

## EFFECTS OF NUTRIENT ENRICHMENT ON *DISTICHLIS SPICATA* AND *SALICORNIA BIGELOVII* IN A MARSH SALT PAN

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**Abstract:** We investigated how nutrient addition affects the abundance, nutrient storage, and competition between *Distichlis spicata* and *Salicornia bigelovii*, two dominant species in salt pans of Northern Gulf of Mexico marshes. Namely, we compared fertilized and unfertilized plots in monospecific areas colonized respectively by *D. spicata* or *S. bigelovii*, and in a mixed area colonized by the two species. Nutrient addition generally increased the aboveground biomass and percent cover of the two species, and those increases were moderate to large in relation to the increases found for other marsh plant species. Nutrient addition also generally decreased the carbon:nitrogen and carbon:phosphorus ratios of aboveground and belowground tissues of the two species. Our results provide evidence that, under enhanced nutrient availability, *D. spicata* is a superior competitor over *S. bigelovii* in the mixed zone of the salt pan where the two species grow together. However, we did not detect large changes in biomass dominance by *D. spicata* following fertilization, possibly because the experiment only lasted 10 months. Our results suggest that nutrient addition, by increasing the structural complexity of the leaf canopy and the nutritional quality of plant tissues for first-order consumers, may enhance the value of salt pans as habitat for organisms

**Key Words:** competition, eutrophication, Gulf of Mexico, nutrient storage

### INTRODUCTION

Plant community structure in salt marshes is affected by competition for light and nutrients and stress induced by varying flooding frequency and salinity levels (Bertness 1991, Pennings and Callaway 1992, Levine et al. 1998, Emery et al. 2001). Ecological theory suggests that the interaction between competitive success and stress tolerance defines the niche for many plant species (Grime 1979, Wilson and Keddy 1986). For example, in the harsh environment of a marsh salt pan, characterized by low rates of tidal recharge and high evaporation rates, clonal plants coexist with non-

clonal succulent plants. Clonal plants have rhizomes and therefore should better compete for nutrients. However, succulent plants store water in their leaves and thus may be more tolerant to water stress. Clonal and non-clonal plants in marsh salt pans utilize different strategies of growth, water conservation, and nutrient storage.

As human populations continue to grow and alter coastal watersheds, the delivery of nutrients into coastal marshes also increases (Valiela et al. 1992, Nixon 1995). This phenomenon, known as anthropogenic eutrophication, is one of the most pervasive human-induced stressors in coastal ecosystems world-wide (Jackson et al. 2000, Tilman et al. 2001). Previous research has examined how increased nutrient availability affects marsh plants, but few studies have focused on the species that

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grow in salt pans (Valiela *et al.* 1975, Jefferies and Perkins 1977, Covin and Zedler 1988). Salt pans provide a good setting to test the effects of increased nutrient availability on interactions between co-occurring species with different competitive abilities and stress tolerance. It is also of importance to examine whether salt pans, by partially absorbing nutrient inputs from the surrounding watershed, can moderate the impacts of anthropogenic eutrophication on coastal waters (Stout 1984, Tobias *et al.* 2001b, Mitsch and Gosselink 2007).

Here we focus on *Distichlis spicata* and *Salicornia bigelovii*, two plant species that co-occur abundantly in salt pans of the Northern Gulf of Mexico. *Distichlis spicata* is a perennial clonal plant that occupies the seaward zone of the salt pan and spreads vegetatively through runners (Bertness 1991). Salt glands, leaf morphology, and water reallocation via rhizomes are all thought to play a role in *D. spicata*'s salt tolerance (Hansen *et al.* 1976, Alpert 1990). *Salicornia bigelovii* is usually situated upland of the *D. spicata* zone and thrives in the salt pan environment through succulence (Stout 1984). Like other annual *Salicornia* species, *S. bigelovii* colonizes bare areas by spreading seeds (Ungar 1987, Alexander and Dunton 2002). In many salt pans, as the one studied in this paper, a mixed zone where the two species grow together can be found.

Our goals were to evaluate the effects of nutrient addition on the abundance, nutrient storage and competition between *D. spicata* and *S. bigelovii* in a marsh salt pan in the Northern Gulf of Mexico. We expected that nutrient addition, by relieving nutrient limitation, would promote plant abundance and nutrient accumulation as plant biomass. We also expected that *D. spicata*, owing to its higher storage capacity and perennial life cycle, would be a superior competitor under enhanced nutrient availability.

## METHODS

### Study Site

The salt pan studied is part of a larger marsh community located in the Northern Gulf of Mexico at Point Aux Pins, Bayou le Batre, Alabama, USA (30°22'28" N, 88°18'52" W). The lower marsh is dominated by *Juncus roemerianus*, with a band of *Spartina alterniflora* at the water edge. The *J. roemerianus* zone gives way to an extensive salt pan at the upper edge of the marsh that borders maritime pine forest. There are three distinct zones in the salt pan studied. Lowest in the salt pan, a stand of *D. spicata* borders the *J. roemerianus* zone. Higher in the salt pan, *D. spicata* becomes mixed

with *S. bigelovii* to then give way to a stand of *S. bigelovii* highest in the salt pan that fringes the upland maritime forest.

### Experimental Design

Within each of the three zones (i.e., monospecific *D. spicata*, mixed *D. spicata*-*S. bigelovii*, and monospecific *S. bigelovii*) we fertilized six plots and left six more unfertilized (controls). We paired the plots in each zone to minimize the influence of environmental patchiness within the zone, with each pair having one fertilized and one control plot selected randomly. Plots were 1 × 1 m<sup>2</sup> and separated 2 m from each other within a pair. Adjacent pairs were 10 m apart.

To fertilize the plots, we applied 56 g nitrogen (N) m<sup>-2</sup> every two weeks from early October to late November 2003, and from early February to mid April 2004. Based on measurements taken before starting the experiment, we estimated this addition would increase the ambient N concentration in the soil porewater approximately seven-fold, which reflects a realistic level of human-induced nutrient enrichment in coastal marshes while not being large enough to produce ammonium toxicity (Levine *et al.* 1998, Valiela *et al.* 2000, 2001). In addition, and also based on the same preliminary measurements, we applied 7 g phosphorus (P) m<sup>-2</sup> simultaneously with the N in order to reach an atomic N:P ratio in the porewater of the fertilized plots that approximated the ratio found in the tissues of marsh plants (mean value of 16:1; Wetzel 1983, Thorman and Bayley 1997). Thus, this procedure represents a realistic, stoichiometrically balanced N and P enrichment. Nutrients were added by hand-casting NH<sub>4</sub>NO<sub>3</sub> and P<sub>2</sub>O<sub>5</sub>. In April 2004, a few months before concluding the experiment, we stopped fertilizing the plots because we found incipient signs of deleterious impacts due to overfertilization (e.g., necrotic or yellow leaf tips). Nevertheless, we continued to find increased nutrient concentrations in the porewater of fertilized plots in relation to control plots for the remainder of the experiment (see results).

### Variables Measured

Sediment porewater was collected in each plot five times over the course of the experiment (October and November 2003; March, April, and June 2004) from wells made of 2.5 cm-diameter PVC pipe with mesh-covered holes in the lower 10 cm of the pipe. At the beginning of the experiment, one well was secured 15 cm into the sediment at the center of each plot and left in place throughout the duration of the

experiment. On each sampling date, the porewater within the well was pumped out with a syringe into acid-washed plastic vials and stored on ice. Upon return to the laboratory, all samples were filtered through 25 mm Whatman GF/F filters and frozen until analysis for nitrite ( $\text{NO}_2^-$ ), nitrate ( $\text{NO}_3^-$ ), ammonium ( $\text{NH}_4^+$ ), and phosphate ( $\text{PO}_4^+$ ), which was conducted following standard wet chemical techniques (Strickland and Parsons 1972) modified for the Skalar SAN<sup>+</sup> Autoanalyzer.

In November 2003 and July 2004 we measured above- and belowground plant biomass in each plot (grams dry weight  $400\text{ cm}^{-2}$ ) by haphazardly tossing a  $20 \times 20\text{ cm}^2$  quadrat in the plot once and harvesting all enclosed above- and belowground material. Samples were returned to the laboratory and washed over a sieve. For each of the two species, plant tissue was separated into above- and belowground components and dried at  $90^\circ\text{C}$  for a minimum of 48 hours.

Percent plant cover was estimated from early October through late November 2003 and again from early February through late June 2004. To estimate percent plant cover, a  $1 \times 1\text{ m}^2$  quadrat was divided into 25 equal subquadrats, the quadrat was placed over each plot, and plant dominance within each subquadrat was visually estimated. The subquadrat was considered to be dominated by a species if the species occupied  $> 50\%$  of the subquadrat area. Thus, each subquadrat was categorized as “dominated by *D. spicata*”, “dominated by *S. bigelovii*”, or “unvegetated”. From the number of subquadrats in each category, values of percent cover for the entire  $1 \times 1\text{ m}^2$  quadrat were calculated for the given species in monospecific plots and for each species in mixed plots (i.e., percent cover by a species in a plot = (number of subquadrats dominated by the species/total number of subquadrats)  $\times 100$ ). This technique may underestimate percent plant cover (i.e., subquadrats where no species covered  $> 50\%$  of the area were considered unvegetated) and it can only detect relatively large changes in percent plant cover (e.g., a change from 10% to 40% cover by a species in a subquadrat is not recorded). However, these limitations did not affect the conclusions reached in this study (see first paragraph in discussion section).

Carbon:nitrogen (C:N) and carbon:phosphorus (C:P) atomic ratios in the above- and belowground components of each species were measured four times during the course of the experiment: October and November 2003 and April and July 2004. We haphazardly collected three individuals of each species from each plot on each date and separated the above- and belowground components. In turn,

aboveground *S. bigelovii* was separated into succulent young stems (fleshy cortex tissue that is green or red in color) and the woody cork layer (Fahn and Arzee 1959, Boyer et al. 2001). Plant tissues were dried at  $90^\circ\text{C}$  for a minimum of 48 hours and ground using a Wiley Mill. A Carlo Erba Auto Analyzer (NA1500 N/C/S) and Costech Elemental Combustion System (ECS 4010 CHNS-O Analyzer) were used to determine C:N ratios. Phosphorus concentrations were determined by measuring the phosphorus-specific absorbance of the samples in a Shimadzu UV-160 spectrophotometer (Strickland and Parsons 1972, Solorzano and Sharp 1980, Fourqurean et al. 1992). To derive C:P ratios, P concentrations were combined with the C concentrations obtained with the Carlo Erba Auto Analyzer and Costech Elemental Combustion System.

#### Data Analysis

We repeatedly sampled the same plants for our measurements of percent cover. In addition, the plants sampled for biomass and nutrient content at different times, particularly for *D. spicata*, could have been connected and corresponded to the same genet (i.e., genetic individual). Thus, we used three-way repeated measures ANOVA to analyze the data. To confirm that nutrient concentrations in the sediment porewater were higher for fertilized than for control plots, we ran three-way repeated measures ANOVA with treatment (fertilized or control plots) and zone (*D. spicata* monospecific, *S. bigelovii* monospecific, or mixed) as the between-subject factors and time as the within-subject factor. To examine the effects of nutrient addition on the abundance and nutrient storage in *D. spicata* and *S. bigelovii*, we ran three-way repeated measures ANOVA for each species separately with treatment and zone (monospecific or mixed) as between-subject factors and time as the within-subject factor. To examine the effects of nutrient addition on the competition between the two species, we ran three-way repeated measures ANOVA with treatment and species (*D. spicata* or *S. bigelovii*) as the between-subject factors and time as the within-subject factor.

Normality was evaluated using normal probability plots and the Shapiro-Wilk statistic (Zar 1999). Homogeneity of variance was determined using Levene's test. Data were log transformed to meet the above requirements except for percent cover data which were arcsine transformed. In addition, Mauchly's criterion was used to confirm that sphericity, a requirement of repeated measures analysis, was met (Crowder and Hand 1990). All

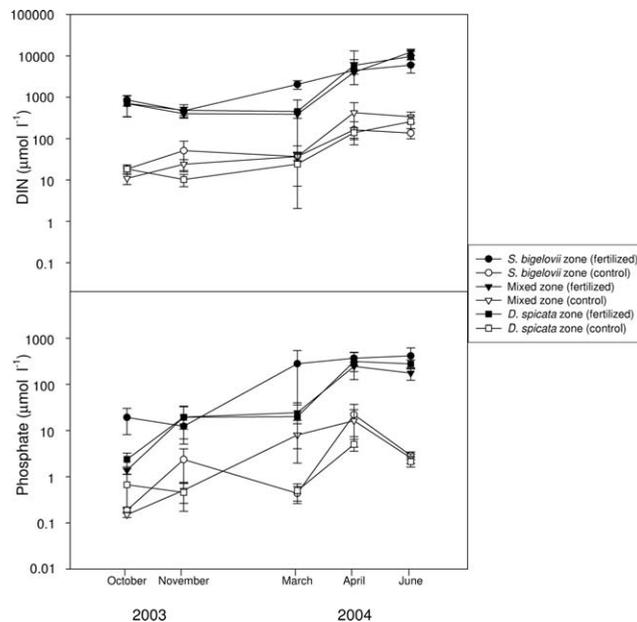


Figure 1. Mean ( $\pm$  SE) porewater dissolved inorganic nitrogen (DIN) and phosphate concentrations.

statistical analyses were done using SYSTAT 10 and JMP 5.0.1 and results were considered significant at  $p < 0.05$ .

## RESULTS

### Fertilization

For both control and fertilized plots, N and P concentrations in the sediment porewater were higher during the last stage than at the beginning of the experiment (Figure 1;  $P < 0.05$  for main time effect,  $P \geq 0.05$  for interaction term between treatment and time), probably due to little rainfall from March 2004 through the end of the experiment. Regardless of this temporal trend, sediment porewater N and P concentrations were higher in the fertilized than in the control plots throughout the experiment ( $P < 0.05$  for main treatment effect), thereby demonstrating that we successfully enriched the fertilized plots.

### Effects of Fertilization on the Abundance and Nutrient Storage by *D. spicata* and *S. bigelovii*

**Biomass.** *Salicornia bigelovii* aboveground biomass did not differ between control and fertilized plots at the beginning of the experiment. Fertilized plots showed higher *S. bigelovii* aboveground biomass than control plots at the end of the experiment, and that increase was much larger in the monospecific than in the mixed zone (Figure 2,  $P < 0.05$  for interaction term between treatment, zone, and time).

*Salicornia bigelovii* belowground biomass did not differ between fertilized and control plots at the beginning of the experiment. At the end of the experiment, fertilized plots showed higher *S. bigelovii* belowground biomass than control plots, but only in the monospecific zone (Figure 2,  $P < 0.05$  for interaction term between treatment, zone, and time).

*Distichlis spicata* aboveground biomass did not differ between control and fertilized plots at the beginning of the experiment, but was higher in fertilized plots at the end of the experiment (Figure 2,  $P < 0.05$  for interaction term between treatment and time). The increase in *D. spicata* aboveground biomass with fertilization was similar in the monospecific and mixed zones ( $P \geq 0.05$  for interaction term between treatment and zone). In contrast, nutrient addition did not increase the belowground biomass of *D. spicata* (Figure 2,  $P \geq 0.05$  for all nutrient effects).

**Percent Cover.** During the middle stages of the experiment, nutrient addition increased the percent cover of *S. bigelovii* in the monospecific zone, but not in the mixed zone (Figure 3,  $P < 0.05$  for interaction term between treatment, zone, and time). Specifically, *S. bigelovii* covered 100% of the ground in control and fertilized plots in the monospecific zone at the beginning of the experiment. One month later senescence began and *S. bigelovii* covered ca. 90% of the ground in both types of plots. We resumed percent cover measurements in February 2004 and, from that date through mid April 2004, fertilized plots had higher *S. bigelovii* percent cover values than control plots in the monospecific zone (one post-hoc comparison between control and fertilized plots for each of those sampling dates,  $P < 0.05$  for all comparisons). From May 2004 to the end of the experiment, control and fertilized plots in the monospecific zone showed similar *S. bigelovii* percent cover. We did not find any significant differences in *S. bigelovii* percent cover between control and fertilized plots in the mixed zone.

Fertilized plots showed higher *D. spicata* percent cover than control plots from mid March to early April 2004 in the mixed zone (Figure 3,  $P < 0.05$  for interaction term between treatment, zone, and time; one post-hoc comparison between control and fertilized plots for each of those sampling dates,  $P < 0.05$  for all comparisons). Control and fertilized plots in the monospecific zone featured ca. 100% *D. spicata* cover throughout the duration of the experiment.

**Carbon:Nitrogen Ratio.** The Carbon:Nitrogen (C:N) ratio of the succulent tissue of *S. bigelovii*

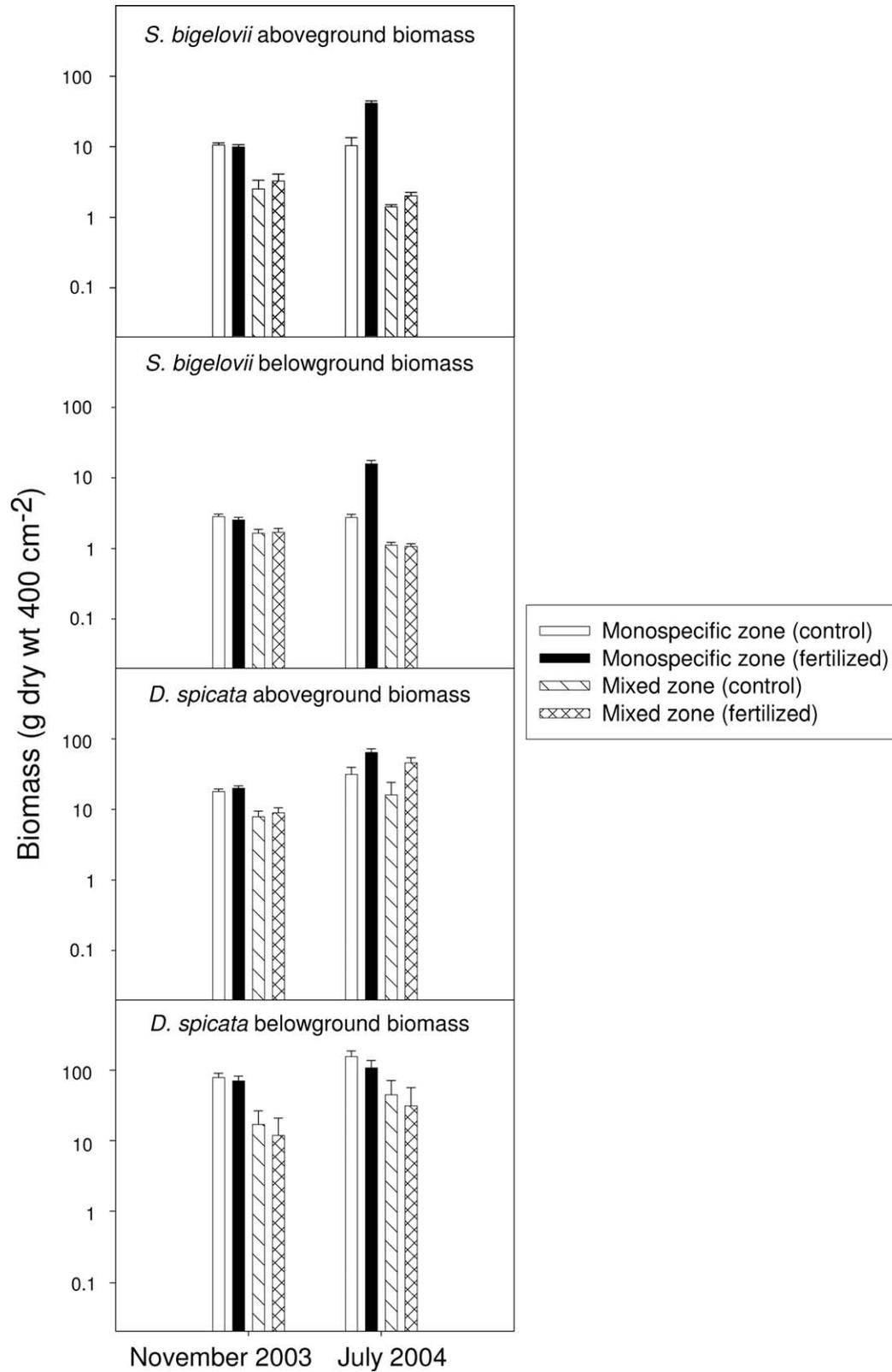


Figure 2. Mean ( $\pm$  SE) above- and belowground biomass of *Salicornia bigelovii* and *Distichlis spicata*.

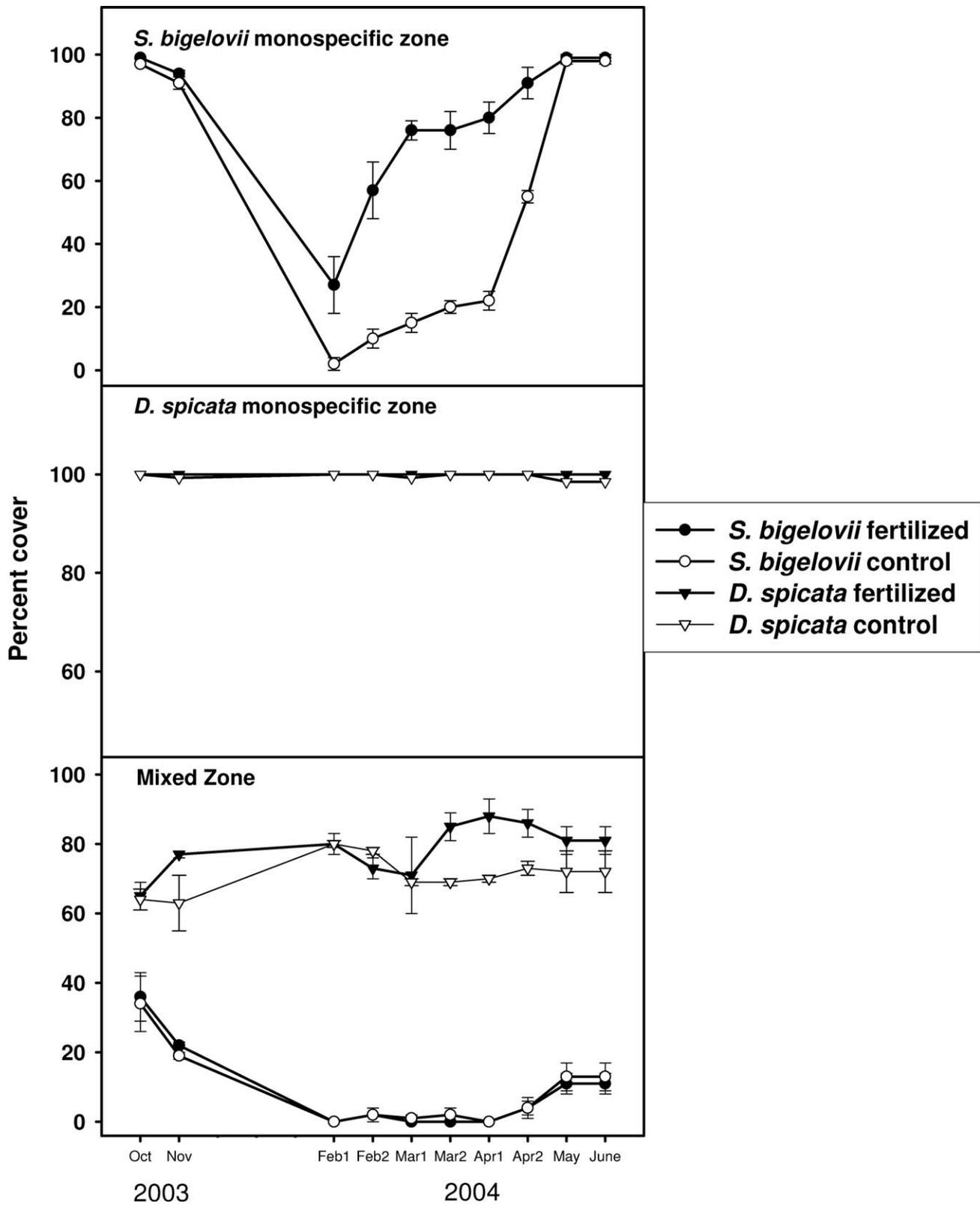


Figure 3. Mean ( $\pm$  SE) percent cover of *Salicornia bigelovii* and *Distichlis spicata*. In February, March and April 2004 percent cover was measured twice per month.

did not differ between fertilized and control plots on the first two sampling dates (October and November 2003, Figure 4), but the ratio was lower in the fertilized plots on the last two sampling dates (April and July 2004;  $P < 0.05$  for interaction term between treatment and time,  $P < 0.05$  for the post-hoc comparisons between control and fertilized plots in April and July 2004,  $P \geq 0.05$  for the post-hoc comparisons in October and November 2003). The decrease in the ratio due to fertilization was similar in the monospecific and mixed zones ( $P \geq 0.05$  for interaction term between treatment and zone).

We could only analyze the C:N ratios in *S. bigelovii* woody tissue in October and November 2003 because sufficient woody tissue had not yet formed by April and May 2004. We did not find a significant impact of nutrient addition for that restricted data set (Figure 4,  $P \geq 0.05$  for all fertilization effects). We did not sample enough *S. bigelovii* belowground tissue for nutrient analysis in mixed plots in July 2004. For the other three sampling dates, lower C:N ratios were found in fertilized than in control plots (Figure 4;  $P < 0.05$  for main fertilization effect,  $P \geq 0.05$  for interaction term between treatment and time). That decrease was similar in the monospecific and mixed zones ( $P \geq 0.05$  for interaction term between treatment and zone).

Nutrient addition decreased the C:N ratio of *D. spicata* aboveground tissue, and that decrease was greater as the experiment progressed (Figure 4;  $P < 0.05$  for interaction term between treatment and time). In addition, the decrease was greater in the mixed than in the monospecific zone ( $P < 0.05$  for interaction term between treatment and zone). Nutrient addition decreased the C:N ratio of *D. spicata* belowground tissue to a similar extent throughout the experiment (Figure 4;  $P < 0.05$  for main fertilization effect,  $P \geq 0.05$  for interaction term between treatment and time) and in monospecific and mixed plots ( $P \geq 0.05$  for interaction term between treatment and zone).

**Carbon:Phosphorus Ratio.** Nutrient addition did not have any significant impacts on the C:P ratios of *S. bigelovii* succulent or woody tissues (Figure 5,  $P \geq 0.05$  for all fertilization effects). However, *S. bigelovii* belowground tissues showed lower C:P ratios in fertilized than in control plots in October and November 2003, and that decrease was greater in the monospecific than in the mixed zone in October 2003, but vice-versa in November 2003 (Figure 5,  $P < 0.05$  for interaction term between treatment, zone, and time).

Nutrient addition decreased the C:P ratio of *D. spicata* aboveground tissues to a similar extent

throughout the experiment (Figure 5;  $P < 0.05$  for main fertilization effect,  $P \geq 0.05$  for interaction term between treatment and time), and that decrease was similar in the monospecific and mixed zones ( $P \geq 0.05$  for interaction term between treatment and zone). Nutrient addition also decreased the C:P ratio of *D. spicata* belowground tissues throughout the experiment, but only in the mixed zone (Figure 5;  $P < 0.05$  for the interaction term between treatment and zone).

#### Effects of Fertilization on the Competition between *D. spicata* and *S. bigelovii*

**Biomass.** *Distichlis spicata* reached a higher aboveground and belowground biomass than *S. bigelovii* in the mixed zone (Figure 2). By the end of the experiment, fertilization seemed to have increased aboveground biomass to a greater extent for *D. spicata* than for *S. bigelovii* in that zone. That observation, however, was not significant ( $P < 0.05$  for main fertilization effect,  $P \geq 0.05$  for interaction term between treatment, species, and time). Nutrient addition did not have any significant effects on the belowground biomass of either species in the mixed zone (Figure 2,  $P \geq 0.05$  for all treatment effects).

**Percent cover.** *Distichlis spicata* had higher percent cover than did *S. bigelovii* in the mixed zone (Figure 3). When comparing the impact of nutrient addition on the percent cover by the two species in the mixed zone, we found no effect on *S. bigelovii* and an apparent, nearly significant increase in the percent cover by *D. spicata* from mid March to early April 2004 (Figure 3;  $P = 0.057$  for interaction term between treatment, species, and time).

**Carbon:Nitrogen Ratio.** Nutrient addition decreased the C:N ratios of the aboveground (succulent for *S. bigelovii*) tissues of *D. spicata* and *S. bigelovii* in the mixed zone, with that decrease being almost significantly higher for the former than for the latter species (Figure 4;  $P < 0.05$  for main fertilization effect,  $P = 0.052$  for interaction term between treatment and species). Nutrient addition also decreased the C:N ratios of the belowground tissues of *D. spicata* and *S. bigelovii* in the mixed zone (comparison only includes October 2003, November 2003, and April 2004), and the extent of the decrease was similar in the two species (Figure 4;  $P < 0.05$  for main fertilization effect,  $P \geq 0.05$  for interaction term between treatment and species).

**Carbon:Phosphorus Ratio.** When comparing the two species in the mixed zone, we found no effect

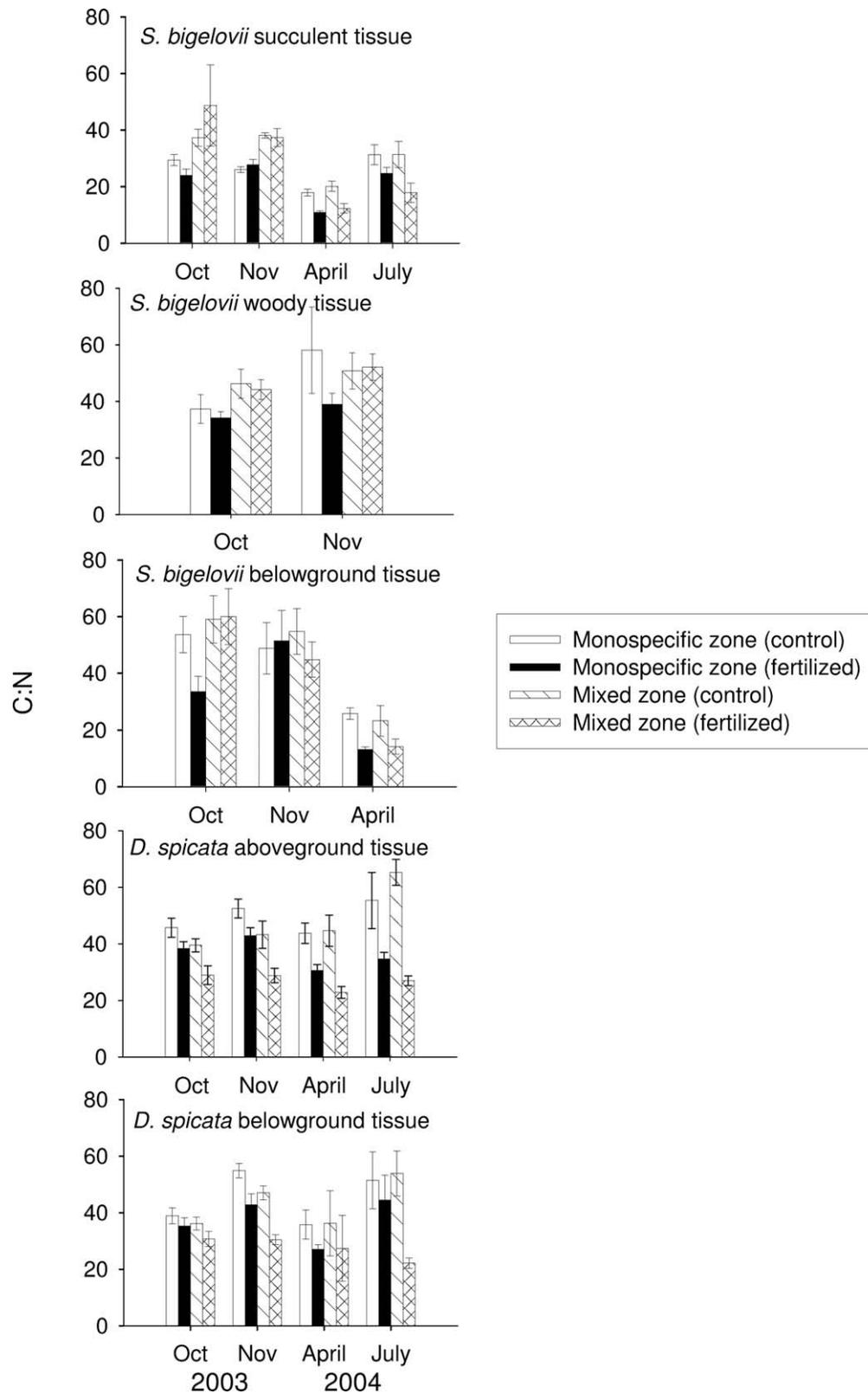


Figure 4. Mean ( $\pm$  SE) C:N ratios in *Salicornia bigelovii* and *Distichlis spicata*. Woody tissue of *S. bigelovii* had not yet formed in April and July 2004. We did not sample enough *S. bigelovii* belowground tissue for nutrient analysis in mixed plots in July 2004.

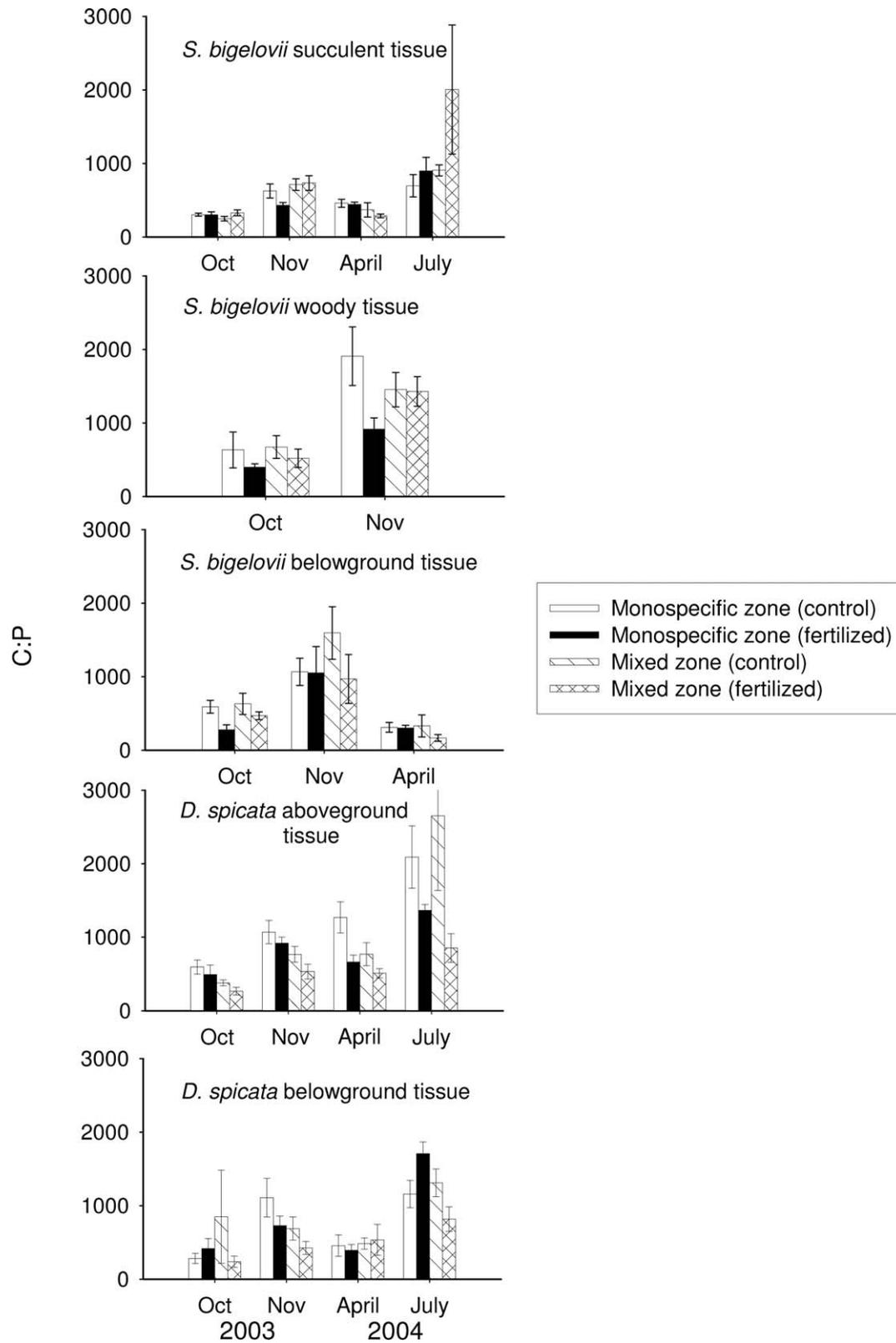


Figure 5. Mean ( $\pm$  SE) C:P ratios in *Salicornia bigelovii* and *Distichlis spicata*.

of nutrient addition on the C:P ratio of *S. bigelovii* succulent tissues, but an apparent, nearly significant decrease in the C:P ratio of *D. spicata* aboveground tissues, (Figure 5,  $P = 0.069$  for interaction term between treatment and species). Despite the significant effects of fertilization on the belowground C:P ratios found for the two species when analyzed separately, fertilization did not have any significant effects on these ratios when the two species were analyzed concomitantly in the mixed zone (Figure 5, comparison only includes October 2003, November 2003, and April 2004;  $P \geq 0.05$  for all treatment effects).

### DISCUSSION

As expected, nutrient addition often increased the aboveground biomass and percent cover of *S. bigelovii* and *D. spicata* in the marsh salt pan studied. We also found that nutrient addition generally decreased the carbon:nitrogen and carbon:phosphorus ratios of *D. spicata* and *S. bigelovii*. The only exceptions were the C:N ratios and C:P ratios of *S. bigelovii* woody tissue, and the C:P ratios of *S. bigelovii* succulent tissue, which remained unaffected by fertilization. Our measurements of percent cover may be underestimates and do not detect small changes. These limitations, however, do not affect our conclusions. It is clear that fertilization only increased *D. spicata* cover in mixed plots, since the species already covered 100% of the ground in monospecific plots. Fertilization could have somewhat increased *S. bigelovii* cover in mixed plots, but our results demonstrate that such a potential increase would certainly have been lower than the increase in *S. bigelovii* cover in monospecific plots and in *D. spicata* cover in mixed plots.

Increases in aboveground biomass due to fertilization were not observed in November 2003, probably because plants senesce in the fall and only one month had elapsed since the onset of fertilization. In accordance with our results, Boyer *et al.* (2001) began fertilizing *Salicornia virginica* in the fall and did not find an impact until the following spring. The only increase in belowground biomass due to fertilization was for *S. bigelovii* in the monospecific zone. We may not have found an increase in *D. spicata* belowground biomass under enhanced nutrient availability because rhizomes may absorb and concentrate extra nutrients for aboveground translocation rather than developing new belowground biomass and diluting the nutrients (Pitelka and Ashmun 1985, Silvertown and Lovett-Doust 1993).

We compiled data from the literature to compare the increases in aboveground plant biomass due to nutrient addition found here with the results of other fertilization experiments in marsh habitats (Table 1). The compilation includes many plant species, elevations (i.e., low, middle, and high marsh), and geographical areas. Increases found in our salt pan varied from moderate to large in relation to changes reported in other studies, as indicated by the ratio of fertilized to unfertilized mean aboveground biomass. In relation to the other ratios in Table 1, the ratios for *D. spicata* in the monospecific zone and for *S. bigelovii* in the mixed zone were intermediate (i.e., approximately 50% of the ratios compiled lie below those two ratios), and the ratios for *D. spicata* in the mixed zone and for *S. bigelovii* in the monospecific zone were high (i.e., approximately 85% of the ratios compiled lie below those two ratios). In general, these two species showed ratios similar to or higher than most other species, except for species known to respond quickly to nutrient addition such as *Spartina alterniflora* (Levine *et al.* 1998, Pennings *et al.* 2002).

As it could be expected based on its rhizomatous structure and perennial life cycle, our experiment suggests *D. spicata* is a superior competitor for nutrient uptake and storage under enhanced nutrient availability. This is based on two results. First, the aboveground C:N ratio and the belowground C:P ratio of *D. spicata* decreased with nutrient addition to a greater extent in mixed plots than they did in monospecific plots. This indicates that, when *D. spicata* grew in the company of *S. bigelovii*, it absorbed and stored nutrient inputs to a greater extent than it did when growing in the monospecific stand. Second, it appears that nutrient addition to the mixed zone may decrease at times the aboveground C:N and C:P ratios to a greater extent for *D. spicata* than for *S. bigelovii*.

Sustained higher rates of nutrient uptake and storage for *D. spicata* than for *S. bigelovii* in the mixed zone under fertilized conditions should have led to an increase in the biomass dominance of the former over the latter species. Accordingly, 10 months after starting our experiment, the increase in aboveground biomass in mixed plots due to nutrient addition seemed to be larger for *D. spicata* than for *S. bigelovii*, although that observation was not statistically significant. Some of our other results also suggest that *D. spicata* is a superior competitor under enhanced nutrient availability and, given enough time, should outgrow *S. bigelovii*. For instance, fertilization did increase at times the cover of *D. spicata*, but never increased the cover of *S. bigelovii*, in the mixed zone. *Salicornia bigelovii* only

Table 1. The ratio of increase in aboveground biomass with fertilization (biomass in fertilized conditions/biomass in control conditions) in marsh plants. All experiments were done in the field and encompassed at least one growing season. The ratio has been calculated with the mean peak biomass under fertilized and unfertilized conditions at the end of the growing season. Fertilized and unfertilized plots were open to grazers in all experiments. Marsh type (MT) corresponds to monocultures (m) or mixed plots (M). Nutrients refer to the specific nutrients added to the fertilized plots. Other abbreviations and symbols are: RU: Russia; SE: Sweden; UK: United Kingdom; USA: United States of America; NL: The Netherlands; HD: High Dosage; LD: Low Dosage; \*: mean for 1993 and 1994; \*\*: mean for 1971, 1972 and 1973; °: short form; °°: tall form.

Species	Location	Nutrients	MT	Ratio	Reference
<i>Armeria maritima</i>	Stiffkey, Norfolk, UK	N (NH <sub>4</sub> )	M	0.77	Jefferies and Perkins 1977
		N (NO <sub>3</sub> )	M	0.77	
		P	M	1.54	
		N (NH <sub>4</sub> )	M	0.96	
		N (NO <sub>3</sub> )	M	0.60	
<i>Batis maritima</i>	Sapelo Island, Georgia, USA	P	M	0.92	
		NPK	M	3.39	Pennings et al. 2002
		NPK	M	0.42	Pennings et al. 2002
		NPK	M	0.99	
<i>Carex subspathacea-Puccinellia phryganodes</i>	Kolokolkova Bay, Tobseba, RU	NPK	M	0.83	Van der Graaf et al. 2007
		NPK	M	2.83	Pennings et al. 2002
<i>Distichlis spicata</i>	Graveline Bayou, Mississippi, USA	NPK	m	1.93	This work
		NP (NH <sub>4</sub> NO <sub>3</sub> ; P <sub>2</sub> PO <sub>5</sub> )	M	2.91	
<i>Festuca rubra</i>	Rhode Island (Rumstick Cove), New England, USA	NPK	M	1.40	Pennings et al. 2002
		NPK	M	1.28	
		NPK	m	2.36*	Levine et al. 1998
		NPK	M	4.30*	
		NPK	M	2.87*	
	Rhode Island (Nag Cove East), New England, USA	NPK	m	1.97	Emery et al. 2001
		NPK	M	5.88	
		NPK	m	3.45	Emery et al. 2001
		NPK	M	2.98	
		NPK	M	2.00	Pennings et al. 2002
<i>Juncus gerardi</i>	Rhode Island (Nag Cove East), New England, USA	NPK	m	1.00	Van der Graaf et al. 2007
		NPK	m	1.00	Van der Graaf et al. 2007
		NPK	m	1.06*	Levine et al. 1998
		NPK	M	0.44*	
		NPK	M	0.98*	
<i>Festuca rubra</i>	Rhode Island (Nag Cove East), New England, USA	NPK	m	1.03	Emery et al. 2001
		NPK	M	0.49	
		NPK	M	0.51	
		NPK	m	0.84	Emery et al. 2001
<i>Juncus gerardi</i>	Rhode Island (Nag Cove West), New England, USA	NPK	M	0.02	
		NPK	M	0.88	

Table 1. Continued.

Species	Location	Nutrients	MT	Ratio	Reference
<i>Juncus roemerianus</i>	Graveline Bayou, Mississippi, USA	NPK	M	2.00	Pennings et al. 2002
	Point aux Pins, Alabama, USA	NPK	M	1.02	Pennings et al. 2002
<i>Limonium vulgare</i>	Sapelo Island, Georgia, USA	N (NH <sub>4</sub> NO <sub>3</sub> )	m	0.89	Gallagher 1975
		NPK	M	0.56	Pennings et al. 2002
	Weeks Bayou, Mississippi, USA	NPK	M	0.75	Pennings et al. 2002
		N (NH <sub>4</sub> )	M	2.24	Jefferies and Perkins 1977
	Stiffkey, Norfolk, UK	N (NO <sub>3</sub> )	M	1.67	
		P	M	1.26	
		N (NH <sub>4</sub> )	M	1.26	
		N (NO <sub>3</sub> )	M	2.17	
		N (NO <sub>3</sub> )	M	2.33	
		P	M	0.97	
<i>Plantago maritima</i>	Stiffkey, Norfolk, UK	N (NH <sub>4</sub> )	M	1.11	Jefferies and Perkins 1977
		N (NO <sub>3</sub> )	M	1.30	
		P	M	0.59	
<i>Polygonum punctatum</i>	East Pearl River, Louisiana, USA	NPK	M	3.95	Gough and Grace 1997
		N (NH <sub>4</sub> )	M	2.00	Jefferies and Perkins 1977
<i>Puccinellia maritima</i>	Stiffkey, Norfolk, UK	N (NO <sub>3</sub> )	M	2.00	
		P	M	0.67	
<i>Sagittaria lancifolia</i>	East Pearl River, Louisiana, USA	NPK	M	1.43	Gough and Grace 1997
		NPK	M	1.66	Gough and Grace 1998
<i>Salicornia bigelovii</i>	Middle Pearl River, Louisiana, USA	NPK	M	1.69	Gough and Grace 1998
		NP (NH <sub>4</sub> NO <sub>3</sub> ; P <sub>2</sub> PO <sub>5</sub> )	m	3.96	This work
<i>Salicornia virginica</i>	Point aux Pins, Alabama, USA	NPK	M	1.38	
		NPK	M	2.02	Pennings et al. 2002
<i>Scirpus americanus</i>	Sapelo Island, Georgia, USA	N	M	1.47	Covin and Zedler 1988
		NPK	M	1.20	Gough and Grace 1998
<i>Scirpus</i> spp.	East Pearl River, Louisiana, USA	NPK	M	0.33	Pennings et al. 2002
		NPK	M	7.50	Pennings et al. 2002
<i>Spartina alterniflora</i>	Point aux Pins, Alabama, USA	NPK	M	3.60	
		NPK	m	2.17*	Levine et al. 1998
<i>Scirpus americanus</i>	Rhode Island (Rumstick Cove), New England, USA	NPK	M	2.34*	
		NPK	m	1.85	Emery et al. 2001
<i>Scirpus americanus</i>	Rhode Island (Nag Cove East), New England, USA	NPK	M	7.00	
		NPK	m	2.25	Emery et al. 2001
<i>Scirpus americanus</i>	Rhode Island (Nag Cove West), New England, USA	NPK	M	4.42	
		N (NH <sub>4</sub> NO <sub>3</sub> )	m	1.70°	Gallagher 1975
<i>Scirpus americanus</i>	Sapelo Island, Georgia, USA	NPK	m	2.58°	
		NPK	m	1.19°°	
<i>Scirpus americanus</i>	Weeks Bayou, Mississippi, USA	NPK	M	5.23	Pennings et al. 2002
		NPK	M	4.12	
<i>Scirpus americanus</i>	Weeks Bayou, Mississippi, USA	NPK	M	6.00	
		NPK	M	2.85	
<i>Scirpus americanus</i>	Weeks Bayou, Mississippi, USA	NPK	M	3.73	Pennings et al. 2002
		NPK	M		

Table 1. Continued.

Species	Location	Nutrients	MT	Ratio	Reference
<i>Spartina alterniflora</i> -( <i>Salicornia</i> spp.)	Great Sippewissett, Massachusetts, USA	HD NPK	M	3.69**	Valiela et al. 1975
<i>Spartina foliosa</i>	Tijuana Estuary, California, USA	LD NPK	M	2.31**	Covin and Zedler 1988
		N	m	1.56	
			M	1.08	
<i>Spartina patens</i>	East Pearl River, Louisiana, USA	NPK	M	1.26	Gough and Grace 1997
			M	3.00	Gough and Grace 1998
	Graveline Bayou, Mississippi, USA	NPK	M	1.15	Pennings et al. 2002
	Middle Pearl River, Louisiana, USA	NPK	M	1.08	Gough and Grace 1998
	Rhode Island (Rumstick Cove), New England, USA	NPK	m	2.00*	Levine et al. 1998
			M	0.69*	
			M	1.94*	
			M	0.92*	
	Rhode Island (Nag Cove East), New England, USA	NPK	m	1.20	Emery et al. 2001
			M	6.22	
			M	0.38	
	Rhode Island (Nag Cove West), New England, USA	NPK	m	2.02	Emery et al. 2001
			M	10.02	
			M	0.81	
<i>Spartina patens</i> - <i>Distichlis spicata</i>	Great Sippewissett, Massachusetts, USA	HD NPK	M	2.27**	Valiela et al. 1975
		LD NPK	M	2.20**	
<i>Triglochin maritima</i>	Stiffkey, Norfolk, UK	N (NH <sub>4</sub> )	M	0.67	Jefferies and Perkins 1977
		N (NO <sub>3</sub> )	M	0.67	
		P	M	1.33	

Table 2. Changes in nitrogen (N) storage from September 2003 to July 2004. Samples of plant biomass and C:N ratios were also obtained in September 2003 before the start of fertilization. Nitrogen storage was calculated by multiplying mean biomass ( $\text{gDW m}^{-2}$ ) times the mean ratio of N per DW. Geometric means were used in these calculations. The change in storage was then expressed as a percentage of the total quantity of N applied throughout the experiment ( $504 \text{ g N m}^{-2} 6 \text{ month}^{-1}$ ). The belowground compartment of *Salicornia bigelovii* in the mixed area was not considered due to insufficient sampling for nutrient analysis.

Plant tissue and marsh zone	g N $\text{m}^{-2}$ September	g N $\text{m}^{-2}$ July	Change in N storage	Percentage of added N retained as plant biomass
<i>S. bigelovii</i> succulent tissue (monospecific zone)	0.36	7.61	7.25	1.4
<i>S. bigelovii</i> belowground tissue (monospecific zone)	0.06	3.65	3.59	0.7
<i>D. spicata</i> aboveground tissue (monospecific zone)	4.36	14.60	10.24	2.0
<i>D. spicata</i> belowground tissue (monospecific zone)	20.72	25.24	4.52	0.9
<i>S. bigelovii</i> succulent tissue (mixed zone)	0.14	0.67	0.53	0.1
<i>D. spicata</i> aboveground tissue (mixed zone)	1.31	12.74	11.43	2.3
<i>D. spicata</i> belowground tissue (mixed zone)	3.54	15.33	11.79	2.3

increased its cover in response to fertilization in the monospecific zone. In addition, when the response of *S. bigelovii* biomass to fertilization was compared between the monospecific and mixed zones, fertilization increased its aboveground biomass to a much greater extent in the monospecific than in the mixed zone, and it increased its belowground biomass in the monospecific zone but not in the mixed zone.

At any rate, we did not find a large change in the biomass dominance of *D. spicata* over *S. bigelovii* in the mixed zone as a result of nutrient addition, in contrast with the results of other studies. In a New England marsh, Levine *et al.* (1998) showed that *Spartina patens* and *Juncus gerardi* dominated over *S. alterniflora* and *D. spicata* under unfertilized conditions, but vice-versa under fertilized conditions. In a comparative study including marshes in Georgia, Alabama, and Mississippi, Pennings *et al.* (2002) documented changes in biomass dominance in four out of seven species mixtures following fertilization, with *S. alterniflora* and *D. spicata* often becoming dominant over other marsh plant species under fertilized conditions. Working in a salt marsh in the Tijuany estuary, Covin and Zedler (1998) found that nutrient addition increased the biomass dominance of *Salicornia virginica* over *Spartina foliosa*. Here, it may be that the duration of the experiment (*i.e.*, 10 months) was not long enough to induce large changes in the biomass dominance of *D. spicata* over *S. bigelovii* in the mixed zone under

fertilized conditions despite higher rates of nutrient uptake and storage by the former species.

Observed increases in aboveground plant biomass and cover due to fertilization suggest that increased anthropogenic nutrient loading may increase the structural complexity of the plant canopy in salt pans, thereby providing better refuge to permanent and transient residents (Stout 1984). In addition, higher plant biomass production could entail higher levels of food availability for the several species of herbivores that feed on *D. spicata* (Pennings *et al.* 2001) and also for the invertebrate detritivores and microbial decomposers that inhabit the marsh soil and whose primary food source is senesced marsh plants (Zimmer *et al.* 2004). Higher nutrient availability may also enhance seed production in salt pan plants (Boyer and Zedler 1999). Therefore, increased nutrient delivery could improve the value of marsh salt pans as habitat for organisms in the Northern Gulf of Mexico.

The general decrease in carbon:nutrient ratios in the tissues of the two species following fertilization suggests two important implications. First, the nutritional quality of *D. spicata* and *S. bigelovii* for first-order consumers should increase with fertilization since the tissues of these two plants have a larger quantity of nutrients per carbon unit when nutrients are added. In turn, enhanced plant nutritional quality following fertilization could promote the growth rates of the herbivores, detritivores, and decomposers that feed on the

plants (Sterner and Elser 2002, Cebrian and Lartigue 2004).

Second, higher nutrient concentrations in the tissues following fertilization, in conjunction with higher levels of biomass, suggests the plants studied can absorb a fraction of the nutrients added and, thus, potentially mitigate the negative impacts of anthropogenic eutrophication on coastal waters. To further explore this, we estimated the percentage of nitrogen added to the fertilized plots that was stored as plant biomass over the course of the experiment. We did these calculations from the changes observed in plant biomass and C:N ratios (Table 2). From October 2003 to April 2004, we added a total of 504 g nitrogen to each fertilized plot. On average, a fertilized monospecific plot of *S. bigelovii* retained 2.1% of that total quantity as plant biomass-bound nitrogen, a monospecific plot of *D. spicata* retained 2.9%, and a mixed plot retained a minimum of 4.7% (i.e., without including the *S. bigelovii* belowground compartment, see Table 2). These numbers are small. Nevertheless, the total percentage of added nitrogen intercepted by the salt pan before it moves into lower areas of the marsh should be much higher. Our calculations do not account for plant biomass senescence and turnover throughout the experiment and, thus, they do not include the nitrogen retained as plant detritus in the salt pan. In addition, a major fraction of nitrogen inputs into marsh soils may be immobilized into particulate organic matter or lost through bacterial denitrification (Tobias et al. 2001a,b). When these processes are invoked, the percentage of nitrogen inputs intercepted by the salt pan studied could well be within the range of estimates for other marshes (i.e., 40%–90%, Valiela et al. 1973, Howard et al. 1986, Tobias et al. 2001b).

This paper clearly shows that nutrient addition increases the abundance and nutrient content of *D. spicata* and *S. bigelovii*, and suggests a superior competitive ability for the former species under enhanced nutrient availability in marsh salt pans of the Northern Gulf of Mexico. However, a longer study could have demonstrated a larger impact on plant abundance, higher nutrient retention as plant biomass, and provided more support for the superior competitive ability of *D. spicata* under fertilized conditions.

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