

Effects of salinity and water level on coastal marshes: an experimental test of disturbance as a catalyst for vegetation change

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Abstract

Wetlands in many coastal areas are threatened by sea level rise. Higher sea level will increase the frequency and duration of inundation in coastal areas and, in some systems, result in higher salinity as well. While the effects of salinity and water level on coastal marsh vegetation have been widely investigated, the role of disturbance in causing shifts in vegetation due to changes in salinity or water level has received little attention. We examined interactions of disturbance (clipping of aboveground vegetation) with salinity and water level treatments in a factorial arrangement using oligohaline marsh mesocosms. The mesocosms all contained soil and vegetation from two adjoining plant communities, one dominated by *Spartina patens* (Ait.) Muhl. and the other by *Sagittaria lancifolia* L. We assessed vegetation responses quarterly for 1 year and related responses to soil redox potential (E_h), sulfide concentration, salinity, and pH. We found that salinity and water level had significant effects on species richness only following disturbance and that similar patterns occurred for aboveground biomass of dominant and subdominant species. Following disturbance, aboveground biomass of *Sagittaria lancifolia* was significantly reduced by salinity but not by flooding (due to a capacity for seed germination under flooded conditions and rapid vegetative growth following disturbance), while the more salt-tolerant *Spartina patens* was eliminated by flooding but not affected by salinity. Disturbance led to almost complete eradication of vegetation under flooded, saline conditions. In the absence of disturbance, *Sagittaria lancifolia* biomass increased while *Spartina patens* was not affected in response to flooding, and neither species was significantly affected by salinity. Responses of vegetation corresponded with lower E_h in flooded

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and saline treatments and higher sulfide concentration in saline treatments. Our results suggest that disturbance is an important component of vegetation change in response to rising sea level, catalyzing rapid shifts in vegetation structure or accelerating wetland loss. © 1998 Elsevier Science B.V. All rights reserved

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1. Introduction

Sea level has risen at an estimated rate of 1.0–2.0 mm/year over the last 100 years 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; Turner, 1997). 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 wetland loss rates observed in coastal Louisiana, estimated at 65.6 km²/year or about 0.35% of the Louisiana coastal plain each year (Britsch and Dunbar, 1993). Higher relative sea level may also result in shifts in vegetation composition of oligohaline and fresh tidal marshes from salt-intolerant to salt-tolerant species. Salinization of coastal marshes is believed to have caused an observed increase in saline and brackish marsh types of 433 km² in coastal Louisiana from 1968–1978 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 water level 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. Natural disturbances are widespread in coastal marshes and include fire, herbivory, deposition of wrack (organic debris), salt water intrusion, hurricanes, and sediment burial (Bertness and Ellison, 1987; Flynn et al., 1995; Guntenspergen et al., 1995; Nyman and Chabreck, 1995; Allison, 1996; Ford, 1996; Taylor et al., 1997; Valiela et al., 1998). Seedling recruitment is an important component of regeneration following disturbances in oligohaline marshes (Baldwin, 1996), and recruitment from seed banks of coastal marshes is altered by salinity and water level (Galinato and van der Valk, 1986; Baldwin et al., 1996). Regeneration via vegetative growth may also be inhibited by increases in salinity or water level (Flynn et al., 1995; Grace and Ford, 1996; Miller et al., 1997). These studies suggest that patterns of establishment and regeneration following disturbance are altered 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), can contain plant communities dominated by species of differing salinity tolerance (Penfound and Hathaway, 1938; Chabreck, 1972; Cowardin

et al., 1979; 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 water level (Chabreck, 1972; Sasser, 1977). 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.

To examine the role of disturbance in vegetation change under different salinity and inundation regimes, we conducted an experiment using mesocosms containing soil and vegetation from two oligohaline marsh communities dominated by species of different salinity tolerance. The mesocosms were subjected to disturbance, salinity, and water level treatments in a factorial arrangement and vegetation was monitored for 1 year. Variation in environmental parameters was also evaluated and related to plant responses. We hypothesized that the effects of salinity and flooding on community structure would be greater in disturbed treatments and that disturbance would result in rapid shifts in the abundance of the community dominants in response to changes in salinity or water level.

2. Materials and methods

2.1. Collection of experimental material

Sections of marsh soil and vegetation were collected on 18 March 1994 from two adjoining oligohaline marsh communities in Madisonville, Louisiana, USA (30°23'N, 90°09'W). One community is dominated by *Sagittaria lancifolia* L. (Alismataceae) and the other by *Spartina patens* (Ait.) Muhl. (Poaceae). 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 25 cm diameter plastic pot (with holes at the bottom and sides for drainage); a total of 40 pots with sods were collected. The objective of combining sections from two marsh communities was to create experimental units containing propagules of both the brackish marsh species (*Spartina patens*) and the intermediate marsh species (*Sagittaria lancifolia* and others) (Chabreck, 1972; Gosselink, 1984). 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. All of the buckets containing the potted sods (experimental units or mesocosms) were filled with fresh water to the level of the soil surface and allowed to acclimate for 1 month before gradually adjusting salinity to the treatment level. Greenhouse temperature was maintained above 10°C throughout the year, and typically reached maxima of 35–40°C during the summer months (slightly above outdoor temperatures). Photoperiod was not controlled.

2.2. Experimental design

The experiment was set up as a randomized block design (RBD) with a factorial arrangement of disturbance, salinity, and water level factors in eight treatment

combinations (all combinations of two levels of each factor: disturbed/undisturbed, fresh/saline, and flooded/nonflooded). Blocking was used because of possible gradients of light and humidity along the length of the greenhouse. Mesocosms were arranged into five groups (blocks) on greenhouse benches extending the length of the greenhouse and the eight treatment combinations were assigned randomly to the experimental units in each block.

2.3. Treatment application

The initial salinity of interstitial water in the mesocosms was low (mean \pm SE: 0.4 \pm 0.3 ppt; $N=40$). Salinity was measured in wells which consisted of PVC pipe (46 cm long, 1.25 cm diameter) with holes drilled in the sides (in the portion of the pipe extending below the soil surface), a rubber stopper on the bottom, and a removable cap on top.

After the acclimation period, salinity of interstitial water was increased gradually in mesocosms receiving the 'saline' treatment over a period of 1 month to 6 ppt by periodically replacing mesocosm water with increasingly concentrated solutions of Bio-Crystals Marinemix sea water formulation (Marine Enterprises, Baltimore, Maryland, USA). The concentration of 6 ppt was chosen as a level that was not expected to cause dieback of aboveground vegetation or reduction of growth of *Spartina patens*, but which might reduce growth of *Sagittaria lancifolia* (Chabreck, 1972; Mendelssohn and McKee, 1987; McKee and Mendelssohn, 1989; R. Howard, National Biological Service, personal communication). Salinity of interstitial water was measured periodically during the experiment and adjusted as necessary to maintain salinity near 6 ppt. Water in mesocosms receiving the 'fresh' treatment was replaced with tap water of approximately the same volume as the solution applied to the mesocosms receiving the saline treatment, which resulted in a fresh mesocosm salinity of about 0.1 ppt.

Disturbance and flooding treatments were applied to the appropriate mesocosms on 18 May 1994. The 'disturbed' treatment consisted of clipping all vegetation at the soil surface. The clipped vegetation was collected and used to calibrate the estimation of aboveground biomass non-destructively (see Section 2.6). Vegetation was left intact in mesocosms receiving the undisturbed treatment. 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; A. Baldwin, personal observation). These disturbances may differ in their effects on edaphic factors but their effect on vegetation is accurately represented by the clipping treatment we used in this experiment. Clipping has been used in to simulate herbivory in other studies (Taylor and Grace, 1995; Grace and Ford, 1996). For the 'flooded' treatment, water level was maintained approximately 10 cm above the surface of the soil; for the 'nonflooded' treatment, water level was maintained 10 cm below the soil surface. Water in the mesocosms was not flowing, but was periodically replaced with water of the appropriate salinity.

2.4. Vegetation sampling

Vegetation in the mesocosms was sampled non-destructively in April 1994 (before applying treatments) and then every 3 months until April 1995 when the experiment was terminated. Within each mesocosm the number of stems of each species were counted. Additionally, the average height of *Spartina patens*, and average height and blade width of *Sagittaria lancifolia*, were visually estimated using a meter stick during each sampling event (measurements of individual stems was not practical due to high stem density). These estimates were used to predict aboveground biomass of the two community dominants (see Section 2.6). On 27 April 1995, all aboveground vegetation was clipped at the soil surface. Harvested plants were sorted by species and as live or dead, dried at 80°C for 3 days, and weighed to the nearest 0.01 g. Plant nomenclature is according to Kartesz (1994).

2.5. Measurement of environmental variables

We measured soil redox potential (E_h) and interstitial water sulfide concentration, salinity, and pH. Three E_h measurements per mesocosm were made at 2 and 15 cm depths in June 1994 using bright platinum electrodes, a calomel reference electrode, and a pH/mV meter. E_h 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), and was not adjusted for pH. In September 1994, a 5 ml sample of well water was collected for sulfide analysis (after drawing water from the wells and allowing them to refill to minimize sulfide oxidation) and immediately placed in an equal volume of antioxidant buffer. Sulfide (S^{2-}) concentration in mV was measured with a sulfide electrode (model DJM-146, Lazar Research Laboratories, Los Angeles, California, USA). A standard curve was prepared from a serial dilution of Na_2S and used to calculate sulfide concentration. 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. Interstitial water pH was measured twice during the experiment using a portable pH meter.

2.6. Data analysis

Data on aboveground biomass and species richness (number of species) of vegetation from quarterly sampling events were analyzed as a RBD using repeated measures analysis of covariance (ANCOVA), with data from the initial sample date used as the covariate. Aboveground biomass data were $\ln(x+1)$ 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-factor analyses of vegetation data, effects of salinity and water level were analyzed by disturbance level. Sulfide concentration and final aboveground biomass were analyzed as a RBD and E_h 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, USA). A significance level of $P=0.05$ was used in interpreting results of statistical tests except when determining the significance of multiple univariate tests to address a single hypothesis; in these instances, a Bonferroni adjustment of significance level was made (Scheiner, 1993). 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.

Aboveground biomass of *Sagittaria lancifolia* and *Spartina patens* was estimated non-destructively from stem count, average height, and average blade width data using no-intercept simple linear regression models. Biomass data used in regressions were based on measurements of vegetation harvested during the initial disturbance treatment and at the end of the experiment. There were significant positive relationships ($P<0.0001$) between biomass and number of stems for *Spartina patens* (biomass= $0.013878 \times$ stems \times height) and between biomass, average height, and average blade width for *Sagittaria lancifolia* (biomass= $0.003177 \times$ stems \times height \times width). Additionally, coefficients of determination were high for both species ($R^2=0.96$ for *Sagittaria lancifolia* and $R^2=0.93$ for *Spartina patens*).

3. Results

3.1. Response of vegetation

Flooding and salinity significantly reduced species richness, but only following disturbance ($P<0.001$; Fig. 1). In the disturbed mesocosms, the effects of flooding and salinity varied significantly over time ($P<0.05$ for time \times water level and time \times salinity interactions) but were additive ($P>0.05$ for water level \times salinity interaction; Fig. 1). Relative to the nonflooded, fresh treatment (the least stressful condition), flooding reduced richness to a greater degree than salinity; the combination of flooding and salinity resulted in the greatest reduction in richness (Fig. 1).

Following disturbance, biomass of *Sagittaria lancifolia* was significantly lower in the saline treatment than in the fresh treatment ($P<0.0001$; Fig. 2(C)). The main effect of water level on *Sagittaria lancifolia* biomass in the disturbed treatment was not significant ($P=0.2084$), although flooding significantly reduced biomass in July 1994 and increased biomass in October 1994 and January 1995 ($P<0.05$; Fig. 2(C)). The water level \times salinity interaction for *Sagittaria lancifolia* biomass in disturbed mesocosms was significant ($P=0.002$) because salinity reduced biomass to a greater extent under flooded than under nonflooded conditions in July and October 1994 ($P<0.01$; Fig. 2(C)). In contrast with *Sagittaria lancifolia*, biomass of *Spartina patens* following disturbance was significantly reduced by flooding ($P<0.0001$) but not salinity ($P=0.9851$) (Fig. 2(D)).

In the absence of disturbance, biomass of *Sagittaria lancifolia* was significantly higher under flooded conditions than under nonflooded conditions overall based on repeated measures ANCOVA ($P=0.0338$) and for the October 1994, January 1995, and April 1995 sample dates ($P<0.05$); however, significant effects of water level within sample dates were not revealed in multiple-comparison tests (Fig. 2(A)). The overall effect of salinity on *Sagittaria lancifolia* in undisturbed mesocosms was not significant ($P=0.1249$),

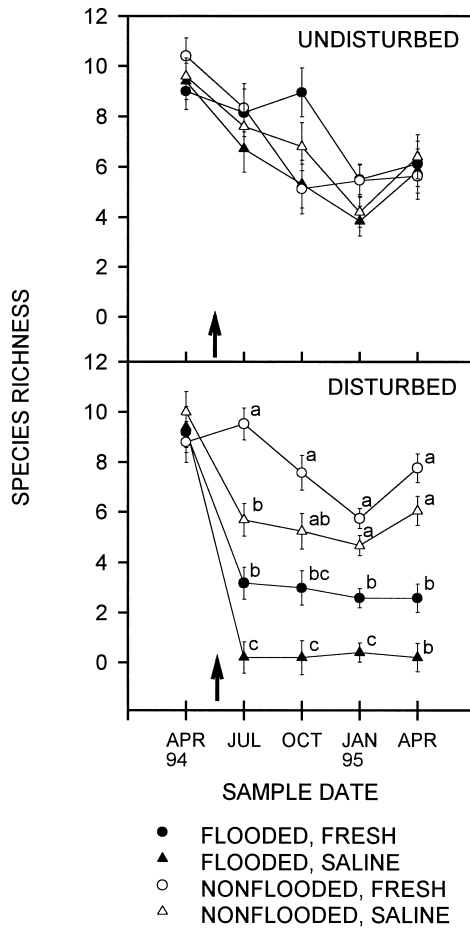


Fig. 1. Variation in species richness in response to salinity and water level in undisturbed and disturbed greenhouse mesocosms. Date of treatment application is indicated by the arrow. Within each level of disturbance and sample date, means with different letters are significantly different. Symbols indicate mean richness in mesocosms; error bars indicate ± 1 SE.

although biomass of *Sagittaria lancifolia* was significantly lower under saline than fresh water conditions for the July 1994 sample date ($P=0.0007$; Fig. 2(A)). Salinity and water level had no significant effects on biomass of *Spartina patens* in undisturbed mesocosms ($P>0.8$; Fig. 2(B)).

Significant effects of salinity or water level on final biomass occurred in five of the 10 most frequently occurring species (Tables 1 and 2). Flooding significantly reduced final biomass in *Alternanthera philoxeroides*, *Aster subulatus*, *Eleocharis fallax*, and *Spartina patens* at probability level of 0.01 (Bonferroni adjustment), but only in disturbed treatments (Tables 1 and 2). In contrast, flooding significantly increased final biomass of *Sagittaria lancifolia* in the undisturbed treatments (Table 1), although this effect was not revealed in means comparison tests (Table 2). Salinity significantly decreased biomass of

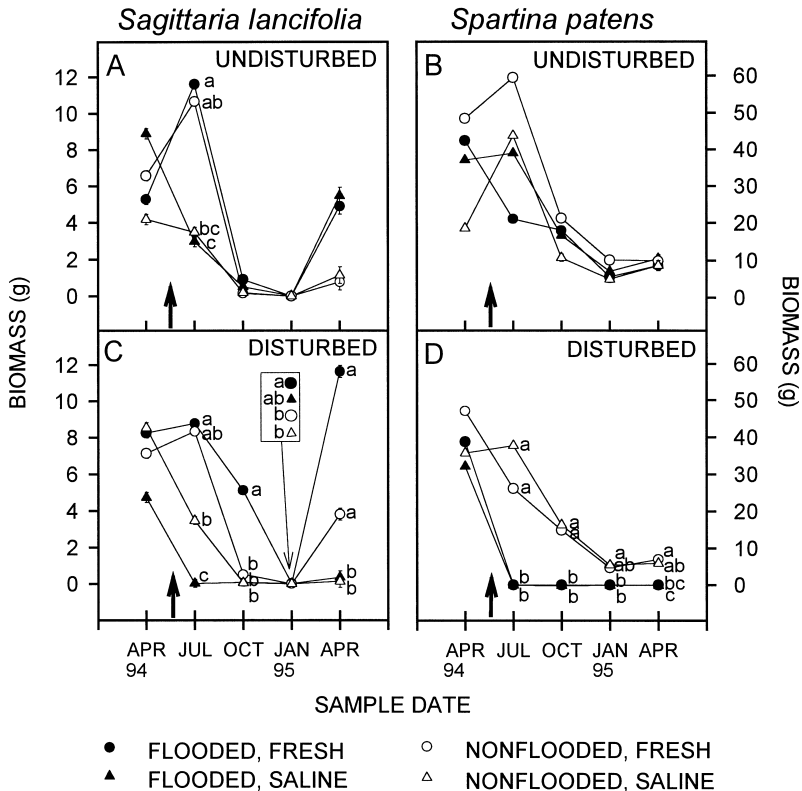


Fig. 2. Effects of salinity and water level on biomass of *Sagittaria lancifolia* and *Spartina patens* in undisturbed and disturbed greenhouse mesocosms. Date of treatment application is indicated by the arrow. Within each level of disturbance and sample date, means with different letters are significantly different. Symbols indicate mean biomass in mesocosms; error bars indicate ± 1 SE. When error bars are not visible they are smaller than symbols.

Sagittaria lancifolia in disturbed treatments at a probability level of 0.01 (Bonferroni adjustment) but had no effect on any species when undisturbed (Table 1).

Total live aboveground biomass for all species combined was not affected by salinity or water level in the absence of disturbance (Tables 1 and 2). However, in disturbed mesocosms the water level \times salinity interaction was significant for total live aboveground biomass (Table 1), with salinity causing a significant reduction in total live aboveground biomass only under flooded conditions (Table 2).

3.2. Environmental variables

Flooding significantly decreased E_h at 2 cm depth under both fresh ($P=0.0017$) and saline ($P<0.0001$) conditions. However, the water level \times salinity effect was significant ($P=0.007$) because flooding reduced E_h to a greater extent under saline than under fresh conditions (Table 3). Both salinity and flooding reduced E_h significantly at 15 cm depth (water level: $P=0.0310$; salinity: $P<0.0001$; Table 3); no interactions were significant.

Table 1

Results of ANOVAs of log-transformed final live biomass of the 10 most frequently occurring species by level of disturbance. Values are *F*-ratios

Species	Undisturbed				Disturbed			
	Water level (W)	Salinity (S)	W×S	Block	Water level	Salinity	W×S	Block
<i>Alternanthera philoxeroides</i>	3.22	0.32	2.55	2.00	17.89 ^a	4.07	4.07	1.95
<i>Ammannia latifolia</i>	3.31	0.38	2.19	4.17	3.23	3.23	3.23	1.00
<i>Aster subulatus</i>	2.30	0.02	0.005	0.63	33.33 ^c	8.85	8.85	1.75
<i>Cyperus odoratus</i>	2.44	0.28	0.28	2.44	1.70	0.18	0.18	0.75
<i>Eleocharis fallax</i>	1.91	1.54	2.74	0.48	14.70 ^a	1.43	0.01	0.26
<i>Phyla nodiflora</i>	0.02	0.08	2.01	0.87	1.57	1.57	1.57	1.00
<i>Polygonum punctatum</i>	2.83	2.83	2.83	1.00	1.00	1.00	1.00	1.00
<i>Sagittaria lancifolia</i>	12.42 ^a	0.20	0.04	0.82	3.99	47.14 ^c	2.65	1.03
<i>Scirpus tabernaemontani</i>	2.14	1.63	0.15	0.76	1.15	4.28	1.15	1.08
<i>Spartina patens</i>	0.14	0.41	0.48	1.15	19.43 ^b	0.0006	0.0006	1.44
Total	0.44	0.07	<0.0001	1.30	59.61 ^c	55.24 ^c	47.68 ^c	0.14

^a *P*<0.01.

^b *P*<0.001.

^c *P*<0.0001.

Table 2

Final live biomass (g) of the 10 most frequently occurring species in greenhouse mesocosms

Species	Undisturbed				Disturbed			
	Nonflooded		Flooded		Nonflooded		Flooded	
	Fresh	Saline	Fresh	Saline	Fresh	Saline	Fresh	Saline
<i>Alternanthera philoxeroides</i>	0.65	0.45	0.07	0.41	1.71 ^a	0.42 ^{ab}	0 ^b	0 ^b
<i>Ammannia latifolia</i>	0	0.05	0.19	0.07	0	0	0.84	0
<i>Aster subulatus</i>	0.37	0.44	0	0.02	0.66 ^b	3.86 ^a	0 ^b	0 ^b
<i>Cyperus odoratus</i>	0	0	0.02	0.04	0.02	0.01	0	0
<i>Eleocharis fallax</i>	1.11	1.47	5.74	1.23	1.78 ^a	1.14 ^{ab}	0.25 ^{ab}	0 ^b
<i>Phyla nodiflora</i>	0.01	0.38	0.35	0.09	0.33	0	0	0
<i>Polygonum punctatum</i>	0	0	0.05	0	0.09	0	0	0
<i>Sagittaria lancifolia</i>	0.81	0.97	4.71	6.13	3.83 ^a	0.16 ^b	11.94 ^a	0.29 ^b
<i>Scirpus tabernaemontani</i>	0	1.06	1.23	2.29	0.45	0	2.19	0
<i>Spartina patens</i>	14.07	4.32	10.71	11.24	6.04 ^a	6.20 ^a	0 ^b	0 ^b
Total	28.92	26.41	36.21	33.00	28.08 ^a	22.49 ^a	21.18 ^a	0.29 ^b

Within species and disturbed and undisturbed treatments, means with different superscripted letters are not significantly different. Absence of letters indicates no significant difference among treatments.

Disturbance had no significant effects on E_h ($P>0.7$). Sulfide concentration was significantly higher in saline treatments than in fresh treatments ($P<0.0001$; Table 3); 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 3), and repeated measures ANOVA indicated a significant difference between fresh and saline treatments ($P<0.0001$). The salinity of mesocosms treated with fresh

Table 3
Summary of environmental measurements in greenhouse mesocosms

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

water was about 0.1 ppt; fresh tidal marshes have been defined as those marshes having a salinity less than 0.5 ppt (Cowardin et al., 1979). The pH of mesocosm interstitial water was slightly but significantly lower in fresh than in saline treatments ($P<0.0001$), although pH values occurred within a narrow range (Table 3).

4. Discussion

The most important finding of this study was that salinity and flooding had a greater effect on community structure when vegetation was disturbed, suggesting that disturbance catalyzes vegetation change in response to environmental variables. Species richness was significantly reduced in response to both salinity and flooding following disturbance, while salinity and flooding did not affect richness in the absence of disturbance (Fig. 1). We observed similar interactions between disturbance, salinity, and water level in their effect on biomass of dominant and subdominant species (Fig. 2 and Tables 1 and 2). Furthermore, salinity resulted in a greater reduction in biomass under flooded conditions than under nonflooded conditions for *Sagittaria lancifolia* and for total aboveground biomass of all species (Tables 1 and 2), suggesting a synergistic effect of salinity and flooding stresses following disturbance.

The responses of individual species to salinity and flooding following disturbance were not uniform. Biomass of *Sagittaria lancifolia*, a common species in fresh and intermediate marshes, was reduced by salinity but not by flooding in disturbed mesocosms. The brackish marsh dominant *Spartina patens*, on the hand, was eliminated by the combination of flooding and disturbance but not affected by salinity. These patterns suggest that disturbance may cause shifts toward more salt- or flood-tolerant communities depending on the water level and salinity at the time of disturbance.

Sagittaria lancifolia persisted in the flooded, fresh, disturbed treatment primarily via prolific seedling recruitment. Seeds of *Sagittaria lancifolia* occur in the seed banks of

oligohaline marshes and, unlike many marsh species, can germinate under flooded conditions (Baldwin et al., 1996). No seedlings of *Sagittaria lancifolia* were observed under saline conditions. Although seeds of *Sagittaria lancifolia* are not killed by temporary exposure to elevated salinity, germination is inhibited by salinities of 2 ppt or higher (Baldwin et al., 1996). We also observed that some *Sagittaria lancifolia* ramets survived through rapid vegetative growth, which restored a pathway for oxygen diffusion to rhizomes. Unlike *Sagittaria lancifolia*, *Spartina patens* did not survive the combination of disturbance and flooding as it did not sprout and was not recruited from seed. The lack of a salinity effect on the regrowth of *Spartina patens* following disturbance under nonflooded conditions is presumably due to its greater physiological tolerance to salinity (Penfound and Hathaway, 1938; Chabreck, 1972; McKee and Mendelsohn, 1989).

That we did not observe a dramatic response to salinity and water level in the absence of disturbance may be due to the relatively short duration of the study. While we did observe some variation in the response of species to salinity and water level in the absence of disturbance, these changes were generally not statistically significant and were smaller than those that occurred following disturbance (Fig. 2 and Tables 1 and 2).

While salinity and flooding may affect plant growth directly (Greenway and Munns, 1980; Kozlowski, 1984), the responses to flooding and salinity we observed may also be due in part to their effects on soil E_h and sulfide concentration. Soil E_h decreased in response to both flooding and salinity, and sulfide concentration was higher in the saline treatments (Table 3). Flooding can result in strongly reducing conditions due to a dramatic decrease in oxygen diffusion rate (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 (Ingold and Havill, 1984; Mendelsohn and McKee, 1987; Bradley and Dunn, 1989; Koch and Mendelsohn, 1989; Bradley and Morris, 1990; Koch et al., 1990; van Diggelen, 1991; Flynn et al., 1995). Lower redox potential also appears to be one of several factors reducing species richness at lower elevations in salt marshes (Brewer et al., 1997).

The responses of the dominant species of fresh and intermediate marshes (*Sagittaria lancifolia*) and brackish marshes (*Spartina patens*) to our experimental treatments suggest that changes in wetland vegetation due to rising sea level depend on disturbance and on the salinity and water level present at the time of disturbance (Fig. 2 and Tables 1 and 2). If water level is high but salinity concentration low, species capable of seed germination under flooded conditions or rapid regrowth such as *Sagittaria lancifolia* may predominate following disturbance. If salinity is high but water level is low, salt-tolerant species that reproduce vegetatively such as *Spartina patens* may prevail after disturbance. If both salinity and water level are high, wetland loss may occur due to the death of all vegetation and the subsequent inability of any 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.

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