

Nutrient Effects on the Composition of Salt Marsh Plant Communities Along the Southern Atlantic and Gulf Coasts of the United States

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ABSTRACT: Nutrient availability is known to mediate plant community structure in many systems, but relatively few studies of nutrient effects have been done in systems where strong gradients in physical stress might constrain the effects of nutrients. Recent studies in New England, United States, salt marshes indicate that nutrients may strongly mediate plant community composition by increasing the competitive ability of stress-tolerant species that are normally displaced by competition to recently-disturbed or low-intertidal habitats. It is unknown whether these results can be generalized to salt marshes in other geographic regions that experience different climates, tidal regimes, and edaphic conditions. To address the generality of these results from New England, we fertilized seven different mixtures of salt marsh plants at study sites on the southeast and Gulf coasts of the U.S. Two of these mixtures were studied in both geographic regions. Consistent with results from New England, fertilization always increased the biomass of the low-marsh dominant *Spartina alterniflora* and usually led to it increasing in dominance at the expense of high-marsh species. Fertilization also led to increased community dominance by *Distichlis*, but only in a mixture where it was already common. Fertilization led to changes in plant dominance patterns in four of the seven types of mixtures that we studied. Results were not a function of edaphic conditions, at least within the range included in our study, and were consistent between the southeastern and Gulf coasts, which experience markedly different tidal regimes. The broad similarity of these results suggests that changes in nutrient input may lead to predictable changes in the composition of similar salt marsh plant communities across large geographic areas despite site to site variation in the abiotic environment.

Introduction

The global nitrogen cycle has been so modified by human activity that more nitrogen is now fixed by human-driven processes than by natural ones (Vitousek 1994). In addition to introducing new nitrogen into ecosystems in the form of fertilizers and sewage, humans also release large amounts of naturally-fixed nitrogen from long-term storage pools through activities such as burning and clearing land (Vitousek 1994). One major symptom of human impact on the global nitrogen cycle is the dramatic and increasing eutrophication of coastal waters (Neilson and Cronin 1981; Howarth 1988; Peierls et al. 1991; Turner and Rabalais 1991; Holligan and Reiners 1992). Estuaries are particularly vulnerable since they concentrate nitrogen inputs from entire watersheds into relatively small systems (Valiela et al. 1992, 1997; Nixon 1995, 1997).

Ecological theory predicts (Tilman 1988; Wish-

eu et al. 1991) and empirical studies have shown that nutrient availability can have strong effects on the diversity and species composition of a variety of terrestrial plant communities (Tilman 1987; Berendse and Elberse 1990; Bobbink 1991; Morris 1991; Theodose and Bowman 1997). Whether these results apply to salt marshes is not immediately obvious, since the strong physical stress gradients of flooding and salinity present in salt marshes (Chapman 1960) might constrain vegetation pattern in spite of nutrient availability. Although many fertilization experiments have been conducted in salt marshes (e.g., Valiela and Teal 1974; Gallagher 1975; Valiela et al. 1978, 1985; Stiling et al. 1991; Van Wijnen and Bakker 1999), most of these studies have focused on monospecific stands, usually of *Spartina alterniflora*, with the goal of evaluating effects on stature and primary production, with the general result that salt marshes are limited by nitrogen, but not by phosphorus. Only a few studies have addressed whether nutrient availability might alter the species composition of salt marsh plant communities (but see Jefferies and Perkins 1977; Covin and Zedler 1988). On the

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Atlantic coast of the United States, a series of studies conducted in New England have either explicitly focused on the community effects of nutrient additions, or have noted such effects in studies primarily focused on monocultures (Valiela et al. 1985; Levine et al. 1998; Emery et al. 2001; Bertness et al. 2002). These researchers found that fertilization typically reverses the competitive hierarchy that creates plant zonation patterns, so that poorer competitors, normally confined by competition to more-stressful, lower elevations or disturbed areas, move up to higher elevations or assume dominance in fertilized plots. Whether these results generalize to other geographic regions is not known; gaining a general understanding of how nutrients affect salt marsh plant communities is an important practical concern for coastal managers. An increased understanding of how nutrients mediate interactions between plants across gradients of non-resource stress is likely to lend new insight into general theories of plant community structure (Tilman 1988; Levine et al. 1998; Emery et al. 2001).

We present results of fertilization experiments conducted in salt marshes on the southeast and Gulf coasts of the U.S. Salt marshes in these two regions experience regimes of climate, flooding, and salinity that differ both from each other and from the northeastern U.S. coast (Pennings and Bertness 2001). Compared to the northeast, both southern regions have a hotter summer, saltier soil, and a milder winter that allows plants to grow nearly year-round, as opposed to seasonally (Turner 1976; Bertness 1999; Pennings and Bertness 1999). The two southern regions differ in that Atlantic coast marshes experience regular, lunar tides of large amplitude (Wiegert and Freeman 1990), whereas Gulf coast marshes experience irregular, climate-driven tides of small amplitude (Stout 1984). The results of field experiments often change as a function of abiotic conditions (Dunson and Travis 1991; Goldberg and Barton 1992; Bertness and Shumway 1993; Bertness and Hacker 1994). A major goal of our study was to test the hypothesis that fertilization would produce similar effects on salt marsh plant communities in different geographic regions, despite marked differences in the abiotic environment.

Materials and Methods

We worked at four study sites. On the southeast coast of the U.S., we worked on Sapelo Island, Georgia (31°27'N, 81°16'W). On the Gulf coast of the U.S., we worked at Point aux Pins, Alabama (30°22'N, 88°18'W), Weeks Bayou, Mississippi (30°24'N, 88°50'W), and Graveline Bayou, Mississippi (30°22'N, 88°40'W). We examined vegetation

mixtures that included the species *Batis maritima*, *Borrhichia frutescens*, *Distichlis spicata*, *Juncus roemerianus*, *Salicornia virginica*, *Scirpus olneyi*, *Scirpus robustus*, *Spartina alterniflora*, and *Spartina patens*. The two species of *Scirpus* were minor components of the vegetation at the Graveline Bayou site only, and were pooled for analysis as *Scirpus* spp. All species other than *S. alterniflora* and *S. patens* will be referred to by their generic names.

Salt marsh vegetation at these study sites commonly occurs in almost monospecific zones, with fairly abrupt borders between zones; areas of mixed vegetation also occur, particularly at Graveline Bayou. The typical zonation pattern in the southeast involves *S. alterniflora* dominating the low marsh and middle marsh, a mixture of meadow species (notably *Batis*, *Distichlis*, and *Salicornia*) dominating the middle marsh at some but not all sites, and *Juncus* and *Borrhichia* dominating the high marsh (Wiegert and Freeman 1990). At Gulf coast sites *S. alterniflora* is typically limited to a smaller portion of the low marsh, and *Juncus* dominates most marsh zones. If present, meadow species typically occur in a break in the *Juncus* zone at middle to high marsh elevations (Stout 1984).

At each site we identified borders between, or mixtures of, plant species common to that site. We located twenty 1 × 1 m (Georgia and Alabama) or 0.5 × 0.5 m (Mississippi) plots along each border or within each mixture, and assigned alternate plots to control and fertilization treatments. At each site we selected the most common vegetation borders or mixtures to study. Because the vegetation differed at each site, we did not fertilize identical mixtures at all sites; we did fertilize *S. alterniflora*-*Juncus* borders in all three states, and *S. alterniflora*-*Distichlis* borders in both Georgia and Alabama. A list of the plant mixtures studied at each site, and associated soil characteristics, are given in Table 1.

Salt marsh vegetation is generally limited by nitrogen rather than phosphorus (Valiela and Teal 1974). Pelletized fertilizer (29% N, 3% P, 4% K) was broadcast into plots by hand at the rate of 60 g m⁻² every 2 wk for the duration of the experiment. This application rate, chosen to be identical to that used by Levine et al. (1998) to facilitate comparison of results, was comparable to previous salt marsh nutrient enrichment studies (Valiela et al. 1985) and never produced signs of burning. Treatments were initiated in May 1996 and ended after two summers in September 1997.

Gas exchange measurements were taken in the summer of 1997 in Georgia and Alabama plots at low tide using an ADC Corporation, Model LCA4 (Dynamax Inc.) open gas exchange system and a portable light source (1.5 mmol m⁻² s⁻¹). Gas ex-

TABLE 1. Vegetation mixtures studied at each site. Species other than those listed for each mixture were rare (< 1% of biomass). General characteristics of soil at each border or mixture are indicated.

Border or Mixture Studied	Marsh Zone	Typical Summer Porewater Salinities (psu)	Bulk Density (g cm ⁻³ , n = 5) mean (SD)	Organic Content (%; n = 5) mean (SD)
Point aux Pins, Alabama				
<i>Spartina alterniflora</i> – <i>Juncus</i> border	Low marsh	~20–35 ¹	0.23 (0.04)	28.2 (6.7)
<i>Spartina alterniflora</i> – <i>Distichlis</i> border	Middle marsh	~30–55 ²	0.41 (0.09)	16.8 (6.0)
<i>Distichlis</i> – <i>Juncus</i> border	Middle marsh	~25–40 ²	0.92 (0.06)	5.2 (1.2)
Sapelo Island, Georgia				
<i>Spartina alterniflora</i> – <i>Juncus</i> border	Low marsh	~25–35 ²	0.54 (0.20)	11.1 (4.3)
<i>Spartina alterniflora</i> – <i>Distichlis</i> border	Middle marsh	~25–50 ²	0.72 (0.18)	8.1 (4.7)
<i>Spartina alterniflora</i> – <i>Borrichia</i> border	Middle marsh	~20–40 ²	1.14 (0.16)	2.8 (0.9)
<i>Spartina alterniflora</i> – <i>Salicornia</i> border	Middle marsh	~40–55 ²	0.75 (0.04)	8.6 (0.2)
<i>Borrichia</i> – <i>Juncus</i> – <i>Batis</i> mixture	High marsh	~25–50 ²	0.98 (0.15)	4.2 (1.4)
Weeks Bayou, Mississippi				
<i>Spartina alterniflora</i> – <i>Juncus</i> border	Low marsh	~20–30 ³	0.32 (0.06)	21.2 (4.4)
Graveline Bayou, Mississippi				
<i>Distichlis</i> – <i>Spartina patens</i> – <i>Juncus</i> – <i>Scirpus</i> spp. mixture	High marsh	~15–25 ³	0.57 (0.15)	12.1 (4.8)

¹ Stanton unpublished data.

² Pennings unpublished data.

³ Brewer unpublished data.

change measurements of any given species within a particular border or mixture were completed on a single day so that fertilizer effects could be examined for a particular species. Time and logistic constraints required that different species and different mixtures or borders be sampled on different days.

The central 0.5 × 0.5 m (Georgia, Alabama) or 0.25 × 0.25 m (Mississippi) of each plot was harvested in September 1997. We measured the height of the tallest individual of each species in each plot. Live plants were sorted to species and dried to a constant mass. Mass data from all sites were converted to units of g 0.25 m⁻² for analysis and presentation. Only aboveground biomass was measured, so results must be interpreted with the caveat that there were likely also changes in allocation patterns and belowground biomass following fertilization.

We measured the organic content and bulk densities of the soils at all sites by taking cores (10 cm deep) adjacent to experimental plots at each site in April 1999. Organic content was determined by loss on ignition. Bulk density was calculated as sediment dry mass (g)/volume of core (cm³).

In cases for which the same mixture of species was studied in multiple states, results were compared with ANOVA, with fertilization treatment and state as main effects. If particular mixtures were studied only in one state, fertilized and control plots were compared with 2-sample *t*-tests. Proportions were arcsine (square root) transformed before analysis.

Results

The fertilization treatment led to shifts in the species composition of some, but not all, plant mixtures. Results from similar plant mixtures were generally consistent between states, despite the large differences in the physical environment between southeast and Gulf coast marshes.

Fertilization of *S. alterniflora*–*Juncus* borders led to similar results in all three states (Fig. 1) despite 2-fold differences among states in bulk density and organic content of soils (Table 1). *S. alterniflora* biomass increased several-fold in fertilized plots. Fertilization significantly increased *S. alterniflora* height (the magnitude of the increase was less in Mississippi than in other states, leading to a significant treatment × state interaction) and showed a marginally-significant (*p* = 0.06) trend towards increasing photosynthetic rates. In fertilized plots, biomass of *Juncus* decreased strongly in Georgia (the state in which *S. alterniflora* attained the greatest mass), was unaffected in Alabama, and increased slightly in Mississippi, leading to a significant treatment × state interaction. Fertilization showed a slight but marginally significant (*p* = 0.054) trend towards increasing *Juncus* height, but had no effect on photosynthetic rates. Because of the large increase in *S. alterniflora* biomass coupled with the decrease or modest increase in *Juncus* biomass, the community composition of the plots shifted away from dominance by *Juncus* and towards dominance by *S. alterniflora*, although the intensity of this shift differed among sites (Fig. 1).

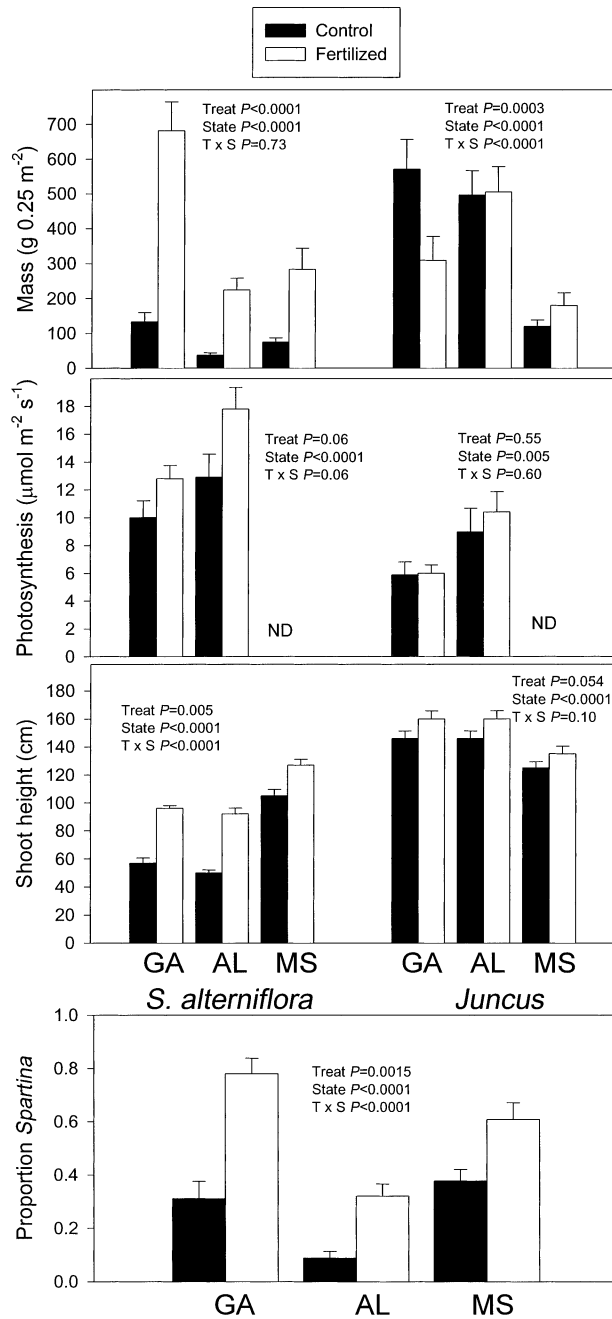


Fig. 1. *Spartina alterniflora*-*Juncus* mixtures. Biomass, photosynthetic rates, and shoot heights of both species, and proportion of the biomass represented by *S. alterniflora* in control and fertilized plots in Georgia, Alabama, and Mississippi. Data are means of 10 plots treatment⁻¹ ± SE.

Fertilization of *S. alterniflora*-*Distichlis* borders (Alabama) or mixtures (Georgia) led to several-fold increases in *S. alterniflora* biomass in both Georgia and Alabama (Fig. 2), despite large differences in soil bulk density and organic content between the two states. The effect of fertilizer on *S.*

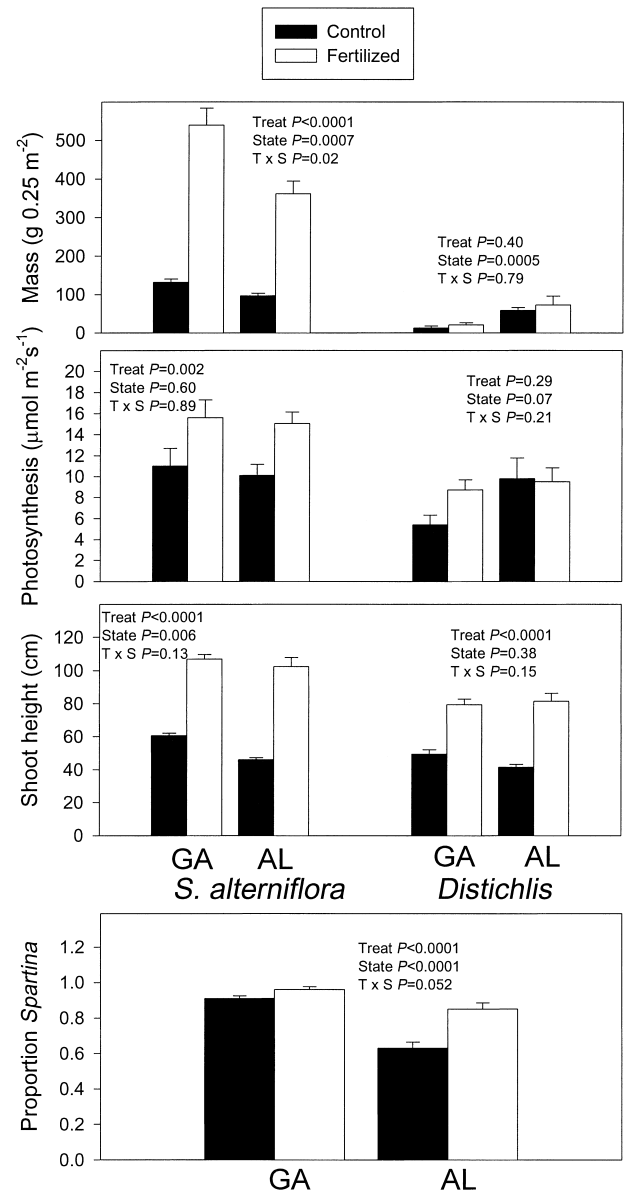


Fig. 2. *Spartina alterniflora*-*Distichlis* mixtures. Biomass, photosynthetic rates, and shoot heights of both species, and proportion of the biomass represented by *S. alterniflora* in control and fertilized plots in Georgia and Alabama. Data are means of 10 plots treatment⁻¹ ± SE.

alterniflora biomass was slightly greater in Georgia than in Alabama, leading to a significant treatment × state interaction. Fertilization increased *S. alterniflora* height and photosynthetic rates. Fertilization increased *Distichlis* height, but had no effect on mass or photosynthetic rates. Community composition in both states shifted towards greater dominance by *S. alterniflora* in fertilized plots, although this effect was modest on a percentage basis since

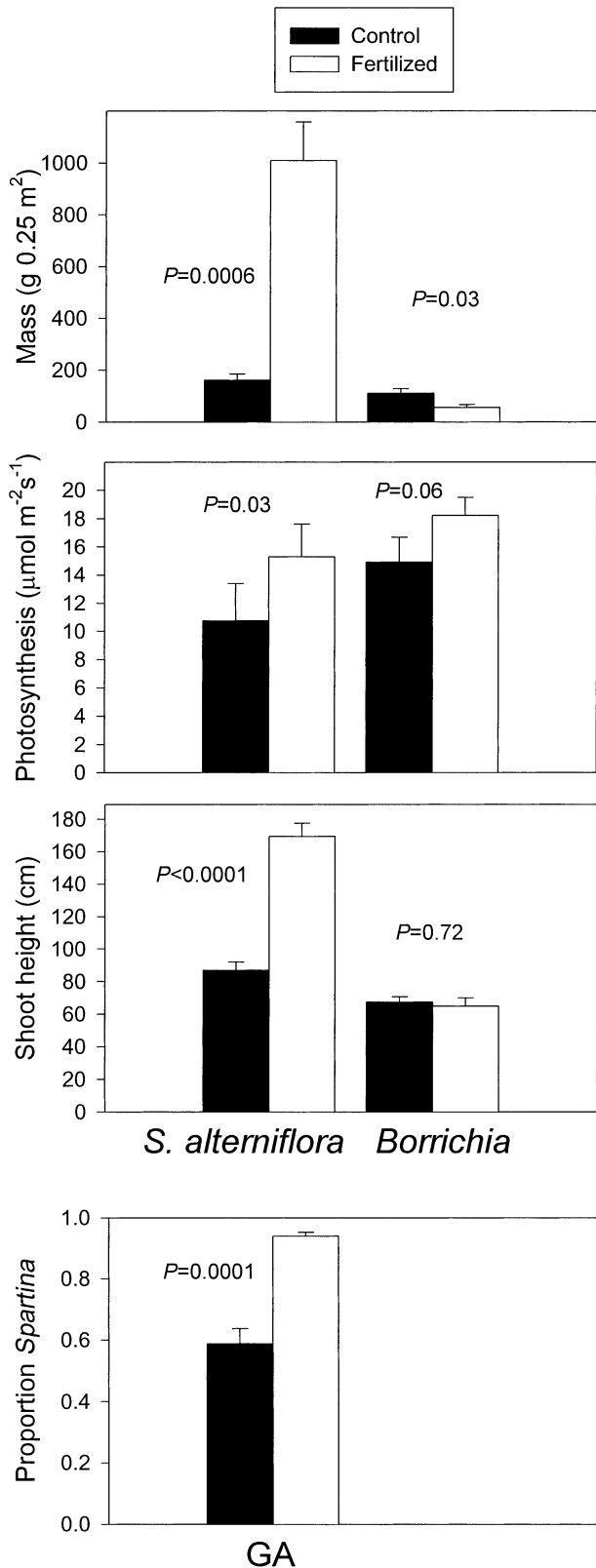


Fig. 3. *Spartina alterniflora*-*Borrighia* mixtures. Biomass, photosynthetic rates, and shoot heights of both species, and pro-

S. alterniflora already dominated the biomass of these mixtures.

Fertilization of *S. alterniflora*-*Borrighia* borders in Georgia led to several-fold increases in *S. alterniflora* biomass (Fig. 3). Fertilization increased *S. alterniflora* height and photosynthetic rates. Fertilization reduced *Borrighia* biomass, had a marginally significant ($p = 0.06$), positive effect on *Borrighia* photosynthetic rates, and had no effect on *Borrighia* height. Community composition in fertilized plots shifted from co-dominance to strong dominance by *S. alterniflora*.

Fertilization of *S. alterniflora*-*Salicornia* borders in Georgia increased biomass and height of both species, but had no effect on photosynthetic rates of either (Fig. 4). Community composition did not differ between fertilized and control plots.

Fertilization of *Borrighia*-*Juncus*-*Batis* mixtures in Georgia led to a striking increase of *Batis* in several replicate plots; however, since only some plots contained *Batis*, results were highly variable and this increase was not significant (Fig. 5). Gas exchange measurements and shoot heights of *Batis* were not taken because *Batis* was initially a minor component of the plant community in these plots and the strength of its increase was not recognized until after plots were harvested. *Borrighia* biomass was not affected by fertilization, but photosynthetic rates and height declined. *Juncus* biomass, photosynthetic rates, and shoot height did not differ between fertilized and control plots. Representation of *Juncus* (the most abundant species) showed a moderate but non-significant ($p = 0.08$) decline in fertilized plots.

Fertilization of *Distichlis*-*Juncus* borders in Alabama increased photosynthetic rates of *Distichlis*, but had no effect on biomass or height of either species (Fig. 6). Community composition did not differ significantly between fertilized and control plots.

Fertilization of mixed-species plots in Mississippi led to an increase in biomass of *Distichlis*, which was initially the most abundant species in the plots, and to a decrease in biomass of *Scirpus* spp., but did not affect biomass of *S. patens* or *Juncus* (Fig. 7). Fertilization did not affect heights of any species. Fertilization led to an increase in dominance of this community by *Distichlis*.

Discussion

Our results indicate that the addition of nutrients often leads to shifts in the composition of salt

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portion of the biomass represented by *S. alterniflora* in control and fertilized plots in Georgia. Data are means of 10 plots treatment⁻¹ ± SE.

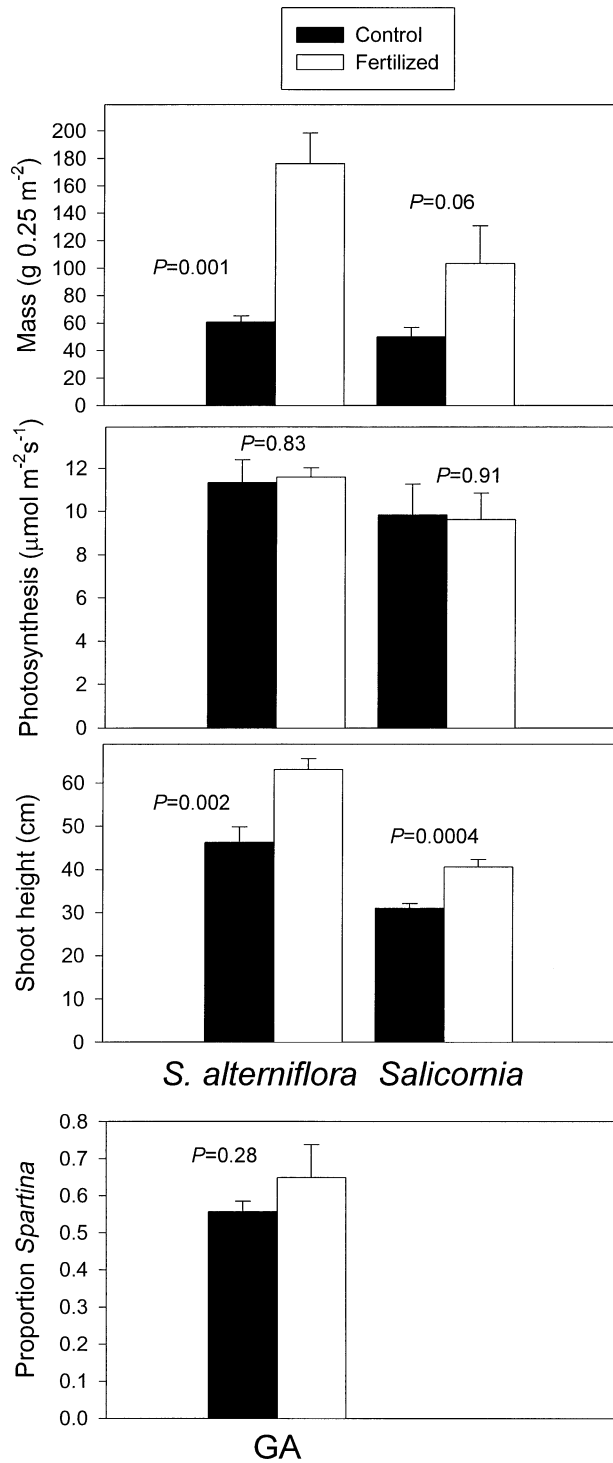


Fig. 4. *Spartina alterniflora*-*Salicornia* mixtures. Biomass, photosynthetic rates, and shoot heights of both species, and proportion of the biomass represented by *S. alterniflora* in control and fertilized plots in Georgia. Data are means of 10 plots treatment⁻¹ ± SE.

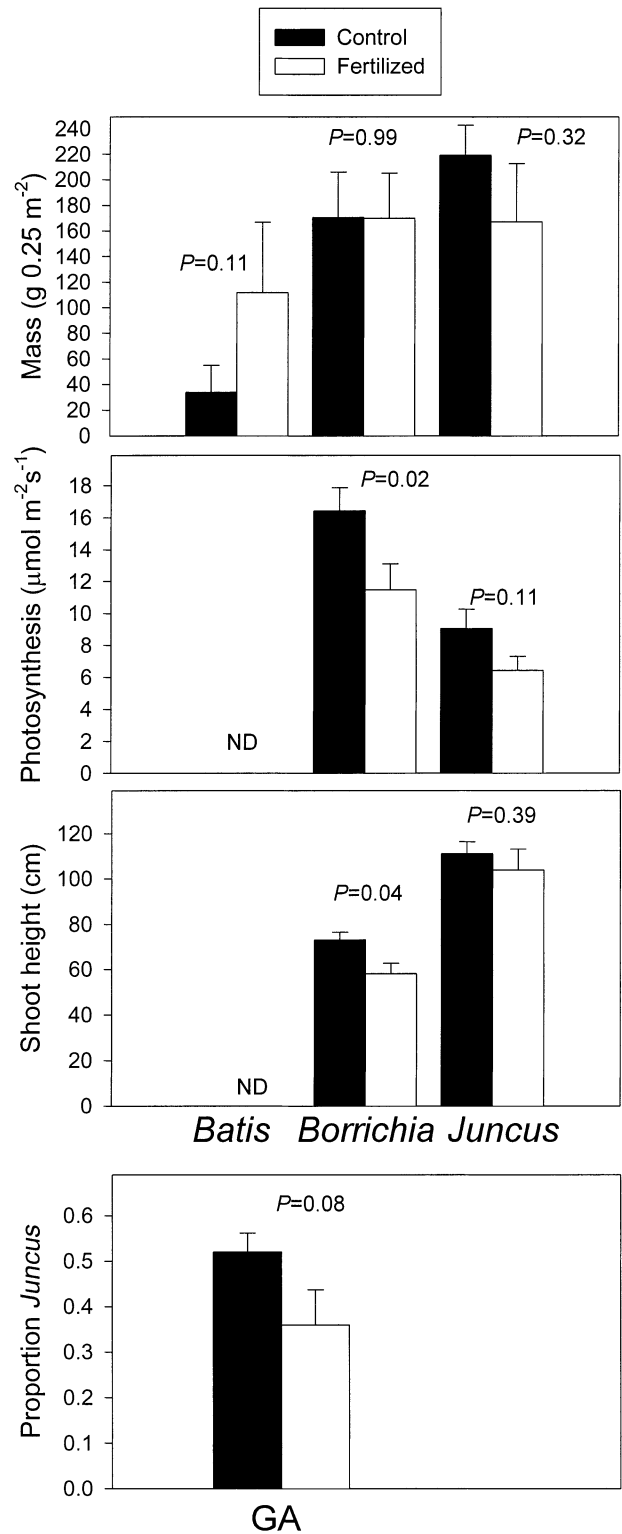


Fig. 5. *Borrichia*-*Juncus*-*Batis* mixtures. Biomass, photosynthetic rates, and shoot heights of each species, and proportion of the biomass represented by *Juncus* in control and fertilized plots in Georgia. Data are means of 10 plots treatment⁻¹ ± SE.

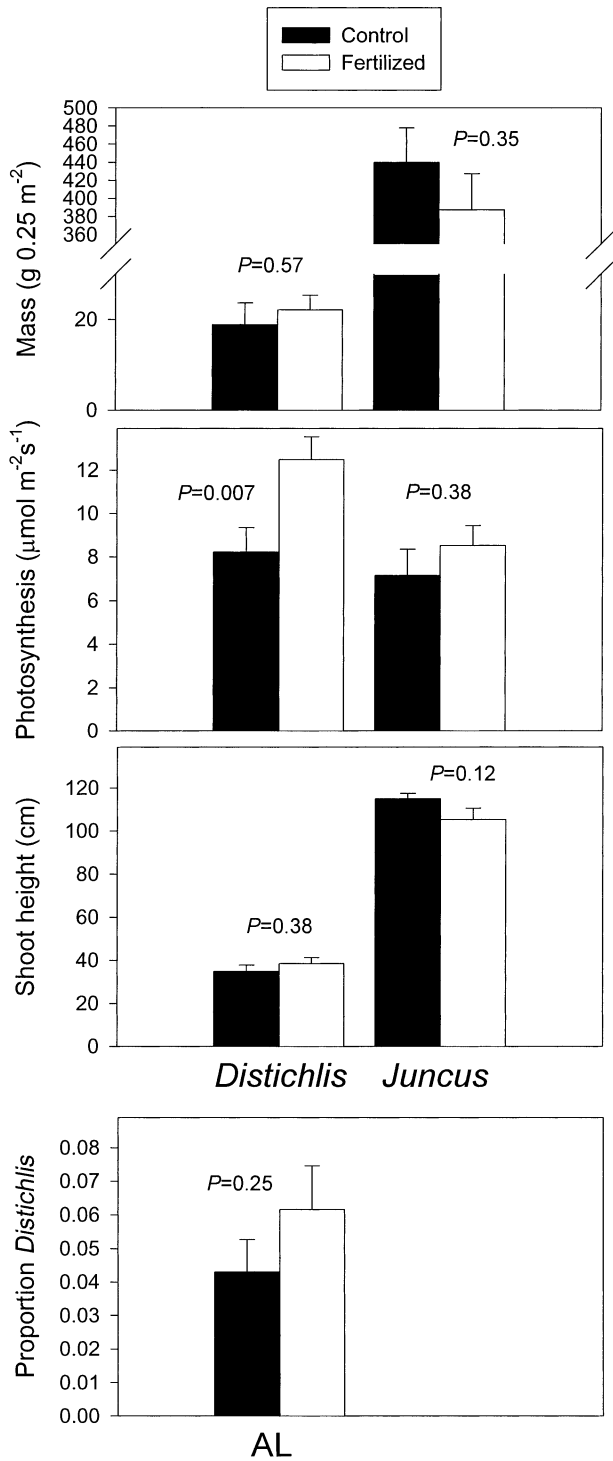


Fig. 6. *Distichlis-Juncus* mixtures. Biomass, photosynthetic rates, and shoot heights of each species, and proportion of the biomass represented by *Distichlis* in control and fertilized plots in Alabama. Data are means of 10 plots treatment⁻¹ ± SE.

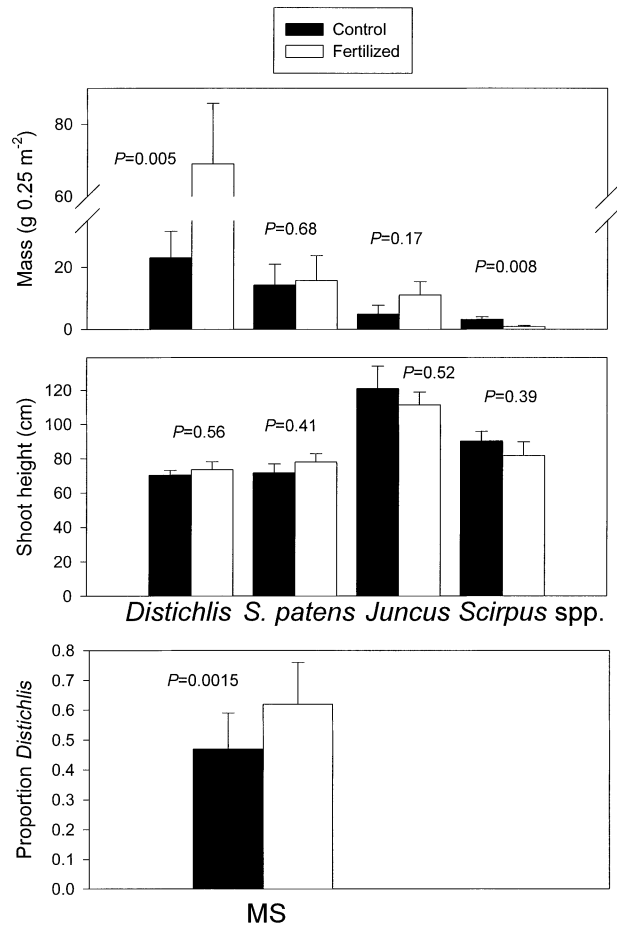


Fig. 7. *Distichlis-Spartina patens-Juncus-Scirpus* spp. mixtures. Biomass and shoot heights of each species, and proportion of the biomass represented by *Distichlis* in control and fertilized plots in Mississippi. Data are means of 10 plots treatment⁻¹ ± SE.

marsh plant communities in the southern U.S. This result was strongly driven by the striking response of *S. alterniflora* to nutrient additions, and communities that do not contain *S. alterniflora* may be less affected. Our results were broadly consistent with results for northeastern U.S. marshes (Valiela et al. 1985; Levine et al. 1998; Emery et al. 2001; Bertness et al. 2002), suggesting that, if the plant composition is similar between geographic regions, community responses to eutrophication may also be similar across regions despite marked differences in the physical environment. A general result of eutrophication may be increased dominance of salt marshes by *S. alterniflora* at the expense of other plant species.

Emery et al. (2001) found that the community effects of fertilization in New England salt marshes were consistent across a gradient of physical stress despite strong edaphic differences across this gra-

dient. We found no relationship between soil traits or hydrology and the response of plant communities to fertilization. The mixtures that were least responsive to fertilizer additions (*Borrichia-Juncus-Batis* and *S. alterniflora-Salicornia* in Georgia, *Distichlis-Juncus* in Alabama) were not unique as a group in terms of porewater salinity, although the *S. alterniflora-Salicornia* border had the highest salinities of any of the mixtures. The three non-responsive mixtures tended to have relatively high bulk densities (0.75–0.98) and low organic contents (4.2–8.6%) but these values were within the range of values of the mixtures that did respond to fertilization. Our results were broadly similar to previous results from New England despite large differences in climate, soil organic content, and salinity between northern and southern marshes (Pennings and Bertness 1999, 2001). Our study sites did not span the full range of variability in edaphic conditions that occurs in salt marsh habitats, and our comparisons across edaphic conditions are partially confounded with differences in species composition. Although we conclude that nutrients can affect salt marsh plant communities over a wide range of edaphic conditions, we cannot rule out the possibility that differences in edaphic conditions may explain some proportion of the variance in how strongly the community responds, particularly under more extreme edaphic conditions.

The most consistent result of our experiments was a strong increase in *S. alterniflora* biomass in fertilized plots, which occurred in 7 of 7 cases. In 6 of 7 cases, *S. alterniflora* also increased in proportional dominance of the plots. The one exception (*S. alterniflora-Salicornia* borders) involved the saltiest plots, and relatively short, low-biomass stands of *S. alterniflora*. It may be that *S. alterniflora* was limited in its ability to respond to nutrients under these salty conditions, and so was unable to significantly increase its dominance over *Salicornia*. It may also be that the duration of the experiment was not long enough to allow *S. alterniflora* biomass to accumulate in these plots to a level high enough to have a competitive effect on *Salicornia*. Regardless of the mechanism, these results suggest the possibility that the impact of nutrients on salt marsh vegetation may be muted under extremely hypersaline conditions where plant biomass is strongly limited by physical stress. Our ability to evaluate this hypothesis was limited in the current study because none of the other mixtures we examined occurred on strongly hypersaline soils. Working in a southern California U.S. marsh, Covin and Zedler (1988) found that adding nutrients increased the ability of *S. virginica* to compete with *Spartina foliosa*, supporting the hypothesis that

Spartina spp. may not be able to take advantage of added nutrients in high-salinity environments.

The response of *Distichlis* to nutrient enrichment varied depending upon initial conditions. When paired with *S. alterniflora* or *Juncus*, *Distichlis* failed to increase in fertilized plots; in the more diverse mixture at Graveline Bayou, *Distichlis* increased in mass several-fold in fertilized plots. One interpretation of these results is that *Distichlis* was only able to increase following fertilization if it already represented a substantial proportion of the biomass in the plot. When paired with *S. alterniflora* or *Juncus*, *Distichlis* represented only a minor proportion of the biomass in the plots, and may have been unable to increase in mass enough to gain a competitive advantage over its taller competitors. Similar results occurred in long-term, sewage-sludge addition plots maintained by Valiela and colleagues (Hersh 1996) in New England marshes, where *Distichlis* only increased following fertilization if it was already common in a plot. Results from New England indicating that *Distichlis* typically increases following fertilization (Levine et al. 1998; Emery et al. 2001) may have been a function of the relatively short stature of the perennial turfs in New England marshes (*S. patens* and *Juncus gerardi*), which are similar in height to *Distichlis* (Emery et al. 2001). In southern marshes, *Distichlis* more often co-occurs with much taller perennials (*S. alterniflora* and *J. roemerianus*), with which it may be unable to compete as effectively, regardless of nutrient levels; however, associated plants at Graveline Bayou were similar in height to *Distichlis* (Fig. 7).

The high-marsh dominants *Juncus* and *Borrichia* consistently failed to benefit from nutrient enrichment in our experiments, and often significantly decreased in parallel with biomass increases of other species. These results suggest that these species are likely to consistently decrease in abundance following anthropogenic eutrophication of coastal sites. A possible explanation for these results lies in the benefit that nitrogen additions provide to plants in salt marsh habitats. Salt marsh soils often contain abundant nitrogen, but the ability of plants to use this nitrogen can be limited, particularly in more flooded habitats, both directly by physical stressors, such as salinity and sulfides, and indirectly by the need to divert nitrogen into physiological mechanisms for dealing with physical stress (Mendelssohn 1979; Mendelssohn et al. 1982). Consequently, plant species which live in higher, less-flooded marsh elevations may experience less of a benefit from nitrogen additions than do plants such as *S. alterniflora* and *D. spicata*, which are typical of more flooded habitats.

Marshes in New England, the southeast coast, and the Gulf coast of the U.S. differ markedly in

climate, tidal range, soil salinity, and soil type (Pennings and Bertness 1999, 2001). Differences in the abiotic environment often lead to different outcomes of experimental studies (Moloney 1990; Dunson and Travis 1991; Goldberg and Barton 1992; Bertness and Shumway 1993; Bertness and Hacker 1994). Our results show several parallels with previous results from northeastern marshes. Studies in New England (Levine et al. 1998; Emery et al. 2001; Bertness et al. 2002) and our study found that *S. alterniflora* benefited from increased nutrient supply, although this result may be reversed over the long term if fertilization increases soil accumulation and turns low-marsh habitats into high-marsh habitats (Hersh 1996). Our results also corroborated New England results that *Distichlis* benefits from increased nutrients (Valiela et al. 1985; Hersh 1996; Levine et al. 1998; Emery et al. 2001), but only if it initially is common and is competing with other plants of similar stature. Although our study did not have any additional species in common with previous studies in New England, these first two parallels are encouraging in that they suggest that the responses of given species to nutrient additions are likely to be consistent between geographic regions. Our results provide cautious support for the conclusion that eutrophication allows low-marsh species to expand at the expense of high-marsh species (Levine et al. 1998; Emery et al. 2001). In every case in which our study found a clear winner between species that differ in elevational range (*S. alterniflora* > *Juncus*, *S. alterniflora* > *Distichlis*, *S. alterniflora* > *Borrichia*), fertilization favored the low-marsh species. Since the low-marsh winner was always *S. alterniflora*, it is unclear whether this result reflects a more general trend that would generalize to marshes elsewhere in the world that lack *S. alterniflora*. We add the caveat that the changes in dominance observed following fertilization in many of our mixtures were not as dramatic as those that were previously reported from New England. For example, although *S. alterniflora* increased in proportional dominance in *S. alterniflora*-*Juncus* mixtures in all three states, only in Georgia was the increase in *S. alterniflora* accompanied by a decrease in biomass of *Juncus*. Although *S. alterniflora* also increased in proportional dominance in mixtures with both *Distichlis* and *Borrichia*, only *Borrichia* showed parallel decreases in biomass. Fertilization experiments in New England consistently showed one species increasing and the other decreasing in biomass following fertilization (Levine et al. 1998; Emery et al. 2001). It may be that competitive displacement takes longer in the south because of the larger sizes of the plants and the longer growing season compared to the north. Some of the details of

plant nutrient relations and competitive interactions may differ between geographic regions for reasons that have yet to be determined.

Our results suggest that, along both the Atlantic and Gulf coasts of the U.S., eutrophication is likely to lead to salt marshes becoming increasingly dominated by *S. alterniflora*. Where *Distichlis* is already common, it too is likely to increase and to dominate high-marsh sites. On the southeast coast, where *S. alterniflora* already dominates salt marshes, eutrophication should lead to increasing community dominance by this species. On the Gulf coast, where *Juncus* typically dominates marshes, eutrophication may lead to a more even mixture of *S. alterniflora* and *Juncus*. These changes will interact with other effects of eutrophication documented elsewhere, such as increases in dominance by *Phragmites* (Bertness et al. 2002) and impacts on biogeochemistry and sedimentation (Hersh 1996; Morris and Bradley 1999). How these changes will affect marsh trophic interactions and function, and how short term effects will translate into long-term effects, is poorly known. These are important topics for future work.

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