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The Role of Seed Banks, Disturbance, and Sea Level Rise in Determining the Plant Community Structure of Oligohaline Coastal Marshes.

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THE ROLE OF SEED BANKS, DISTURBANCE, AND SEA LEVEL RISE
IN DETERMINING THE PLANT COMMUNITY STRUCTURE
OF OLIGOHALINE COASTAL MARSHES

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Plant Biology

by
Andrew Hamilton Baldwin
B.S., Tufts University, 1983
August 1996

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TABLE OF CONTENTS

ACKNOWLEDGEMENTS	iii
ABSTRACT	vi
CHAPTER	
1 INTRODUCTION	1
2 THE INFLUENCE OF VEGETATION, SALINITY, AND INUNDATION ON SEED BANKS OF OLIGOHALINE COASTAL MARSHES	9
3 COMMUNITY RESPONSES TO DISTURBANCE INTENSITY IN OLIGOHALINE MARSHES	38
4 EFFECTS OF SALINITY AND INUNDATION ON COASTAL MARSHES: DISTURBANCE AS A CATALYST FOR VEGETATION CHANGE	80
5 SUMMARY AND CONCLUSIONS	108
LITERATURE CITED	116
APPENDIX: LETTER OF PERMISSION	128
VITA	130

ABSTRACT

Coastal wetlands worldwide are threatened by sea level rise, which is expected to affect the growth and survival of wetland vegetation by increasing water level and salinity. While the effects of salinity and inundation on adult vegetation of oligohaline marshes have been widely studied, the species composition of the seed bank and its response to elevated salinity and water level have not been examined. Additionally, the role of disturbances of different intensities in structuring marsh plant communities and possible interactions between disturbance and rising sea level have received little attention. Disturbances in coastal marshes include nonlethal disturbances such as fire and herbivory (which can remove aboveground vegetation but leave rhizomes intact), and lethal disturbances such as wrack deposition, sedimentation, scouring, or fire or herbivory followed by flooding.

I conducted a series of experiments to examine the role of seed banks, disturbance, and sea level rise in structuring the plant communities of oligohaline marshes in coastal Louisiana, USA. I found that seed banks of three oligohaline marsh communities were similar despite differences in the adult vegetation, and that higher salinity or water level reduced the germination of most species. In a field experiment lethal disturbances promoted the establishment of species via seedling recruitment, leading to persistent changes in community composition. Regeneration following less intense nonlethal disturbances, however, was primarily via vegetative growth which quickly restored the pre-disturbance community structure. The effects

of salinity and inundation on community structure in greenhouse mesocosms were greater and occurred more rapidly following disturbance than occurred in the absence of disturbance. Disturbance coupled with both higher water level and salinity killed almost all vegetation.

These results suggest that regeneration patterns in oligohaline marshes are a function of seed banks, disturbance intensity, and salinity and water level. Higher salinity and water level associated with sea level rise may inhibit seedling recruitment or vegetative growth following disturbance, resulting in shifts in species composition or wetland loss. Understanding the effects of salinity and inundation on patterns of regeneration following disturbance is critical to predicting the responses of coastal marsh communities to rising sea level.

CHAPTER 1

INTRODUCTION

The effects of global climate change and sea level rise on coastal wetland ecosystems may be ecologically and economically disastrous, and the ecological consequences of changes in global climate have been identified as a research priority (Lubchenco et al., 1991). Sea level has risen at an estimated rate of 1.0-2.0 mm/yr over the last 100 yr, and is expected to increase an additional 48 cm by the year 2100 (Barnett, 1990; Gornitz, 1993; Woodworth, 1993; Gornitz, 1995). Global sea level is sensitive to long-term climatic variations in climate, and future increases in sea level are predicted based on estimated global atmospheric warming of 2-5 °C over the next 1000 years associated with increasing concentrations of carbon dioxide (CO₂) and other greenhouse gases (Gornitz, 1995). Global warming increases sea level through thermal expansion of ocean water and melting of large ice sheets, mountain glaciers, and small ice caps (Geophysics Study Committee, 1990).

In some areas of coastal Louisiana, rates of relative sea level rise are nearly 10 times the eustatic rate due to the effects of compactional subsidence of Holocene sediments (Boesch et al., 1994; Gornitz, 1995). Estimated rates of relative sea level rise in the delta plain range from 0.33-1.31 cm/yr, and an increase in relative sea level of 150-200 cm over the next century is predicted for coastal Louisiana (Penland et al., 1989). In addition to problems related to subsidence, a natural

process, the deltaic plain has been extensively altered by construction of levees, canals, and other structures that have deprived coastal marshes of sediment and nutrients and increased saltwater intrusion (Mendelssohn et al., 1983; Gosselink, 1984; Boesch et al., 1994). The combined effect of subsidence, eustatic sea level rise, and anthropogenic activities are thought to be responsible for estimated rates of wetland loss in coastal Louisiana of 65.6 km²/yr (Britsch and Dunbar, 1993; Boesch et al., 1994).

Wetland deterioration is occurring across the range of wetland types in Louisiana's coastal zone; however, low-salinity marshes are experiencing some of the greatest losses (Leibowitz, 1989) because they are susceptible to increases in salinity as well as rising water levels (McKee and Mendelssohn, 1989). Low-salinity marshes include tidal fresh marshes, which have salinity levels of < 0.5 parts per thousand (ppt), and oligohaline marshes, which have salinities of 0.5 - 5 ppt (according to the classification system of Cowardin et al., 1979). The oligohaline salinity modifier corresponds roughly to the intermediate marsh type category, which is based on vegetation associations described by Penfound and Hathaway (1938) and Chabreck (1972) rather than on salinity level (Gosselink, 1984). The more saline marsh types and their salinity modifiers are brackish marsh (mesohaline, 5 - 18 ppt salinity) and salt marsh (polyhaline, 18 - 30 ppt salinity) (Cowardin et al., 1979; Gosselink, 1984).

In addition to causing wetland loss, higher relative sea level may result in shifts in vegetation composition from salt-intolerant to salt-tolerant species.

Salinization of interior marshes is thought to have caused an observed increase in saline and brackish marsh types of 433 km² in coastal Louisiana from 1968-78 and an equivalent decrease in the extent of less saline marsh types (Boesch et al., 1994). Greater increases in salinity occurred in wetlands where input of fresh water was reduced by levees or near dredged canals that facilitated saltwater intrusion.

In coastal marshes of the Gulf of Mexico, conversion from intermediate to brackish marsh may occur when communities dominated by the relatively salt-intolerant species Sagittaria lancifolia L. (bulltongue) are replaced by communities dominated by the more salt-tolerant species Spartina patens Ait. Muhl. (marsh hay cordgrass). Intermediate marshes are generally more species-rich than brackish marshes (Chabreck, 1972), meaning that conversion to the more salt-tolerant community represents a reduction in biological diversity.

While conversion to more saline marsh types under high rates of relative sea level rise makes intuitive sense, the mechanisms of community conversion are complex and not well-understood. First, salinity levels do not increase linearly or gradually, but are thought to increase in "pulses" as a result of storm winds pushing saline water inland into low-salinity marshes (Brewer and Grace, 1990; Grace and Ford, 1996). These salt pulses sometimes cause dieback of the aboveground parts of salt-intolerant marsh vegetation (e.g., Guntenspergen et al., 1995). Second, patterns of regeneration via seedling recruitment and vegetative growth in marsh species following salt pulses or other disturbances, while likely to be important in predicting the response of marsh plant communities to sea level rise, have received little

attention. Regeneration may also be affected by sea level rise, favoring species capable of seedling recruitment or vegetative growth under conditions of elevated salinity or water level, or leading to wetland loss if conditions unsuitable for regeneration are present at the time of a disturbance. And finally, competitive interactions among plant species may influence community composition differently if salinities or water levels are higher than they are now. More stress-tolerant species may be weaker competitors (e.g., Grace and Wetzel, 1981; Bertness and Ellison, 1987; Bertness, 1991a,b), and increases in water level or salinity may favor adults of more salt-tolerant or flood-tolerant species. The changes in marsh plant communities that occur as sea level rises may, therefore, be due to interactions between mechanisms of regeneration, environmental variables, and natural and anthropogenic disturbance, as well as the physiological tolerance of adult plants to salinity and inundation.

As part of my dissertation research I conducted a series of experiments to investigate the importance of regeneration, disturbance, and environmental variables in structuring oligohaline marsh communities under a sea level rise scenario. This included two growth chamber studies, a two-year field study, and a one-year greenhouse study. These experiments are described in Chapters 2, 3, and 4 of this dissertation; Chapter 5 presents my overall conclusions drawn from this research.

Chapter 2 describes two growth chamber experiments I conducted on the soil seed bank (buried viable seeds and propagules) of oligohaline marshes. Seed banks are important to the development, regeneration, and maintenance of vegetation in

many plant communities (Grubb, 1977; Fenner, 1985; Parker et al., 1989; Middleton et al., 1991), including tidal marshes (Leck and Graveline, 1979; Parker and Leck, 1985; Leck and Simpson, 1987). However, the species composition of seed banks of oligohaline marshes has not been described, nor have the effects of elevated water level and salinity on seedling emergence from oligohaline marsh seed banks been investigated. In the first experiment described in Chapter 2 I characterized the species composition of seed banks and vegetation in three oligohaline marsh communities. Because seeds may be more widely dispersed among vegetation types than adults (Parker and Leck, 1985; Wilson et al., 1993), I hypothesized that the seed banks of the three communities would be similar in composition despite differences in emergent vegetation. The second experiment examined how differences in salinity and water level modified emergence of seedlings from the seed bank. Salinity and flooding have been found to reduce seed germination in other wetland systems (Ungar, 1978; van der Valk and Davis, 1978; Galinato and van der Valk, 1986; Shumway and Bertness, 1992), so I hypothesized that seedling emergence would be reduced at higher salinity levels and under flooded conditions.

In Chapter 3 I describe a two-year field study which investigated the effects of disturbance intensity on patterns of regeneration of vegetation in two oligohaline marsh communities. Along with disturbance frequency, predictability, areal extent, and rotation period, the intensity of disturbance has been recognized as an important descriptor of disturbance regimes (Connell, 1978; Malanson, 1984; Sousa, 1984;

Pickett and White, 1985; Glenn-Lewin and van der Maarel, 1992). Disturbances in coastal marshes vary widely in their intensity and include fire, herbivory, wrack deposition, salt water intrusion, hurricanes, sedimentation, and oil spills (Bertness and Ellison, 1987; Mendelssohn et al., 1990; Flynn et al., 1995; Guntenspergen et al., 1995; Nyman and Chabreck, 1995; Taylor and Grace, 1995; and others).

However, the effects of intensity of disturbance on regeneration in marshes have received little attention, despite the potential for disturbance to aggravate the effects of sea level rise. Because the critical threshold for intensity of disturbance may be whether the disturbance kills the vegetation or only removes a portion of the vegetation, in this experiment I subjected vegetation in two marsh communities (one dominated by Spartina patens and the other by Sagittaria lancifolia) to three disturbance treatments (undisturbed, nonlethal disturbance, and lethal disturbance) and monitored patterns of regeneration. In the nonlethal disturbance aboveground vegetation was clipped and in the lethal disturbance vegetation was killed using herbicide. I hypothesized that the stability and resilience (sensu Underwood, 1989) of the marsh community would vary as a function of disturbance intensity and pre-disturbance community structure, and that colonization would be primarily via seedling recruitment in the lethal disturbance treatment and via vegetative propagation in the nonlethal treatment.

The objective of the greenhouse experiment I describe in Chapter 4 was to examine the role of disturbance in vegetation change under different salinity and inundation regimes. Some studies have suggested that changes in salinity and water

level may have a greater effect on community structure if marsh vegetation is disturbed than in the absence of disturbance (Flynn et al., 1995; Grace and Ford, 1996). Additionally, disturbance may accelerate the conversion of low-salinity marsh types to brackish or saline marsh types by creating gaps in the vegetation that stimulate recruitment (see Chapter 3; Pickett and White, 1985; van der Valk, 1992), and the species recruited may depend on salinity and water level (see Chapter 2). However, previous studies have not determined whether disturbance results in greater response of community structure to salinity and inundation than would occur in the absence of disturbance and, if this is true, whether species with differential tolerance to salinity and inundation are favored under different salinity and inundation regimes. In my greenhouse experiment I exposed mesocosms of oligohaline marsh communities, each containing two half-sections of soil and vegetation from adjoining plant communities (one dominated by Sagittaria lancifolia and the other by Spartina patens), to two levels each of disturbance (disturbed and undisturbed), salinity (fresh and saline), and inundation (flooded and nonflooded) in a factorial arrangement. I hypothesized that the effects of salinity and inundation on community structure would be greater in disturbed treatments, and that disturbance might result in more rapid shifts in the abundance of the community dominants than would occur without disturbance.

In summary, while the responses of adult plants to salinity and inundation may be important in understanding the response of oligohaline marshes to rising sea level, review of the literature suggests that disturbance and regeneration may also be

of considerable importance. In my dissertation research I have investigated the mechanisms of regeneration of oligohaline marsh species following disturbance, the influence of environmental variables on patterns of regeneration, and the role of disturbance in vegetation change under a sea level rise scenario. I hope that the findings of my research further our understanding of the dynamics of coastal marshes under conditions of rising sea level and in finding management solutions to address this global problem.

CHAPTER 2

THE INFLUENCE OF VEGETATION, SALINITY, AND INUNDATION ON SEED BANKS OF OLIGOHALINE COASTAL MARSHES*

INTRODUCTION

Understanding the relationships among seed banks, vegetation, and environmental conditions may be important in predicting the effects of sea level rise on plant communities of coastal oligohaline marshes. The importance of the soil seed bank (buried viable seeds and propagules) to the development, regeneration, and maintenance of vegetation in many plant communities has been recognized (Grubb, 1977; Fenner, 1985; Parker et al., 1989; Middleton et al., 1991), and noted specifically for tidal freshwater marshes in New Jersey (Leck and Graveline, 1979; Parker and Leck, 1985; Leck and Simpson, 1987; Leck and Simpson, 1994; Leck and Simpson, 1995). However, no one has examined the role of seed bank dynamics in controlling the response of coastal marsh plant communities to elevated water levels and salinities, which are anticipated due to an estimated increase in global sea level of 46-100 cm by the year 2100 (Warrick, 1993; Boesch et al., 1994). In coastal Louisiana, where subsidence of Holocene sediments decreases marsh elevation, sea level relative to the marsh surface may increase 150-200 cm over the next century (Penland et al., 1989). An increase of 433 km² of brackish

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and salt marsh types (and an equivalent loss of less saline marshes) in coastal Louisiana between 1968 and 1978 has been attributed to salt water intrusion associated with high rates of relative sea level rise (Boesch et al., 1994).

Increases in water level and salinity may affect recruitment from the seed bank. Salinity and flooding have been found to decrease seed germination in a variety of wetland plant species (Ungar, 1978; van der Valk and Davis, 1978; Galinato and van der Valk, 1986; Shumway and Bertness, 1992; Poljakoff-Mayber et al., 1994). Additionally, the abundance of buried seeds may be affected by the presence or absence of standing vegetation (Smith and Kadlec, 1985a), suggesting that the composition of the seed bank may differ between vegetated areas and the patches of open water typical of deteriorating coastal marshes (Boesch et al., 1994). Seed bank composition may also vary among wetland types, although seeds may be more widely dispersed among vegetation types than adults (Parker and Leck, 1985; Wilson et al., 1993).

We asked three main questions relevant to the effects of vegetation, salinity, and inundation on seed bank dynamics of oligohaline marshes. First, how does the species composition of seed banks differ among three oligohaline marsh communities? Second, does the composition of the seed bank differ between vegetated and nonvegetated (i.e., open water or mud flat) areas? And third, how do salinity and inundation affect the viability and germination of buried seeds in oligohaline coastal marshes? We conducted two experiments to address these questions, the first experiment to study the relationships between seed banks and

vegetation, and the second to examine the effects of salinity and inundation on recruitment from the seed bank. In this second experiment we investigated both the effects of a temporary increase in salinity (to simulate a salt water intrusion event) on the viability of buried seeds as well as the effects of salinity on seed germination.

MATERIALS AND METHODS

Field site

Seed banks were studied in three tidal marsh communities in the deltaic plain of the Mississippi River (LaFourche Parish, Louisiana, USA; 29°30'N, 90°25'W). The three marsh communities, which are dominated by Paspalum vaginatum Sw. (Poaceae), Sagittaria lancifolia L. (Alismataceae), or Spartina patens (Ait.) Muhl. (Poaceae), respectively, are located within ≈ 7 km of each other and are classified as oligohaline (0.5-5 ppt salinity; Cowardin et al., 1979). Mean interstitial water salinity \pm SE (N) between May 1991 and September 1992 was 3.4 ± 0.5 ppt (10) for the Paspalum vaginatum community, 2.3 ± 0.4 ppt (20) for the Sagittaria lancifolia community, and 3.8 ± 0.4 (20) for the Spartina patens community (E. Webb, Louisiana State University, personal communication). The region is experiencing wetland deterioration, evident as small (generally < 5 m diameter) pools of open water or tidally-exposed mud flats interspersed among stands of vegetation. Approximate mean monthly temperatures for the region range from 14 C in December/January (freezing temperatures do occur infrequently in winter) to 30 C in July/August, and annual precipitation is ≈ 160 cm (Gosselink, 1984).

Relationships between seed banks and vegetation

Seed banks and vegetation were sampled at 20 plots in each of the three marsh communities on 16 November 1992 (total = 60 plots), a time of year following seed dispersal in most species at our study sites. Within each community, ten plots were located in areas containing emergent vegetation ("vegetated") and ten plots were located in open water or mud flat areas where emergent vegetation was mostly absent ("nonvegetated"). The vegetated and nonvegetated plots were in pairs, generally within 5 m of each other, and the ten pairs of plots in each community were established along transects 0.5-1.5 km long.

Each seed bank sample consisted of five cores of marsh soil collected within a 1-m² area, combined in the field to yield one composite sample at each plot. The coring device was a 5 cm long aluminum pipe of 4.76 cm inner diameter, yielding a sampling area of 17.8 cm² and a sampling volume of 89 cm³ per core (for 5 cores, total area = 89 cm² and total volume = 445 cm³). Composite sampling was performed to minimize small-scale heterogeneity; a large number of small sampling units appears to be more appropriate than a few large sampling units for seed bank studies (Simpson et al., 1989; Warr et al., 1993). The depth of 5 cm was selected because of the importance of surficial seeds for recruitment and to be consistent with work by other authors (van der Valk and Davis, 1978; Keddy and Reznicek, 1982; Hopkins and Parker, 1984; Parker and Leck, 1985; Hartman, 1988; Poiani and Johnson, 1988; Grelsson and Nilsson, 1991; and others).

Vegetation was described on 16 November 1992 by visually estimating percent of total area covered by each species in 1-m² quadrats adjoining each of the 60 plots where seed bank samples were collected. The time of year vegetation was sampled provided representative sampling of the dominant perennials but may have missed certain annual species, based on comparison with long-term studies conducted in the same communities (E. Webb, Louisiana State University, unpublished data).

The seed bank samples were transported to Louisiana State University and stored in darkness at 4 C for 2 d, at which time the samples were processed. Refrigeration of seed bank samples until processing is a common procedure (e.g., van der Valk and Davis, 1978; Wilson et al., 1993; and others) and was not expected to affect the viability of buried seeds given that low winter temperatures do occur periodically at our study sites. Living (white) roots and coarse organic material were removed, scraping off soil and checking for any adhering seeds before discarding. Each sample was then mixed thoroughly and spread in a layer \approx 1.3 cm thick on the surface of sand in labeled plastic pots (11 cm diameter) with slits cut in the pot sides near the bottom for drainage.

The pots, containing soils from vegetated or nonvegetated sites in each of the three communities, were subjected to flooded and nonflooded conditions in plastic tanks (26.5 liters) in a walk-in growth chamber maintained at a 30 C day/25 C night thermoperiod and 14-hr light/10-hr dark photoperiod. Light and alternating high temperatures have been reported to increase percentage germination in wetland

species (Galinato and van der Valk, 1986). Flooded treatments were implemented by maintaining the tank water level 4-5 cm above the soil surface. Nonflooded treatments were implemented by elevating the pots within the tanks so that the resulting water level was maintained 1-2 cm below the soil surface. The experimental design used was a $3 \times 2 \times 2$ factorial in a randomized block: all 12 possible combinations of community type, vegetation state, and inundation regime were placed randomly in each of ten tanks (blocks), which were randomly placed in the growth chamber. Tank water levels and minimum and maximum temperatures in the growth chamber were checked (and adjusted if necessary) every 2 d for the duration of the experiment.

Seedlings emerging from the marsh soils were counted daily for the first 12 d and then every other day for 16 d (to monitor emergence rates), during which time little additional seedling emergence was occurring. The seedlings were allowed to grow an additional 20 d to facilitate species identification (time elapsed = 48 d), and a final count of seedlings of each species made. While it was possible to identify most seedlings as distinct species at an early age (usually after the first true leaves emerged), taxonomic identification to species level was generally not possible until flowering. Five seedlings of each species (or fewer for rare species) were transplanted to a commercial potting mixture in plastic containers and grown until flowering in the greenhouse. All seedlings were identified to species level, and voucher specimens were placed in the Herbarium of Louisiana State University.

The technique of collecting soils and exposing them to favorable germination conditions in a greenhouse or growth chamber (the "emergence method"), has been found to provide an accurate measure of wetland seed bank composition, particularly if flooded as well as nonflooded treatments are incorporated (Poiani and Johnson, 1988). Additionally, germination methods have been found to provide a more complete listing of species present than other methods (Gross, 1990).

Influence of salinity and inundation on seedling emergence

Approximately 38 liters of marsh soil was collected from the top 5 cm of the surface of the Sagittaria lancifolia community using aluminum corers on 16 November 1992. Coarse organic matter was removed from the soil, which was then mixed thoroughly and divided into five separate containers. Instant Ocean (Aquarium Systems, Inc., Mentor, OH) was added to these containers to create five "pretreatment" salinity concentrations (0, 2, 4, 8, and 16 ppt), and the treated soils stored in the dark at 4 C (to reduce bacterial and fungal activity). The purpose of the pretreatment was to assess the effects of a temporary increase in salinity (such as might occur during a salt water intrusion event) on the viability of buried seeds. After 2 mo, the soils were transferred to plastic pots and exposed to two water levels (flooded and nonflooded) and five "germination" salinities (0, 2, 4, 8, and 16 ppt) in tanks in a growth chamber. Each tank contained the ten pretreatment \times inundation treatment combinations, and there were three tanks for each level of germination salinity (150 experimental units total). Pots were flushed first with tap water (\approx 400 ml) to reduce and equalize salinities and then with water of the

appropriate germination salinity before placing them in tanks. Water level was maintained 3-4 cm below the soil surface of the nonflooded treatments and 4-5 cm above the soil surface of the flooded treatments. Plastic pots, tanks, water levels, and growth chamber environmental settings were identical to those described previously. The number of seedlings of each species in each experimental unit was determined after 5 wk.

The experimental design was a split-plot with three fixed experimental factors in a $5 \times 5 \times 2$ factorial arrangement (five pretreatment salinity levels, five germination salinity levels, and two inundation levels). Germination salinity was the wholeplot factor (three tanks at each of five germination salinity levels) and pretreatment salinity and inundation were the subplot factors (all ten treatment combinations of pretreatment salinity and inundation were in each of the 15 germination salinity tanks).

Data analysis

Analyses were performed on final count data for the numbers of seedlings of all species emerging from marsh soils and on vegetation cover data. Data were analyzed using the SAS statistical package (SAS, 1990), and a significance level of $P = 0.05$ was used in interpreting results of statistical tests unless otherwise noted.

For the seed bank and vegetation experiment, data on the number of seedlings of each species in seed bank samples were first converted to density (number per square meter based on surface area of original cores) to facilitate comparison with other studies. These data were summarized by calculating mean

and standard error for flooded and nonflooded treatments and vegetated and nonvegetated areas for each of the three communities. Additionally, the antilog of the Shannon-Weaver species diversity index (the number of equally common species that would yield the same index value as that actually observed; Peet, 1974) was calculated using relative frequency data, and species richness (number of species) tabulated. Analyses were performed on the actual numbers of seedlings observed for the salinity and inundation experiment.

Analysis of variance (ANOVA) was conducted on species richness and seedling abundance data. When three-way interactions were significant, the two-way treatment structures were analyzed for each level of the third factor. Tukey's Studentized Range test was used to compare treatment means in the seed bank and vegetation experiment, and the multiple comparison procedure for split-plot designs (Milliken and Johnson, 1992) with a Bonferroni correction used to compare least squares means in the salinity and inundation experiment. The experimentwise error rate for the Bonferroni comparisons was controlled at 0.1 because many comparisons were made, resulting in a low comparisonwise error rate (Milliken and Johnson, 1992). Least squares means were necessary for the salinity and inundation experiment because of removal of an outlier (abnormal value) identified during data set diagnostics. The outlier was caused by high seedling mortality in one experimental unit subjected to 0 ppt salinity and nonflooded conditions due to an unknown cause (possibly fungal infection). Analyses of seedling numbers were limited to species comprising $\geq 1\%$ of the total number of seedlings because the

low number of occurrences for the rarer species prevented meaningful statistical examination of treatment effects. Seedling abundance data were log transformed [$\ln(x+1)$] to reduce heterogeneity of variances.

Percent cover data for vegetation were summarized by calculating mean and standard error for vegetated and nonvegetated areas for the three communities. Additionally, the antilog of the Shannon-Weaver index (Peet, 1974) and species richness were determined.

RESULTS

Relationships between seed banks and vegetation

The seed banks of the three communities had similar species richness and diversity, and exhibited considerable overlap in species composition (Table 2.1). Out of a total of 15 seed bank species observed, 11 occurred in at least two communities and five occurred in all three communities. Species richness and diversity of vegetation were lower, approaching the richness and diversity of the seed bank only in the Sagittaria lancifolia community. Although Paspalum vaginatum and Spartina patens were present at high relative frequencies in the vegetation of their communities, they were not observed in the seed bank.

Flooding significantly reduced species richness (Fig. 2.1; $P < 0.00001$) as well as seedling numbers for most species (Tables 2.2 and 2.3). The exceptions were Eleocharis parvula and Sagittaria lancifolia, for which the effect of inundation was not significant (Table 2.3).

Table 2.1. Relative frequency (%) of plant species in the seed bank and standing vegetation of three oligohaline marsh communities. Species richness and antilog Shannon-Weaver (S-W) diversity tabulated below each column. P = perennial, A = annual, F = floating. Nomenclature according to Kartesz (1994).

Species	Community type					
	<u>Paspalum vaginatum</u>		<u>Sagittaria lancifolia</u>		<u>Spartina patens</u>	
	Seed bank	Vegetation	Seed bank	Vegetation	Seed bank	Vegetation
<u>Amaranthus australis</u> (Gray) Sauer (A)	1.47				6.45	
<u>Ammannia latifolia</u> L. (A)	5.88				21.0	
<u>Bacopa monnieri</u> (L.) Pennell (P)	19.1	23.3	19.2	23.2	12.9	
<u>Cyperus odoratus</u> L. (A)	7.35	3.33	5.48		11.3	
<u>Echinochloa crus-galli</u> (L.) Beauv. (A)	1.47		1.37			
<u>Eclipta prostrata</u> (L.) L. (A)			1.37			
<u>Eleocharis fallax</u> Weatherby (P)	11.8		2.74		1.61	
<u>Eleocharis parvula</u> (Roemer & J.A.Schultes) Link ex Bluff, Nees & Schauer (P)	23.5		11.0		33.9	5.56
<u>Eleocharis</u> sp. (P)				5.36		
<u>Hydrocotyle</u> sp. (P)				1.79		
<u>Lemna minor</u> L. (F)	1.47		9.59			
<u>Leptochloa fascicularis</u> (Lam.) Gray (A)	23.5		8.22		4.84	
<u>Ludwigia leptocarpa</u> (Nutt.) Hara (P)	2.94					
<u>Lythrum lineare</u> L. (P)	1.47				3.23	11.1
<u>Paspalum vaginatum</u> Sw. (P)		66.7				
<u>Phyla nodiflora</u> (L.) Greene (P)		6.67		8.93		
<u>Pluchea odorata</u> (L.) Cass. var. <u>odorata</u> (A)					1.61	
<u>Ranunculus sceleratus</u> L. (A)			4.11			

(table con'd)

Species	Community type					
	<u>Paspalum vaginatum</u>		<u>Sagittaria lancifolia</u>		<u>Spartina patens</u>	
	Seed bank	Vegetation	Seed bank	Vegetation	Seed bank	Vegetation
<u>Sacciolepis striata</u> (L.) Nash (P)				21.4		
<u>Sagittaria lancifolia</u> L. (P)			37.0	25.0	3.23	
<u>Salvinia minima</u> Baker (F)				14.3		
<u>Scirpus americanus</u> Pers. (P)						5.56
<u>Spartina alterniflora</u> Loisel (P)						5.56
<u>Spartina patens</u> (Ait.) Muhl. (P)						72.2
Species richness	11	4	10	7	10	5
Antilog (S-W diversity)	7.10	2.47	6.45	5.69	6.57	2.07

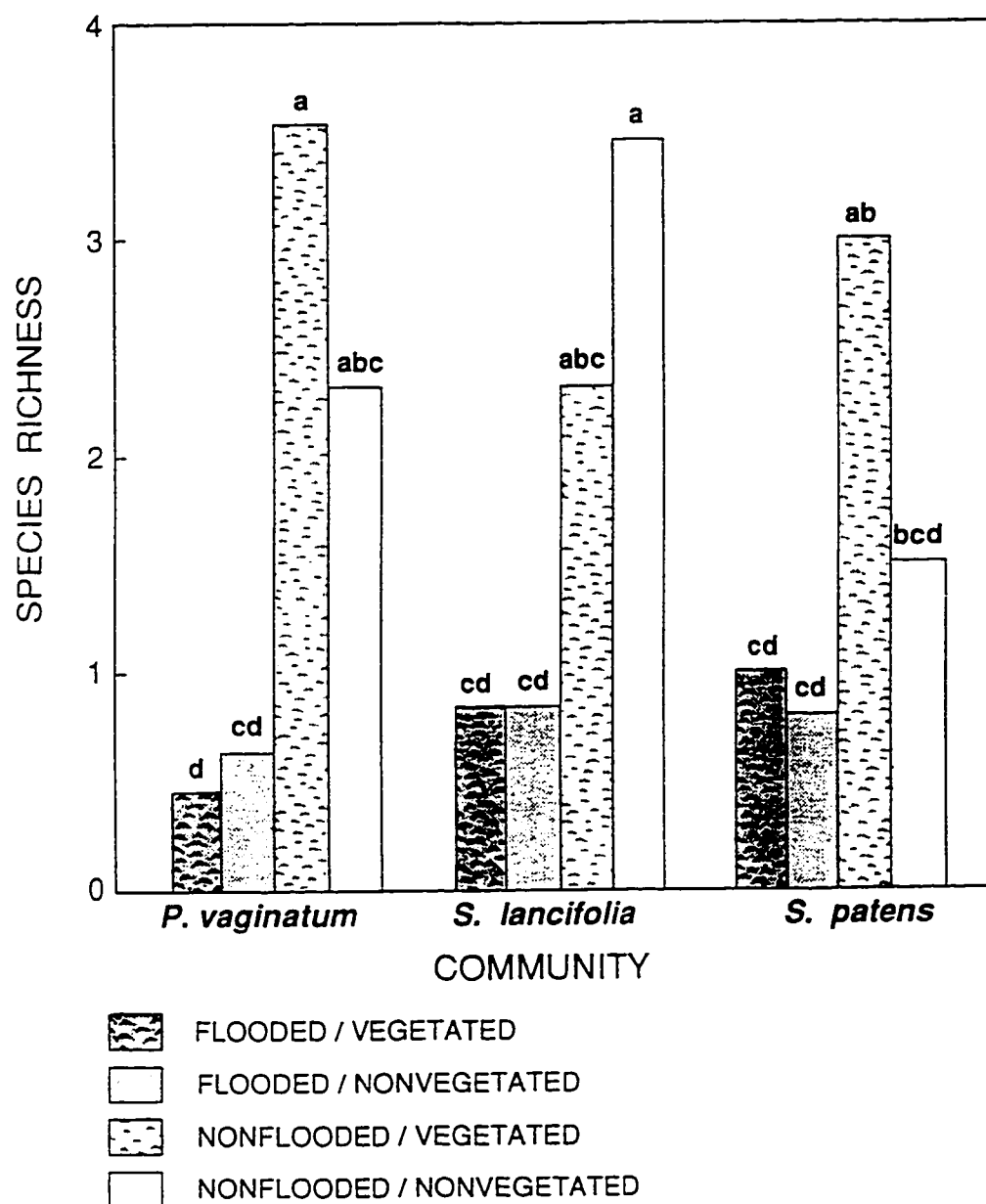


Fig. 2.1. Species richness of seedlings emerging from soils collected from vegetated and nonvegetated areas in three oligohaline marsh communities and subjected to flooded and nonflooded conditions. Treatment means having the same letter are not significantly different among or within communities, inundation regime, or vegetation status (Tukey's Studentized Range test).

Table 2.2. Density of seedlings (no./m²) emerging from soils collected in three oligohaline marsh communities and exposed to flooded and nonflooded conditions. Values are mean density \pm SE (N = 20); total number of seedlings observed given in parentheses.

Species	Community type					
	<u>Paspalum vaginatum</u>		<u>Sagittaria lancifolia</u>		<u>Spartina patens</u>	
	Flooded	Nonflooded	Flooded	Nonflooded	Flooded	Nonflooded
<u>Amaranthus australis</u>	0	5.61 \pm 5.61 (1)	0	0	0	50.5 \pm 29.9 (9)
<u>Ammannia latifolia</u>	0	281 \pm 171 (50)	0	0	5.61 \pm 5.61 (1)	1,160 \pm 421 (207)
<u>Bacopa monnieri</u>	16.8 \pm 16.8 (3)	595 \pm 385 (106)	163 \pm 140 (29)	1,440 \pm 547 (257)	50.5 \pm 36.9 (9)	354 \pm 206 (63)
<u>Cyperus odoratus</u>	0	89.8 \pm 41.2 (16)	0	61.7 \pm 29.9 (11)	0	101 \pm 43.0 (18)
<u>Echinochloa crus-galli</u>	0	5.61 \pm 5.61 (1)	0	5.61 \pm 5.61 (1)	0	0
<u>Eclipta prostrata</u>	0	0	0	5.61 \pm 5.61 (1)	0	0
<u>Eleocharis fallax</u>	0	225 \pm 73.3 (40)	0	16.8 \pm 12.3 (3)	0	5.61 \pm 5.61 (1)
<u>Eleocharis parvula</u>	561 \pm 188 (100)	909 \pm 432 (162)	241 \pm 174 (43)	898 \pm 435 (160)	1,180 \pm 316 (210)	1,780 \pm 574 (317)
<u>Lemna minor</u>	0	5.61 \pm 5.61 (1)	0	89.8 \pm 37.0 (16)	0	0
<u>Leptochloa fascicularis</u>	5.61 \pm 5.61 (1)	281 \pm 73.5 (50)	0	89.8 \pm 42.8 (16)	0	44.9 \pm 29.8 (8)
<u>Ludwigia leptocarpa</u>	0	16.8 \pm 12.3 (3)	0	0	0	0
<u>Lythrum lineare</u>	0	11.2 \pm 11.2 (2)	0	0	0	39.3 \pm 27.3 (7)
<u>Pluchea odorata</u>	0	0	0	0	0	5.61 \pm 5.61 (1)
<u>Ranunculus sceleratus</u>	0	0	0	22.5 \pm 13.1 (4)	0	0
<u>Sagittaria lancifolia</u>	0	0	202 \pm 51.3 (36)	331 \pm 63.3 (59)	16.8 \pm 12.3 (3)	0
Total	584 \pm 185 (104)	2,430 \pm 667 (432)	606 \pm 224 (108)	2,960 \pm 698 (528)	1,250 \pm 323 (223)	3,540 \pm 823 (631)
Species richness	3	11	3	10	4	9

Table 2.3. Probability values from three-way ANOVAs of numbers [$\ln(x+1)$ transformed] of seedlings emerging from marsh soils collected from vegetated and nonvegetated areas in three communities (Paspalum vaginatum, Sagittaria lancifolia, and Spartina patens) and exposed to two inundation levels (flooded and nonflooded). Analyses were performed only for species comprising $\geq 1\%$ of the total number of seedlings.

Species	Community (C)	Vegetation (V)	Inundation (I)	C \times V	C \times I	V \times I	C \times V \times I	Block
<u>Ammannia latifolia</u>	<0.0001	0.0009	<0.0001	0.0178	<0.0001	0.0017	0.0334	0.3220
<u>Bacopa monnieri</u>	0.0346	0.9715	<0.0001	0.0613	0.1348	0.6629	0.5004	0.3477
<u>Cyperus odoratus</u>	0.7307	0.1506	<0.0001	0.0665	0.7307	0.1506	0.0665	0.7946
<u>Eleocharis fallax</u>	0.0007	0.7122	0.0005	0.8866	0.0007	0.7122	0.8866	0.5395
<u>Eleocharis parvula</u>	0.0052	0.0050	0.6059	0.1681	0.5851	0.6716	0.5089	0.0102
<u>Leptochloa fascicularis</u>	<0.0001	0.3823	<0.0001	0.0012	<0.0001	0.5723	0.0038	0.4663
<u>Sagittaria lancifolia</u>	<0.0001	0.0019	0.1357	0.0018	0.0121	0.4758	0.8728	0.0524

Within level of inundation, species richness of the seed bank did not vary significantly among communities (Fig. 2.1; flooded: $P = 0.2014$; nonflooded: $P = 0.2839$). However, the abundance of most species varied significantly among communities (Tables 2.2 and 2.3), with only Cyperus odoratus showing no significant main effect of community. The majority of Sagittaria lancifolia seedlings were restricted to soils of the Sagittaria lancifolia community. The density of emerging Eleocharis parvula seedlings was significantly higher in the Spartina patens community than in the Sagittaria lancifolia community; seedling density in the Paspalum vaginatum community was intermediate (Tukey's Studentized Range test). Eleocharis fallax seedlings emerged at significantly higher densities from soils of the Paspalum vaginatum community than from those of the other two communities.

The presence of vegetation affected the abundance of some species in the seed bank, but in general had little impact on species composition (Tables 2.3 and 2.4). Species richness was not affected by vegetation within both levels of inundation (flooded: $P = 0.8451$; nonflooded: $P = 0.1531$), but the community \times vegetation interaction for nonflooded treatments was significant (Fig. 2.1; $P = 0.0109$). Seed bank species richness was higher in vegetated plots than nonvegetated plots in the Paspalum vaginatum and Spartina patens communities, while the opposite pattern occurred in the Sagittaria lancifolia community. Seedlings of Sagittaria lancifolia emerged at significantly higher densities from soils of vegetated sites than from those of nonvegetated sites. Seedlings of Ammannia latifolia emerged at their highest densities from soils of vegetated sites in the

Table 2.4. Density of seedlings (no./m²) emerging from soils collected from vegetated and nonvegetated areas in three oligohaline marsh communities. Values are mean density \pm SE (N = 20; total number of seedlings observed given in parentheses).

Species	Community type					
	<u>Paspalum vaginatum</u>		<u>Sagittaria lancifolia</u>		<u>Spartina patens</u>	
	Vegetated	Nonvegetated	Vegetated	Nonvegetated	Vegetated	Nonvegetated
<u>Amaranthus australis</u>	5.61 \pm 5.61 (1)	0	0	0	44.9 \pm 29.8 (8)	5.61 \pm 5.61 (1)
<u>Ammannia latifolia</u>	275 \pm 171 (49)	5.61 \pm 5.61 (1)	0	0	926 \pm 393 (165)	241 \pm 213 (43)
<u>Bacopa monnieri</u>	500 \pm 385 (89)	112 \pm 71.0 (20)	387 \pm 195 (69)	1,220 \pm 553 (217)	337 \pm 206 (60)	67.4 \pm 42.6 (12)
<u>Cyperus odoratus</u>	89.8 \pm 41.2 (16)	0	22.5 \pm 22.5 (4)	39.3 \pm 22.0 (7)	67.4 \pm 41.0 (12)	33.7 \pm 20.1 (6)
<u>Echinochloa crus-galli</u>	0	5.61 \pm 5.61 (1)	0	5.61 \pm 5.61 (1)	0	0
<u>Eclipta prostrata</u>	0	0	5.61 \pm 5.61 (1)	0	0	0
<u>Eleocharis fallax</u>	129 \pm 63.2 (23)	95.4 \pm 51.7 (17)	5.61 \pm 5.61 (1)	11.2 \pm 11.2 (2)	5.61 \pm 5.61 (1)	0
<u>Eleocharis parvula</u>	376 \pm 192 (67)	1,090 \pm 418 (195)	0	1,140 \pm 444 (203)	1,450 \pm 456 (258)	1,510 \pm 480 (269)
<u>Lemna minor</u>	5.61 \pm 5.61 (1)	0	73.0 \pm 37.6 (13)	16.8 \pm 9.20 (3)	0	0
<u>Leptochloa fascicularis</u>	219 \pm 76.6 (39)	67.4 \pm 30.9 (12)	5.61 \pm 5.61 (1)	84.2 \pm 43.0 (15)	33.7 \pm 28.3 (6)	11.2 \pm 11.2 (2)
<u>Ludwigia leptocarpa</u>	11.2 \pm 11.2 (2)	5.61 \pm 5.61 (1)	0	0	0	0
<u>Lythrum lineare</u>	11.2 \pm 11.2 (2)	0	0	0	39.3 \pm 27.3 (7)	0
<u>Pluchea odorata</u>	0	0	0	0	5.61 \pm 5.61 (1)	0
<u>Ranunculus sceleratus</u>	0	0	16.8 \pm 12.3 (3)	5.61 \pm 5.61 (1)	0	0
<u>Sagittaria lancifolia</u>	0	0	382 \pm 65.4 (68)	152 \pm 37.6 (27)	16.8 \pm 12.3 (3)	0
Total	1,620 \pm 538 (289)	1,390 \pm 526 (247)	898 \pm 219 (160)	2,670 \pm 744 (476)	2,920 \pm 780 (521)	1,870 \pm 530 (333)
Species richness	10	7	8	9	10	6

Spartina patens community, while the highest densities of Leptochloa fascicularis seedlings emerged from soils of vegetated sites in the Paspalum vaginatum community. Unlike most other species, Eleocharis parvula seedlings emerged at significantly higher densities from soils of nonvegetated areas than from soils of vegetated areas.

Vegetation in the Paspalum vaginatum and Spartina patens communities (Table 2.5: vegetated areas) differed from that of the seed bank in both species composition and abundance. Paspalum vaginatum and Spartina patens, which were not observed in the seed bank, predominated and formed extensive monocultures in their respective communities; Paspalum vaginatum occurred at 67% mean cover and Spartina patens occurred at 96% mean cover. Other species were present at relatively low percent cover in these communities. Bacopa monnieri occurred at 11.5% mean cover in the Paspalum vaginatum community, primarily in patches surrounded by monocultures of Paspalum vaginatum. All species in the Spartina patens community other than Spartina patens occurred at 1% mean cover or less. The predominance of Paspalum vaginatum and Spartina patens over other species in their communities is reflected in and low diversity index values for their vegetation (Table 2.1).

In contrast with the two grass-dominated communities, several of the species in the seed bank were well represented in the vegetation of the Sagittaria lancifolia community (Table 2.5). Sagittaria lancifolia occurred at 29.5% mean cover and Bacopa monnieri occurred at 16% mean cover in vegetated plots in this community.

Table 2.5. Percent cover of species of standing vegetation in vegetated and nonvegetated areas in three oligohaline marsh communities. Values are mean cover (%) \pm SE (N = 10).

Species	Community type					
	<u>Paspalum vaginatum</u>		<u>Sagittaria lancifolia</u>		<u>Spartina patens</u>	
	Vegetated	Nonvegetated	Vegetated	Nonvegetated	Vegetated	Nonvegetated
<u>Bacopa monnieri</u>	11.5 \pm 3.34	0.500 \pm 0.500	16.0 \pm 3.64	2.50 \pm 1.12	0	0
<u>Cyperus odoratus</u>	0.500 \pm 0.500	0	0	0	0	0
<u>Eleocharis parvula</u>	0	0	0	0	0	0.500 \pm 0.500
<u>Eleocharis</u> sp.	0	0	1.50 \pm 0.764	0	0	0
<u>Hydrocotyle</u> sp.	0	0	0.500 \pm 0.500	0	0	0
<u>Lythrum lineare</u>	0	0	0	0	1.00 \pm 0.667	0
<u>Paspalum vaginatum</u>	67.0 \pm 7.79	13.5 \pm 7.96	0	0	0	0
<u>Phyla nodiflora</u>	1.50 \pm 1.07	0	3.00 \pm 1.11	0	0	0
<u>Sacciolepis striata</u>	0	0	7.50 \pm 1.54	2.00 \pm 0.817	0	0
<u>Sagittaria lancifolia</u>	0	0	29.5 \pm 3.02	2.00 \pm 0.817	0	0
<u>Salvinia minima</u>	0	0	5.50 \pm 3.29	8.00 \pm 5.83	0	0
<u>Scirpus americanus</u>	0	0	0	0	0.500 \pm 0.500	0
<u>Spartina alterniflora</u>	0	0	0	0	1.00 \pm 1.00	0
<u>Spartina patens</u>	0	0	0	0	96.0 \pm 1.63	1.50 \pm 0.764
Total	80.5 \pm 8.93	14.0 \pm 7.92	63.5 \pm 4.41	14.5 \pm 5.13	98.5 \pm 1.30	2.00 \pm 0.817
Species richness	4	2	7	4	4	2

Two species observed in the seed bank of the Sagittaria lancifolia community during the salinity and inundation experiment, Sacciolepis striata (L.) Nash and Phyla nodiflora (L.) Greene, also occurred in the vegetation (Table 2.5).

The nonvegetated sites were not completely devoid of vegetation, but contained a few species present at low mean percent cover (Table 2.5: nonvegetated areas). An exception was Salvinia minima, a floating aquatic fern, which occurred at higher mean percent cover in open water or mud flat sites than in vegetated sites.

Influence of salinity and inundation on seedling emergence

There was a significant interaction between germination salinity and inundation for species richness ($P < 0.0001$) and seedling numbers for most species (Table 2.6). Under nonflooded conditions there were significant trends toward decreasing species richness (Fig. 2.2) and seedling numbers (Fig. 2.3) with increasing germination salinity. However, species richness and seedling numbers in flooded treatments were low at all germination salinities and did not vary significantly.

Most species did not show appreciable germination above 4 ppt salinity, and Amaranthus australis, Eleocharis fallax, and Ranunculus sceleratus did not germinate above 2 ppt (Fig. 2.3). However, Bacopa monnieri, Eleocharis parvula, and Leptochloa fascicularis exhibited some germination at 8 ppt. Under flooded conditions a few Sagittaria lancifolia seedlings emerged at 4 ppt and some Eleocharis parvula seedlings emerged at 16 ppt (data not shown).

Table 2.6. Probability values from three-way ANOVAs of numbers [$\ln(x+1)$ transformed] of seedlings emerging from marsh soils exposed to five pretreatment salinities (0, 2, 4, 8, and 16 ppt), five germination salinities (0, 2, 4, 8, and 16 ppt), and two inundation levels (flooded and nonflooded). Analyses were performed only for species comprising $\geq 1\%$ of the total number of seedlings.

Species	Pretreatment salinity (P)	Germination salinity (G)	Inundation (I)	P \times G	P \times I	G \times I	P \times G \times I	Tank
<u>Amaranthus australis</u>	0.4384	0.0032	0.0154	0.8986	0.4384	0.0229	0.8986	0.9607
<u>Bacopa monnieri</u>	0.1188	0.0005	<0.0001	0.4649	0.3778	<0.0001	0.3224	0.1036
<u>Cyperus odoratus</u>	0.2369	0.0007	<0.0001	0.0590	0.2369	<0.0001	0.0590	0.5523
<u>Eleocharis fallax</u>	0.0473	0.0011	<0.0001	0.0151	0.0473	<0.0001	0.0151	0.0217
<u>Eleocharis parvula</u>	0.3453	0.0007	0.0386	0.4403	0.0356	0.0033	0.2468	0.6329
<u>Leptochloa fascicularis</u>	0.0734	0.1523	<0.0001	0.0112	0.0734	0.0034	0.0112	0.0418
<u>Phyla nodiflora</u>	0.9935	0.0038	<0.0001	0.4167	0.4395	<0.0001	0.4167	0.1151
<u>Polygonum punctatum</u>	0.2254	0.0046	<0.0001	0.3173	0.2254	0.0005	0.3173	0.6891
<u>Ranunculus sceleratus</u>	0.1168	0.0035	0.3131	0.2054	0.4620	0.7632	0.1728	0.9222
<u>Sagittaria lancifolia</u>	0.1099	0.0071	0.3685	0.0029	0.3984	<0.0001	0.7576	<0.0001
<u>Sacciolepis striata</u>	0.5664	<0.0001	<0.0001	0.8570	0.5664	<0.0001	0.8570	0.8734

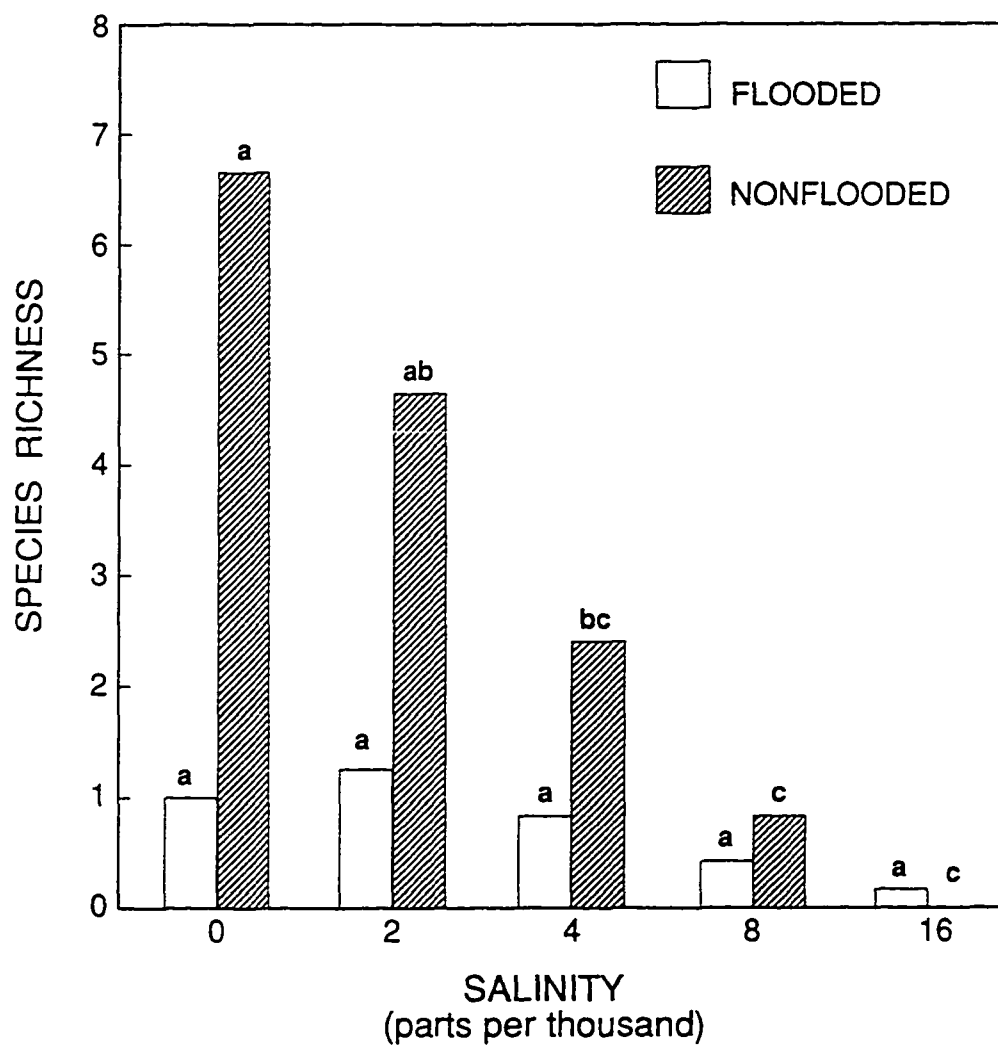


Fig. 2.2. Species richness of seedlings emerging from marsh soils exposed to five germination salinities under flooded and nonflooded conditions. Within flooded or nonflooded treatments, germination salinity means having the same letter are not significantly different (Bonferroni procedure).

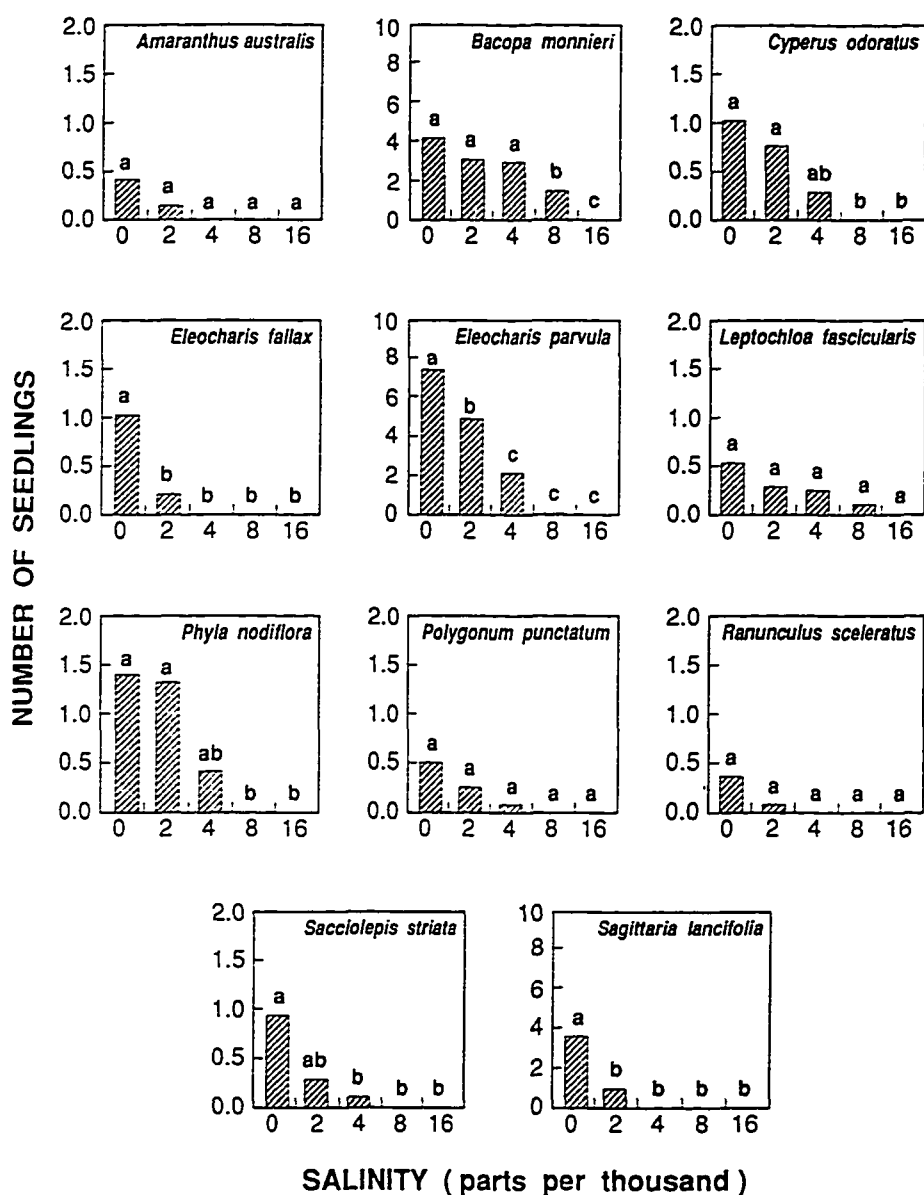


Fig. 2.3. Responses of 11 common species emerging from marsh soils exposed to five germination salinities under nonflooded conditions. Germination salinity means having the same letter are not significantly different (Bonferroni procedure). Seedling emergence was not significantly affected by germination salinity in flooded treatments (data not shown).

Pretreatment salinity had no significant effect on species richness ($P = 0.4080$) or on seedling emergence in most species (Table 2.6). However, there were significant interactions between pretreatment salinity and germination salinity or inundation for several species. Increasing pretreatment salinity significantly decreased seedling emergence in Eleocharis fallax at 0 and 2 ppt germination salinities under nonflooded conditions (Bonferroni procedure). Similarly, seedling emergence decreased significantly in Leptochloa fascicularis with increasing pretreatment salinity at 0, 2, and 4 ppt germination salinities under nonflooded conditions. Although there were significant differences in emergence of Sagittaria lancifolia seedlings among pretreatment salinities, no trend was evident.

A total of 14 species emerged from Sagittaria lancifolia marsh soils in the salinity and inundation experiment, ten of which were also observed in the seed bank and vegetation experiment. The species emerging only in the salinity and inundation experiment were Lilaeopsis carolinensis Coult. & Rose, Phyla nodiflora, Polygonum punctatum Ell., and Sacciolepis striata.

To assess the effect of storage at 4 C during the pretreatment on seedling emergence, we compared seedling densities for the "nonstressed" treatments in both experiments (no salinity exposure and nonflooded conditions). Mean total seedling density was 2,920/m² for the nonstressed treatment in the salinity and inundation experiment, while densities ranged from 2,430/m² to 3,540/m² in the seed bank and vegetation study (Table 2.2). Similarly, densities of individual species in the salinity and inundation study were either within or very close to the ranges observed in the

seed bank and vegetation study. These results indicate that there was little effect of storage during the pretreatment on afterripening or viability.

DISCUSSION

While the species composition and seed density of seed banks varies among wetland types (Leck, 1989), total seedling densities we observed in nonflooded treatments from the three communities (2,430-3,540 seedlings/m²) are similar to those observed at 0-5 cm depth in freshwater tidal marshes in New Jersey (1,645-3,620 seedlings/m²; Parker and Leck, 1985). Additionally, several of the species and genera we observed also occur in the New Jersey marshes, including Ranunculus sceleratus, Polygonum punctatum, Amaranthus sp., Cyperus sp., Sagittaria sp., Echinochloa crus-galli, Lythrum sp., and Ludwigia sp. (Leck and Graveline, 1979; Parker and Leck, 1985; Leck and Simpson, 1987; Leck and Simpson, 1994; Leck and Simpson, 1995). These similarities suggest a comparable role of seed banks in the vegetation dynamics of certain oligohaline and freshwater tidal marshes. However, changes in sea level may lead to changes in vegetation, salinity level, and hydrologic regime, altering patterns of recruitment from the seed bank in these wetlands.

Effects of vegetation on marsh seed banks

Despite considerable differences in species composition of vegetation, the seed banks of the three communities had similar species richness and diversity. There was also considerable overlap in species composition of seed banks, indicating that seed dispersal by wind or water may be important for several of the seed bank

species. These findings suggest that changes in dominant vegetation associated with sea level rise may not immediately affect the species composition of oligohaline marsh seed banks.

While changes in dominant vegetation may not affect the composition of the seed bank, they may alter patterns of seedling recruitment. Seed bank species occurred at higher percent cover in the vegetation of the Sagittaria lancifolia community than in the Paspalum vaginatum or Spartina patens communities. Paspalum vaginatum and Spartina patens persist year-round (Hopkinson et al., 1978; Brewer and Grace, 1990) and have high mean percent cover (67% for Paspalum vaginatum and 96% for Spartina patens in our study); Sagittaria lancifolia dies back during the winter months (Hopkinson et al., 1978; Platt and Brantley, 1989; Brewer and Grace, 1990) and has lower cover ($\approx 30\%$). Dense, persistent canopies of clonal perennials have been reported to inhibit seedling recruitment (Thomas and Dale, 1975; Cook, 1979; Schmid, 1984; Metcalfe et al., 1986; Falinska, 1991; Shumway and Bertness, 1992), which may explain the lower occurrence of seed bank species in the vegetation of the Paspalum vaginatum and Spartina patens communities.

Within a community type, the presence or absence of vegetation may affect seed densities for some species, but appears to have little effect on the species composition of buried seeds. Seeds or fruits of many aquatic species float (Leck, 1989), and vegetation may act as a barrier that traps floating seeds (Smith and Kadlec, 1985a). The capacity for prolonged seed flotation (> 2 mo in Sagittaria

lancifolia; Collon and Velasquez, 1989) may explain the presence of seeds of some species at higher densities in vegetated areas.

Effects of environmental factors on seedling recruitment

In coastal marshes of the Gulf of Mexico and elsewhere, salt water intrusion events or salt pulses may occur during storms when winds push saline water into fresh or oligohaline marsh areas, sometimes stressing or killing the vegetation (Turner and Cahoon, 1987; Odum, 1988; McKee and Mendelssohn, 1989; Brewer and Grace, 1990; Guntenspergen et al., 1995). After storms, salinities have been observed to decrease to prestorm levels (A. Baldwin, Louisiana State University, unpublished data), presumably due to leaching by precipitation (Gosselink, 1984) or tidal flushing. The general lack of a pretreatment salinity effect on germination in our study suggests that the viability of buried seeds in oligohaline marshes would not be significantly reduced by such temporary increases in soil salinity. Recruitment from the seed bank may thus be an important mechanism for regeneration of vegetation following salt pulses.

While salt pulses may not affect seed viability, the long-term increase in salinity and water level anticipated as global sea level continues to rise (Boesch et al., 1994) may result in conditions unfavorable for seedling recruitment. Our results indicate that higher salinities and water levels will inhibit seedling emergence in most of the seed bank species studied. Only Sagittaria lancifolia and Eleocharis parvula germinated well under flooded conditions, and few species germinated at salinities above 4 ppt. Germination was significantly reduced in Eleocharis parvula

and Sagittaria lancifolia by salinities as low as 2 ppt. Trends toward decreasing emergence with increasing salinity were not significant in some species, probably because of the low numbers of their seedlings observed. Other authors have also noted the inhibitory effects of salinity (Ungar, 1978; Galinato and van der Valk, 1986; Shumway and Bertness, 1992; Poljakoff-Mayber et al., 1994) and flooding (van der Valk and Davis, 1978; Smith and Kadlec, 1985a; Galinato and van der Valk, 1986; Willis and Mitsch, 1995) on germination in wetland plant species.

Seed banks, environmental conditions, and species distribution

The distribution of dominant species across the Mississippi delta region has been attributed to differences in the salinity tolerance of adult plants (Penfound and Hathaway, 1938; Chabreck, 1972). However, the mean salinity levels at our study sites of < 4 ppt are well within the tolerance ranges of adults of all three community dominants (Penfound and Hathaway, 1938; Chabreck, 1972; McKee and Mendelssohn, 1989), suggesting that the action of salinity on adult plants is not responsible for the distribution of the three species on a local level. Rather, salinity may affect species distributions by inhibiting seed germination, reducing the abundance of species reliant on seedling recruitment while allowing continued growth of species capable of vegetative reproduction. Salinity levels of 4 ppt reduced seed germination in most species in our study, and a significant reduction in germination occurred at 2 ppt for some species. These data suggest that the salinities of ≈ 3.5 ppt in the Paspalum vaginatum and Spartina patens communities

may be partly responsible for the underrepresentation of seed bank species in the vegetation of these communities.

The changes that occur in community structure may depend on the rate of sea level rise relative to the marsh surface. If sea level rises quickly and permanently submerges the marsh surface, flooding will probably act as the primary stressor by reducing vegetative growth rates (McKee and Mendelssohn, 1989; Reed and Cahoon, 1992) and precluding seedling establishment by most species. Under this scenario, species such as Sagittaria lancifolia that can germinate under flooded conditions may become more abundant or, if water levels are too high, all vegetation may succumb to flooding stress and the marsh would convert to open water. If sea level rise is relatively slow (the more likely scenario), the frequency and duration of inundation will on average be greater (Reed and Cahoon, 1992) but low tides will still expose the marsh surface periodically. In this case salinity will act as the most important stressor by reducing seed germination, possibly resulting in communities dominated by salt-tolerant clonal perennials that colonize areas of high salinities via clonal fragments rather than by seedling establishment. Conversion to marshes dominated by monospecific stands of clonal perennials such as Spartina patens would continue until water levels become so high as to stress and kill the vegetation, and the marsh would become open water. Patterns of wetland change and loss in many regions of the Mississippi River delta plain, including our study area, appear to conform to this mechanism of community response.

CHAPTER 3

COMMUNITY RESPONSES TO DISTURBANCE INTENSITY IN OLIGOHALINE MARSHES

INTRODUCTION

Along with disturbance frequency, predictability, and areal extent, the magnitude of disturbance has been recognized as an important descriptor of disturbance regimes (Connell, 1978; Malanson, 1984; Sousa, 1984; Pickett and White, 1985; Underwood, 1989; Glenn-Lewin and van der Maarel, 1992). Magnitude has been divided into disturbance intensity, which refers to the physical force of a disturbance, and disturbance severity, which refers to the amount of damage caused to organisms, communities, or ecosystems (Sousa, 1984; Pickett and White, 1985). However, the terms intensity and severity have been used interchangeably (Sousa, 1984). In terrestrial communities exposed to fire, as the intensity of disturbance increases, plant mortality often increases and the probability that regeneration will be by vegetative propagation of surviving plants decreases (Keeley and Zedler, 1978; Sousa, 1984; Christensen, 1985). Similarly, in limestone grasslands successful seedling recruitment is promoted by increasingly intense disturbances, which damage dominant species and increase the amount of bare ground produced (Burke and Grime, 1996). Thus, as disturbance intensity increases, colonization is more likely to be a result of propagules dispersed into the

disturbed patch than from vegetative colonization by neighboring clonal plants, possibly leading to a change from the structure of the community present before the disturbance.

The role of disturbance intensity in other communities has received little attention. A recent study found that highest species richness occurred at intermediate intensities of disturbance (determined based on the areal extent of damage to vegetation) in a Louisiana coastal marsh (Grace and Pugsek, 1996). However, little else is known about how disturbance intensity affects marsh community structure or patterns of regeneration following disturbance.

Coastal marshes experience a wide array of natural and anthropogenic disturbances which differ markedly in their intensity. Examples of disturbance in coastal marshes include fire (Hoffpauer, 1968; Nyman and Chabreck, 1995; Ford and Grace, 1996), herbivory (Smith and Kadlec, 1985b; Hik and Jefferies, 1990; Shaffer et al., 1992; Taylor and Grace, 1995), salt water intrusion (Turner and Cahoon, 1987; Odum, 1988; Shaffer et al., 1992; Flynn et al., 1995), deposition of dead plant debris ("wrack"; Bertness and Ellison, 1987; Valiela and Rietsma, 1995), sedimentation (Shaffer et al., 1992), submergence (McKee and Mendelssohn, 1989; Webb et al., 1995), and oil spills (Stebbins, 1970; Mendelssohn et al., 1990; Mendelssohn et al., 1993). Storms or hurricanes may result in multiple disturbances including wrack deposition, scouring, sedimentation (burial), salt burning, and elevational changes due to marsh compression (Guntenspergen et al., 1995). In Louisiana, the vertebrate herbivore nutria (Myocastor coypus) may be one of the

most important disturbance agents affecting the vegetation of coastal marshes (Chabreck, 1988; Shaffer et al., 1992; Llewellyn and Shaffer, 1993; Taylor and Grace, 1995; Grace and Ford 1996).

These disturbances differ in the severity of damage they inflict upon marsh vegetation. For example, cover fires may burn off aboveground vegetation but leave rhizomes unscathed and allow vegetation to resprout, while peat or root burns may kill vegetation entirely (Thompson and Shay, 1985; van Arman and Goodrick, 1979; Nyman and Chabreck, 1995). Similarly, the effects of wrack deposition can range from a decrease in shoot density to complete eradication of vegetation (Bertness and Ellison, 1987; Valiela and Rietsma, 1995; Guntenspergen et al., 1995). And under nonflooded conditions, nutria herbivory may merely damage plants by removing their aboveground parts but in the presence of flooding may kill them (Shaffer et al., 1992; see Chapter 4). Multiple disturbances applied simultaneously have been found to result in a greater impact on dominant vegetation than single disturbances (Turner, 1988; Grace and Ford, 1996; Ford and Grace, 1996).

In some salt marshes, regeneration following disturbances occurs rapidly via vegetative colonization of disturbed patches by surrounding dominant perennials (Bertness and Ellison, 1987; Hartman, 1988; Shumway and Bertness, 1992). However, seedling dynamics are an important component of the vegetation dynamics of fresh and oligohaline tidal marshes (Odum, 1988; Leck and Simpson, 1995; Baldwin et al., 1996) and may be an important component of regeneration following disturbances. Marshes are classified as fresh if salinity levels are less than 0.5 parts

per thousand (ppt) and oligohaline if salinities are 0.5 - 5 ppt (Cowardin et al., 1979). Resprouting of perennial dominants of oligohaline marshes following disturbances that do not kill the plant such as herbivory or fire (Guntenspergen et al, 1995; Grace and Ford, 1996) may inhibit seedling recruitment and quickly reestablish the pre-disturbance structure of the community. Populations of dominant marsh species may therefore be relatively "stable" and "resilient" (both terms sensu Underwood, 1989) in response to nonlethal disturbances. Conversely, patches created by disturbances that kill dominant vegetation (e.g., wrack or herbivory followed by flooding) may be colonized primarily by seedlings recruited from the seed bank (Baldwin et al., 1996) or propagules dispersed into the patch via water, wind, or other means (Fenner, 1985). Because colonization of patches lacking vegetation by community dominants may occur slowly, their populations may be viewed as being relatively unstable in response to lethal disturbances. Furthermore, if recruited seedlings competitively inhibit vegetative colonization by perennials surrounding the disturbed patch, populations may not be resilient to lethal disturbances, and a shift in community structure may occur. Therefore, the critical threshold for intensity of disturbance may be whether the disturbance kills or only damages the vegetation. I will hereafter refer to these as lethal and nonlethal disturbances.

To examine the effects of disturbance intensity on subsequent patterns of colonization, I subjected vegetation in two oligohaline marsh communities, (one dominated by Spartina patens (Ait.) Muhl. and the other by Sagittaria lancifolia L.)

to three levels of disturbance intensity (lethal, nonlethal, and no disturbance) and quantified vegetation change for two years. I also assessed the potential for recruitment from the seed bank and measured salinity, water level, redox potential (Eh), and light level. I hypothesized that the stability and resilience (*sensu* Underwood, 1989) of the marsh community would vary as a function of disturbance intensity and pre-disturbance community structure. I also hypothesized that colonization would be primarily via seedling recruitment in the lethal disturbance treatment and via vegetative propagation in the nonlethal treatment, and that establishment of species previously absent from the community in the lethal treatment might lead to a persistent change in community structure.

METHODS

Study site

This study was conducted from July 1993 through July 1995 in two oligohaline marsh communities adjacent to the Tchefuncte River, which flows into the northern edge of Lake Pontchartrain in St. Tammany Parish, Louisiana. One community is dominated by the broadleaf perennial Sagittaria lancifolia L. (Alismataceae) and the other by the perennial grass Spartina patens (Ait.) Muhl. (Poaceae), hereafter referred to respectively as the Sagittaria and Spartina communities. The Sagittaria community (30°23'21"N, 90°09'37"W) is located adjacent to Balford Bayou, a small natural bayou flowing into the Tchefuncte River about 1.5 km from Lake Pontchartrain, while the Spartina community (30°22'51"N, 90°09'39"W) is located adjacent to a small man-made channel about 0.5 km from

Lake Pontchartrain. These community types are widespread in coastal marshes of the Gulf of Mexico and elsewhere (Penfound and Hathaway, 1938; Chabreck, 1972; Tiner, 1993).

The vegetation structure of the two communities differs substantially. The canopy of Sagittaria is relatively open and dies back during the winter (Hopkinson et al., 1978; Platt and Brantley, 1989; Brewer and Grace, 1990; Baldwin et al., 1996), possibly explaining the abundance of annual species which are present in this community. The canopy of Spartina, however, often forms dense monocultures that persist year-round (Hopkinson et al., 1978; Brewer and Grace, 1990; Baldwin et al., 1996), possibly preventing colonization by annual species (Gosselink, 1984). There are discrete patches of marsh dominated by Sagittaria embedded in the Spartina community.

The climate of the region is subtropical and strongly influenced by the Gulf of Mexico (National Climatic Data Center, 1995). Annual mean temperatures between 1961 and 1990 recorded in Covington, Louisiana (30°32'N, 90°07'W) were 19.3°C, with monthly means ranging from 10.1°C in January to 27.3°C in July (Owenby and Ezell, 1992). The lowest mean minimum temperature (3.8°C) and highest mean maximum temperature (33.2°C) also occur in January and July, respectively (Owenby and Ezell, 1992). The beginning and end of the "growing season" are indistinct, as seedling recruitment and growth of some native marsh species occur year-round (Baldwin, personal observation; Hopkinson et al., 1978). An indication of the length of the growing season are the average first and last

occurrences of freezing temperatures in the region recorded from 1951-1980, which were December 5 and February 20, respectively (National Climatic Data Center, 1995). Average annual precipitation at the Covington station between 1961 and 1990 was 1,592 mm (Owenby and Ezell, 1992). More than 356 mm of rain can fall in a 24-hr period; snowfall is infrequent and light (National Climatic Data Center, 1995). Diurnal lunar tides are only about 30 cm at the coast, but wind effects combined with lunar tides can result in water level shifts of > 1 m within 12 hours in Louisiana coastal marshes (Gosselink, 1984).

Experiment setup

In July 1993 I established 10 randomly selected blocks in each of the two marsh communities. Each block consisted of three $2\text{ m} \times 2\text{ m}$ plots (separated by a 1 m buffer) subjected to one of three disturbance intensity treatments applied in random order. These were (1) no disturbance, (2) a nonlethal disturbance created by removing aboveground vegetation with a gasoline-powered weed clipper, and (3) a lethal disturbance where vegetation was killed by applying Roundup herbicide (the isopropylamine salt of glyphosate; Monsanto, St. Louis, Missouri, USA) to the plots. Standing dead vegetation was removed two wk after the herbicide was applied. Roundup has several properties that make it suitable for this experiment. First, it has been found to be effective in controlling various species of aquatic vegetation found in fresh and oligohaline marshes, including Eleocharis spp., Scirpus spp., Alternanthera philoxeroides, and Typha spp. (Barrett, 1985). Second, Roundup is not believed to adversely affect seeds in soil (M. Braverman, Louisiana

State University, personal communication). Finally, Roundup has been used to create gaps in other studies with no evident effect on recruitment of seedlings following gap creation (Hughes, 1992; Bertness et al., 1992). After treatments were applied I installed permanent 0.5 m \times 0.5 m quadrats divided into 25-10 cm \times 10 cm cells in the center of each plot.

The objective of the disturbance treatments was to simulate effects of a wide range of natural and anthropogenic disturbance agents occurring in coastal marshes. Fire, vertebrate herbivory, and salt burning (to due storm-generated salt pulses) in coastal marshes often result in removal or dieback of aboveground vegetation, after which vegetative growth occurs from rhizomes (Guntenspergen et al., 1995; Nyman and Chabreck, 1995; personal observation). While these disturbances may differ in their effects on edaphic factors, their effect on vegetation is accurately represented by the removal of aboveground vegetation in the nonlethal disturbance treatment. Vegetation can be killed by wrack deposition, sedimentation, and scouring; fire and herbivory may also kill vegetation if they are very intense or if they are followed by flooding (Bertness and Ellison, 1987; Shaffer et al., 1992; Guntenspergen et al., 1995; Nyman and Chabreck, 1995). These types of disturbances result in effects on vegetation similar to those of the lethal disturbance treatment. Actual disturbances in coastal marshes may not be uniform in their intensity and severity, resulting in death of vegetation in some areas but only damaging it in others.

Vegetation sampling

I sampled vegetation by counting the number of seedlings or ramets of each species in each of the 25 cells in the 60 quadrats every three months beginning in July 1993. Additionally, I measured heights of three seedlings or ramets of each species in each quadrat and determined percent cover by estimating the number of quadrat cells filled by each species. Percent cover was also determined monthly for the duration of the study, except in March 1995 when water elevation was too high to accurately determine cover. Also, one sampling event was conducted in early December 1993 to represent both November and December 1993. Otherwise, monthly sampling was conducted near the 15th day of each month. In July 1995 the aboveground vegetation was clipped, sorted by species and as alive or dead, dried at 80 C for at least 3 d, and weighed to the nearest 0.01 g. Throughout the text species are referred to generically, with specific epithets given only for congeneric species.

Seed bank assessment

In June 1994 I collected one seed bank sample in each block. Each sample consisted of five shallow cores (5 cm deep by 4.76 cm diameter) collected within a 1 m² vegetated area outside of the plots subjected to disturbance treatments. This sampling procedure has been described elsewhere in detail (Baldwin et al., 1996). Coarse organic material and living roots were removed from the samples, which were then mixed thoroughly and spread in a layer \approx 1.3 cm thick on the surface of sand in plastic pots (11 cm diameter) with slits cut in the pot sides near the bottom

for drainage. The pots were placed in tanks in a greenhouse at Louisiana State University on July 19, 1994. Seedlings emerging from the soils were counted by species and removed at 1 mo, 2 mo, and 3 mo, after which no new seedlings were emerging.

Environmental measurements

I measured salinity of interstitial and standing water, water level relative to the marsh surface, photosynthetically active radiation (PAR; 400 - 700 nm wavelength), and Eh. Interstitial water salinity and water level were measured monthly in monitoring wells (screened from the soil surface to 70 cm depth) installed in each block. Salinity of standing water was also measured if water levels were above the marsh surface. Salinity measurements were made with a portable salinity-conductivity-temperature meter. Photosynthetically Active Radiation flux density through the canopy was measured monthly throughout the study (except in October 1994 and March and April 1995 when water level was > 15 cm above the marsh surface) using a LICOR LI-185B meter equipped with an LI-190SA Quantum Sensor (LICOR, Lincoln, Nebraska, USA). Flux densities were measured at various times during daylight hours with the sensor pointed upward at a height of approximately 15 cm in the center of each quadrat. Flux density readings for full sunlight were made at each site by pointing the sensor toward the sun at a height of approximately 2 m so that quadrat readings could be normalized as percentage of full sunlight. Three redox potential measurements were made in each quadrat in September 1993 using brightened platinum electrodes inserted to a depth of 10 cm, a

calomel reference electrode, and a portable pH/mV meter. The potential of the calomel reference electrode (+244 mV) was added to each measured value to calculate Eh (Faulkner et al., 1989).

Statistical analyses

Quarterly and monthly data were analyzed as a randomized block design using univariate repeated measures Analysis of Variance (ANOVA) computed with SAS version 6.10 for Windows (SAS Institute, Cary, North Carolina, USA). A significance level of $P = 0.05$ was used in interpreting results of statistical tests; P -values of 0.05 - 0.1 were considered to be marginally significant. Greenhouse-Geisser adjusted P -values were used in determining statistical significance in repeated measures analyses and the Tukey-Kramer method used as a post-hoc test to compare treatment least squares means. Dependent variables analyzed using ANOVA were species richness (number of species), relative abundance, relative dominance, final biomass, percent cover, salinity concentration, water level, proportion of full sunlight, and redox potential (analyzed as a nested design). Biomass data were $\ln(x+1)$ transformed to reduce heterogeneity of variances; means were detransformed for presentation (Neter et al., 1990). Species richness was determined from monthly cover data. A fire consumed four plots in the Spartina community in February 1995; vegetation and light data from these plots for the remainder of the study were not included in analyses.

Relative frequency of occurrence of species in the vegetation during the study (based on monthly cover data) and in the seed bank was calculated by dividing the

frequency of each species by the sum of the frequencies of all species and multiplying by 100%. For quarterly sampling events, relative abundance of species was calculated by dividing the number of seedlings or ramets of a particular species in a sample by the total number of seedlings or ramets for that sample. Relative dominance was calculated by multiplying the average height of each species by its percent cover in each quadrat, and dividing this dominance measure by the sum of the dominance values for that sample. This measure of dominance is an index of the volume occupied by each species and has been used by other authors (Brewer and Grace, 1990). Because many species occurred at low frequency, ANOVAs of relative abundance and dominance were limited to the five species occurring at highest relative frequency in all disturbance treatments combined in each community.

Principal components analysis (PCA) of monthly cover data was conducted using the PRINCOMP procedure of SAS. To examine seasonal differences in community structure I prepared separate ordinations for monthly cover estimates made in two seasons, April - October and November - March, over the two-year study in both communities. These time periods seemed to represent two distinct seasons for plant growth and community composition based on climatological data and the observed phenology and life history of plant species at the study site. Scores from the first two PCA axes were used to prepare ordination diagrams of plots subjected to the three disturbance treatments. I conducted Pearson

correlation analysis of PCA axis scores and proportion of full sunlight to examine the relationship between light penetration and community structure.

RESULTS

Response of vegetation to disturbance

Frequency of occurrence in the vegetation and seed bank.—In the vegetation species tended to be distributed more evenly among disturbance treatments in the Sagittaria community than in the Spartina community (Table 3.1). Similar numbers of species were observed in the three disturbance treatments in the Sagittaria community, while the number of species observed increased with increasing disturbance intensity in the Spartina community (Table 3.1).

The effect of disturbance was not uniform across species (Table 3.1). Of species occurring at > 5% relative frequency in any of the disturbance treatments in the Sagittaria community, the relative frequencies of Aster, Eleocharis fallax, and Ptilimnium were similar (within a range of 2%) in all three treatments, while the frequencies of Alternanthera, Cyperus haspan, Diodia, Polygonum, Sagittaria, and Vigna differed among treatments. In the Spartina community, Spartina occurred at a much higher frequency than other species in the undisturbed and nonlethal treatments, but at a low frequency in the lethal treatment (Table 3.1). Most other species in the Spartina community occurred at their highest frequency in the lethal treatment. Polygonum occurred at high relative frequencies in the nonlethal and lethal treatments, and Scirpus and Vigna were the only species other than Spartina that occurred at their highest frequency in the undisturbed treatment in this

Table 3.1. Relative frequency (%) of species in vegetation subjected to three disturbance treatments (U = undisturbed, NL = nonlethal disturbance, and L = lethal disturbance) throughout the study and in seed banks of two oligohaline marsh communities. Life history type indicated after species name (A = annual, P = perennial). Nomenclature according to Kartesz (1994).

Species	<u>Sagittaria</u> Community				<u>Spartina</u> Community			
	Vegetation			Seed bank	Vegetation			Seed bank
	U	NL	L		U	NL	L	
<u>Alternanthera philoxeroides</u> (Mart.) Griseb. (P)	7.9	7.6	2.4	0	0	0.2	0	0
<u>Amaranthus australis</u> (Gray) Sauer (A)	0	0.4	0.3	2.5	0	0.2	2.6	6.5
<u>Ammannia latifolia</u> L. (A)	0	0	0	0	0	0.5	2.4	16.1
<u>Aster subulatus</u> Michx. (A)	12.1	11.5	11.2	10	0.7	5.6	8.6	3.2
<u>Baccharis halimifolia</u> L. (P)	0.1	0.1	0.1	0	0	4.2	8.5	0
<u>Bacopa monnieri</u> (L.) Pennell (P)	0	0	0	0	0	0	0.6	0
<u>Cuscuta pentagona</u> Engelm. (A)	0.2	0.1	0.3	0	0	0	0	0
<u>Cyperus polystachyos</u> Rottb. var. <u>filicinus</u> (Vahl) C.B. Clarke (A)	0	0	0	2.5	0	0	0.5	0
<u>Cyperus haspan</u> L. (A)	0.2	1.1	8.1	15	0	0	0	1.6
<u>Cyperus odoratus</u> L. (A)	0	0.1	0.8	0	0	0.7	2.7	16.1
<u>Cyperus</u> sp.	0.1	0.3	1.8	0	0	1.5	5.9	0
<u>Diodia virginiana</u> L. (P)	2.8	5.4	6.2	5	0	0	1.5	0
<u>Echinochloa crus-galli</u> (L.) Beauv. (A)	0	0.2	1.8	2.5	0	0	3.0	9.7
<u>Eclipta prostrata</u> (L.) L. (A)	0	0	0	0	0	0	0.8	0
<u>Eleocharis fallax</u> Weatherby (P)	15.2	16.4	16.8	17.5	0	0	1.5	0

(table con'd)

Species	<u>Sagittaria</u> Community				<u>Spartina</u> Community			
	Vegetation			Seed bank	Vegetation			Seed bank
	U	NL	L		U	NL	L	
<u>Eleocharis parvula</u> (Roemer & J.A. Schultes) Link ex Bluff, Nees & Schauer (P)	0	0	0	0	0	0	0	8.1
<u>Galium tinctorium</u> (L.) Scop. (P)	4.6	3.2	1.1	0	0	0	0	0
<u>Ipomoea sagittata</u> Poir. (P)	3.7	3.3	0.1	0	0.3	0	1.6	0
<u>Kosteletzkya virginica</u> (L.) K. Presl ex Gray (P)	0.1	3.4	1.1	0	0.3	2.9	4.0	0
<u>Leptochloa fascicularis</u> (Lam.) Gray (A)	0	0	0	0	0	0	1.7	0
<u>Ludwigia leptocarpa</u> (Nutt.) Hara (P)	0	0	0	0	0	0	0.2	0
<u>Lythrum lineare</u> L. (P)	3.0	0.5	1.7	7.5	0	4.6	2.3	4.8
<u>Phyla nodiflora</u> (L.) Greene (P)	4.4	2.3	1.3	2.5	0	0	0	0
<u>Polygonum punctatum</u> Ell. (P)	16.3	15.8	22.1	17.5	2.3	19.5	20.0	8.1
<u>Ptilimnium capillaceum</u> (Michx.) Raf. (A)	8.4	7.8	8.7	0	0	3.4	6.0	0
<u>Sagittaria lancifolia</u> L. (P)	13.6	14.3	7.2	15	0	0	2.5	12.9
<u>Sacciolepis striata</u> (L.) Nash (P)	0.9	0.2	3.7	0	0.3	2.2	3.0	0
<u>Scirpus tabernaemontani</u> K.C. Gmel. (P)	0	0	0	0	16.7	0.5	4.2	9.7
<u>Sesbania exaltata</u> (Raf.) Rydb. ex A.W. Hill (A)	0	0	0	0	0.3	10.2	5.9	3.2
<u>Sium suave</u> Walt. (P)	0.1	0.7	0	0	0	0	0	0
<u>Spartina patens</u> (Ait.) Muhl. (P)	0	0	0	0	70.9	36.9	5.6	0
<u>Vigna luteola</u> (Jacq.) Benth. (P)	6.1	5.6	3.4	2.5	8.2	7.1	4.4	0
Species richness	19	22	21	12	9	16	25	12

community. The deciduous shrub Baccharis halimifolia was the only woody species identified, and this species occurred almost exclusively in the lethal and nonlethal disturbance treatments in the Spartina community.

Most of the 17 species observed in the seed bank were also observed in the vegetation (Table 3.1). All of the seed bank species observed in the Sagittaria community were observed in the vegetation except Cyperus polystachyos, and seed bank species occurred in all three disturbance treatments. Except for Cyperus haspan and Eleocharis parvula, all of the species observed in the seed bank of the Spartina community were observed in the vegetation, although seed bank species occurred almost exclusively in the disturbed treatments. The seed banks of the two communities contained similar numbers of annual and perennial species.

Species richness.—The overall effect of disturbance on species richness was significant in both the Sagittaria community (Fig. 3.1; $P = 0.0005$) and the Spartina community (Fig. 3.1; $P < 0.0001$). The time \times disturbance interaction was also significant ($P < 0.0001$) for both communities (Fig. 3.1). For sampling dates when significant differences occurred among disturbance treatments, species richness in the Sagittaria community was significantly lower in the lethal treatment than in the nonlethal or undisturbed treatments, which differed significantly on only one sampling date (Fig. 3.1). In contrast with the Sagittaria community, species richness in the Spartina community was significantly higher in the lethal treatment than in the undisturbed treatment on all sampling dates where significant differences occurred (Fig. 3.1). The species richness of the nonlethal treatment was generally

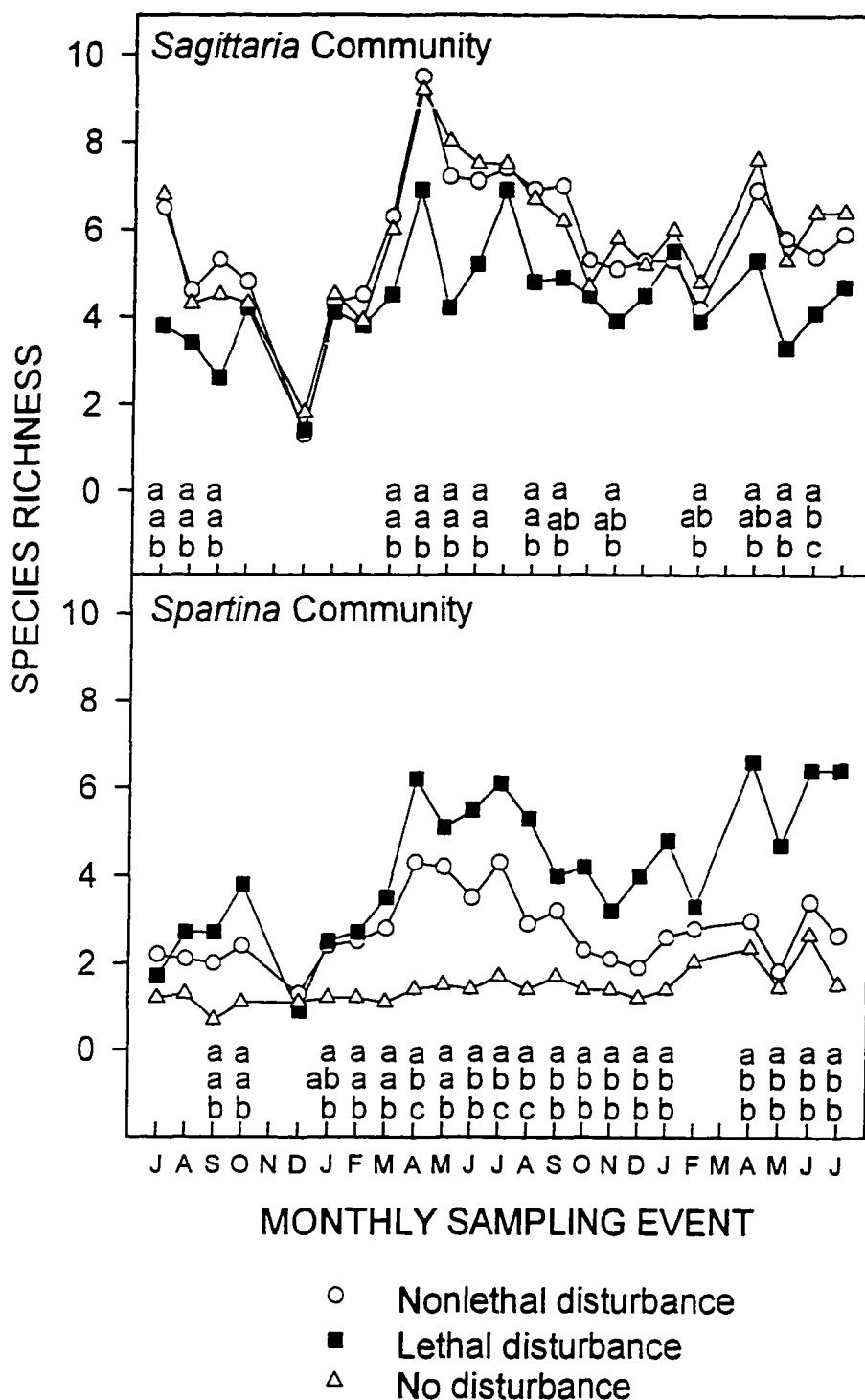


Fig. 3.1. Dependence of species richness (in 0.25 m² plots) on disturbance intensity in two oligohaline marsh communities. Where differences between treatment means were significant, letters corresponding to the plotted means are shown below them at the bottom of each graph. Means with different letters are significantly different.

intermediate to the lethal and undisturbed treatments, differing significantly from the undisturbed treatment initially and from the lethal treatment during the second half of the experiment.

Relative abundance and dominance.—In ANOVAs of the relative abundance of the five most frequently occurring species, the overall effect of disturbance in the Sagittaria community was significant for Aster, Polygonum, and Sagittaria, but not for Eleocharis fallax and Ptilimnium (Table 3.2). However, the time \times disturbance interaction was significant for all of these species, and significant effects of disturbance occurred for all of these species on certain sample dates (Fig. 3.2). For sample dates where significant differences occurred, the relative abundance of Aster, Ptilimnium, and Sagittaria was always lower in the lethal treatment than in the undisturbed or nonlethal treatment, which generally did not differ (Fig. 3.2). Polygonum occurred at its highest relative abundance in the lethal treatment throughout the study. Eleocharis occurred at low relative abundance in the lethal treatment early in the study but eventually reached its highest abundance in the lethal treatment late in the study. In the Spartina community, the effect of disturbance was marginally significant for Baccharis and not significant for Sesbania, but significant for the other species (Table 3.2). All species occurred at their highest abundance in the lethal treatment in this community except Spartina (Fig. 3.2). The pattern of significance of overall effects of disturbance on relative dominance was almost identical to that of relative abundance (Table 3.2), as was the pattern of significance within sample dates, so graphs of relative dominance data are not presented.

Table 3.2. Results of repeated measures ANOVAs of relative abundance and relative dominance of the five most frequently occurring species in the Sagittaria and Spartina marsh communities. Values are *P*-levels from ANOVAs of relative abundance (relative dominance in parentheses).

Species	Between subjects		Within subjects		
	Disturbance (D)	Block (B)	Time (T)	T × D	T × B
<u>Sagittaria</u> community					
<u>Aster</u>	<0.0001 (0.0106)	0.1353 (0.3954)	<0.0001 (<0.0001)	0.0008 (0.0182)	0.4072 (0.6666)
<u>Eleocharis</u>	0.5795 (0.2165)	0.1019 (0.2866)	<0.0001 (<0.0001)	<0.0001 (<0.0001)	0.1332 (0.0091)
<u>Polygonum</u>	<0.0001 (<0.0001)	0.0219 (0.4734)	<0.0001 (<0.0001)	0.0421 (<0.0001)	0.6365 (0.5784)
<u>Ptilimnium</u>	0.1566 (0.9287)	0.6169 (0.1924)	<0.0001 (<0.0001)	0.0049 (<0.0001)	0.5181 (0.0234)
<u>Sagittaria</u>	<0.0001 (<0.0001)	0.7111 (0.7811)	<0.0001 (<0.0001)	<0.0001 (<0.0001)	0.4535 (0.2208)
<u>Spartina</u> community					
<u>Aster</u>	0.0302 (0.0412)	0.5396 (0.6185)	0.0491 (0.3015)	0.1408 (0.3342)	0.3973 (0.5603)
<u>Baccharis</u>	0.0540 (0.0445)	0.2321 (0.0949)	0.0162 (0.0018)	0.0502 (0.0684)	0.2164 (0.1590)
<u>Polygonum</u>	<0.0001 (<0.0001)	0.3234 (0.2768)	<0.0001 (<0.0001)	<0.0001 (<0.0001)	0.3384 (0.5308)
<u>Sesbania</u>	0.1744 (0.1766)	0.3067 (0.1342)	0.0110 (0.0047)	0.1980 (0.1879)	0.3002 (0.2006)
<u>Spartina</u>	<0.0001 (<0.0001)	0.3801 (0.2302)	0.3204 (0.1774)	0.2733 (0.1514)	0.7071 (0.7002)

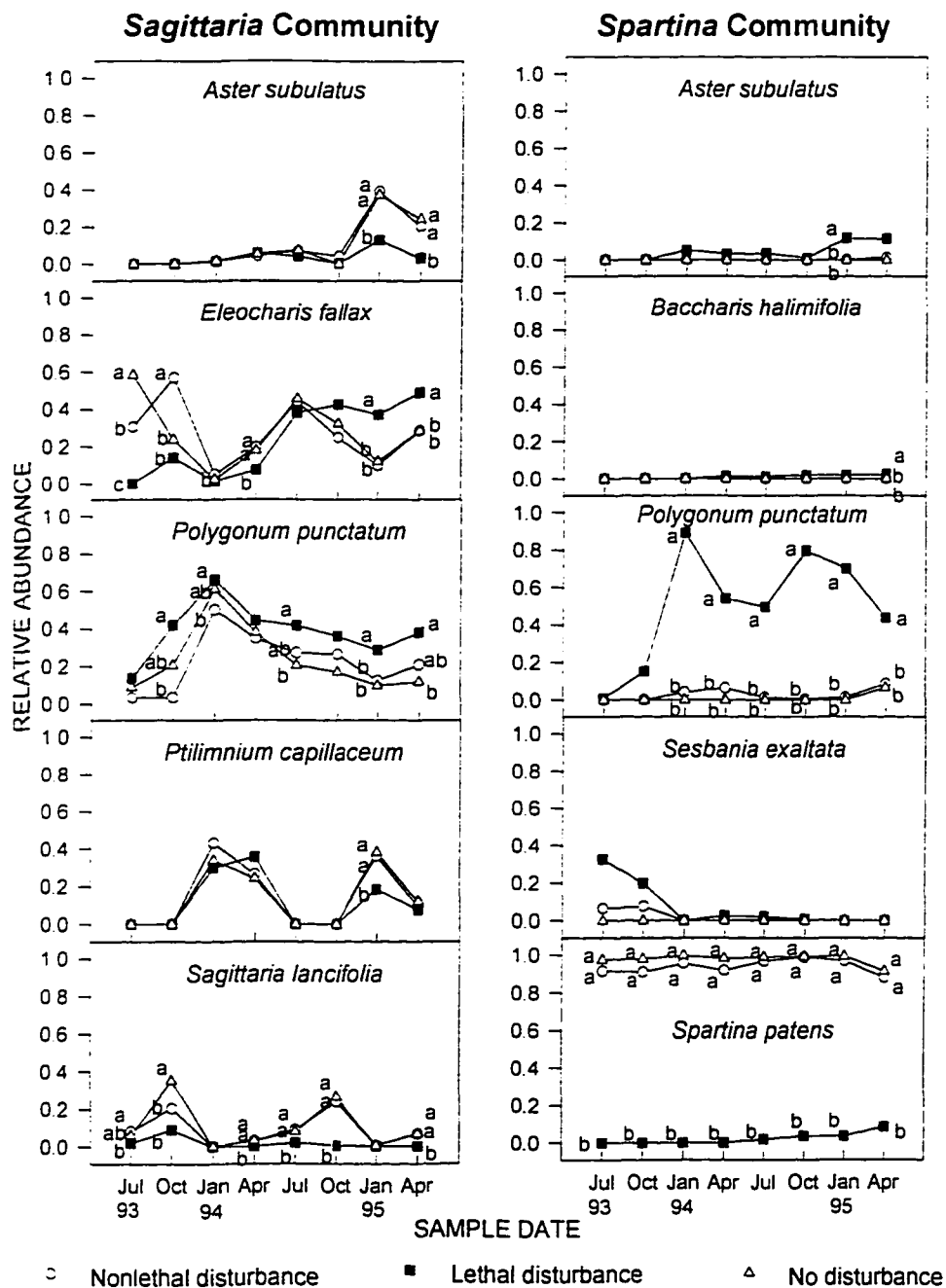


Fig. 3.2. Disturbance-induced changes in relative abundance of seedlings or ramets of the five most frequently occurring species in two marsh communities. Means having different letters are significantly different.

There was very little successful colonization of plots subjected to a lethal disturbance by the community dominants Sagittaria and Spartina via vegetative propagation or seedling recruitment (Fig. 3.2). Seedlings of Sagittaria did colonize following a lethal disturbance in both communities, but the majority of these did not survive. No Spartina seedlings were observed during the study. Aster, Polygonum, and Ptilimnium seedlings were recruited at relatively high densities during the winter months of one or both of the years sampled (Fig. 3.2). Ptilimnium and Aster behaved as annuals, but many Polygonum seedlings overwintered, resprouting early in the following spring. In the Sagittaria community, the perennial Eleocharis fallax increased in abundance and dominance in the lethal treatment via vegetative propagation after initially colonizing via seedling recruitment. The woody shrub Baccharis, while recruited at low densities, occurred at significantly higher relative abundance in the lethal treatment than in other treatments by the end of the experiment. Although differences were not significant, Sesbania initially colonized some plots at high densities following lethal and nonlethal disturbances in the Spartina community; in some cases Sesbania grew to form thickets > 2 m in height, flowered, and subsequently occurred at low abundance and dominance for the remainder of the study.

Final biomass.—Total live biomass two years after the disturbance treatments were applied was significantly reduced by the lethal treatment in the Spartina community but not in the Sagittaria community (Table 3.3). However, the proportion of all living and nonliving biomass that was dead was significantly lower

Table 3.3. Mean live biomass (g) and mean percent of total biomass that was dead (in parentheses) of species in two oligohaline marsh communities two years after three disturbance treatments were applied (U = undisturbed, NL = nonlethal disturbance, L = lethal disturbance). Within community type, means having different superscripted letters are significantly different. Biomass values were $\ln(x + 1)$ transformed prior to analysis.

Species	<u>Sagittaria</u> Community			<u>Spartina</u> Community		
	U	NL	L	U	NL	L
<u>Alternanthera philoxeroides</u>	3.33	1.93	1.09	0	0	0
<u>Amaranthus australis</u>	0	0	0	0.01	0.01	0.10
<u>Ammannia latifolia</u>	0	0	0	0.0 ^b	0.0 ^b	0.29 ^a
<u>Aster subulatus</u>	43.01 ^{**} (0.2)	24.36 ^{ab} (0.2)	14.86 ^{b*}	0.36 ^{b*}	0.64 ^{ab}	1.71 ^{a*}
<u>Baccharis halimifolia</u>	0	0	0	0.67 ^{b*}	0.83 ^{b*}	8.23 ^{a*}
<u>Bacopa monnieri</u>	0	0	0	0	0	0.03
<u>Cyperus haspan</u>	0.0 ^b	0.24 ^b	1.88 ^a (0.4)	0	0	0
<u>Cyperus polystachyos</u>	0	0	0	0	0	0.16
<u>Cyperus</u> sp.	0	0	0	0.08	0.08	0.15
<u>Diodia virginiana</u>	0.93	0.50	0.47	0.41	0.41	0.41
<u>Echinochloa crus-galli</u>	0	0	0.06	0	0	0.05
<u>Eleocharis fallax</u>	8.65 ^b (11.2)	6.94 ^b (7.4)	31.02 ^a (11.8)	0	0	0.41 (8.6)
<u>Galium tinctorium</u>	0.16	0.18	0	0	0	0
<u>Ipomoea sagittata</u>	0.89 ^{ab}	1.43 ^a	0.0 ^b	0	0	0.45
<u>Kosteletzkya virginica</u>	0.0 ^{b*}	1.55 ^{a*}	0.11 ^{ab}	0	0	1.17
<u>Leptochloa fascicularis</u>	0	0	0	0	0	0.21

(table con'd)

Species	<u>Sagittaria</u> Community			<u>Spartina</u> Community		
	U	NL	L	U	NL	L
<u>Lythrum lineare</u>	0.88	0.07	0.51	0	0	0.65 (6.2)
<u>Mikania scandens</u>	0	0	0	0	0	0.07
<u>Phyla nodiflora</u>	1.55 (0.2)	0.46 (0.2)	0.35 (0.2)	0	0	0
<u>Polygonum punctatum</u>	8.78 ^c	22.24 ^b	72.73 ^a (0.3)	0.0 ^b (34.6)	0.77 ^b (33.8)	27.91 ^a (34.9)
<u>Ptilimnium capillaceum</u>	0	0.0 (69.9)	0.11 (40.5)	0	0	0.0 (100)
<u>Sagittaria lancifolia</u>	106.91 ^a (19.0)	81.83 ^a (24.2)	0.85 ^b (34.2)	0	0	0.38 (49.7)
<u>Sacciolepis striata</u>	0	0.10	0.06	0.33	0.58	0.33
<u>Scirpus robustus</u> Pursh	0	0	0.16	0	0	0.34
<u>Scirpus tabernaemontani</u>	0	0	0	2.40 ^{ab} (31.3)	0.13 ^{b*} (0.5)	5.44 ^{a*} (31.9)
<u>Sesbania exaltata</u>	0	0	0	0.04	0.21	0.38
<u>Sium suave</u>	0	0.12	0	0	0	0
<u>Spartina patens</u>	0	0	0	323.16 ^a (42.0 ^a)	395.37 ^a (37.6 ^a)	5.78 ^b (15.2 ^b)
<u>Vigna luteola</u>	1.36 ^{a*}	0.40 ^{ab}	0.16 ^{b*}	0.25	0.34	0.33
Total	204.2 (11.7 ^a)	184.8 (13.4 ^a)	150.9 (5.1 ^b)	377.3 ^a (33.6 ^a)	434.0 ^a (33.6 ^a)	142.7 ^b (17.1 ^b)

* Marginally significant difference ($P = 0.05 - 0.10$)

in the lethal treatment in both communities (Table 3.3). The lethal treatment stimulated colonization and growth of Cyperus haspan, Eleocharis fallax, and Polygonum in the Sagittaria community; biomass of Aster, Ipomoea, Sagittaria, and Vigna was higher in nonlethal or undisturbed treatments in this community. In the Spartina community Aster, Baccharis, Polygonum, and Scirpus tabernaemontani had higher biomass in the lethal treatment; only Spartina occurred at lower biomass in the lethal treatment. Spartina was the only species to exhibit significant differences in the proportion of total biomass that was dead; a lower proportion of dead biomass occurred in the lethal treatment (Table 3.3). The amount of dead biomass of Spartina in the undisturbed and nonlethal treatments was considerably higher than that of other species, comprising a majority of the dead biomass and over a third of the total biomass present.

Cover.—In the absence of disturbance Spartina occurred at high percent cover in its community throughout the year (Table 3.4). In contrast, the cover of Sagittaria in undisturbed vegetation was lower than that of Spartina in its community during the spring and summer and decreased to very low cover during the winter due to dieback (Table 3.4). With the exception of Sesbania, the cover of the other most frequently occurring species did not differ significantly between the undisturbed and nonlethal treatments in either season (Table 3.4). Cover of Eleocharis, Polygonum, Baccharis, and Sesbania was significantly higher in the lethal treatment than in the nonlethal or undisturbed treatments (Table 3.4). The cover of Ptilimnium, Sagittaria, and Spartina, on the hand, was lowest in the lethal

Table 3.4. Mean cover (%) of the five most frequently occurring species in two oligohaline marsh communities during two seasons (over a period of two years) in vegetation subjected to three disturbance treatments (U = undisturbed, NL = nonlethal disturbance, and L = lethal disturbance). Within season and community type, means having different superscripted letters are significantly different.

Species	April — October			November — March		
	U	NL	L	U	NL	L
<u>Sagittaria</u> community						
<u>Aster subulatus</u>	6.1 ^a	5.4 ^a	1.7 ^b	5.2 ^a	4.3 ^{a*}	2.6 ^{b*}
<u>Eleocharis fallax</u>	4.8 ^b	4.2 ^b	7.5 ^a	2.4 ^b	2.8 ^b	4.2 ^a
<u>Polygonum punctatum</u>	13.1 ^b	10.7 ^b	24.1 ^a	14.5 ^{ab}	13.3 ^{b*}	18.2 ^{a*}
<u>Ptilimnium capillaceum</u>	4.7 ^a	3.7 ^{ab}	2.3 ^b	8.2	9.6	7.2
<u>Sagittaria lancifolia</u>	22.4 ^a	20.5 ^a	1.4 ^b	1.8 ^a	2.0 ^a	0.35 ^b
<u>Spartina</u> community						
<u>Aster subulatus</u>	0.03 ^b	0.42 ^b	1.9 ^a	0.01 ^b	0.13 ^b	1.7 ^a
<u>Baccharis halimifolia</u>	0.13 ^b	0.38 ^b	4.9 ^a	0.03 ^b	0.28 ^b	2.9 ^a
<u>Polygonum punctatum</u>	0.09 ^b	1.9 ^b	25.1 ^a	0.09 ^b	2.3 ^b	19.4 ^a
<u>Sesbania exaltata</u>	0.86 ^b	4.8 ^a	4.6 ^a	<0.01	0.06	0.09
<u>Spartina patens</u>	86.3 ^a	59.8 ^b	1.5 ^c	79.4 ^a	53.1 ^b	1.6 ^c

* Marginally significant difference ($P = 0.05 - 0.10$)

treatment. Aster cover was lowest in the lethal treatment in the Sagittaria community but reached its greatest cover in this treatment in the Spartina community. Differences persisted through the winter months for all species except Sesbania and Ptilimnium (Table 3.4).

Ordination diagrams based on monthly cover data graphically illustrate the similarity in community structure between plots subjected to the undisturbed and nonlethal treatments, and their distinction from the structure of plots receiving the lethal treatment (Figs. 3.3 and 3.4). Differences among treatments are evident primarily during the spring and summer months in the Sagittaria community, with less separation among treatments occurring during the winter months (Fig. 3.3). In the Spartina community the difference of the lethal treatment from the other treatments is evident in both seasons (Fig. 3.4). Plots receiving the undisturbed and nonlethal treatments in the Spartina community are clustered closely together, primarily because they were predominantly composed of Spartina, while the cover and species composition of vegetation in plots receiving the lethal treatment in this community were more variable.

Environmental conditions

Light.—The overall effect of disturbance on light penetration was significant in both marsh communities ($P < 0.0001$), with significantly higher light levels occurring in the lethal treatment than in the nonlethal or undisturbed treatments (which generally did not differ significantly) on most sample dates (Fig. 3.5). Light levels were low (generally $< 20\%$ full sun) below the canopy in the nonlethal and

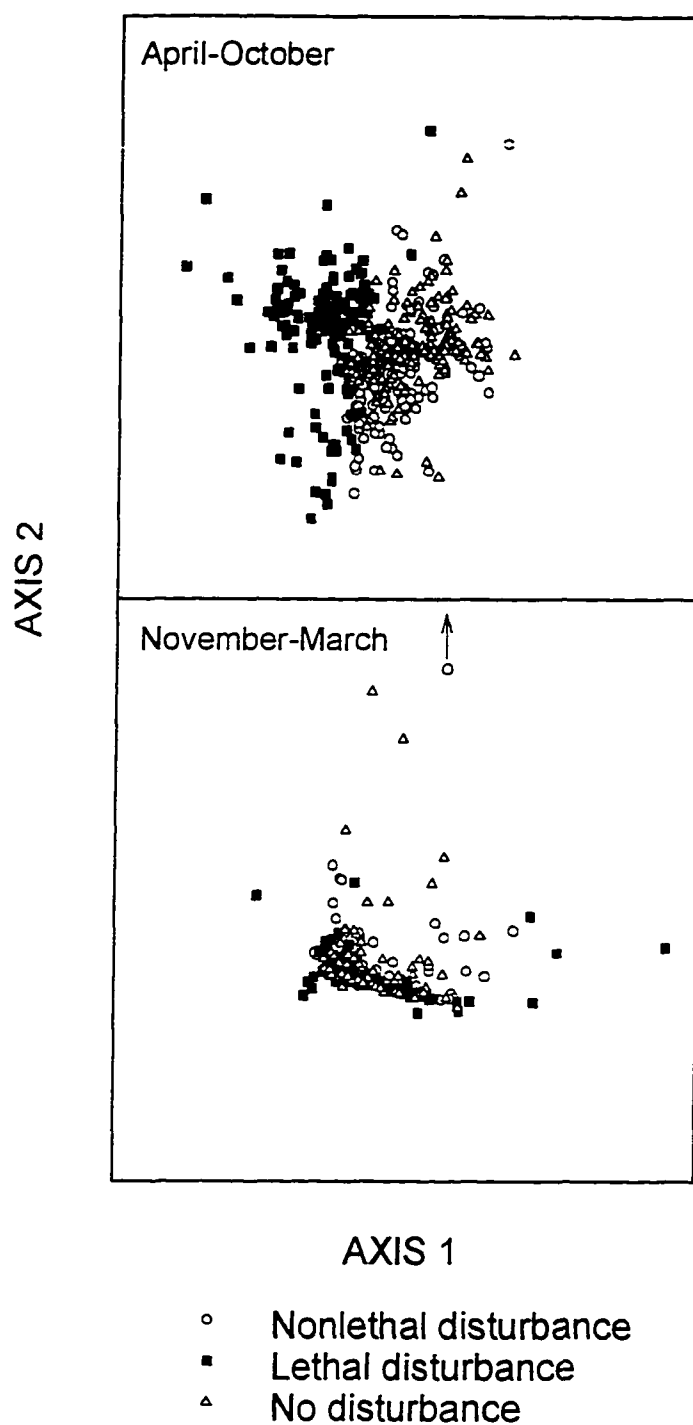


Fig. 3.3. Seasonal variation in community structure in the *Sagittaria* marsh community following disturbances of three intensities. Points are axis scores for field plots from Principal Components Analysis of cover data collected monthly for two years.

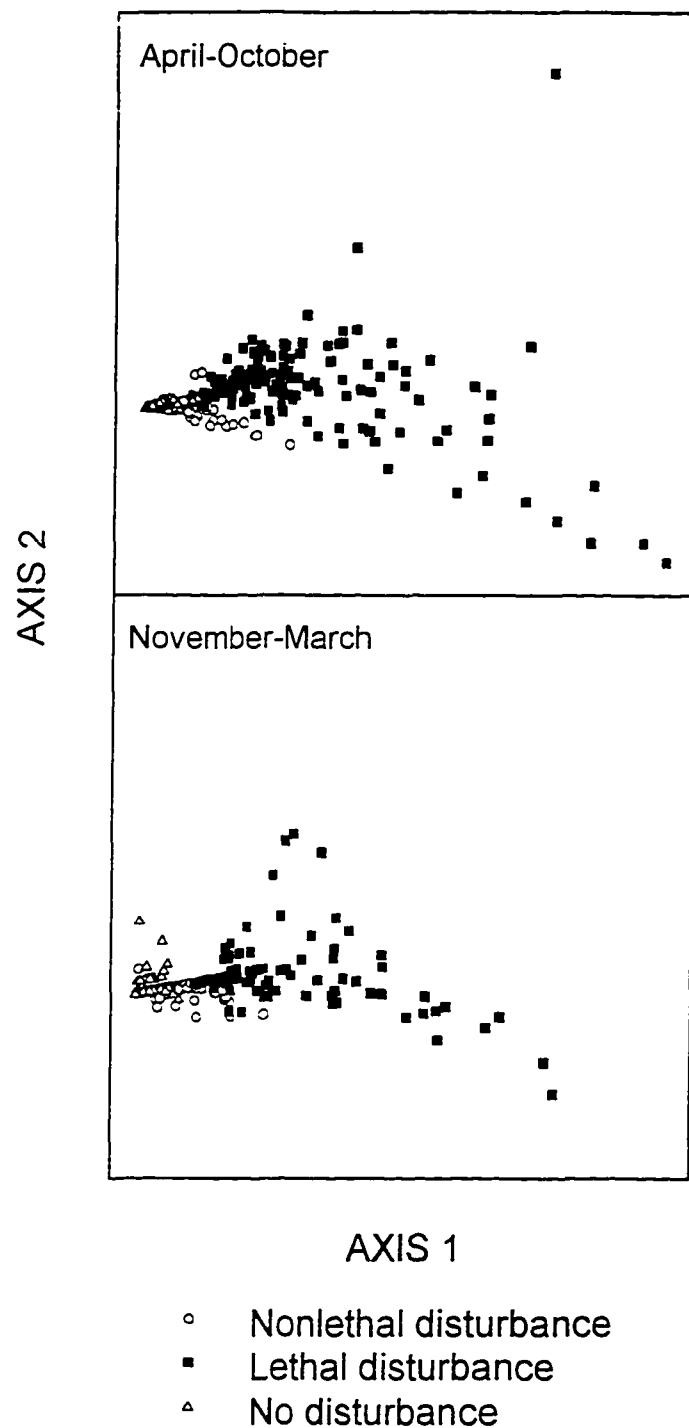


Fig. 3.4. Seasonal variation in community structure in the Spartina marsh community following disturbances of three intensities. Points are axis scores for field plots from Principal Components Analysis of cover data collected monthly for two years.

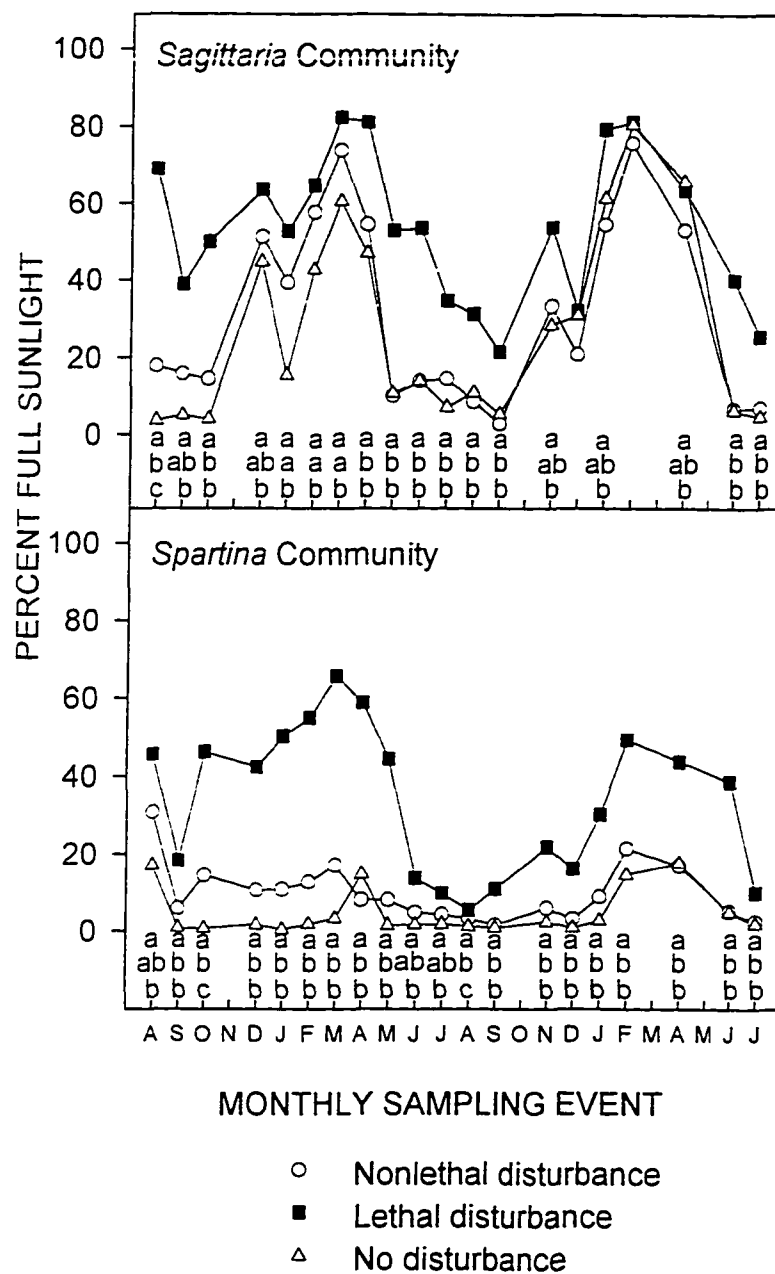


Fig. 3.5. Differences in light penetration in vegetation subjected to disturbances of three intensities in two oligohaline marsh communities. Where differences between treatment means were significant, letters corresponding to the plotted means are shown below them at the bottom of each graph. Means with different letters are significantly different.

undisturbed treatments of the Spartina community throughout the study, while low light levels in these treatments occurred only during the summer months in the Sagittaria community. During the winter and spring months when dominant vegetation had died back, high light levels (> 40% full sun) occurred in all treatments in the Sagittaria community.

Light penetration was moderately but significantly correlated with PCA axis scores (Table 3.5). Correlation coefficients reflect the higher light levels in plots subjected to the lethal treatment relative to plots subjected to other treatments (Figs. 3.3 and 3.4). The magnitude of the correlation coefficients for Axis 1 was greater for April - October for the Sagittaria community and for November - March for the Spartina community. During November - March, most of the vegetation in the Sagittaria community had died back or occurred as seedlings, and differences in light penetration among disturbance treatments were smaller than during April - October (Fig. 3.5). The canopy of Spartina, however, persisted throughout the year, and the greatest differences among treatments occurred during November - March when dominant vegetation in the lethal treatment had died back or consisted primarily of seedlings.

Salinity.—Salinity levels were low in both communities, although slightly higher mean and range values occurred in the Spartina community than in the Sagittaria community (Table 3.6). Salinity of standing water tended to fluctuate to a greater degree than that of interstitial water. There was a significant overall effect of community type on salinity level of interstitial water ($P < 0.0001$) and standing

Table 3.5. Pearson correlation analysis of PCA axis scores and light level.

Season	Community			
	<u>Sagittaria</u>		<u>Spartina</u>	
	<u><i>r</i></u>	<u><i>P</i></u>	<u><i>r</i></u>	<u><i>P</i></u>
April — October				
PCA axis 1	-0.31	<0.0001	0.30	<0.0001
PCA axis 2	0.26	<0.0001	0.12	0.0269
November — March				
PCA axis 1	0.17	0.0080	0.62	<0.0001
PCA axis 2	-0.19	0.0025	0.07	0.2518

Table 3.6. Summary of salinity, relative water level, and redox potential (Eh) measurements in two oligohaline marsh communities. Values are mean \pm SE (N) and range (minimum — maximum). Positive water level indicates elevation above marsh surface, negative water level depth below marsh surface.

Parameter	Community	
	<u>Sagittaria</u>	<u>Spartina</u>
Salinity (parts per thousand)		
Interstitial water	0.96 \pm 0.03 (229)	1.32 \pm 0.04 (223)
	0.17 — 1.7	0.64 — 2.4
Standing Water	0.88 \pm 0.05 (143)	1.28 \pm 0.05 (160)
	0.13 — 2.1	0.45 — 2.5
Relative Water Level (cm)		
	5.13 \pm 0.9 (231)	7.24 \pm 0.8 (225)
	-21.7 — +47.5	-3.8 — +46.2
Redox potential (mV)		
Undisturbed	-8.0 \pm 16.8 (30)	-149.5 \pm 16.9 (30)
Nonlethal disturbance	-28.3 \pm 16.8 (30)	-141.5 \pm 16.9 (30)
Lethal disturbance	-69.4 \pm 16.8 (30)	-124.4 \pm 16.9 (30)

water ($P < 0.0001$), although the time \times community interaction was significant for interstitial water salinity ($P = 0.001$). Interstitial salinity was significantly higher in the Spartina community than the Sagittaria community on 48% of the sample dates, while standing water salinity was significantly higher in the Spartina community on 60% of the sample dates. Otherwise, differences between communities were not significant.

Relative water level.—Water levels fluctuated markedly relative to the marsh surface but tended to be slightly higher in the Spartina community than in the Sagittaria community (Table 3.6). Differences in water levels between communities were marginally significant overall ($P = 0.0536$), although effects of time and time \times community were highly significant ($P < 0.0001$). On 48% of the sample dates water levels were significantly higher in the Spartina community than in the Sagittaria community, while on 13% of the sample dates water levels were significantly higher in the Sagittaria community. Differences were not significant during other sample dates.

Redox potential.—Redox potential was significantly lower in the Spartina community than in the Sagittaria community ($P < 0.0001$), although the effect of disturbance on Eh was not significant ($P = 0.5566$; Table 3.6). Mean Eh was -138.5 mV in the Spartina community and -35.2 mV in the Sagittaria community. The community \times disturbance interaction was significant ($P = 0.0375$), but the effect of disturbance was not significant ($P > 0.15$) when analyzed by community. There was, however, a trend toward lower Eh with increasing intensity of

disturbance in the Sagittaria community; no trend was evident in the Spartina community (Table 3.6).

DISCUSSION

One of the most striking results of this experiment was the persistent effect of an intense lethal disturbance on community structure compared with that of a milder nonlethal disturbance, soon after which the vegetation resembled that of the undisturbed treatment. This pattern occurred in both the Sagittaria and the Spartina communities, which have very different assemblages of species. Analyses of relative frequency, species richness, relative abundance, relative dominance, final biomass, and cover all indicate that community structure differed between the lethal treatment and the nonlethal and undisturbed treatments (which were similar), and that these differences persisted throughout the study. Following the nonlethal disturbance community dominants resprouted rapidly and quickly reestablished the structure of the community. In this sense the populations of dominant perennials were stable and resilient (*sensu* Underwood, 1989) in response to a nonlethal disturbance, such as might occur due to low intensity grazing pressure or fires. All vegetation was killed by the lethal disturbance treatment as might occur due to wrack deposition, sedimentation, scouring, or flooding after fire or herbivory. There was very little successful colonization by community dominants in the lethal treatment during the study, suggesting that differences would persist for some time. Seedlings of Sagittaria were periodically observed in the lethal treatment, but most of these did not survive, possibly because of herbivory by nutria. No Spartina

seedlings were observed during the study and Spartina was slow to colonize vegetatively, possibly because of competitive inhibition by the high densities of Polygonum, Baccharis, and other species recruited from seed. Dominant perennials therefore appear to be relatively unstable and not resilient (at least locally) in response to lethal disturbances.

The influence of dominant perennials on regeneration

The similarity in structure between the nonlethal disturbance treatment and undisturbed vegetation is due to the rapid resprouting of the community dominants Sagittaria and Spartina. While more seedlings did become established following nonlethal disturbances than when no disturbance occurred in the Spartina community, these were quickly displaced by resprouting Spartina. Due to the more open canopy of Sagittaria and its dieback in the winter months, seedling recruitment rates were higher in the undisturbed vegetation of the Sagittaria community than in that of the Spartina community and were little affected by the temporary opening of the canopy caused by the nonlethal disturbance.

The low abundance and dominance of the dominant species in the lethal treatments appears to have had differential effects on the establishment and growth of individual colonizing species, and may be the primary cause for the differences in community structure I observed. In many plant communities there are species requiring special conditions or disturbance for germination (van der Valk, 1992), and different species may have distinct requirements for regeneration (Grubb, 1977). Additionally, competitive interactions among species are important in structuring

many plant communities (Grime, 1977; Silander and Antonovics, 1982; Grace and Tilman, 1990; Bertness, 1991a). In crossed-gradient experiments of effects of productivity and disturbance, the importance of interspecific competition as a determinant of vegetation structure was found to decrease with increasing intensity of disturbance (Campbell and Grime, 1992; Turkington et al., 1993). The low abundance and dominance of dominant perennials I observed following the lethal disturbance undoubtedly altered the competitive environment, apparently favoring some species and inhibiting others.

The importance of seedling recruitment following disturbance

My results indicate that seedling recruitment is an important component of regeneration following intense disturbances which kill dominant vegetation in oligohaline marshes. Several perennial species, including Baccharis, Cyperus haspan, Eleocharis fallax, Polygonum, and Scirpus tabernaemontani became established via seedling recruitment at higher frequency, abundance, dominance, biomass, or cover in the lethal disturbance treatment than in other treatments. These findings suggest that lethal disturbances may lead to a change in vegetation structure, and may be important for the establishment and persistence of some species in the community. Additionally, the prevalence of seed bank species in the vegetation following disturbances illustrates the importance of the seed bank as a source of propagules for regeneration following intense disturbances in oligohaline marshes. Seedling recruitment is less important following nonlethal disturbances, when some species may become established temporarily and even reproduce (e.g.,

Sesbania) but are quickly displaced by the rapidly vegetative regrowth of perennial dominants.

The importance of seedling recruitment in regeneration following intense disturbances I observed in oligohaline marshes contrasts with patterns of regeneration observed by other authors in salt marshes. Because of the high soil salinity of salt marshes, bare patches generated by lethal disturbances can become hypersaline, reducing seed germination and colonization via seedling recruitment (Bertness, 1991a; Shumway and Bertness, 1992). Bare patches are colonized vegetatively by more salt-tolerant but competitively inferior perennials which reduce substrate salinity through shading and facilitate vegetative colonization of the patch by less salt-tolerant but competitively superior species (Bertness, 1991a). Seedling recruitment of some species may occur (Ellison, 1987), but the patches are nonetheless quickly colonized by surrounding perennials and close completely, generally in less than two growing seasons for patches of about 1.4 m² or less (Ellison, 1987; Bertness and Ellison, 1987). A 15 m² patch closed in three growing seasons (Ellison, 1987). Consequently, the colonization of disturbance patches in these salt marshes is primarily a function of clonal growth processes (Bertness, 1991a; Shumway and Bertness, 1992).

While increases in salinity also reduce germination rates of many species present in seed banks of oligohaline marshes (Baldwin et al., 1996), my results indicate that disturbances do not result in substrate salinities high enough to inhibit seedling recruitment. Colonization rates for perennial community dominants in my

4 m² patches created by lethal disturbances appear to be considerably slower than those observed in salt marshes, especially when the considerably longer growing season at my study site is taken into account (canopy closure had not occurred in some plots as of April 1996; A. Baldwin, personal observation). The slower colonization rates may be due to the abundance of vegetation recruited via seed which reduced light penetration, possibly competitively inhibiting vegetative colonization by surrounding perennials into the patches. If this is the case, succession following lethal disturbances in oligohaline marshes may adhere to an inhibition model (*sensu* Connell and Slatyer, 1977) rather than a facilitation model, as appears to be the case in salt marshes (Bertness and Ellison, 1987).

The slower colonization rates may be due to differences in the morphology of species in oligohaline and salt marshes. Spartina patens in New England salt marshes has a dense turf morphology and is typically less than 30 cm tall (Bertness, 1991a), while at my study site it has a sprawling tussock morphology and a mean height \pm SE of 108 ± 1.1 cm (some culms were as long as 160 cm). I observed that Spartina colonized bare space either by plantlets produced at the end of long culms that fell over or via sparse culms emerging from subterranean rhizomes, but did not advance as a dense front as occurs in New England salt marshes (Bertness, 1991a). The sprawling morphology of Spartina in Louisiana may not be effective for invading patches containing perennial plants recruited as seedlings. These included the woody shrub Baccharis and semi-woody herb Polygonum, both of which occurred in plots subjected to the lethal treatment, often at high cover values

and heights of > 100 cm during the study. The slow rates of vegetative invasion of Sagittaria lancifolia (which does not occur in salt marshes) may be due primarily to its habit of advancing slowly by producing leaves in a distichous arrangement from subterminal apices of stout (4-5 cm diameter) horizontal rhizomes (Lieu, 1979).

Effects of environmental variables

Disturbances of different intensity may affect community structure in large part by altering light level; the lethal disturbance created higher light levels than did the nonlethal disturbance in both communities. Additionally, light level was correlated with ordination axis scores, indicating a relationship between disturbance intensity, light level, and community structure. Light also appears to be an important requirement for seedling recruitment in the undisturbed vegetation of the Sagittaria community. Higher light levels during the winter months (resulting from dieback of dominant vegetation) coincided with high rates of seedling recruitment by Aster, Polygonum, and Ptilimnium.

Other environmental variables did not explain differences in recruitment patterns between communities or disturbance treatments. Salinity was generally slightly higher in the Spartina community than in the Sagittaria community, but was not sufficiently high to prevent recruitment from the soil seed bank (Baldwin et al., 1996). Salinity did not explain the distribution of the two communities in another study (Brewer and Grace, 1990), although fewer salinity measurements were made. Additionally, the salinities I observed (< 2.5 ppt) are well within the tolerance ranges of the community dominants at my study site (Penfound and Hathaway,

1938; Chabreck, 1972; McKee and Mendelssohn, 1989), suggesting that their distribution is not a result of differential physiological tolerance to salinity.

Water levels tended to be slightly higher and redox potential slightly lower in the Spartina community than in the Sagittaria community. Greater frequency and duration of inundation resulting from lower elevation can decrease redox potential (Reed and Cahoon, 1992; Webb et al., 1995). While Spartina may occur at lower elevation sites experiencing significantly greater duration and frequency of inundation than Sagittaria, these two species may also occur co-occur at the same site (Sasser, 1977), suggesting that elevation does not explain the distribution of the Spartina and Sagittaria communities. Disturbances might be predicted to affect redox potential by changing the availability of carbon available for microbial respiration or the degree of plant-induced soil aeration (Ponnamperuma, 1972; Mendelssohn and Burdick, 1988). Although there was a trend toward lower redox potential with increasing intensity of disturbance in the Sagittaria community, the effect of disturbance on Eh was not significant in either community.

Implications for distribution of community types

Some coastal wetland communities, notably salt marshes and mangroves, exhibit conspicuous zonation of vegetation in response to steep environmental gradients (e.g. Lugo and Snedaker, 1974; Bertness and Ellison, 1987; Bertness, 1991b; McKee, 1993, 1995). In salt marshes a decrease in elevation creates gradients of increasing tidal inundation, increasing salinity, and decreasing redox potential (Bertness and Ellison, 1987). These factors combine to result in a gradient

of increasing stress to vegetation, which allows only the most stress-tolerant species to grow at the seaward end of the gradient. However, the more stress-tolerant species tend to be the weakest competitors, and while physiologically capable of growing over a wide range of elevations, are competitively displaced to more stressful lower elevations by better competitors unable to tolerate the more stressful conditions (Bertness and Ellison, 1987).

In contrast with mangroves and salt marshes, elevational gradients in oligohaline marshes are very weak, with slight changes in elevation, salinity, and inundation occurring over scales of kilometers rather than meters (Penfound and Hathaway, 1938; Chabreck, 1972; Gosselink, 1984). Despite the relative uniformity of environmental conditions as compared with salt marshes and mangroves, boundaries between oligohaline marsh communities are often distinct (Baldwin, personal observation). For example, at my study site there are abrupt boundaries between sections of marsh dominated by Sagittaria and Spartina. Because of the proximity and degree of interspersed of the two community types and the relative uniformity of environmental conditions at my study site, it seems unlikely that differences in environmental conditions explain their distribution. Rather, the distribution of communities and their discrete boundaries may be maintained by competitive interaction among species. Lethal disturbances in the Spartina community may create opportunities for colonization by Sagittaria and other species that, once established, persist indefinitely. At my study site patches of Sagittaria-dominated marsh are embedded in a matrix of Spartina monoculture, and individual

Baccharis shrubs are scattered throughout the Spartina community. My results suggest that these patterns of distribution are the result of colonization following lethal disturbances. In the absence of disturbance the dense, persistent canopy of Spartina and layer of dense standing dead biomass inhibit seedling recruitment, acting to maintain its distribution in the absence of strong salinity or inundation gradients.

In conclusion, my results indicate that patterns of regeneration following disturbance in oligohaline marshes depend on disturbance intensity. Following nonlethal disturbances, regeneration is primarily via vegetative regrowth of dominant clonal perennials. This type of disturbance may provide an opportunity for temporary establishment of other species via seedling recruitment, but the structure of the community is quickly reestablished by the rapid resprouting of the dominant species. Lethal disturbances, on the other hand, create bare soil that is colonized primarily by seedlings which grow rapidly, possibly inhibiting invasion by clonal perennials surrounding the disturbed patch. Competitive inhibition of colonization via seedling recruitment in undisturbed vegetation and following mild disturbances, or via vegetative means following intense disturbances, may be more important than slight differences in salinity and elevation in controlling the community structure of oligohaline marshes.

CHAPTER 4

EFFECTS OF SALINITY AND INUNDATION ON COASTAL MARSHES: DISTURBANCE AS A CATALYST FOR VEGETATION CHANGE

INTRODUCTION

Sea level has risen at an estimated rate of 1.0-2.0 mm/yr over the last 100 yr, and is expected to increase an additional 48 cm by the year 2100 (Gornitz, 1995). In coastal Louisiana, rates of relative sea level rise are nearly 10 times the eustatic rate due to the effects of subsidence and anthropogenic activities such as levee and canal construction (Boesch et al., 1994; Gornitz, 1995). Rising sea level is expected to result in greater frequency and duration of inundation, and in some cases higher salinities, in coastal wetlands (Titus, 1988; Boesch et al., 1994). A high rate of relative sea level rise may be the cause of the rapid land loss rates observed in coastal Louisiana (estimated at 65.6 km²/yr; Britsch and Dunbar, 1993). Higher relative sea level may also result in shifts in vegetation composition from salt-intolerant to salt-tolerant species; salinization of coastal marshes is thought to have caused an observed increase in saline and brackish marsh types of 433 km² in coastal Louisiana from 1968-78 and an equivalent decrease in the extent of less saline marsh types (Boesch et al., 1994).

While numerous studies have examined the effects of salinity and inundation on coastal marsh species (Mendelssohn and McKee, 1987; McKee and Mendelssohn,

1989; Blits and Gallagher, 1991; van Diggelen, 1991; Marcum and Murdoch, 1992; Broome et al., 1995; and others), the effects of salinity and water level on regeneration following disturbances have received little attention. Disturbances in coastal marshes include fire, herbivory, wrack deposition, salt water intrusion, hurricanes, sedimentation, and oil spills (Bertness and Ellison, 1987; Mendelssohn et al., 1990; Flynn et al., 1995; Guntenspergen et al., 1995; Nyman and Chabreck, 1995; Taylor and Grace, 1995; and others). In Louisiana, herbivory by the rodent nutria (Myocastor coypus) may be the most important disturbance affecting coastal marsh vegetation (Chabreck, 1988; Shaffer et al., 1992; Llewellyn and Shaffer, 1993; Taylor and Grace, 1995; Grace and Ford 1996). Seedling recruitment is an important component of regeneration following disturbances in oligohaline marshes (Chapter 3), and seedling emergence from seed banks of coastal marshes is altered by salinity and inundation (Baldwin et al., 1996). Regeneration via vegetative growth may also be inhibited by increases in salinity and water level (Flynn et al., 1995; Grace and Ford, 1996). This suggests that establishment and regeneration following disturbance are affected by increases in salinity and water level.

Another effect of disturbance may be to accelerate the conversion of low salinity marsh types to brackish or saline marsh types. Oligohaline marshes, which have salinities of 0.5 - 5 parts per thousand (ppt; Cowardin et al., 1979), can contain plant communities dominated by species of differing salinity tolerances (Penfound and Hathaway, 1938; Chabreck, 1972; Baldwin et al., 1996). In the absence of disturbance, community structure may change slowly in response to

changes in water level or salinity because the community dominants are typically perennials tolerant of fairly wide ranges of salinity and inundation (Chabreck, 1972; Sasser, 1977). Assuming that the more stress-tolerant species are weaker competitors, as has been found in other wetland systems (Grace and Wetzel, 1981; Bertness and Ellison, 1987; Bertness, 1991a,b), encroachment of more salt- or flood- tolerant species due to increases in salinity or water level would occur gradually as competitively superior but less stress-tolerant species were displaced to fresher or more elevated areas. Disturbances create gaps in the vegetation that stimulate recruitment (Pickett and White, 1985; van der Valk, 1992), possibly resulting in rapid colonization by more stress-tolerant species. For example, salt-tolerant species may be able to sprout following disturbance and prevail under higher salinity levels than would salt-intolerant species, and species capable of germinating under flooded conditions may become established and predominate if water levels are elevated.

To examine the role of disturbance in vegetation change under different salinity and inundation regimes, I conducted an experiment using mesocosms containing soil and vegetation from two oligohaline marsh communities dominated by Sagittaria lancifolia L. and Spartina patens (Ait.) Muhl. While these species occur over a wide range of salinity levels, Spartina predominates in brackish marshes, while Sagittaria is most abundant in fresh and intermediate marshes (intermediate marsh type corresponds closely with the oligohaline salinity modifier; Chabreck, 1972; Gosselink, 1984). The mesocosms were exposed to two levels

each of disturbance, salinity, and inundation in a factorial arrangement, and vegetation monitored quarterly for one year. The objective of the disturbance treatment was to simulate a disturbance which removed aboveground plant material such as herbivory or fire. I also measured soil Eh, sulfide and salinity concentration, and pH.

I hypothesized that the effects of salinity and inundation on community structure would be greater in disturbed treatments, and that disturbance might result in more rapid shifts in the abundance of the community dominants than would occur without disturbance. Because Spartina is more salt-tolerant than Sagittaria (Penfound and Hathaway, 1938; Chabreck, 1972; McKee and Mendelssohn, 1989), I expected Spartina to predominate under saline, nonflooded conditions both in the presence and absence of disturbance. Seeds of Sagittaria can germinate under flooded (but fresh) conditions and occur in the seed bank of oligohaline marshes (Baldwin et al., 1996; Chapter 3), suggesting that Sagittaria might become established via seedling recruitment in the flooded, freshwater treatment following disturbance. Salinity inhibits seed germination in many oligohaline marsh species (Baldwin et al., 1996), so I anticipated little seedling recruitment in the saline treatment. Flooding following disturbance may kill vegetation (Hoffpauer, 1968; Sale and Wetzel, 1983; Grace and Ford, 1996), and I therefore expected that the combination of flooding and disturbance might be lethal to most species.

METHODS

Collection of experimental material

Sections of marsh soil and vegetation were collected on March 18, 1994 from two adjoining oligohaline marsh communities, one dominated by Sagittaria lancifolia and the other by Spartina patens, adjacent to the Tchefuncte River in Madisonville, Louisiana (see site description in Chapter 3). Within each community type cylindrical sections of marsh soil and vegetation ("sods") approximately 25 cm in diameter and 25 cm deep were excavated using a shovel. Each sod was cut in half vertically with a hacksaw and combined in the field with a half-sod from the other community type in a plastic pot (with holes at the bottom and sides for drainage); a total of 40 pots with sods were collected. The objective of combining the two sections of marsh community was to have propagules of both brackish marsh species (Spartina) and intermediate marsh species (Sagittaria and others) in each experimental unit. Although Spartina is the predominant brackish marsh species in coastal Louisiana and Sagittaria is most abundant in fresh and intermediate marshes (Chabreck, 1972) they may occur together in some oligohaline marshes (A. Baldwin, personal observation). The sods were transported to Louisiana State University in Baton Rouge, where they were placed in 18.9 l plastic buckets (28.5 cm diameter by 34 cm tall) in a greenhouse. The buckets containing the potted sods (experimental units or mesocosms) were filled with fresh water to just below the rim of the plastic pot and allowed to acclimate for 1 mo.

Experimental design

The experiment was set up as a randomized block design (RBD) with a factorial arrangement of two levels each of disturbance, salinity, and inundation, for a total of eight treatments. Blocking was used because of possible gradients of light and humidity along the length of the greenhouse. Mesocosms were arranged into 5 groups (blocks) on greenhouse benches extending the length of the greenhouse, and the eight treatment combinations assigned randomly to the experimental units in each block.

Treatment application

Salinity was adjusted in the appropriate mesocosms before implementing disturbance and flooding treatments. Salinity of interstitial water measured in wells inserted in each sod before adjusting salinity to the treatment level was 0.37 ± 0.32 ppt ($N = 40$). The wells were constructed from PVC pipe (46 cm long, 1.25 cm diameter) with a rubber stopper on the bottom, a removable cap on top, and holes drilled on the sides up to 20 cm from the bottom. After sods had acclimated for 1 mo, salinity of interstitial water was increased gradually over a period of 1 mo to 6 ppt, the desired treatment level, by adding Bio-Crystals Marinemix sea water formulation (Marine Enterprises, Inc., Baltimore, Maryland). This concentration was chosen as a level which was not expected to cause dieback of aboveground vegetation, but which might reduce growth rates of Sagittaria but not of Spartina (Chabreck, 1972; Mendelssohn and McKee, 1987; McKee and Mendelssohn, 1989; R. Howard, National Biological Service, personal communication). Salinity of

interstitial water was measured periodically and adjusted as necessary to maintain salinities near 6 ppt.

Disturbance and flooding treatments were applied to the appropriate mesocosms on May 18, 1994. The disturbance treatment consisted of clipping all vegetation at the soil surface; the clipped vegetation was collected for estimating biomass non-destructively (see Data Analysis methods). Vertebrate herbivory, fire, and storm-generated salt pulses in coastal marshes often result in removal or dieback of aboveground vegetation, after which plants sprout from rhizomes (Guntenspergen et al., 1995; Nyman and Chabreck, 1995; personal observation). These disturbances may differ in their effects on edaphic factors, but their effect on vegetation is accurately represented by the clipping treatment I used in this experiment. The flooded treatment was implemented by filling the buckets to the rim, resulting in a water level approximately 10 cm above the surface of the soil. In the nonflooded treatment, water level was maintained 10 cm below the soil surface. Water level was checked frequently and water added as necessary to maintain levels within 2-3 cm of their original level.

Vegetation sampling

Vegetation was sampled in April 1994 (before applying treatments) and then every three months until April 1995 when the experiment was terminated. Within each mesocosm the number of stems of each species were counted and the average height of each species estimated during each sampling event. For Sagittaria, average blade width was also estimated. These measurements were used to estimate

biomass non-destructively (see Data Analysis methods). On April 27, 1995 all aboveground vegetation was clipped at the soil surface. Harvested plants were sorted by species and as alive and dead, dried at 80°C for at least 3 days, and weighed to the nearest 0.01 g.

Measurement of environmental variables

Environmental variables I measured during the study were soil redox potential (Eh), sulfide concentration, salinity, and pH. Soil Eh was measured at 2 cm and 15 cm depth in June 1994. Three Eh measurements were made at each depth using brightened platinum electrodes, a calomel reference electrode, and a pH/mV meter. Eh was calculated by adding the potential of the calomel electrode against a standard hydrogen electrode (+244 mV) to each millivolt reading (Faulkner et al., 1989).

A 5 ml sample of well water was collected for sulfide analysis (after purging wells once) and immediately placed in an equal volume of antioxidant buffer in September 1994. Sulfide (S^{2-}) concentration in mV was measured with a sulfide electrode (model DJM-146, Lazar Research Laboratories, Los Angeles, California). A standard curve was prepared from a serial dilution of Na_2S and used to calculate sulfide concentration in parts per million.

Salinity of interstitial water samples from all mesocosms was measured before applying the salinity treatment and at four times during the remainder of the experiment using a portable salinity-conductivity-temperature meter. I also periodically measured salinity of the mesocosms that received salt. Measurements

of interstitial water pH were made using a hand-held pH meter twice during the experiment.

Data analysis

Biomass and species richness (number of species) of vegetation from quarterly sampling events were analyzed as a RBD using repeated measures analysis of covariance, with data from the initial sample date used as the covariate. Biomass data were $\ln(\text{biomass} + 1)$ transformed prior to analysis to reduce heterogeneity of variances; means were detransformed for presentation (Neter et al., 1990). Because interactions involving disturbance were generally significant in three-way ANOVAs of vegetation data, effects of salinity and inundation were analyzed by disturbance level. Sulfide concentration and final biomass were analyzed as a RBD and Eh as a nested RBD using analysis of variance (ANOVA). Salinity concentration and pH were analyzed using repeated measures ANOVA. All statistical tests were performed using SAS version 6.10 for Windows (SAS Institute, Cary, North Carolina). A significance level of $P = 0.05$ was used in interpreting results of statistical tests. Greenhouse-Geisser adjusted P -values were used in determining statistical significance in repeated measures analyses and the Tukey-Kramer method used to compare treatment least squares means.

Biomass for all sample dates except April 1995 was estimated non-destructively from stem count and average height and blade width data using linear regression. Biomass data used in regressions were from vegetation collected during the initial disturbance treatment and the final harvest. Significant relationships

between stem count multiplied by average height (and by average blade width for Sagittaria) were found for 19 of the 24 species encountered in biomass harvests. R^2 values for most species were > 0.8 , and for over half were > 0.9 . Biomass was estimated only for species with significant regressions.

Principal components analysis (PCA) of untransformed estimated biomass data was conducted separately for disturbed and undisturbed treatments using the PRINCOMP procedure of SAS. Mesocosm scores from the first two PCA axes were used to prepare ordination diagrams and were subjected to ANOVA.

Relative frequency was calculated both by treatment and for all treatments combined by dividing the frequency of each species by the sum of frequencies for all species and multiplying by 100%.

RESULTS

Response of vegetation

The combination of disturbance, salinity, and inundation resulted in an almost complete eradication of vegetation which persisted throughout the experiment (Table 4.1). Sagittaria persisted in only one of the mesocosms subjected to this treatment by sprouting immediately following the disturbance, and an Aster seedling was present during one sample date (the high relative frequencies for these species are due to the absence of other species). The combination of disturbance and flooding with fresh water also resulted in death of many plants, but seedlings of Ammannia, Sagittaria, and Scirpus were subsequently recruited at relatively high frequencies in this treatment (Table 4.1). The only species which survived the combination of

Table 4.1. Relative frequency (%) of plant species in greenhouse mesocosms during the four sample events following treatment application ($N = 20$). Species rank based on overall frequency is given in parentheses; species with the same two ranks occurred at the same frequency. Nomenclature according to Kartesz (1994).

Species	Undisturbed				Disturbed			
	Nonflooded		Flooded		Nonflooded		Flooded	
	Fresh	Saline	Fresh	Saline	Fresh	Saline	Fresh	Saline
<u>Alternanthera philoxeroides</u> (Mart.) Griseb. (4)	10.5	12.0	5.1	12.1	10.3	14.8	3.4	0
<u>Ammannia latifolia</u> L. (10)	0	1.6	5.9	2.8	1.3	0	23.6	0
<u>Aster subulatus</u> Michx. (5)	10.5	12.0	6.6	6.5	9.6	10.2	1.8	20.0
<u>Baccharis halimifolia</u> L. (21/22)	0	4.0	0	0	0	0	0	0
<u>Cyperus polystachyos</u> Rottb. var. <u>filicinus</u> (Vahl) C.B. Clarke (13)	1.5	5.6	5.9	2.8	1.9	0.9	0	0
<u>Cyperus haspan</u> L. (23)	0	0.8	2.2	0	0	0	0	0
<u>Cyperus odoratus</u> L. (9)	4.5	2.4	4.4	2.8	5.8	2.8	0	0
<u>Cyperus</u> sp. (17)	3.0	0	0	4.7	1.3	0.9	1.8	0
<u>Diodia virginiana</u> L. (21/22)	0.8	0	0	0	1.9	0	1.8	0
<u>Echinochloa crus-galli</u> (L.) Beauv. (12)	3.8	3.2	0.7	0	4.5	7.4	0	0
<u>Eleocharis fallax</u> Weatherby (2)	12.8	15.2	14.7	13.1	12.8	18.5	12.7	0
<u>Ipomoea sagittata</u> Poir. (18/19)	2.3	0.8	0	2.8	0.6	0	1.8	0
<u>Kosteletzkya virginica</u> (L.) K. Presl ex Gray (24/25)	2.3	0	0	0	0	0	0	0
<u>Leptochloa fascicularis</u> (Lam.) Gray (16)	3.8	0	0	0	1.3	6.5	0	0

(table con'd)

Species	Undisturbed				Disturbed			
	Nonflooded		Flooded		Nonflooded		Flooded	
	Fresh	Saline	Fresh	Saline	Fresh	Saline	Fresh	Saline
<u>Lythrum lineare</u> L. (11)	0.8	8.8	0.7	0.9	3.8	6.5	0	0
<u>Phyla nodiflora</u> (L.) Greene (6)	4.5	6.4	6.6	5.6	4.5	1.9	0	0
<u>Polygonum punctatum</u> Ell. (8)	7.5	0	8.1	0.9	6.4	0	1.8	0
<u>Ptilimnium capillaceum</u> (Michx.) Raf. (18/19)	3.0	0	0	0	1.9	1.9	0	0
<u>Sagittaria lancifolia</u> L. (1)	7.5	11.2	11.8	17.8	10.3	10.2	34.5	80.0
<u>Sacciolepis striata</u> (L.) Nash (15)	0	0	0.7	0	9.0	0	0	0
<u>Scirpus tabernaemontani</u> K.C. Gmel. (7)	0	4.0	5.9	9.3	1.9	0	14.5	0
<u>Sesbania exaltata</u> (Raf.) Rydb. ex A.W. Hill (20)	2.3	2.4	0	0.9	0	0	0	0
<u>Spartina patens</u> (Ait.) Muhl. (3)	15.0	9.6	12.5	15.9	10.9	16.7	0	0
<u>Utricularia gibba</u> L. (24/25)	0	0	2.2	0	0	0	0	0
<u>Vigna luteola</u> (Jacq.) Benth. (14)	3.8	0	5.9	0.9	0	0.9	1.8	0

disturbance and flooding by sprouting were Sagittaria and Eleocharis, although this occurred in only two of the five mesocosms subjected to this treatment for Sagittaria and in one mesocosm for Eleocharis.

Most of the other frequently occurring species were fairly evenly distributed among the other treatments. The five most frequent species overall (Sagittaria, Eleocharis, Spartina, Alternanthera, and Aster, together comprising about 60% of the relative frequency of all species) occurred in all undisturbed treatments and in the nonflooded disturbed treatments (Table 4.1). Within undisturbed treatments, Ammannia and Scirpus occurred at higher frequencies in the flooded treatments, while Aster occurred at lower frequencies under flooded conditions. The frequency of Polygonum was lower under saline conditions in both disturbed and undisturbed treatments.

Flooding and salinity significantly reduced species richness in the disturbed treatments but not in the undisturbed treatments (Fig. 4.1, Table 4.2). In the disturbed treatments, the effects of inundation and salinity varied significantly over time but were additive (Fig. 4.1, Table 4.2). Relative to the nonflooded, fresh treatment, flooding reduced richness to a greater degree than salinity; the combination of flooding and salinity resulted in the greatest reduction in richness (Fig. 4.1). There were no significant differences in richness among undisturbed treatments.

Following disturbance, biomass of Sagittaria was significantly lower in the saline treatments than in the fresh treatments throughout the study ($P < 0.0001$;

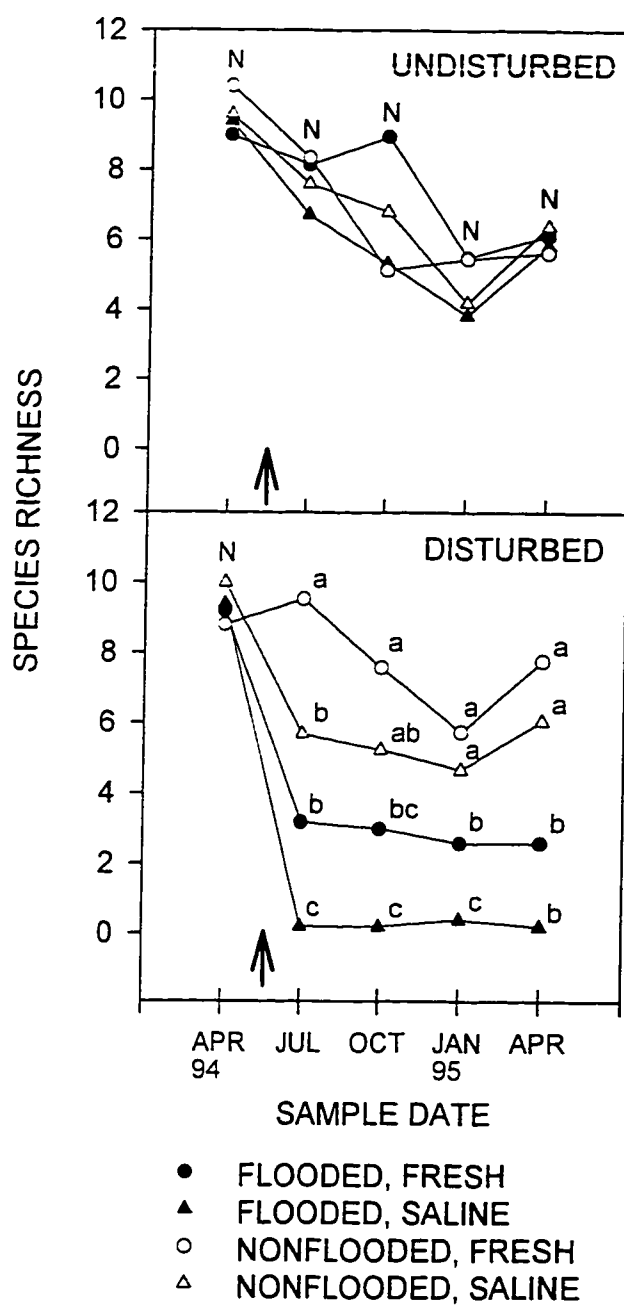


Fig. 4.1. Variation in species richness in response to salinity and inundation in undisturbed and disturbed greenhouse mesocosms. Date of treatment application is indicated by the arrow. Within each level of disturbance and sample date, means with different letters are significantly different. N = no significant differences among treatments.

Table 4.2. Two-way ANOVA by level of disturbance for effects of inundation and salinity on species richness in greenhouse mesocosms. NS = Not significant ($P > 0.05$).

Source	d.f.	MS	F	P	Sig.
<u>Undisturbed</u>					
<i>Between Subjects</i>					
Inundation	1	0.22	0.02	0.8891	NS
Salinity	1	13.44	1.23	0.2901	NS
I × S	1	16.46	1.51	0.2444	NS
Covariate	1	18.87	1.73	0.2147	NS
Block	4	6.77	0.62	0.6562	NS
Error	11	10.88			
<i>Within Subject</i>					
Time	3	0.62	0.55	0.6236	NS
Time × I	3	2.49	2.23	0.1154	NS
Time × S	3	2.71	2.42	0.0955	NS
Time × I × S	3	6.32	5.65	0.0054	**
Time × Covariate	3	1.63	1.46	0.2498	NS
Time × Block	12	1.09	0.97	0.4869	NS
Error (Time)	33	1.12			
<u>Disturbed</u>					
<i>Between Subjects</i>					
Inundation	1	496.20	111.62	<0.0001	****
Salinity	1	109.58	24.65	0.0004	***
I × S	1	0.56	0.13	0.7285	NS
Covariate	1	1.32	0.30	0.5963	NS
Block	4	4.57	1.03	0.4353	NS
Error	11	4.45			
<i>Within Subject</i>					
Time	3	0.23	0.31	0.7182	NS
Time × I	3	4.65	6.21	0.0091	**
Time × S	3	2.76	3.68	0.0463	*
Time × I × S	3	0.87	1.16	0.3288	NS
Time × Covariate	3	0.06	0.07	0.9170	NS
Time × Block	12	0.97	1.30	0.2984	NS
Error (Time)	33	0.75			

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$

Fig. 4.2). The effect of inundation in the disturbed treatments was not significant ($P = 0.2084$), but the inundation \times salinity interaction was ($P = 0.002$). Biomass of Spartina following disturbance, on the other hand, was significantly reduced by flooding ($P < 0.0001$) but not salinity ($P = 0.9851$) during the study (Fig. 4.2). In the absence of disturbance, the biomass of Sagittaria was significantly higher under flooded conditions ($P = 0.0338$; Fig. 4.2), while salinity had no effect ($P = 0.1249$; Fig. 4.2). Salinity and inundation had no effect on biomass of Spartina in undisturbed treatments ($P > 0.8$; Fig. 4.2). Within sampling dates disturbance resulted in more significant differences among salinity and inundation treatments than occurred without disturbance (Fig. 4.2).

Significant effects of salinity or inundation on final biomass occurred in the five most frequently occurring species (Tables 4.1 and 4.3). Flooding significantly reduced final biomass in Alternanthera, Aster, Eleocharis, and Spartina, but only in disturbed treatments (Tables 4.3 and 4.4). In contrast, flooding significantly increased final biomass of Sagittaria in the undisturbed treatments (Table 4.3), although this effect was not revealed in post-hoc tests (Table 4.4). Salinity significantly increased final biomass of Aster and decreased that of Sagittaria in disturbed treatments but had no effect in any species when undisturbed (Tables 4.3 and 4.4).

Ordination diagrams of mesocosm PCA scores indicate greater separation among salinity and inundation treatments following disturbance than in the absence of disturbance (Fig. 4.3). Higher eigenvalues for the disturbed treatment ordination

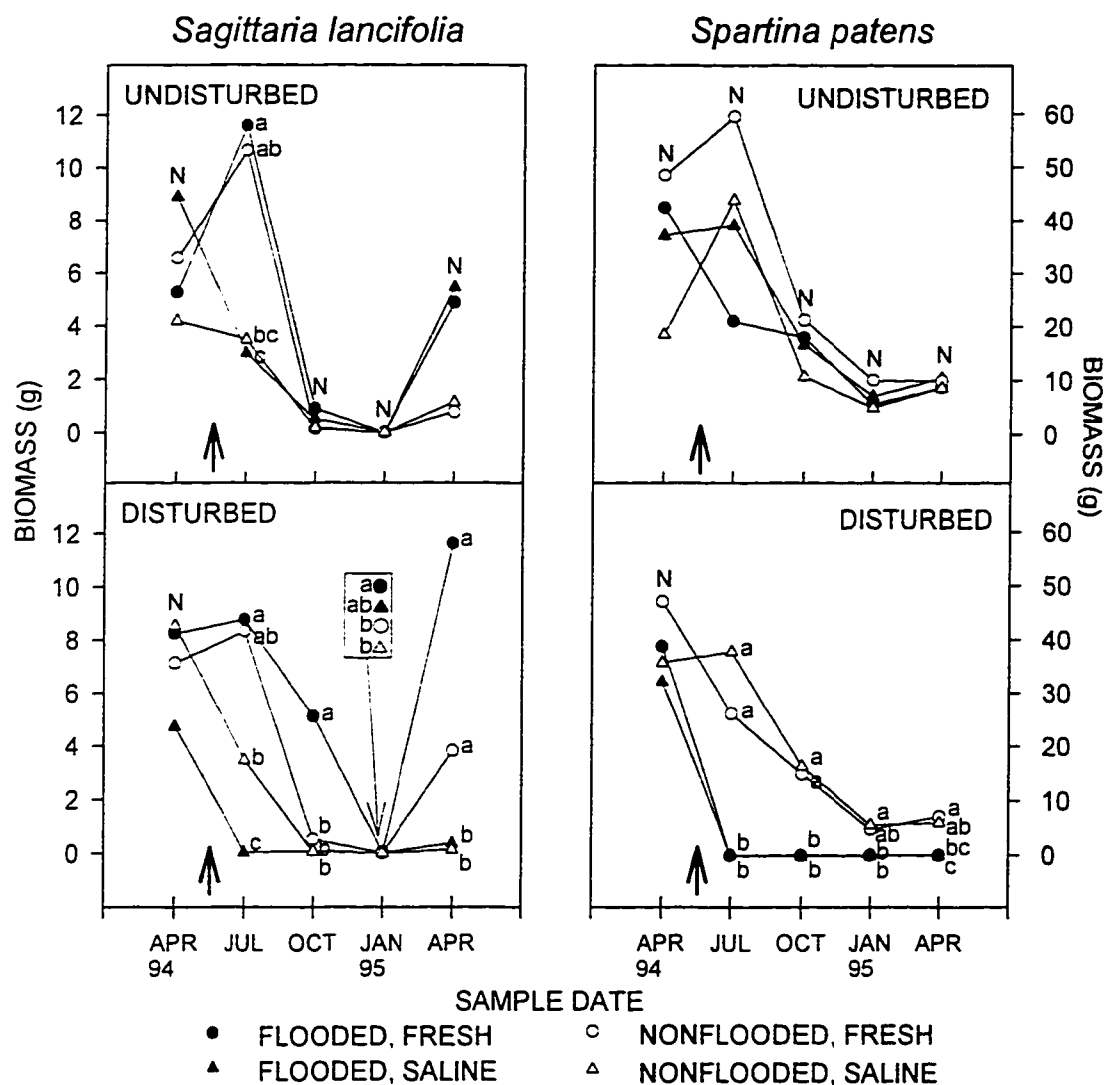


Fig. 4.2. Effects of salinity and inundation on biomass of *Sagittaria lancifolia* and *Spartina patens* in undisturbed and disturbed greenhouse mesocosms. Date of treatment application is indicated by the arrow. Within each level of disturbance and sample date, means with different letters are significantly different. N = no significant differences among treatments.

Table 4.3. Results of ANOVAs of log-transformed live biomass of the 10 most frequently occurring species by level of disturbance in greenhouse mesocosms after one year. Values are *F*-ratios.

Species	Undisturbed				Disturbed			
	Inundation	Salinity	I × S	Block	Inundation	Salinity	I × S	Block
<u>Alternanthera philoxeroides</u>	3.22	0.32	2.55	2.00	17.89**	4.07	4.07	1.95
<u>Ammannia latifolia</u>	3.31	0.38	2.19	4.17*	3.23	3.23	3.23	1.00
<u>Aster subulatus</u>	2.30	0.02	0.005	0.63	33.33****	8.85*	8.85*	1.75
<u>Cyperus odoratus</u>	2.44	0.28	0.28	2.44	1.70	0.18	0.18	0.75
<u>Eleocharis fallax</u>	1.91	1.54	2.74	0.48	14.70**	1.43	0.01	0.26
<u>Phyla nodiflora</u>	0.02	0.08	2.01	0.87	1.57	1.57	1.57	1.00
<u>Polygonum punctatum</u>	2.83	2.83	2.83	1.00	1.00	1.00	1.00	1.00
<u>Sagittaria lancifolia</u>	12.42**	0.20	0.04	0.82	3.99	47.14****	2.65	1.03
<u>Scirpus tabernaemontani</u>	2.14	1.63	0.15	0.76	1.15	4.28	1.15	1.08
<u>Spartina patens</u>	0.14	0.41	0.48	1.15	19.43***	0.0006	0.0006	1.44

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$

Table 4.4. Live biomass (g) of the 10 most frequently occurring species in greenhouse mesocosms after one year. Within disturbed and undisturbed treatments, means with different superscripted letters are not significantly different.

Species	Undisturbed				Disturbed			
	Nonflooded		Flooded		Nonflooded		Flooded	
	Fresh	Saline	Fresh	Saline	Fresh	Saline	Fresh	Saline
<u>Alternanthera philoxeroides</u>	0.65	0.45	0.07	0.41	1.71 ^a	0.42 ^{ab}	0 ^b	0 ^b
<u>Ammannia latifolia</u>	0	0.05	0.19	0.07	0	0	0.84	0
<u>Aster subulatus</u>	0.37	0.44	0	0.02	0.66 ^b	3.86 ^a	0 ^b	0 ^b
<u>Cyperus odoratus</u>	0	0	0.02	0.04	0.02	0.01	0	0
<u>Eleocharis fallax</u>	1.11	1.47	5.74	1.23	1.78 ^a	1.14 ^{ab}	0.25 ^{ab}	0 ^b
<u>Phyla nodiflora</u>	0.01	0.38	0.35	0.09	0.33	0	0	0
<u>Polygonum punctatum</u>	0	0	0.05	0	0.09	0	0	0
<u>Sagittaria lancifolia</u>	0.81	0.97	4.71	6.13	3.83 ^a	0.16 ^b	11.94 ^a	0.29 ^b
<u>Scirpus tabernaemontani</u>	0	1.06	1.23	2.29	0.45	0	2.19	0
<u>Spartina patens</u>	14.07	4.32	10.71	11.24	6.04 ^a	6.20 ^a	0 ^b	0 ^b

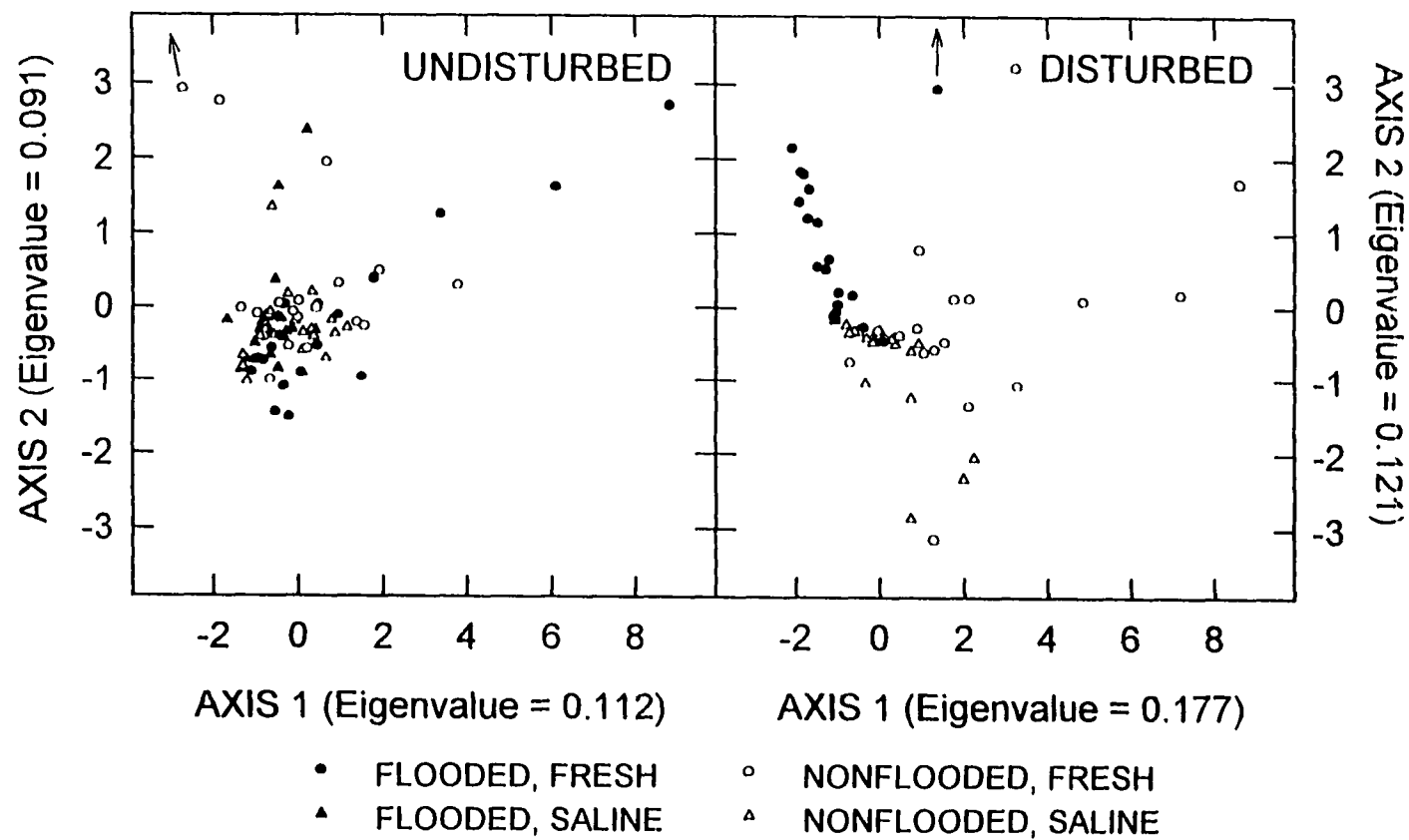


Fig. 4.3. Differences in community structure in undisturbed and disturbed greenhouse mesocosms subjected to salinity and inundation treatments. Points are axis scores for mesocosms from Principal Components Analysis of biomass determined during four sample dates following treatment application.

indicate the PCA axes were more important in explaining variability among treatments than occurred in the undisturbed treatment ordination. In disturbed treatments separation of salinity and inundation treatments can be seen along the first two PCA axes, and ANOVA of mesocosm scores indicated significant effects of both salinity and inundation ($P < 0.05$). Some separation of salinity treatments appears along the first axis for undisturbed treatments, and ANOVA indicated a significant effect of salinity ($P = 0.0296$) but not inundation ($P = 0.5125$) on mesocosm scores. Little separation of treatments can be seen along the second axis for the undisturbed treatments, and the effects of inundation and salinity were not significant ($P > 0.05$).

Environmental variables

The inundation \times salinity effect on Eh at 2 cm depth was significant ($P = 0.007$), and inundation significantly decreased Eh at 2 cm depth under both fresh ($P = 0.0017$) and saline ($P < 0.0001$) conditions (Table 4.5). Both salinity and inundation reduced Eh significantly at 15 cm depth (inundation: $P = 0.0310$; salinity: $P < 0.0001$; Table 4.5); no interactions were significant. Disturbance had no significant effects on Eh ($P > 0.7$). Sulfide concentration was significantly higher in saline treatments than in fresh treatments ($P < 0.0001$; Table 4.5); no other main effects or interactions were significant. Treatment of mesocosms with sea water formulation was successful in maintaining salinities near the desired level of 6 ppt (Table 4.5), and repeated measures ANOVA indicated a significant difference between fresh and saline treatments ($P < 0.0001$). Mesocosm interstitial

Table 4.5. Summary of environmental measurements in greenhouse mesocosms.

Parameter	Treatment	Mean \pm SE (N)
Eh 2 cm depth (mV)	Nonflooded, Fresh	46.3 \pm 15.5 (30)
	Nonflooded, Saline	65.9 \pm 26.4 (30)
	Flooded, Fresh	-64.7 \pm 15.5 (30)
	Flooded, Saline	-132.0 \pm 26.4 (30)
Eh 15 cm depth (mV)	Nonflooded	-56.4 \pm 7.3 (60)
	Flooded	-83.0 \pm 7.3 (60)
	Fresh	-38.1 \pm 7.3 (60)
	Saline	-101.3 \pm 7.3 (60)
Sulfide (parts per million)	Fresh	1.2 \pm 0.04 (20)
	Saline	6.7 \pm 0.04 (20)
Salinity (parts per thousand)	Fresh	0.1 \pm 0.01 (80)
	Saline	6.1 \pm 0.1 (80)
pH	Fresh	6.46 \pm 0.05 (40)
	Saline	6.81 \pm 0.03 (40)

water was slightly but significantly lower in fresh than in saline treatments ($P < 0.0001$), although pH values occurred within a narrow range (Table 4.5).

DISCUSSION

The widespread occurrence of natural and anthropogenic disturbances in coastal marshes suggests that disturbance may be an important component of their vegetation dynamics. Disturbances of different intensity result in markedly different effects on patterns of regeneration in oligohaline marsh communities (Chapter 3), and herbivory, fire, hurricanes, and wrack affect the structure of marsh vegetation (Bertness and Ellison, 1987; Shaffer et al., 1992; Guntenspergen et al., 1995; Ford and Grace, 1996). Additionally, salinity and inundation have been implicated as factors associated with changes in community structure related to sea level rise (Gosselink, 1984; Mendelssohn and McKee, 1987; Turner and Cahoon, 1987; McKee and Mendelssohn, 1989; Howard and Mendelssohn, 1995). Only recently, however, have some of the effects of salinity and flooding on regeneration been investigated.

Salinity and inundation were found to strongly influence the recovery of freshwater marsh vegetation following a simulated saltwater intrusion event which caused dieback of aboveground vegetation, although interactions between disturbance and salinity or inundation were not examined (Flynn et al., 1995). In another study, biomass of Sagittaria lancifolia was significantly reduced by the combination of a salt pulse, simulated herbivory (clipping), and flooding, but not in single or pairwise combinations of these treatments (Grace and Ford, 1996). These studies suggest

that post-disturbance salinity and water level are important in determining patterns or regeneration. A question not addressed in these studies is whether disturbance results in greater response of community structure to salinity and inundation than would occur in the absence of disturbance. Also, if this is true, are species with differential tolerances to salinity and inundation favored under different salinity and inundation regimes?

My results indicate that salinity and inundation do have a greater effect on community structure when vegetation is disturbed. Species richness was significantly reduced in response to both salinity and flooding following disturbance, while salinity and inundation did not affect richness in the absence of disturbance (Fig. 4.1). I observed similar interactions between disturbance, salinity, and inundation in their effect on biomass of dominant species (Fig. 4.2, Tables 4.3 and 4.4) and community structure (Fig. 4.3). Frequency of species also reflects this pattern (Table 4.1). Disturbance seemed to act as a catalyst for vegetation change in response to environmental variables.

The responses of individual species to salinity and inundation following disturbance were not uniform. Biomass of the intermediate marsh species Sagittaria following disturbance was reduced under saline conditions but not affected by flooding. The brackish marsh dominant Spartina, on the hand, was eliminated by the combination of flooding and disturbance but not affected by salinity. These patterns are likely due to differences in mode of reproduction, morphology, and physiological tolerance to environmental variables of the two species.

Sagittaria persisted in flooded, fresh, disturbed treatments primarily via prolific seedling recruitment. Unlike many marsh species, seeds of Sagittaria occur in the seed banks of oligohaline marshes and can germinate under flooded conditions (Baldwin et al., 1996; Chapter 3). Individuals recruited from seed were responsible for a majority of the regeneration following disturbance and flooding with fresh water. No seedlings of Sagittaria were observed under saline conditions, probably because germination of Sagittaria seeds is inhibited by salinities of 2 ppt or higher (Baldwin et al., 1996). While net photosynthesis in Sagittaria may be reduced in response to a short-term increase in water level (Pezeshki et al., 1987), other studies have found no significant effect of flooding on aboveground biomass of adult plants (McKee and Mendelssohn, 1989; Howard and Mendelssohn, 1995). In the absence of disturbance, I found that growth of Sagittaria was actually promoted by flooding.

I also observed that some Sagittaria ramets survived through rapid vegetative growth, quickly pushing the clipped bases of new leaves above water. The rate of oxygen diffusion through water is much slower than through porous media (Greenwood, 1961; Gambrell and Patrick, 1978), and many aquatic plants maintain aerobic respiration in their roots by having aerenchyma tissue that allows diffusion of oxygen to their roots (Armstrong, 1979; Mendelssohn and Burdick, 1988). If the pathway for oxygen diffusion to roots is cut off by removing aboveground vegetation and flooding, anaerobic conditions can develop quickly (1-2 days; Turner and Patrick, 1968) and vegetation may die. This pattern has been observed in other aquatic emergent species in response to clipping and flooding (Sale and Wetzel,

1983) and burning and flooding (Hoffpauer, 1968). In some of the mesocosms Sagittaria appeared to quickly restore the oxygen diffusion pathway and thereby survive disturbance followed by flooding.

Unlike Sagittaria, Spartina did not survive the combination of disturbance and flooding as it did not sprout and was not recruited from seed. However, regrowth of Spartina following disturbance under nonflooded conditions was not affected by salinity, presumably because of its greater salinity tolerance.

While salinity and flooding may affect plant growth directly (Greenway and Munns, 1980; Kozlowski, 1984), the responses to flooding and salinity I observed may also be due in part to their effects on soil Eh and sulfide concentration. Soil Eh decreased in response to both flooding and salinity, and sulfides were higher in the saline treatments (Table 4.5). Flooding can result in strongly reducing conditions due to the dramatic decrease in oxygen diffusion (Greenwood, 1961; Gambrell and Patrick, 1978) and the continued use of oxygen by plant roots and soil microorganisms (Turner and Patrick, 1968). Under highly reducing conditions sulfate present in seawater is reduced to the phytotoxin hydrogen sulfide (Ponnamperuma, 1972), which has been found to adversely affect growth of wetland vegetation (Ingoll and Havill, 1984; Mendelssohn and McKee, 1987; Bradley and Dunn, 1989; Koch and Mendelssohn, 1989; Bradley and Morris, 1990; Koch et al., 1990; van Diggelen, 1991; Flynn et al., 1995).

The differences I observed in the responses of the dominant species of intermediate and brackish marsh types suggest that conversion of wetland vegetation

in response to rising sea level may depend on disturbance and the salinity and inundation levels present at the time of the disturbance. If water level is high but salinity concentration low, species capable of seed germination under flooded conditions or rapid resprouting such as Sagittaria may predominate following disturbance. If salinities are high but water levels low, more salt-tolerant species that reproduce vegetatively such as Spartina may prevail after disturbance. These consequences are suggested by the effects of salinity and inundation on biomass of these species I observed in disturbed mesocosms (Fig. 4.2, Tables 4.3 and 4.4). If both salinity and water level are high, wetland loss may occur due to the death of all vegetation and the subsequent inability of species to colonize the disturbed area via vegetative growth or seedling recruitment. In the absence of disturbance, clonal perennials may be able to persist for extended periods under conditions of elevated salinity or water level by reproducing vegetatively.

That I did not observe a dramatic response to salinity and inundation in the absence of disturbance may be due to the relatively short duration of the study. Shifts in relative abundance due to changes in environmental conditions may occur gradually over a period of several years (e.g., Bertness, 1991b). While I did observe some variation in the response of species to salinity and inundation in the absence of disturbance, these changes were generally not statistically significant and were smaller than those which occurred following disturbance (Fig. 4.2, Tables 4.3 and 4.4).

In conclusion, the results of this study suggest that disturbance may act to catalyze rapid vegetation change in response to rising sea level. Disturbance creates opportunities for colonization via vegetative propagation or seedling recruitment, and the success of colonizing species depends on water level and salinity. Under conditions of high water level and salinity, no colonization may occur and wetlands may convert to open water, as is currently occurring on a large scale in coastal Louisiana. In the absence of disturbance, vegetation may be able to tolerate considerable fluctuations in salinity and water level and persist via vegetative propagation. These findings indicate that disturbance and mechanisms of colonization, in addition to the tolerance of adults of individual species to environmental variables, are critical factors affecting the response of coastal marsh communities to sea level rise.

CHAPTER 5

SUMMARY AND CONCLUSIONS

As sea level continues to rise, changes in inundation regimes and salinity levels can be expected to affect the vegetation structure and dynamics of coastal wetlands. Increases in salinity and water level may have differential effects on the growth and competitive ability of adult plants in wetland vegetation, resulting in shifts in community structure. In coastal Louisiana, where rates of relative sea level rise are about 10 times those of eustatic rates, shifts to more salt-tolerant vegetation have been attributed to increased salinity in interior marshes (Boesch et al., 1994). Responses of adult plants to salinity and inundation may be one factor responsible for changes in plant community structure in response to rising sea level (e.g., McKee and Mendelssohn, 1989). However, seedling dynamics are important in many low-salinity marshes (e.g., Odum, 1988; Leck and Simpson, 1994), and sea level rise may affect patterns of seedling recruitment by altering salinity and water level (Baldwin et al., 1996). Additionally, natural and anthropogenic disturbances such as hurricanes, fire, herbivory, wrack, and oil spills may create gaps in marsh vegetation, creating opportunities for colonization via vegetative propagation or seedling recruitment (Pickett and White, 1985). Patterns of colonization may be strongly influenced by water level and salinity concentration present at the time of disturbance (Flynn et al., 1995; Grace and Ford, 1996). Disturbance, salinity, and

inundation may therefore interact to alter the community structure of coastal marshes in ways that might not be predicted based solely on the physiological tolerances of adult plants to salinity and inundation.

As part of this dissertation I conducted a series of experiments to examine the influence of disturbance and sea level rise on the community structure of oligohaline marshes. Because of the importance of the soil seed bank in regeneration in some marsh communities (e.g., van der Valk and Davis, 1978; Middleton et al., 1991; Leck and Simpson, 1995), I described the composition and abundance of species in seed banks of oligohaline marshes in coastal Louisiana and investigated the role of salinity and inundation in controlling recruitment from the seed bank (Chapter 2). I had observed seedlings of seed bank species present following fires in oligohaline marshes, and hypothesized that the establishment and growth of recruited seedlings might be determined in large part by the ability of the dominant species to colonize vegetatively following disturbance and the degree of damage the vegetation sustained. To examine how patterns of colonization depended on community composition and intensity of disturbance I conducted a two-year field experiment (Chapter 3). Finally, I hypothesized that disturbance might lead to greater and more rapid shifts in community structure in response to changes in salinity and water level than would occur in the absence of disturbance, and I tested this hypothesis in a greenhouse experiment (Chapter 4). Important results and conclusions from these studies are summarized here.

SEED BANKS OF OLIGOHALINE MARSHES

I found that soils of oligohaline marshes contain a viable seed bank, and that recruitment of seedlings from the seed bank depends on salinity and water level.

The seed banks of oligohaline marsh communities dominated by Paspalum vaginatum, Sagittaria lancifolia, or Spartina patens all had similar species richness (10-11) and diversity (antilog Shannon-Weaver diversity index = 6.5-7.1). The presence or absence of standing vegetation within a community affected the abundance of some species in the seed bank but had little effect on species composition. Higher salinities and flooding reduced seedling emergence for most species; few species emerged at salinities above 4 ppt, and only Sagittaria lancifolia and Eleocharis parvula germinated well under flooded conditions. A temporary increase in salinity (applied before the germination portion of the experiment to simulate a salt water intrusion event) did not affect species richness or seedling emergence of most species.

These results suggest that differences in vegetation of some oligohaline marshes have little effect on the composition of seed banks. Additionally, transient salt water intrusion events may not reduce the viability of buried seeds. However, higher salinities and greater depth and duration of inundation associated with sea level rise may decrease recruitment of seed bank species and reduce their abundance in oligohaline marsh communities.

COMMUNITY RESPONSES TO DISTURBANCE INTENSITY

In this study I monitored changes in two oligohaline marsh communities (one dominated by Sagittaria lancifolia and the other by Spartina patens) in response to three levels of disturbance intensity (undisturbed, nonlethal disturbance, and lethal disturbance). In the nonlethal disturbance aboveground vegetation was clipped to simulate disturbances such as fire and herbivory. Vegetation was killed using herbicide in the lethal disturbance to simulate disturbances such as wrack deposition, sedimentation, scouring, and flooding following fire or herbivory. Despite differences in the vegetation of the two communities, they exhibited a similar overall response to disturbance intensity during the two-year study. Following a nonlethal disturbance the dominant species resprouted and quickly reestablished the structure of the vegetation. In contrast, colonization following lethal disturbances occurred primarily via seedling recruitment, which resulted in differences in community structure that persisted throughout the study. Many of the species recruited as seedlings occurred in the seed bank, indicating that the seed bank is an important source of propagules for regeneration. Measurements of relative frequency, species richness, relative abundance, relative dominance, final biomass, and cover all supported this pattern of regeneration. While the two communities responded similarly overall to disturbance, the response of individual species was not uniform; frequency, abundance, dominance, biomass, or cover of some species increased while others decreased in response to disturbance. Of the environmental variables

measured, light penetration appeared to be the variable most closely related to the effect of disturbance intensity on community structure.

The results of this study indicate that the observed distribution of plant communities may be in part due to disturbance. Because gradients of salinity and water level are not steep in oligohaline marshes, community structure may be maintained by competitive inhibition of colonization by other species. Disturbances in these communities increase light availability, which stimulates colonization that may lead to a persistent change in vegetation.

DISTURBANCE, SEA LEVEL RISE, AND VEGETATION CHANGE

To investigate how community response to disturbance might depend on salinity or water level I examined the interactive effects of disturbance, salinity, and inundation using mesocosms of oligohaline marsh communities (each containing two half-sections of soil and vegetation from two adjoining plant communities, one dominated by Spartina patens and the other by Sagittaria lancifolia). I found that salinity and inundation had a significant effect on species richness only when vegetation was disturbed, and observed similar patterns for biomass of dominant species and for community structure as depicted in ordination diagrams. Also, disturbance accelerated shifts in the relative dominance of the two community dominants and under flooded, saline conditions led to almost complete eradication of vegetation. Following disturbance, biomass of Sagittaria was significantly reduced by salinity but unaffected by flooding, while Spartina was eliminated by flooding but not affected by salinity. In the absence of disturbance, Sagittaria biomass increased

while Spartina was not affected in response to flooding, and neither species was significantly affected by salinity. The responses of vegetation I observed can be attributed in part to changes in Eh and sulfides; Eh decreased due to flooding and salinity, while sulfide concentration increased in response to salinity. These results suggest that disturbance is an important component of vegetation change in response to rising sea level, acting as a catalyst for rapid change in vegetation structure or accelerating wetland loss.

OVERALL CONCLUSIONS

The results this research support a number of conclusions relative to the role of seed banks and disturbance in structuring the vegetation of oligohaline coastal marshes as sea level rises:

- 1) Seed banks are an important component of the vegetation dynamics of oligohaline marshes. I observed relatively similar seed banks in three marsh communities, and observed recruitment of seed bank species following disturbance in two oligohaline marsh communities as well as in undisturbed vegetation of marsh dominated by Sagittaria lancifolia.
- 2) Community response to disturbance depends on disturbance intensity. In two oligohaline marsh communities I found that seedling recruitment was the most important mechanism of regeneration following intense disturbances that killed dominant vegetation, while vegetative propagation predominated

following milder nonlethal disturbances which removed aboveground biomass but did not damage rhizomes. Nonlethal disturbances common in coastal marshes include fire and herbivory, while lethal disturbances may include wrack deposition, sedimentation, scouring, or fire or herbivory followed by flooding. Several perennial species became established at higher frequency, abundance, dominance, biomass, or cover in the lethal disturbance treatment than in other treatments, suggesting that lethal disturbances may lead to a change in vegetation structure. While this overall pattern held for both communities, responses of individual species to disturbance intensity varied.

- 3) Because steep gradients of elevation and salinity are generally absent in oligohaline marshes, distinct community types may be maintained primarily by competitive inhibition of seedling recruitment rather than competitive displacement of competitively inferior but more stress-tolerant species to more stressful locations. I found that disturbances which removed aboveground plant biomass or were lethal to vegetation stimulated prolific seedling recruitment of both annual and perennial species in communities where these species were otherwise rare in adult vegetation.
- 4) Disturbance catalyzes shifts in marsh community structure in response to rising sea level. My results indicate that salinity and inundation had a

greater effect on marsh community structure when a disturbance was applied than occurred in the absence of disturbance.

- 5) The reproductive biology of individual species is critical to our understanding of oligohaline marsh community dynamics under conditions of rising sea level. I found that salinity and inundation generally reduced seed germination but that the capacity for germination under different salinity or inundation levels differed among species, suggesting that seedling recruitment patterns may be altered by higher salinity and water levels. Also, capacity for vegetative colonization following disturbance in the community dominants Sagittaria lancifolia and Spartina patens was differentially affected by salinity and water level. Responses of adult plants to changes in salinity or water level in the absence of disturbance were small and generally not significant.

I hope that the findings of my research further our understanding of how oligohaline marshes respond to changes in environmental variables associated with sea level rise. At a minimum, my research indicates that an understanding of disturbance processes and regeneration mechanisms is critical to predicting changes in these complex systems as sea level continues to rise. This information may be useful in developing management strategies for addressing problems of vegetation change and loss of coastal wetlands associated with this global issue.

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APPENDIX: LETTER OF PERMISSION



LOUISIANA STATE UNIVERSITY
AND AGRICULTURAL AND MECHANICAL COLLEGE
Department of Plant Biology

March 21, 1996

Kim Hiser
Business Manager
American Journal of Botany
Botanical Society of America
1735 Neil Ave
Columbus, Ohio 43210-1293

Dear Ms. Hiser:

Thanks for calling me today. As part of my dissertation work at Louisiana State University I prepared a manuscript entitled "The influence of vegetation, salinity, and inundation on seed banks of oligohaline coastal marshes" (coauthored with K. McKee and I. Mendelssohn). The ms. was accepted for publication in Vol 83(4) of the *American Journal of Botany* (manuscript No. 95-41, Galley D-121). In order to include this paper in my dissertation LSU requires that I receive written permission from the journal or copyright holder, and include this documentation in my dissertation. I would not photocopy the article but rather include it in the same format as the rest of the dissertation (no abstract, references separate, etc.).

I would greatly appreciate it if you could send the permission letter or form to me here at the Department of Plant Biology. I can be reached at (504)388-8554 or (504)767-3405 if you require any additional information. Thank you for your help.

Sincerely,

Andrew H. Baldwin

Permission granted for the use of the material above.

Kimberly E. Hiser
Business Manager

Date

VITA

Andrew Baldwin was born in Buffalo, New York, on August 11, 1960 and moved to Houston, Texas, before he was two years old. In 1967, he and his family moved to Trieste, Italy, for four years and then to Brussels, Belgium, for six months. During this European stint he became fluent in Italian and French, and experienced some of the art, history, culture, and skiing of Europe. At 12 he went to West Hartford, Connecticut, for his formative adolescent years and graduated from Watkinson School in 1979. He then pursued bachelor of science degrees in both biology and engineering at Tufts University in Medford, Massachusetts, and graduated with Cum Laude honors in 1983. Andrew subsequently found work as an environmental engineer at a consulting firm.

Although he had training in engineering, his love lay with plants. He gradually became involved in ecological work, eventually becoming a full-time ecologist at another environmental firm. In this position he traveled the country, visiting sites ranging from pristine wetlands to hazardous waste sites and describing their flora and fauna. After about eight years of consulting, however, he wanted a deeper and more quantitative understanding of plants and their ecology, and decided to pursue doctoral studies in botany at Louisiana State University. He became interested in plant communities of Louisiana coastal marshes and how disturbance and sea level rise might affect their dynamics, and chose to investigate these issues in his dissertation research. Outside of his dissertation he studied the effects of Hurricane Andrew on mangroves in south Florida. On August 1, 1996 he will

receive his doctorate of philosophy degree in botany from the Department of Plant Biology at Louisiana State University. His future is now wide open, but one thing is certain: it will involve plants.

DOCTORAL EXAMINATION AND DISSERTATION REPORT


Candidate: Andrew Hamilton Baldwin

Major Field: Botany

Title of Dissertation: The Role of Seed Banks, Disturbance, and Sea Level Rise in Determining the Plant Community Structure of Oligohaline Coastal Marshes

Approved:

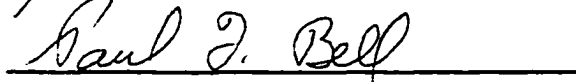

Major Professor and Chairman

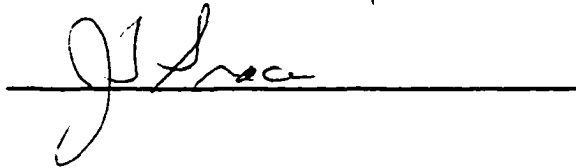

Dean of the Graduate School

EXAMINING COMMITTEE:









Date of Examination:

May 31, 1996