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Effects of flooding, salinity and herbivory on coastal plant communities, Louisiana, United States

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Abstract Flooding and salinity stress are predicted to increase in coastal Louisiana as relative sea level rise (RSLR) continues in the Gulf of Mexico region. Although wetland plant species are adapted to these stressors, questions persist as to how marshes may respond to changed abiotic variables caused by RSLR, and how herbivory by native and non-native mammals may affect this response. The effects of altered flooding and salinity on coastal marsh communities were examined in two field experiments that simultaneously manipulated herbivore pressure. Marsh sods subjected to increased or decreased flooding (by lowering or raising sods, respectively), and increased or decreased salinity (by reciprocally transplanting sods between a brackish and fresh marsh), were monitored inside and outside mammalian herbivore exclosures for three growing seasons. Increased flooding stress reduced species numbers and biomass; alleviating flooding stress did not significantly alter species numbers while community biomass increased. Increased salinity reduced species numbers and biomass, more so if herbivores were present. Decreasing salinity had an unexpected effect: herbivores selectively consumed plants transplanted from the higher-salinity site. In plots protected from herbivory, decreased salinity had little effect on species numbers or biomass, but community composition changed. Overall, herbivore pressure further reduced species richness and biomass under conditions of in-

creased flooding and increased salinity, supporting other findings that coastal marsh species can tolerate increasingly stressful conditions unless another factor, e.g., herbivory, is also present. Also, species dropped out of more stressful treatments much faster than they were added when stresses were alleviated, likely due to restrictions on dispersal. The rate at which plant communities will shift as a result of changed abiotic variables will determine if marshes remain viable when subjected to RSLR.

Key words Biomass · Louisiana · Nutria · Species density · Species diversity

Introduction

Coastal plant communities are structured by both ambient salinity levels and the degree of flooding stress, determined to a large extent by elevation of the marsh and tidal inundation rates (Bertness and Ellison 1987; Mendelssohn and McKee 1987; Flynn et al. 1995; Howard 1995; Brewer et al. 1997). Broad expanses of different assemblages of plant species grade into each other across very slight elevational changes in the coastal zone of Louisiana. Relative sea level rise (RSLR) is increasing in this region, bringing more saline water into fresh and brackish marsh and subjecting marsh plants to greater degrees of flooding (Turner and Cahoon 1987; Boesch et al. 1994). Although marsh plant species are adapted to such conditions, they are naturally segregated along these gradients so that if conditions change, the species that had been located in that area may no longer be able to survive. Questions persist about how salt- or flood-tolerant species may migrate and successfully establish in previously more benign locations.

Mammalian herbivores undoubtedly affect the response of these plant communities to changing abiotic conditions. Herbivores may directly remove individuals from a particular area, or may indirectly affect interactions among the plants themselves, e.g., by selectively

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removing a competitive dominant and encouraging co-existence among the other species (Crawley 1983). There is well-documented herbivore pressure in many marshes by both native and non-native vertebrate herbivores (Weller 1981; Smith and Kadlec 1985; Bazely and Jefferies 1986; Mitsch and Gosselink 1986). In Louisiana, nutria (non-native rodents) have had a significant impact on wetland plants, especially as animal populations continue to increase (Chabreck 1988; Wilsey et al. 1991; Nyman et al. 1993; Taylor et al. 1994). With the exception of a study examining the effect of salinity, flooding and simulated herbivory on a dominant plant species (Grace and Ford 1996), we are not aware of any field studies of the interaction of herbivory with these other processes in Louisiana coastal marshes (for correlations among these factors see Grace and Pugsek 1997).

The objectives of this study were to address the following questions in two coastal plant communities:

1. Do altered flooding stress, altered ambient salinity, and exclusion of herbivores affect plant species composition and richness?
2. Do herbivores affect the plant community response to salinity or water depth changes?

To examine these questions, sods were raised, lowered, reciprocally transplanted between sites of different salinities, and protected from herbivory in two marsh communities in coastal Louisiana, and responses were measured for three growing seasons.

Methods

Study site

Two study sites were located within the Pearl River Wildlife Management Area, on the coastal boundary between Louisiana and Mississippi (White 1983; Gough 1996). The *Sagittaria* site was located along the Middle Pearl River in a fresh/oligohaline marsh (water salinities ranged from 0 to 2 ppt) dominated by *Sagittaria lancifolia* L. and *Spartina patens* (Ait.) Muhl., with a variety of annual species present. The brackish *Spartina* site was located along the East Pearl River where it widens to empty into Lake Borgne and the Gulf of Mexico (water salinity range: 6–14 ppt); this site was dominated by *S. patens* and *Scirpus americanus* Pers. [*Scirpus olneyi* Gray], with graminoids comprising most of the rest of the vegetation. Several mammalian herbivore species were present at both sites including wild boar (*Sus scrofa*), rabbit (*Sylvilagus* sp.), muskrat (*Ondatra zibethicus*), deer (*Odocoileus virginianus*) and most abundantly, nutria (*Myocaster coypus*). Although the nutria (large rodents introduced to Louisiana from South America in the 1930s) have increased in number over the past decade, they consume vegetation in a manner similar to the native muskrats.

Experimental design

Flooding

The flooding treatments were raised, lowered, and control; methods follow those of McKee and Mendelssohn (1989). For all treatments, circular sods (0.33 m diameter, 15 cm deep) were cut out of the marsh, placed in black plastic weed cloth, and tied with string. To construct the raised treatments, the hole left by the sod was filled and the sods placed on top at approximately 10 cm above the

marsh surface. Bamboo stakes were used to hold sods in place. Lowered sods were placed with the surface 10 cm below the marsh surface after sediment had been removed from the hole. Control sods were placed back in the hole flush with the marsh surface. Undisturbed control plots of 0.33 m diameter were marked and regarded as a separate treatment throughout the study. All treatments were carried out in June 1993.

Salinity

Reciprocal transplants of sods between the two marshes were performed (see McKee and Mendelssohn 1989). These sods were dug up, and placed in weed cloth in the same manner as the flooding experiment; the same control and undisturbed control sods were used. Sods were replaced randomly at both sites in holes left by the other sod removals in June 1993.

Herbivory

Eight fenced exclosures were constructed at each site following the implementation of the flooding and salinity treatments to prevent herbivory by nutria, muskrat, rabbit, deer and wild boar. Wooden corner posts and 1.2-m-wide plastic coated fencing wire (with 5 × 5 cm openings) were used to construct the approximately 7 × 7 m exclosures. The wire was sunk approximately 10 cm into the soil to prevent burrowing. All plots were located at least 1 m from the fences to avoid edge effects. Each fence surrounded one replicate of each treatment. For the flooding experiment this resulted in a total of 108 sods; for the salinity experiment this resulted in 96 sods.

Data collection

Plots were sampled in July, October, and April of 1993, 1994, and through July 1995. Non-destructive sampling included recording the species found in each plot (species density), estimating aerial percent cover, counting number of stems, and measuring the average height of each species. Vine species were censused by percent cover only as it is impossible during the growing season to determine where the vines are rooted and how long the stems are. Water levels in relation to sod height were also recorded for the flooding treatments, and signs of herbivory were noted for all unfenced treatments. In late July 1995 elevation of the flooding treatment plots was recorded using a laser survey system (Spectra-Physics Instruments, Dayton, Ohio, USA). Salinity was measured in standing water on the marsh surface using a portable salinity-conductivity meter (YSI, Yellow Springs, Ohio, USA).

In early August 1995, destructive harvests were performed by removing all aboveground biomass (including standing dead and litter) from each plot. Samples were brought to the laboratory and sorted to species. Those species with easily identifiable dead ramets were divided into live and dead, while litter that could not be identified to species was lumped into one category. Plants were dried for at least 48 h at 80°C and then weighed.

Data analysis

The flooding and salinity experiments were analyzed separately following the same procedures outlined here. Species density was analyzed as a split-split plot design. The whole plot was the marsh by fence interaction, since each treatment was replicated within each marsh by fence combination. The flooding or salinity treatments were the first split, and time was the second. Error terms are shown in the tables directly beneath the effects they tested. PROC GLM (SAS version 6.0, SAS Institute, Cary, N.C., USA) with a repeated statement was used to perform the overall analysis, determine sphericity, and generate univariate results for each census date. All effects were evaluated for significance using type III sums of squares, and least square means with Tukey's HSD test were used for pairwise comparisons. Alpha levels were judged significant at 0.05 unless otherwise specified.

The same analysis was performed on biomass without repeated measures. The analysis of variance was run on total biomass, live and dead biomass separately, and mass of individual species. Normality was evaluated using the Shapiro-Wilks statistic, and homogeneity of variances was determined with residual plots. Biomass data for individual species were log-transformed as necessary to meet model assumptions.

Results

Flooding

Although sods were initially established at 10 cm above or below the marsh surface, the raised sods settled an average of 3 cm and the lowered sods gradually filled in an average of 3 cm over the three growing seasons of this study. Since treatment effects in the undisturbed control plots were not significantly different from the disturbed control plots (data not shown), only results from the disturbed control plots are reported here. The disturbed control plots will be referred to as “controls” throughout the remainder of this paper.

Species density

The repeated-measures analysis for species density over the length of the experiment revealed consistently higher species density in the *Sagittaria* marsh and strong effects of time of year (Table 1, Fig. 1). Because the marsh × fence × flood interaction was not significant (Table 1), we evaluated the two-way interactions separately. Lowered sods contained fewer species than raised sods in the *Sagittaria* marsh throughout the experiment, but only significantly in April and July 1994, and July 1995 in the *Spartina* marsh (Table 1, Fig. 1). Lowered sods contained fewer species than controls at all dates in the unfenced plots, but only significantly in the fenced plots at the final date (Table 1, Fig. 2).

The shifts in species composition in these plots were complex; species were lost from some plots but established in others within the same treatment. The loss of species in the lowered plots in the *Sagittaria* marsh was mostly due to dicots dropping out, particularly *Phyla nodiflora* (L.) Greene, *Galium tinctorum* L., and *Polygonum punctatum* Elliott, in addition to two vine species. Species gained in the raised plots were mostly dicots as well, especially *P. punctatum*, *Ph. nodiflora*, and *Aster subulatus* Michx. *A. subulatus* increased in the raised *Spartina* sods while *Spartina alterniflora* Loiseleur and *Sagittaria lancifolia* dropped out of the lowered plots.

Biomass

The plants in the raised plots accumulated significantly more biomass than the controls while the lowered sods contained less biomass than controls (lowered 37.5 ± 1.6 g/0.1 m², control 58.0 ± 1.9 g/0.1 m², raised 77.9 ± 2.0 g/0.1 m²; Table 2). These differences were

Table 1 Repeated-measures analysis of species density for flooding experiment. Since the dataset did not meet sphericity requirements for univariate analysis (Mauchly’s criterion = 0.528, *P* = 0.03), within-subject effects (time and its interactions) are reported using Greenhouse-Geiser adjusted univariate *P*-values (Moser et al. 1990). Significant *P*-values (<0.05) are in boldface. Rep = replicate

Source	df	MS	F	P
Marsh	1	549.37	84.71	0.0001
Fence	1	25.09	3.87	0.06
Marsh × fence	1	0.001	0	0.99
Rep (marsh × fence)	28	6.48		
Flood	2	245.89	72.62	0.0001
Marsh × flood	2	33.08	9.77	0.0002
Fence × flood	2	25.65	7.58	0.001
Marsh × fence × flood	2	5.67	1.68	0.20
Error	55	3.38		
Time	6	46.12	32.96	0.0001
Time × marsh	6	17.44	11.21	0.0001
Time × fence	6	4.20	2.70	0.02
Time × marsh × fence	6	0.91	0.58	0.74
Time × rep (marsh × fence)	168	1.56		
Time × flood	12	3.88	2.77	0.003
Time × marsh × flood	12	1.95	1.40	0.18
Time × fence × flood	12	1.86	1.33	0.22
Time × marsh × fence × flood	12	1.02	0.73	0.70
Error (Time)	330	1.40		

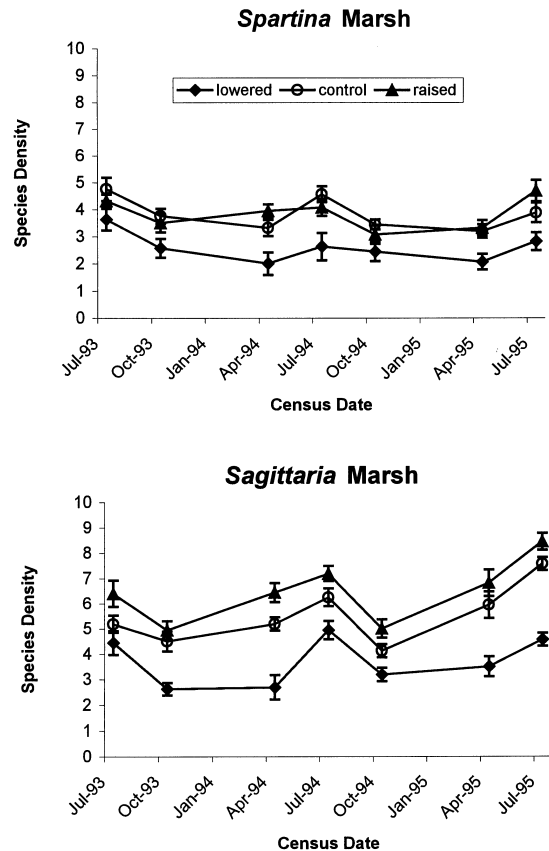


Fig. 1 Mean species density (number of species/0.1 m²) over time for the flooding experiment in the *Spartina* marsh and *Sagittaria* marsh. Error bars represent ± 1 SE (*n* = 8)

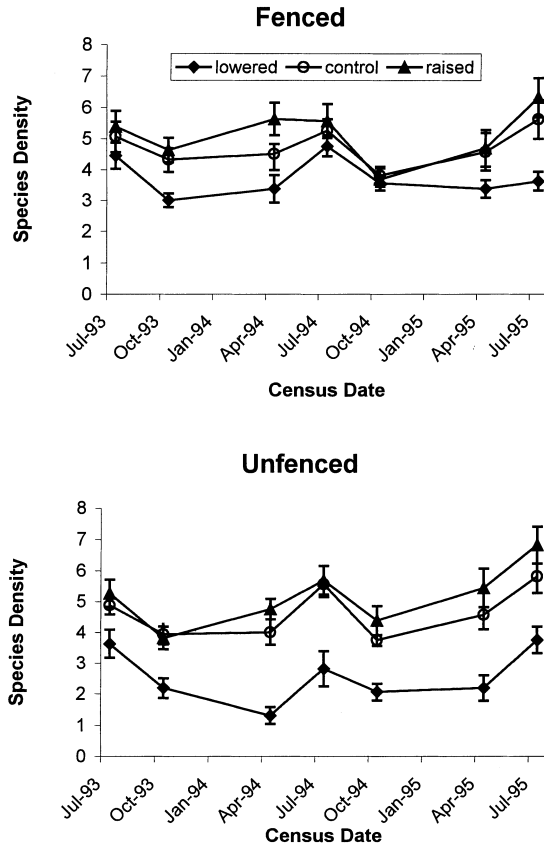


Fig. 2 Mean species density (number of species/0.1 m²) over time for the flooding experiment in fenced and unfenced plots. Error bars represent ±1 SE (*n* = 8)

more pronounced in the *Sagittaria* marsh, but not significantly so (Fig. 3). Live biomass exhibited a similar pattern, while dead biomass (which included standing dead and litter) was significantly different in many cases (Table 2). Greater live biomass in the *Spartina* marsh counteracted greater amounts of litter in the *Sagittaria* marsh resulting in a nonsignificant marsh effect for total biomass (Table 2, Fig. 3).

Several species were examined individually for biomass results. *Scirpus americanus*, a clonal sedge, occurred solely in the *Spartina* marsh where it was a dominant species. This species accumulated more total biomass inside the fences, resulting from greater litter accumulation; live biomass alone was not different across treatments (*P* > 0.05, Table 3). *S. patens*, a clonal grass, was dominant or codominant in both marshes. This species accumulated more biomass in the raised sods than controls (flooding treatment *P* = 0.0008; Table 3); control and lowered sods were not significantly different (pairwise *P* > 0.05). There was no effect of fencing on biomass accumulation of this species (*P* > 0.05). *Sagittaria lancifolia*, a clonal broad-leafed monocot, was a dominant in both marshes but was more prevalent in the *Sagittaria* marsh (*P* = 0.0001, Table 3). Raised sods had significantly greater biomass than the lowered sods (*P* = 0.03); more litter accumulated in the fenced, raised

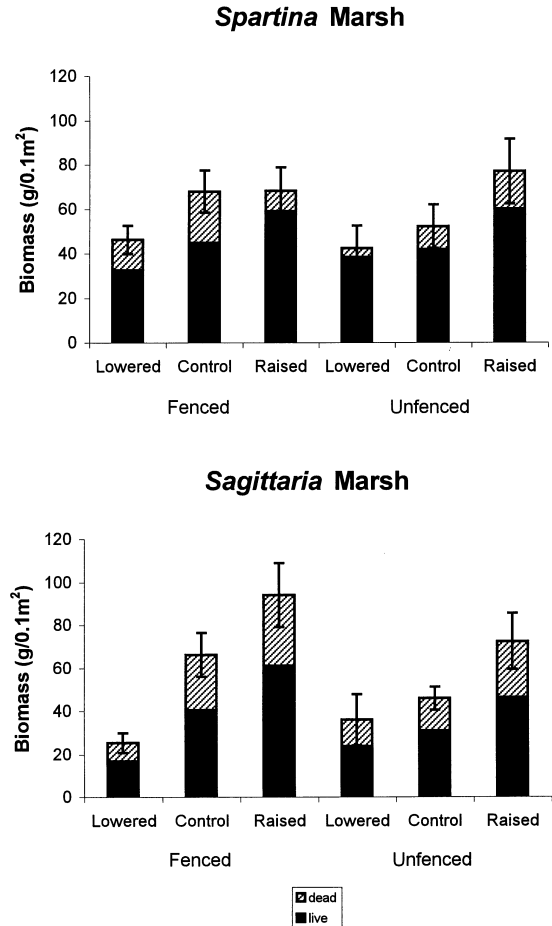


Fig. 3 Community biomass results for the flooding experiment from August 1995 for *Spartina* marsh and *Sagittaria* marsh. Error bars represent ±1 SE for total biomass (live + dead)

Table 2 Biomass analysis of flooding experiment

Source	df	P		
		Total	Live	Dead
Marsh	1	0.73	0.08	0.02
Fence	1	0.30	0.67	0.11
Marsh × fence	1	0.61	0.51	0.97
Rep (marsh × fence)	28			
Flood	2	0.0001	0.0001	0.0001
Marsh × flood	2	0.24	0.74	0.004
Fence × flood	2	0.33	0.49	0.03
Marsh × fence × flood	2	0.29	0.78	0.01
Error	56			

plots than the fenced, lowered plots in the *Sagittaria* marsh (*P* = 0.05, Table 3).

Salinity

Species density

The three-way interaction of marsh by fence by treatment was significant in the salinity experiment (Fig. 4,

Fig. 4 Mean species density (number of species/0.1 m²) over time for the salinity experiment in *Spartina* marsh, fenced plots; *Spartina* marsh, unfenced plots; *Sagittaria* marsh, fenced plots; and *Sagittaria* marsh, unfenced plots. *Marsh type* indicates the origin site of the sods. *Error bars* represent ± 1 SE ($n = 8$)

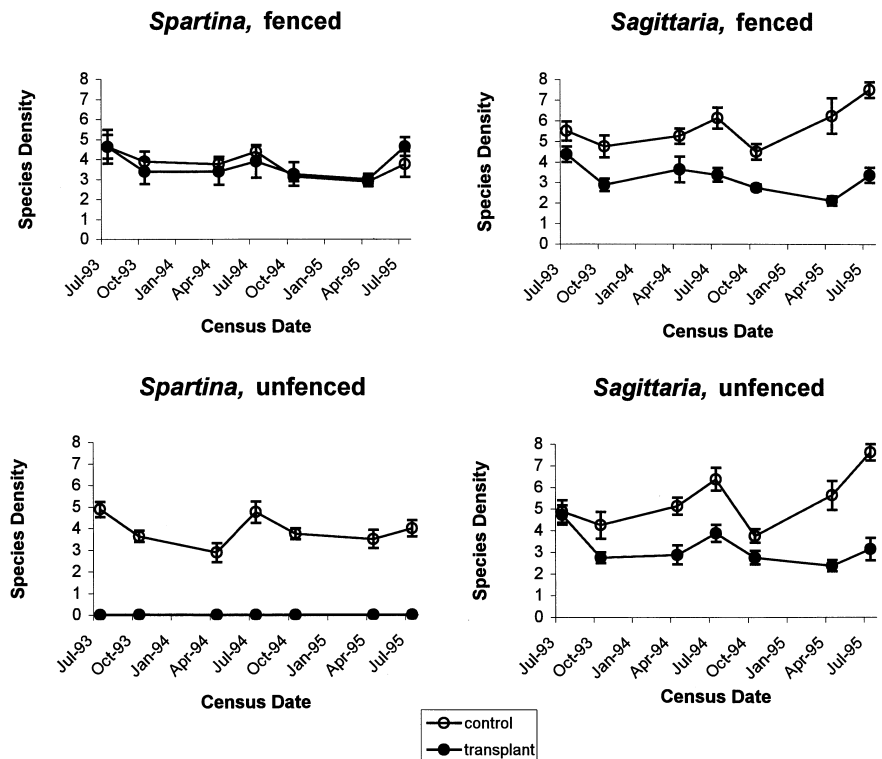


Table 4 Repeated measures analysis of species density for salinity experiment. Data maintained sphericity so univariate results for within subject factors (time and its interactions) are reported

Source	df	MS	F	P
Marsh	1	239.12	77.77	0.0001
Fence	1	99.12	32.24	0.0001
Marsh \times fence	1	68.75	22.36	0.0001
Rep (marsh \times fence)	28	3.07		
Salinity	1	477.37	85.68	0.0001
Marsh \times salinity	1	3.19	0.57	0.46
Fence \times salinity	1	81.87	14.69	0.0007
Marsh \times fence \times salinity	1	113.46	20.36	0.0001
Error	26	5.57		
Time	6	18.48	17.86	0.0001
Time \times marsh	6	4.52	3.74	0.002
Time \times fence	6	1.02	0.84	0.54
Time \times marsh \times fence	6	1.14	0.94	0.47
Time \times rep (marsh \times fence)	168	1.21		
Time \times salinity	6	4.38	4.23	0.0006
Time \times marsh \times salinity	6	8.12	7.84	0.0001
Time \times fence \times salinity	6	0.63	0.61	0.73
Time \times marsh \times fence \times salinity	6	1.53	1.48	0.19
Error (time)	156	1.04		

Herbivory had complex effects on plant biomass

Overall, herbivores altered biomass of individual species but had no effect on community biomass (except in the transplanted sods), implying selective herbivory of individual plant species and compensatory growth of unpalatable species. An unexpected event occurred when brackish marsh sods transplanted to the unfenced areas in the *Sagittaria* marsh were completely consumed by

Table 5 Biomass analysis of salinity experiment

Source	df	P		
		Total	Live	Dead
Marsh	1	0.51	0.98	0.10
Fence	1	0.002	0.03	0.002
Marsh \times fence	1	0.02	0.05	0.12
Rep (marsh \times fence)	28			
Salinity	1	0.0003	0.0080	0.0001
Marsh \times salinity	1	0.22	0.14	0.92
Fence \times salinity	1	0.83	0.30	0.13
Marsh \times fence \times salinity	1	0.01	0.01	0.36
Error	27			

herbivores. Muskrat and nutria may have been attracted to these sods because they contained *Scirpus americanus*, a preferred forage species not normally found at the *Sagittaria* site. The range of herbivore impacts includes drastic effects such as these, where vegetation is destroyed, and less drastic effects where one dominant species is selectively removed thus favoring other plant species (see next section).

In some instances, the combination of a stress, such as increased salinity or increased flooding, and a disturbance (in our case herbivory) results in mortality of plant species that otherwise withstand such stresses individually (see Sale and Wetzel 1983, Grace and Ford 1996, Baldwin 1996 for clipping; Herndon et al. 1991, Ford and Grace 1998 for fire; Brewer et al. 1997, 1998 for litter removal). Such an extenuated loss of species can be expected if there is a trade-off in adaptations to stress and disturbance. For instance, in some cases

flooding and herbivory tolerance may be inversely related, for example, where plants increase stem internode length in response to anoxic soils, thus increasing susceptibility to herbivory (Etherington 1984, Oosterheld and McNaughton 1991; see next section). Although not examined here, the combination of salinity and flooding may also severely impact vegetation by increasing mortality when neither factor alone would cause plant death, and may detrimentally affect subsequent recolonization (McKee and Mendelssohn 1989, Flynn et al. 1995, Howard 1995, Baldwin 1996). Overall, we found that herbivory caused variable reductions in components of

the community rather than an overall decrease in community biomass unless combined with increased flooding or salinity.

Treatments affected relative abundance of dominant species

Increased abiotic stress affects plant community structure directly by killing individuals or preventing germination, and indirectly by providing conditions favorable to certain species and shifting competitive dominance. The latter case may be particularly important if stress tolerance (e.g., of salinity or flooding) involves a trade-off with competitive ability, as documented for several wetland plant species (e.g., Grace and Wetzel 1981, Bertness 1991a,b). *Scirpus americanus* is flood tolerant (Broome et al. 1995) but more susceptible to herbivory (Chabreck et al. 1981, Ford 1996, Gough and Grace 1998) than other brackish marsh species. In flooded sods, *Spartina patens* decreased biomass, perhaps in response to the increase in biomass of *S. americanus*, particularly inside the exclosures. We cannot separate the effects of competition from the inability to tolerate stressful abiotic conditions in this study, but factors such as herbivory or increased water depth may tip the balance towards dominance by one species over another (also see Gough and Grace 1998).

The Fresh marsh dominant species, *Sagittaria lancifolia*, was relatively tolerant of flooding and herbivory. Herbivory did not affect biomass accumulation, probably because nutria and muskrat usually avoid this species (Chabreck et al. 1981). Biomass decreased in both transplant experiments: increased salinity likely restricted growth in the brackish marsh (as seen along natural gradients, Chabreck 1972, Grace and Pugsek 1997, Gough and Grace 1999), but increased dominance by *S. patens* may have suppressed growth of *S. lancifolia* in the fresh marsh. These trade-offs in degree and direction of response by the dominant plant species demonstrate how difficult it is to predict responses of marsh communities to changing abiotic conditions because of both competitive and facilitative interactions (also see Gough and Grace 1999).

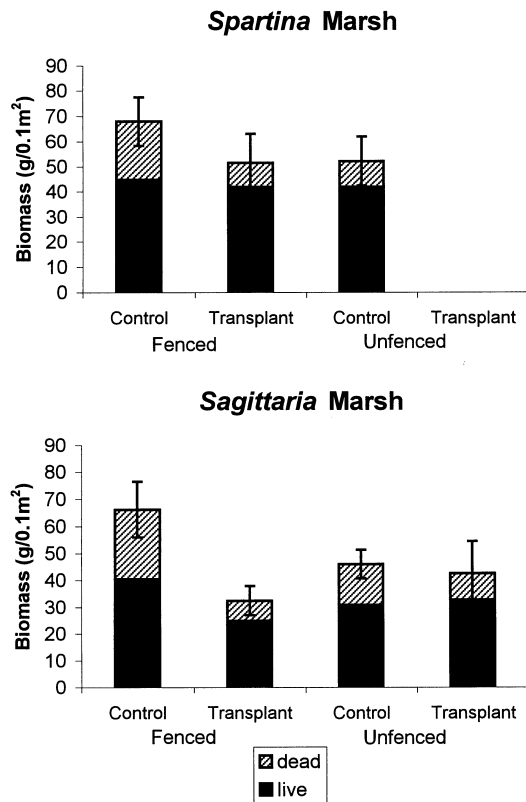


Fig. 5 Community biomass results for the salinity experiment from August 1995 for sods from the *Spartina* marsh and *Sagittaria* marsh. Error bars represent ± 1 SE for total biomass (live + dead)

Table 6 Individual species biomass from salinity experiment. All units are g/0.1 m² for means (1 S.E. (n = 8)). “-” indicates all sods transplanted from the *Spartina* marsh into unfenced areas in the *Sagittaria* marsh were consumed by herbivores

Species	Origin site	Origin site							
		<i>Spartina</i> marsh				<i>Sagittaria</i> marsh			
		Fenced		Unfenced		Fenced		Unfenced	
		Control	Transplant	Control	Transplant	Control	Transplant	Control	Transplant
<i>Scirpus americanus</i>	Live	11.4 ± 3.4	0.1 ± 0.0	5.7 ± 2.9	-				
<i>S. americanus</i>	Dead	13.2 ± 4.1	2.5 ± 1.4	2.4 ± 1.0	-				
<i>Spartina patens</i>	Live	11.3 ± 7.1	27.7 ± 9.8	16.2 ± 4.2	-	14.2 ± 7.0	11.5 ± 3.5	9.2 ± 3.8	20.6 ± 7.5
<i>Sagittaria lancifolia</i>	Live	3.7 ± 2.4	0.8 ± 0.6	3.6 ± 1.8	-	9.7 ± 2.4	7.1 ± 1.0	11.7 ± 1.5	5.9 ± 1.7
<i>S. lancifolia</i>	Dead	2.3 ± 1.1	1.2 ± 1.0	1.3 ± 0.6	-	12.8 ± 2.1	4.9 ± 0.9	8.4 ± 0.8	3.8 ± 1.3

Species more often lost than gained

In general, plant species numbers decrease as abiotic stresses increase along natural gradients (Grime 1979, Keddy 1990, Huston 1994). Nonexperimental studies indicate such a relationship for salinity and flooding gradients in Gulf Coast wetlands (Gough et al. 1994, Grace and Pugsek 1997). Our results show that experimentally increasing these abiotic stressors caused a rapid loss of species as well as decreased biomass. An expected increase in biomass occurred when stresses were ameliorated, reflecting more favorable growing conditions. However, species numbers did not increase under more benign conditions, perhaps because of dispersal limitations (e.g., Marrs et al. 1996) or intensified dominance effects (Tilman 1993, Gough and Grace 1998). The relative importance of these two processes is yet to be determined, but effects on successful colonization will undoubtedly play a central role in community responses to both relative sea level rise and herbivory.

Implications for relative sea level rise

The rate at which species are able to migrate successfully among communities will affect the sustainability of ecosystems such as marshes in response to environmental change. The experiments reported here demonstrate that although coastal species may be adapted to frequently stressful flooding and salinity regimes, the addition of herbivory can further affect plant survival, both directly by creating unfavorable conditions and indirectly by altering the competitive regime and dominance of individual species. Because species drop out of communities more quickly than they re-colonize, we do not know if coastal plants can respond to increased sea level rapidly enough to prevent an overall loss of diversity. Herbivory may preclude the establishment of brackish species in lower salinity marshes as plants are forced to migrate inland by unfavorable flooding and salinity levels at the coast. Because of the additional pressure they place on some plant populations, the effects of herbivores must be taken into consideration when attempting to predict responses of coastal ecosystems to potential global change and current relative sea level rise.

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