *S. alterniflora* were unvegetated tidal creeks.

Table 1. *Frequency of species within 1 m^2* plots by sampling date along permanent transect established on an overwash fan (n = 122 per zone). Percentage total number of species out of 32 are labeled as "% of Spec".

DATE	ZONE	% of Spec.	Total # Spec.	ANGL 1	AVGE 2	BAHA 3	BAMA 4	BOFR 5	CRPU 6	CYPA 7	CYOD 8	DISP 9	EUEX 10	FISP 11	HECU 12	HYBO 13	IPST 14	OEHE 15
Oct-93	HIGH	43.75	14	0	2	0	1	0	0	1	0	1	0	7	0	1	0	0
Apr-94	HIGH	53.13	17	0	0	2	1	1	0	0	0	2	0	5	1	2	0	0
Oct-94	HIGH	68.75	22	0	3	11	1	0	0	0	2	0	0	49	0	3	4	1
Apr-95	HIGH	81.25	26	0	3	16	1	0	1	0	2	3	26	52	22	10	4	0
Oct-93	MED	15.63	5	0	11	0	0	0	0	0	0	1	0	0	0	0	0	0
Apr-94	MED	31.25	10	0	8	0	0	0	0	0	0	2	0	0	0	0	0	0
Oct-94	MED	31.25	10	0	15	0	0	0	0	0	0	4	0	2	0	0	0	0
Apr-95	MED	40.63	13	0	15	0	1	0	0	0	0	5	0	0	0	0	0	0
Oct-93	LOW	21.88	7	0	15	1	2	0	0	0	0	7	0	0	0	0	0	0
Apr-94	LOW	21.88	7	0	9	0	1	0	0	0	0	10	0	0	0	0	0	0
Oct-94	LOW	28.13	9	4	7	0	3	0	0	0	0	15	0	1	0	0	0	0
Apr-95	LOW	28.13	9	0	13	0	4	0	0	0	0	22	0	1	0	0	0	0
Oct-93	REF	9.38	3	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0
Apr-94	REF	9.38	3	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Oct-94	REF	15.63	5	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0
Apr-95	REF	15.63	5	0	3	0	2	0	0	0	0	0	0	0	0	0	0	0

DATE	ZONE	PAVA 16	PHAU 17	PHNO 18	PLSP 19	PTCA 20	SAST 21	SABI 22	SAVI 23	SCAM 24	SEPO 25	SOSE 26	SPAL 27	SPPA 28	SPVI 29	STHE 30	SULI 31	VILU 32
Oct-93	HIGH	3	2	0	0	0	0	0	9	0	10	0	41	14	3	0	1	0
Apr-94	HIGH	0	4	0	0	0	0	4	6	0	12	0	49	26	4	2	14	2
Oct-94	HIGH	4	10	3	0	0	2	4	8	0	24	7	55	40	6	7	28	3
Apr-95	HIGH	5	13	2	0	1	16	7	11	1	25	17	62	61	2	0	34	29
Oct-93	MED	0	0	0	0	0	0	5	30	0	0	0	36	0	0	0	0	0
Apr-94	MED	0	0	0	0	0	0	33	27	0	1	0	43	1	1	0	2	1
Oct-94	MED	0	0	0	2	0	5	34	41	0	1	0	53	0	0	0	2	0
Apr-95	MED	0	0	0	2	0	2	48	46	0	2	0	58	1	1	0	9	2
Oct-93	LOW	0	0	0	0	0	0	5	22	0	0	0	61	0	0	0	0	0
Apr-94	LOW	0	0	0	0	0	0	17	37	0	0	0	68	0	1	0	0	0
Oct-94	LOW	0	0	0	0	0	0	30	48	0	0	0	71	1	0	0	0	0
Apr-95	LOW	0	0	0	0	0	0	50	70	0	0	0	82	1	0	0	1	0
Oct-93	REF	0	0	0	0	0	0	1	0	0	0	0	98	0	0	0	0	0
Apr-94	REF	0	0	0	0	0	0	0	1	0	0	0	98	0	0	0	0	0
Oct-94	REF	0	0	0	0	0	0	2	2	0	0	0	98	0	0	0	0	0
Apr-95	REF	0	0	0	0	0	0	5	6	0	0	0	98	0	0	0	0	0

Species Key:

ANGL = *Andropogon glomeratus*
AVGE = *Avicennia germinans*
BAHA = *Baccharis halimifolia*
BAMA = *Batis maritima*
BOFR = *Borrichia frutescens*
CRPU = *Croton punctatus*
CYPA = *Cynanchum palustre*
CYOD = *Cyperus odoratus*
DISP = *Distichlis spicata*
EUEX = *Eustoma exaltatum*
FISP = *Fibristylis* sp.
HECU = *Heliotropium carassavicum*
HYBO = *Hydrocotyle bonariensis*
IPST = *Ipomoea stolonifera*
OEHE = *Oenethera heterophylla*
PAVA = *Paspalum vaginatum*
PHAU = *Phragmites australis*
PHNO = *Phyla nodiflora*
PLSP = *Pluchea* sp.

PTCA = *Ptilimnium capillaceum*
SAST = *Sabatia stellaris*
SABI = *Salicornia bigelovii*

SAVI = *Salicornia virginica*
SCAM = *Scirpus americanus*
SEPO = *Sesuvium portulacastrum*
SOSE = *Solidago sempervirens*
SPAL = *Spartina alterniflora*
SPPA = *Spartina patens*
SPVI = *Sporobolus virginicus*
STHE = *Strophostyles helvola*
SULI = *Suaeda linearis*
VILU = *Vigna luteola*

Permanent Plot Data

Vegetative Response

The species composition within permanent plots was extremely similar to that found in the transect plots. Of the 32 species observed along the transects, 31 were found within permanent plots. At the termination of the study the high zone contained 29 of these species. Species richness was less in the lower three zones with 7, 6, and 2 species in the medium, low, and reference zones, respectively (Figure 4).

Although species richness increased with time in all of the overwashed zones, the high zone displayed the greatest increase (Figure 4). The species richness of barren plots became significantly similar to vegetated plots on the final sampling date in both the high and medium zones. Species richness did increase in the low zones but at a much slower rate. The species composition within the reference zones remained constant throughout the entire study. Herbivore exclusion had no significant effect on species richness.

Total vegetative percentage cover within permanent plots differed significantly between zones, zones by date, and zones by treatment ($P<0.01$; Figure 5). Percentage cover of all treatments within the high zone increased steadily through time. Percent cover in the barren plots in the medium and low zones also increased consistently throughout the experiment. However, only the barren plots within the medium zone achieved percentage covers similar to the vegetated plots by the termination of sampling (Figure 5). Vegetated plot types within the medium and low zones displayed little change, whereas the reference zone was relatively constant over time until the final sampling when it significantly decreased.

Plots that were originally vegetated, both fenced and unfenced, were similar in percentage cover throughout the experiment (Figure 5). None of the statistical contrasts indicated that vegetated fenced and unfenced plots were not significantly different within zones on any date, supporting the conclusion that herbivory was not an important control on species occurrence (data not shown).

Species importance values indicated that of the 29 species present in the high zone, 7 species were dominant (Figure 6). For most species in the high zone, modified species importance values varied little between sampling dates (Figure 6). However, *S. alterniflora,* the most important early colonizer on this site, decreased in importance over time while *S. patens* became most important.

Within the medium zone, *A. germinans* decreased in importance over time, while the salt-tolerant succulents, *S. bigelovii* and *S. virginica,* increased (Figure 6). Importance values within the low zone resembled those in the medium zone both in species and in value (Figure 6). Neither the low nor the medium zones resembled the reference zone, which was a virtual monoculture of *S. alterniflora* with a small number of *A. germinans* and only an occasional *Salicornia* spp. or *B. maritima.*

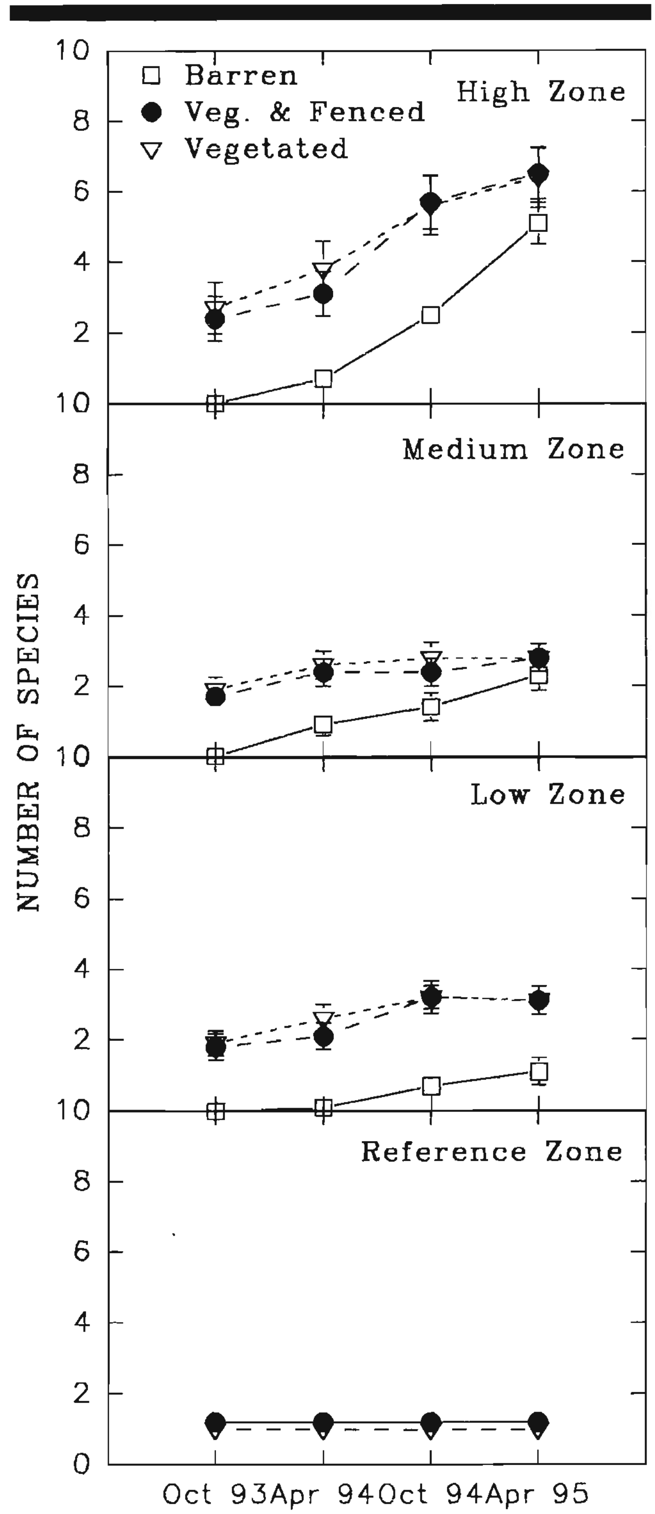

Figure 4. Total number of species (species richness) by sampling date, strata, and plot type (n = 10).

Soil Response to Overwash

Except for percentage soil moisture, all soil variables (conductivity, percentage organic matter, pH, phosphorus, iron,

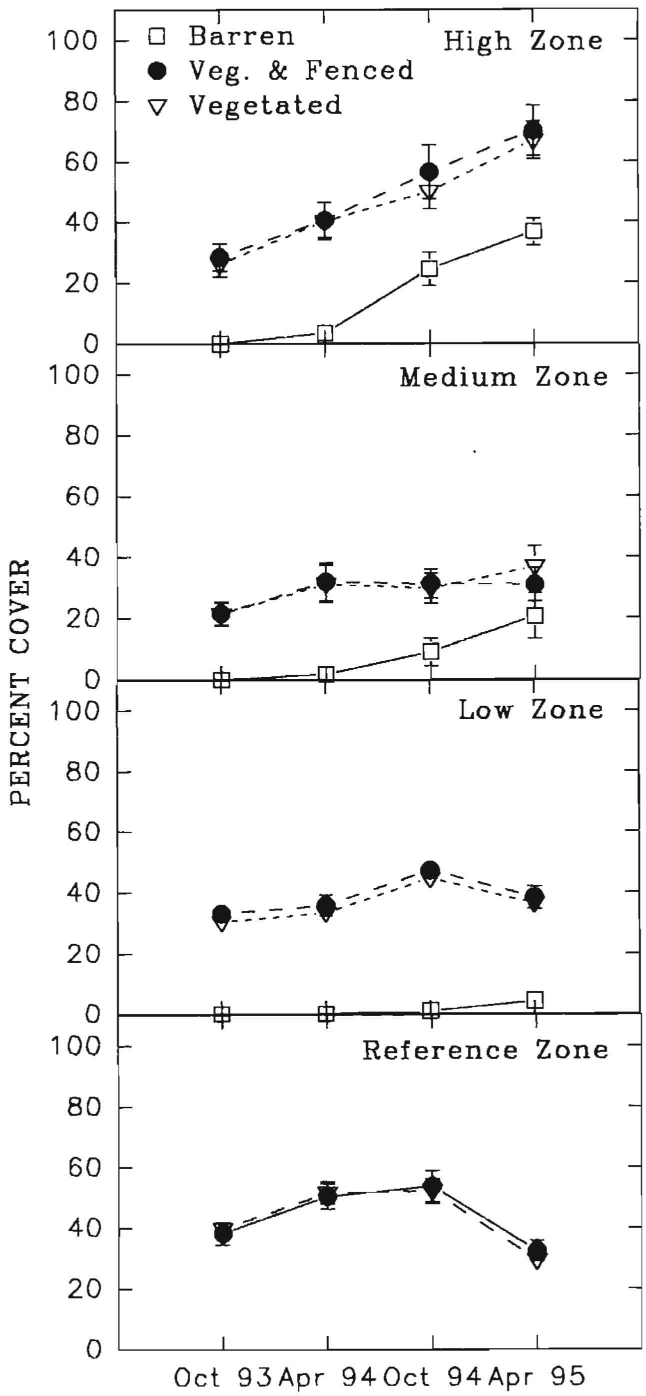

Figure 5. Total percent cover by sampling date, strata, and plot type (n = 10).

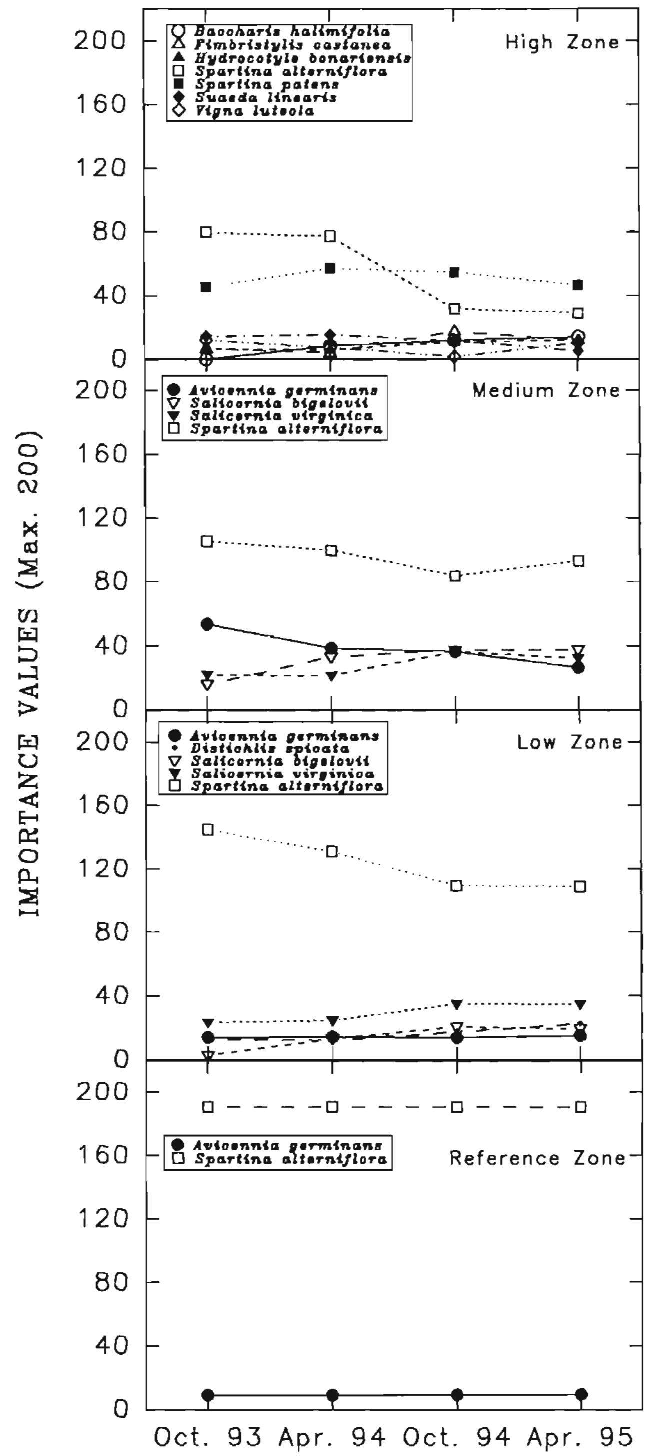

Figure 6. Importance values of major plant species within each strata over the four sampling dates.

and total inorganic nitrogen) displayed highly significant three-way interactions between date, zone and treatment ($P<0.01$). The basis for this interaction was largely due to differences in zone responses over time and secondarily due to differences in the barren plot responses on certain dates relative to the vegetative plots.

Percentage soil moisture varied significantly by zones ($P<0.01$). The highest soil moisture values occurred in the reference zone and the lowest values within the high zone. Furthermore, soil moisture displayed a significant interaction between zones and treatment ($P<0.01$; Table 2). All vegetated plot types were statistically similar on all sampling dates within each zone. However, barren plots contained soil moistures that were statistically different than the vegetated plots ($P=0.02$). Closer examination of the significant differences indicated that the soil moisture within the barren plot types were generally lower, particularity in the medium and low zones.

There was a significant effect of zones on soil conductivity ($P<0.01$). Conductivities were low in the high zone and increased significantly in the medium and low zones (Table 2). Soil conductivity also displayed a highly significant ($P<0.01$) treatment effect with higher conductivities in the barren plots than in the vegetated plots ($P<0.01$). Higher conductivities in barren plots were especially evident in the low zone (Table 2) and contributed heavily to the overall contrast. Soil sodium, magnesium, and potassium concentrations (data not shown), major components of soil conductivity, followed the same trends as soil conductivity.

Organic matter was virtually absent in the high zone soil and had values between 0.25% to 0.75% in the medium, low and reference zones (data not shown). Plot type had no significant effect on soil organic matter ($P=0.11$), and there was no discernable increase through time.

Soil pH significantly differed between zones ($P<0.01$). Highest pH values (≈ 8.5) were consistently found in the high zone and decreased as elevation decreased into the reference zone ($pH \approx 7.5$; Table 2). Although variation within zones was generally low, soil pH was significantly higher in the barren plots compared to the vegetated plots on many dates ($P<0.01$).

Soil total inorganic nitrogen varied greatly with zones, time and treatment (data not shown). The high zone contained the lowest concentrations of inorganic nitrogen (0.5–1.0 mg/kg soil), whereas other zones generally fluctuated between 0.5–2.0 mg/kg soil. No other discernable trends were evident (Table 2).

Available soil phosphorus varied between zones and through time ($P<0.01$), but there were no differences between treatments ($P=0.51$). The general trend was for soil phosphorus to increase through time within all zones. The highest concentrations were found in the reference zone. The greatest increase in phosphorus was also within this zone (Table 2).

Soil iron content also exhibited a significant interaction between date, zones and treatment ($P<0.01$; data not shown). In general, soil iron was lowest in the high zone ($\approx$50 mg/kg), increased in the medium zones ($\approx$250 mg/kg), and was highest in the low and reference zones ($\approx$400–800 mg/kg). There were no significant overall differences between treatments; soils associated with fenced plots did not exhibit any significant differences in iron concentration from unfenced plots.

Relationship Between Biotic and Abiotic Responses

A canonical correlation analysis conducted on elevation and edaphic variables with species cover greatly reduced the number of abiotic variables associated with explaining plant zonation. Of the 20 abiotic variables, 8 were correlated with 5 of the 31 vegetation variables. From this analysis, two variate pairs were determined to be highly significant, which accounted for 41% and 27%, respectively, of the common variance (Table 3).

The first variate pair was interpreted as an elevation factor based on a 0.92 loading of elevation. Soil pH was directly related to this factor, whereas soil moisture, iron, and potassium displayed strong negative loadings with elevation. In this first variate pair, strong positive loadings of total percentage plant cover of *Hydrocotyle bonariensis*, *S. patens*, and *Vigna luteola* (Table 3) indicated a positive association with elevation. However, the percentage cover of *S. alterniflora* displayed a negative loading, indicating a negative association with elevation. The second variate pair was interpreted as a salinity factor, based on strong negative loadings of soil conductivity, magnesium and sodium. In this second variate pair, *A. germinans* also displayed a negative loading, and was therefore associated with areas of higher salinities than *S. alterniflora,* which had a positive loading.

DISCUSSION AND CONCLUSIONS

The overwash fan associated with Hurricane Andrew altered the backbarrier marsh by eroding the beach front and depositing sands onto the marsh vegetation. Field observations indicated that marsh plants nearest the new shoreline, receiving the highest sand deposition, were unable to survive. However, at moderate sand loadings (25 to 35 cm), survivorship of some of the pre-storm dominant marsh species such as *S. alterniflora* and *A. germinans* did occur. Survivorship increased with diminishing sand burial toward the backbarrier marsh.

Although some *A. germinans* did survive immediately after the storm, most individuals did not persist beyond the first year. Over time new mangrove propagules became established in the low and medium zone, which were occasionally flooded by high tides. Due to the floating nature of these propagules, they were often deposited at slightly higher elevations due to extreme high tidal events, as previously observed (PATTERSON and MENDELSSOHN, 1991; PATTERSON *et al.,* 1993).

Annual plants are often thought to be better adapted to the recovery of disturbed environments (PEMADASA *et al.,* 1974; WATKINSON, 1978). However, the post-overwash vegetative communities on Trinity Island were mainly dominated by perennial species such as *S. alterniflora* and *S. patens.* During the growing season following the hurricane, "islands" of *S. alterniflora* developed from a combination of vegetative regrowth of buried plants in conjunction with new seedling establishment. Seed recruitment on all zones of sand burial appeared to have been facilitated by nearby surviving species of the backbarrier marsh plant community. Adjacent plant communities have similarly been reported by others to be important in defining the species composition of colonizing veg-

Table 2. *Selected abiotic variables of soils sampled within each zone of deposition between plot type and sampling date. Variables presented as a mean with plus or minus standard error (n = 10).*

		Sample Date			
Zone	Treatment	Oct-93	Apr-94	Oct-94	Apr-95
Soil Moisture (%)					
High	Vegetated Fenced	19.23 ± 1.47	16.36 ± 1.90	23.68 ± 1.02	15.92 ± 1.81
	Vegetated Unfenced	18.27 ± 1.48	16.37 ± 1.82	22.42 ± 1.22	16.84 ± 2.59
	Non-vegetated Unfenced	17.77 ± 0.74	15.93 ± 1.25	22.25 ± 0.66	15.64 ± 1.07
Medium	Vegetated Fenced	37.52 ± 3.72	27.17 ± 1.54	28.90 ± 2.81	25.95 ± 2.23
	Vegetated Unfenced	34.86 ± 3.69	25.03 ± 1.03	27.26 ± 1.58	23.17 ± 1.20
	Non-vegetated Unfenced	34.99 ± 3.52	23.70 ± 1.04	24.98 ± 0.62	22.86 ± 1.20
Low	Vegetated Fenced	25.38 ± 1.23	27.37 ± 1.01	31.99 ± 1.84	35.14 ± 2.56
	Vegetated Unfenced	23.69 ± 1.21	24.77 ± 0.61	31.92 ± 1.12	34.74 ± 2.03
	Non-vegetated Unfenced	25.68 ± 1.21	25.16 ± 2.12	27.95 ± 1.35	32.51 ± 3.45
Reference	Vegetated Fenced	38.84 ± 4.68	33.31 ± 5.03	43.22 ± 4.00	48.46 ± 3.09
	Vegetated Unfenced	48.58 ± 7.24	40.41 ± 6.55	48.63 ± 7.96	49.45 ± 5.82
Soil Conductivity (mmhos/cm)					
High	Vegetated Fenced	0.48 ± 0.14	0.10 ± 0.02	0.17 ± 0.05	0.14 ± 0.03
	Vegetated Unfenced	0.45 ± 0.15	0.08 ± 0.01	0.20 ± 0.08	0.12 ± 0.03
	Non-vegetated Unfenced	0.59 ± 0.39	0.10 ± 0.03	0.22 ± 0.08	0.25 ± 0.08
Medium	Vegetated Fenced	3.35 ± 0.22	3.02 ± 0.83	4.70 ± 1.18	5.29 ± 1.07
	Vegetated Unfenced	3.64 ± 0.37	3.08 ± 0.95	4.76 ± 1.25	4.73 ± 1.34
	Non-vegetated Unfenced	5.92 ± 0.52	3.93 ± 1.00	4.75 ± 0.89	4.20 ± 0.72
Low	Vegetated Fenced	5.44 ± 1.18	4.19 ± 0.60	3.68 ± 0.28	4.95 ± 0.55
	Vegetated Unfenced	4.75 ± 1.01	3.61 ± 0.37	4.19 ± 0.24	5.07 ± 0.41
	Non-vegetated Unfenced	4.06 ± 0.77	7.05 ± 1.03	5.11 ± 0.45	7.03 ± 0.51
Reference	Vegetated Fenced	4.33 ± 0.44	4.10 ± 0.26	4.94 ± 0.52	4.14 ± 0.41
	Vegetated Unfenced	4.14 ± 0.49	6.45 ± 1.53	5.05 ± 0.82	4.31 ± 0.55
pH					
High	Vegetated Fenced	8.40 ± 0.06	8.43 ± 0.08	8.12 ± 0.10	8.22 ± 0.13
	Vegetated Unfenced	8.37 ± 0.09	8.38 ± 0.09	8.04 ± 0.09	8.24 ± 0.07
	Non-vegetated Unfenced	8.36 ± 0.07	8.58 ± 0.07	8.33 ± 0.11	8.25 ± 0.15
Medium	Vegetated Fenced	8.04 ± 0.11	8.16 ± 0.11	8.05 ± 0.07	7.96 ± 0.11
	Vegetated Unfenced	8.12 ± 0.08	8.30 ± 0.10	7.91 ± 0.11	8.01 ± 0.11
	Non-vegetated Unfenced	8.17 ± 0.02	8.49 ± 0.07	7.25 ± 0.03	8.14 ± 0.12
Low	Vegetated Fenced	7.94 ± 0.05	7.74 ± 0.07	7.33 ± 0.05	7.71 ± 0.08
	Vegetated Unfenced	7.89 ± 0.05	7.71 ± 0.08	7.91 ± 0.07	7.49 ± 0.07
	Non-vegetated Unfenced	8.13 ± 0.04	8.03 ± 0.07	7.84 ± 0.11	7.92 ± 0.06
Reference	Vegetated Fenced	7.68 ± 0.10	7.04 ± 0.09	7.75 ± 0.06	7.08 ± 0.09
	Vegetated Unfenced	7.47 ± 0.06	6.88 ± 0.10	7.59 ± 0.07	7.04 ± 0.05
Total Inorganic Nitrogen (mg/kg dry soil)					
High	Vegetated Fenced	0.37 ± 0.04	0.53 ± 0.06	0.18 ± 0.02	0.72 ± 0.13
	Vegetated Unfenced	0.38 ± 0.05	7.75 ± 0.12	0.25 ± 0.04	1.11 ± 0.36
	Non-vegetated Unfenced	0.24 ± 0.02	0.57 ± 0.10	0.11 ± 0.02	0.60 ± 0.12
Medium	Vegetated Fenced	1.02 ± 0.34	0.99 ± 0.34	0.17 ± 0.03	0.74 ± 0.09
	Vegetated Unfenced	0.81 ± 0.16	1.15 ± 0.51	0.23 ± 0.05	1.20 ± 0.41
	Non-vegetated Unfenced	3.15 ± 0.31	1.21 ± 0.25	0.42 ± 0.22	0.72 ± 0.14
Low	Vegetated Fenced	0.54 ± 0.08	1.30 ± 0.33	0.24 ± 0.07	1.98 ± 0.40
	Vegetated Unfenced	0.90 ± 0.31	1.04 ± 0.28	0.30 ± 0.05	2.50 ± 1.18
	Non-vegetated Unfenced	0.74 ± 0.28	2.73 ± 0.46	0.41 ± 0.05	2.04 ± 0.44
Reference	Vegetated Fenced	1.56 ± 0.49	0.55 ± 0.09	1.53 ± 0.58	1.85 ± 0.38
	Vegetated Unfenced	3.15 ± 0.85	0.97 ± 0.15	1.43 ± 0.41	1.82 ± 0.37
Phosphorus (mg/kg dry soil)					
High	Vegetated Fenced	53.83 ± 1.91	66.24 ± 4.28	68.86 ± 4.33	77.44 ± 4.28
	Vegetated Unfenced	54.26 ± 2.72	63.69 ± 4.31	63.29 ± 2.80	64.57 ± 4.93
	Non-vegetated Unfenced	51.41 ± 1.26	65.19 ± 5.84	69.76 ± 5.15	68.36 ± 3.62
Medium	Vegetated Fenced	79.44 ± 6.08	81.57 ± 5.52	68.98 ± 2.73	104.88 ± 8.73
	Vegetated Unfenced	78.00 ± 6.69	72.21 ± 3.78	84.72 ± 9.53	92.54 ± 18.00
	Non-vegetated Unfenced	77.42 ± 3.71	79.78 ± 3.99	108.00 ± 7.39	102.20 ± 6.58
Low	Vegetated Fenced	83.16 ± 6.81	77.79 ± 5.47	129.31 ± 4.95	131.87 ± 5.14
	Vegetated Unfenced	86.30 ± 6.64	78.03 ± 4.74	109.00 ± 6.10	121.86 ± 6.50
	Non-vegetated Unfenced	92.79 ± 5.51	90.90 ± 5.94	95.71 ± 13.52	120.80 ± 11.75
Reference	Vegetated Fenced	101.03 ± 9.57	119.70 ± 9.41	108.46 ± 7.34	181.87 ± 7.69
	Vegetated Unfenced	107.21 ± 12.31	132.13 ± 11.22	117.50 ± 6.69	186.47 ± 10.50

Table 3. *Canonical correlations between abiotic variables and percent cover by species. Canonical correlation and structure: squared canonical correlations, proportion of variance in common to the two variable sets that is explained by each variate pair and correlations of variables with complementary canonical variates.*

	Variate Pairs	
	First	Second
Correlations of variables with the complementary canonical variate		
Abiotic variables (8 out of 20 variables represented)		
Na	−0.47	−0.54
K	−0.62	—
Mg	−0.45	−0.57
Fe	−0.63	—
pH	0.52	—
Conductivity	—	−0.57
% Soil moisture	−0.53	−0.57
Elevation	0.92	—
% Cover by species (Biotic Variables) (5 species out of 31 represented)		
Avicennia germinans	—	−0.61
Hydrocotyle bonariensis	0.44	—
Spartina alterniflora	−0.69	0.60
S. patens	0.67	—
Vigna luteola	0.42	—
Squared canonical correlation	0.63	0.52
% Common variance explained by variate pair	41%	27%

etation within disturbed areas (DOING, 1985; CORDAZZO and SEELIGER, 1993).

The patchiness in vegetative colonization at the site was influenced by the differential recovery success of certain pre-storm plants (biotic affect) as well as debris deposited from the hurricane (abiotic affect). Both provided protected areas where seeds could become established (REIDENBAUGH and BANTA, 1980; HARTMAN *et al.,* 1983). Much of the successful colonization from seed recruitment was observed to be on the lee sides of shells, wrack, and previously established vegetation. This was especially true in the high and medium zones, where wind erosion was high and much of pre-existing vegetation died because of the storm effects.

The importance of vegetative lateral spread in colonization varied between zones. During the two-year study, plants in the high zone were able to colonize fairly rapidly from adjacent dune plants. Precipitation also quickly leached salts from the high zone soil. In the irregularly flooded areas of higher soil conductivities (medium and low zones), plants appear more stressed and were located much further from unstressed vegetation that could tiller and spread into the area. As a result, successful vegetative colonization of barren areas in the medium and low zones was greatly reduced. An exception, *D. spicata,* often invaded barren areas within the low zone solely from vegetative means. BERTNESS and ELLISON (1987) and BREWER and BERTNESS (1996) have similarly reported the importance of *D. spicata* in facilitating secondary succession in high marsh habitats via vegetative spread.

The number of plants found on the overwash site increased through time in all zones. More than half of all species found at the study site occurred on the new dune and swale environments of the high zone where soil salinity was lowest. Percentage cover followed a similar pattern in relation to the salt stress. The high zone also had the greatest percentage cover and largest increase in species richness over time, possibly because the high zone was less stressful in terms of salinity and flooding stresses. In general, species richness is low in highly stressful environments (MITCH and GOSSELINK, 1993; BARBOUR *et al.,* 1985; GOUGH *et al.,* 1994; BREWER *et al.,* 1997).

Importance values showed that in the high zone, the dominance of *S. alterniflora* decreased as other species became established. Although *S. alterniflora* was able to initially survive severe burial in the high zone, through time it decreased in vigor in this new higher elevation, lower soil moisture environment. Therefore, in the high zone, the overwash severely increased elevations and resulted in a shift in the back-barrier marsh plant community to one fairly typical of a rear dune and swale. This community was characterized by species such as *Baccharis halimifolia, Solidago sempervirens,* and *S. patens.*

Elevational gradients have been shown to affect zonation patterns of the pioneer plant communities (GODFREY, 1977; DE LEEUW *et al.,* 1993; YOUNG *et al.,* 1995). Site elevation was the primary factor determining plant zonation as supported by the results of the canonical correlation.

The area between the new dune plant community and the tidal marsh (*i.e.* the medium and low zones) received only infrequent tides. Reduction of tidal flushings created hypersaline conditions (DAY *et al.,* 1989; MITSCH and GOSSELINK, 1993), especially in these low and medium levels of sand burial (10 to 35 cm). In these zones, soil conductivities were slightly higher than those presently found in the backbarrier marsh reference zone. At both low and moderate levels of sand burial, halophytic species other than *S. alterniflora,* such as *D. spicata* and the succulents *S. bigelovii* and *S. virginica,* were better able to colonize and survive. Therefore, low to moderate sand deposition resulted in a shift of the plant community to communities more characteristic of high marsh and salt pan habitats.

Conductivities within the different plot treatments were similar in all zones except for the low zone. In this zone it appears that areas of vegetative cover adequately shaded the soil surface, reducing evaporation rates and thereby lowering soil conductivities (BERTNESS, 1992). The additional stresses associated with infrequent flushings and increased soil conductivities resulted in an obvious slowing of plant recovery after the storm.

Another factor that affects plant establishment is soil fertility (MENDELSSOHN, 1981; CUTSHALL, 1985). In coastal dune environments, nitrogen is often the most limiting soil nutrient (MONTEFERRANTE *et al.,* 1982; DOUGHERTY *et al.,* 1990; HESTER and MENDELSSOHN, 1992). However, soil nitrogen concentrations exhibited considerable variation along the sand burial gradient and indicated no discernable trend relative to the establishment of new vegetation.

Available phosphorus can also be a limiting nutrient in sandy environments (PATRICK *et al.,* 1985). However, soil concentrations of phosphorus were fairly high in all zones, indicating that phosphorus was probably not limiting on Trinity Island after the storm (DOUGHERTY *et al.*, 1990).

Although many wetland and barrier island areas of Louisiana are negatively affected by large populations of herbivores such as nutria, muskrat, and swamp rabbit (FULLER *et al.*, 1985; HESTER *et al.*, 1994), there was limited herbivory on Trinity Island. Vegetated fenced and unfenced plots maintained nearly identical vegetative composition and cover throughout the experiment. However, some signs of nutria herbivory were observed on the third and fourth sampling dates mainly on *Paspalum vaginatum* rhizomes, yet no grazing was observed in the research plots. Although grazing could slow recruitment of denuded areas, field observations indicate that herbivory had minor affects on this island. This could change should populations of herbivores increase.

A number of factors interacted to determine vegetative colonization and the resultant barrier island plant communities following extensive hurricane-induced overwash and sand burial of backbarrier marshes. Biotic factors such as seed dispersal and establishment and vegetative regrowth interacted within the abiotic constraints imposed by the post-overwash environment. We found that excessive overwash deposits (>50 cm) can drive plant secondary succession of a previous backbarrier marsh community to a more xeric dune plant community by creating an environment less conducive to the growth of *S. alterniflora* and more conducive to the recruitment and growth of *B. halimifolia, Fimbristylis castanea, Suaeda linearis,* and *S. patens.* Areas of intermediate overwash appear to be on a trajectory toward a high marsh/swale plant community, whereas areas of low sand deposition are expected to exhibit characteristics of a high marsh or salt pan habitat.

ACKNOWLEDGMENTS

The authors would like to express their gratitude to the U.S. Fish and Wildlife Service (USFWS) and the U.S. Biological Survey for the support that made this research possible. Special thanks must be given to Dr. Glenn Guntenspergen and Dr. James Grace for their input and interest in the Isles Dernieres work.

LITERATURE CITED

BARBOUR, M.G.; DE JONG, T.M., and PAVLIK, B.M., 1985. Marine beach and dune communities. *In:* CHABOT, B.F. and MOONEY, H.A. (ed.). *Physiological ecology of North American plant communities.* Chapman and Hall, New York, pp. 296–322.

BARBOUR, M.G.; REJMANEK, M.; JOHNSON, A.F., and PAVLIK, B.M., 1987. Beach vegetation and plant distribution patterns along the northern Gulf of Mexico. *Phytocoencia,* 15(2), 201–233.

BERTNESS, M.D., 1991. Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. *Ecology,* 72, 138–148.

BERTNESS, M.D., 1992. The ecology of a New England salt marsh. *American Scientist,* 8 (May/June), 260–268.

BERTNESS, M.D. and ELLISON, A.M., 1987. Determinants of pattern in a New England salt marsh plant community. *Ecological Monographs,* 57, 129–147.

BREWER, J.S. and BERTNESS, M.D., 1996. Disturbance and intraspecific variation in the clonal morphology of salt marsh perennials. *Oikos,* 77, 107–116.

BREWER, J.S.; LEVINE, J.M., and BERTNESS, M.D., 1997. Effects of biomass removal and elevation on species richness in a New England salt marsh. *Oikos,* 80, 333–341.

CORDAZZO, C.V. and SEELIGER U., 1993. Zoned habitats of southern Brazilian coastal foredunes. *Journal of Coastal Research,* 9(2), 317–323.

COSTA, C.S.B.; CORDAZZO, C.V., and SEELIGER, U., 1996. Shore disturbance and dune plant distribution. *Journal of Coastal Research,* 12(1), 132–140.

CUTSHALL, J.R., 1985. Vegetative establishment of smooth cordgrass (*Spartina alterniflora*) for shoreline erosion control. *Fourth Coastal Marsh and Estuary Management Symposium,* 1985, 63–69.

DAY, J.W.; HALL, C.A.S.; KEMP, W.M., and YANEZ-ARANCIBIA, A., 1989. *Estuarine Ecology.* New York: Wiley-Interscience, 558p.

DE LEEUW, J.; DE MUNCK, W.; OLFF, H., and BAKKER, J.P., 1993. Does zonation reflect the succession of salt marsh vegetation? A comparison of an estuarine and a coastal bar island marsh in The Netherlands. *Acta Bot. Neerl.,* 42(4), 435–445.

DOING, H., 1985. Coastal fore-dune zonation and succession in various parts of the world. *Vegetatio,* 61, 65–75.

DOUGHERTY, K.M.; MENDELSSOHN, I.A., and MONTEFERRANTE, F.J., 1990. Effect of nitrogen, phosphorus and potassium additions on plant biomass and soil nutrient content of a swale barrier strand community in Louisiana. *Annals of Botany,* 66, 265–271.

FAHRIG, L.; HAYDEN, B., and DOLAN, R., 1993. Distribution of barrier island plants in relation to overwash disturbance: A test of life history theory. *Journal of Coastal Research,* 9(2), 403–412.

FULLER, D.A.; SASSER, C.E.; JOHNSON, W.B., and GOSSELINK, J.G., 1985. The effects of herbivory on vegetation on islands in Atchafalaya Bay, Louisiana. *Wetlands,* 4, 105–114.

GODFREY, P.J., 1977. Climate, plant response and development of dunes on barrier beaches along the U.S. east coast. *International Journal of Biometeorology,* 21(3), 203–215.

GOUGH, L.; GRACE, J.B., and TYLOR, K.L., 1994. The relationship between species richness and community biomass: the importance of environmental variables. *Oikos,* 70, 271–279.

HARTMAN, J.; CASWELL, H., and VALIELA, I., 1983. Effects of wrack accumulation on salt marsh vegetation. *In:* Proceedings of the Seventh European Marine Biology Symposium, *Oceanologica Acta,* Special Issue, pp. 99–102.

HESTER, M.W. and MENDELSSOHN, I.A., 1991. Expansion patterns and soil physicochemical characterization of three Louisiana populations of *Uniola paniculata* (sea oats). *Journal of Coastal Research,* 7(2), 387–401.

HESTER, M.W. and MENDELSSOHN, I.A., 1992. *Texaco USA barrier island vegetation dynamics: Stabilization and maintenance projects on Timbalier Island.* 1992 Final Report. Wetland Biogeochemistry Institute, Louisiana State University, Baton Rouge, Louisiana.

HESTER, M.W.; WILSEY, B.J., and MENDELSSOHN, I.A., 1994. Grazing of *Panicum amarum* in a Louisiana barrier island dune plant community: Management implications for dune restoration projects. *Ocean & Coastal Management,* 23, 213–224.

MAUN, M.A., 1994. Adaptations enhancing survival and establishment of seedlings on coastal dune systems. *Vegetatio,* III, 59–70.

MENDELSSOHN, I.A., 1981. Sand dune vegetation and stabilization in Louisiana. *In: Proceedings of the Conferences on Coastal Erosion and Wetland Modification in Louisiana: Causes, Consequences and Options.* Oct. 5–7, 1981, 107–207.

MITSCH, W.J. and GOSSELINK, J.G., 1993. *Wetlands.* New York: Van Nostrand Reinhold, 722p.

MONTEFERRANTE, F.J.; MENDELSSOHN, I.A., and HESTER, M.W., 1982. Vegetative investigation for the management of barrier islands and beaches in Louisiana. *In: Proceedings of Coastal Society 8,* Oct. 12, 1982, 231–236.

OLFF, H.; HUISMAN, J., and VAN TOOREN, B.F., 1993. Species dynamics and nutrient accumulation during early primary succession in coastal sand dunes. *Journal of Ecology,* 81, 693–706.

OLSON, J.S., 1957. Rates of succession and soil changes on southern Lake Michigan sand dunes. *Botanical Gazette,* 119, 125–169.

OOSTING, H.J. and BILLINGS, W.D., 1942. Factors effecting vegetational zonation on coastal dunes. *Ecology,* 23, 131–142.

PATRICK, W.H.; MIKKELSEN, D.S., and WELLS, B.R., 1985. Plant nutrient behavior in flooded soil. *Fertilizer Technology and Use.* Soil Science Society of America. 197–228.

PATTERSON, C.S. and MENDELSSOHN, I.A., 1991. A comparison of physicochemical variables across plant zones in a mangal/salt marsh community in Louisiana. *Wetlands*, 11(1), 139–161.

PATTERSON, C.S.; MENDELSSOHN, I.A., and SWENSON, E.M., 1993. Growth and survival of *Avicennia germinans* seedlings in a mangal/salt marsh community in Louisiana, U.S.A. *Journal of Coastal Research*, 9(3), 801–810.

PEMADASA, M.S.; GREIG-SMITH, P., and LOVELL, P.H., 1974. A quantitative description of the distribution of annuals in the dune system at Aberffraw, Anglesey. *Journal of Ecology*, 62, 379–402.

REIDENBAUGH, T.G. and BANTA, W.C., 1980. Origin and effects of tidal wrack in a Virginia salt marsh. *Gulf Research Reports*, 6, 393–401.

ROBERTSON, G.P., 1982. Factors regarding nitrification in primary and secondary succession. *Ecology*, 63, 1561–1573.

ROBERTSON, G.P. and VITOUSEK, P.M., 1991. Nitrification potentials in primary and secondary succession. *Ecology*, 62, 376–386.

SAS, 1985. *SAS User's Guide: Statistics.* Cary, North Carolina. SAS Institute, Inc.

STONE, G.W.; GRYMES, J.M.; ROBBINS, K.D.; UNDERWOOD, S.G.; STEYER, G.D., and MULLER, R.A., 1993. A chronologic overview of climatological and hydrological aspects associated with Hurricane Andrew and its morphological effects along the Louisiana coast, U.S.A. *Shore and Beach*, 61(2), 2–12.

U.S. ENVIRONMENTAL PROTECTION AGENCY, 1979. *Methods for chemical analysis of water and wastes.* Environmental Monitoring and Support Laboratory, Cincinnati, Ohio. EPA-600/4-79-020.

VAN DER MEIJDEN, E. and VAN DER WAALS-KOOI, R.E., 1979. The population ecology of *Senecio jacobaea* in a sand dune system. I. Reproductive strategy and the biennial habit. *Journal of Ecology*, 67, 131–153.

VAN DER VALK, A.G., 1975. Ecological investigations of the foredune vegetation of Cape Hatteras National Seashore. *Chesapeake Science*, 16, 115–126.

WATKINSON, A.R., 1978. The demography of a sand dune annual, *Ulpia fasciculata.* III. The dispersal of seeds. *Journal of Ecology*, 66, 483–498.

WATKINSON, A.R. and DAVY, A.J., 1985. Population biology of salt marsh and sand dune annuals. *Vegetatio*, 62, 487–497.

WILSEY, B.J.; MCKEE, K.L., and MENDELSSOHN, I.A., 1992. Effects of increased elevation and macro- and micronutrient additions on *Spartina alterniflora* transplant success in salt marsh die-back areas in Louisiana. *Environmental Management*, 16(4), 505–511.