

Mechanisms mediating plant distributions across estuarine landscapes in a low-latitude tidal estuary

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Abstract. Understanding of how plant communities are organized and will respond to global changes requires an understanding of how plant species respond to multiple environmental gradients. We examined the mechanisms mediating the distribution patterns of tidal marsh plants along an estuarine gradient in Georgia (USA) using a combination of field transplant experiments and monitoring. Our results could not be fully explained by the “competition-to-stress hypothesis” (the current paradigm explaining plant distributions across estuarine landscapes). This hypothesis states that the upstream limits of plant distributions are determined by competition, and the downstream limits by abiotic stress. We found that competition was generally strong in freshwater and brackish marshes, and that conditions in brackish and salt marshes were stressful to freshwater marsh plants, results consistent with the competition-to-stress hypothesis. Four other aspects of our results, however, were not explained by the competition-to-stress hypothesis. First, several halophytes found the freshwater habitat stressful and performed best (in the absence of competition) in brackish or salt marshes. Second, the upstream distribution of one species was determined by the combination of both abiotic and biotic (competition) factors. Third, marsh productivity (estimated by standing biomass) was a better predictor of relative biotic interaction intensity (RII) than was salinity or flooding, suggesting that productivity is a better indicator of plant stress than salinity or flooding gradients. Fourth, facilitation played a role in mediating the distribution patterns of some plants. Our results illustrate that even apparently simple abiotic gradients can encompass surprisingly complex processes mediating plant distributions.

Key words: *Altamaha River estuary, Georgia, USA; biotic interaction; competition; estuary; facilitation; flooding; physical gradient; salinity; tidal marsh; transplant experiments; zonation.*

INTRODUCTION

Determining the mechanisms underlying spatial distribution patterns of organisms has long been a goal of ecological research. This goal has become more critical with accelerating biodiversity losses (Pimm et al. 1995) and increasing global changes such as sea level rise (Nicholls and Cazenave 2010), global warming (Petchey et al. 1999), climate changes (Pearson 2006), and eutrophication (Harpole and Tilman 2007). One classic approach to this goal is to compare how ecological processes differ across environmental gradients (Grime 1973, 1977, Tilman 1982, 1987, Grace 1993, Keddy et al. 1997). It is widely accepted that abiotic stress and biotic interactions (e.g., competition and facilitation) are important factors affecting organism distributions (Grime 1973, Tilman 1982, Callaway 1995, Bruno et al. 2003), but there has been no consensus on how the relative role of biotic interactions vary across abiotic stress gradients (Grace 1993, Brooker et al. 2005, Maestre et al. 2006).

Coastal tidal marshes are characterized by striking zonation patterns of plant communities across elevation (Chapman 1974). A number of studies in salt marshes have addressed the mechanisms responsible for these patterns (Snow and Vince 1984, Bertness 1991a, b, Pennings and Moore 2001, Pennings et al. 2005). These studies showed that there is a trade-off in marsh plants between competitive ability and stress tolerance; competitive dominants are typically unable to survive in physically harsh environmental conditions (e.g., high salinity, frequent flooding, and low productivity), while stress-tolerant but competitively subordinate plants grow in more stressful habitats because they are displaced from benign habitats by dominant competitors (Bertness et al. 1992, Pennings and Bertness 2001). Similar processes mediate plant zonation in nonsaline wetlands (Grace and Wetzel 1981, Grace 1989, Keddy 1989). Although attractive for its simplicity, this paradigm has proven difficult to apply under more complicated environmental conditions when it is not clear which habitats are the most stressful (Pennings and Callaway 1992, Costa et al. 2003, Farina et al. 2009).

Far less attention has been paid to the mechanisms mediating plant distributions across estuarine landscapes from tidal freshwater to tidal salt marsh sites. Although it has long been recognized that plant

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communities change along estuaries (Simpson et al. 1983, Odum 1988), the underlying mechanisms responsible for these patterns have been examined in only two field studies, both conducted at relatively high latitudes. In New England, Crain et al. (2004) concluded that changes in the composition of marsh plant communities across the estuarine salinity gradient were driven by competitively superior freshwater marsh plants displacing stress-tolerant plants to physically harsh salt-marsh habitats, whereas freshwater marsh plants were restricted from salt marshes by physical stresses. We will refer to this set of mechanisms as the “competition-to-stress hypothesis.” Similar mechanisms were also deemed responsible for the distribution patterns of tidal marsh plants in Elbe estuary in Germany (Engels and Jensen 2010).

These studies, although laying a foundation for a mechanistic understanding of plant distributions along estuarine salinity gradients, only included two or three levels of salinity along the estuaries. A more accurate picture of how processes change along a gradient would emerge if the study included more positions along the gradients (Kawai and Tokeshi 2007, le Roux and McGeoch 2010). Moreover, how species respond to ecological gradients is a function of species-specific adaptations (Körner 2003, Liancourt et al. 2005). Differences in climate and soils between high- and low-latitude sites may lead to differences in ecological processes (Pennings and Bertness 1999, Bertness and Pennings 2000), and low-latitude plants may not respond to these in the same ways as high-latitude plants (Pennings et al. 2003). Thus, results from systems at high latitudes (41–53° N) may not predict processes at lower latitudes. Finally, neither Crain et al. (2004) nor Engels and Jensen (2010) discussed the possible role of facilitation in along-estuary plant zonation patterns, although the broader literature discussed previously suggests that facilitation could play a role in mediating distribution patterns at the most stressful habitats.

In this study, we examined the mechanisms mediating the distribution of tidal marsh plants across estuarine landscapes in Georgia, USA, using a combination of field transplant experiments and monitoring to test the predictions of the competition-to-stress hypothesis that (1) the upstream limits of plant distribution are determined by competition, and (2) the downstream limits of plant distribution are set by abiotic stress. Our results indicate that the initial formulation of the competition-to-stress hypothesis was incomplete, and that it needs to be elaborated to make it more general.

METHODS

Study sites

Fieldwork was conducted in tidal marshes in and near the Altamaha River estuary, Georgia, USA (31.4° N, 81.4° W). We located six pairs of sites along the salinity gradient of the estuary, and refer to the salinity zones

represented by these pairs of sites as freshwater, brackish, salt-1, salt-2, salt-3, and salt-4 (Fig. 1). The average soil pore-water salinity of sites in each salinity zone was 0.4 ± 0.7 , 14 ± 5 , 27 ± 7 , 33 ± 7 , 38 ± 8 , and 49 ± 12 psu, respectively (mean \pm SD of 160 samples over three years), and differences in salinity within each zone among years were modest (Appendix C: Fig. C1). Soil pore-water salinity was measured monthly in individual plots throughout the growing seasons of 2007–2009 by determining water content gravimetrically, rehydrating dried soils in a known volume of distilled water, measuring the salinity of the supernatant, and back-calculating to the original pore-water volume (Pennings and Richards 1998).

The tidal freshwater marshes were dominated by *Zizaniopsis miliacea*, *Pontederia cordata*, and *Cicuta maculata*; brackish marsh sites by *Juncus roemerianus*, *Schoenoplectus americanus*, *Schoenoplectus robustus*, and *Spartina cynosuroides*; and the four types of salt marshes by *Spartina alterniflora*, *Batis maritima*, and *Sarcocornia* sp. (see Plate 1). The taxonomy of *Sarcocornia* is under debate, with the USDA (2010) and the Flora of North America (2003) disagreeing about how to name the common perennial succulent previously widely known as “*Salicornia virginica*”; therefore, we refer to this species as *Sarcocornia* sp. Otherwise, all taxonomy follows the USDA (2010), and all plant species will be referred to generically hereafter.

Plots were located on the marsh platform at each site. To quantify flooding, the proportion of time that study plots were flooded was determined by comparing the elevations of study plots (determined for each replicate plot at each site with a Real-Time Kinematic GPS with a vertical error of ~ 2 cm; Appendix C: Fig. C2) with water-level data recorded by Seabird MicroCAT sondes (Sea-Bird Electronics, Bellevue, Washington, USA; recording at 30-min intervals) deployed near the study sites during the growing season of 2009. Plots were scored as “flooded” any time that the sea level measured at the sonde was greater than the measured elevation of the plot. Estimates of flooding determined this way were confirmed by directly measuring flooding at several of the sites using StowAway TidBit temperature loggers (Onset Computer, Bourne, Massachusetts, USA), which recorded abrupt changes in temperature during nighttime flooding events when water temperature differed from air temperature. Direct measures of flooding were highly consistent with estimates based on measured elevation ($r^2 = 0.90$, $n = 10$ sites; data not shown). Across the 12 study sites, flooding and salinity gradients were largely independent (Appendix C: Fig. C3). We also estimated marsh productivity along the estuary by measuring aboveground biomass of the ambient marsh vegetation. In August 2009, we harvested aboveground biomass from six 1×1 m quadrats near the experimental plots at each site. Biomass was dried for 3 d at 60°C and weighed (Appendix C: Fig. C4).

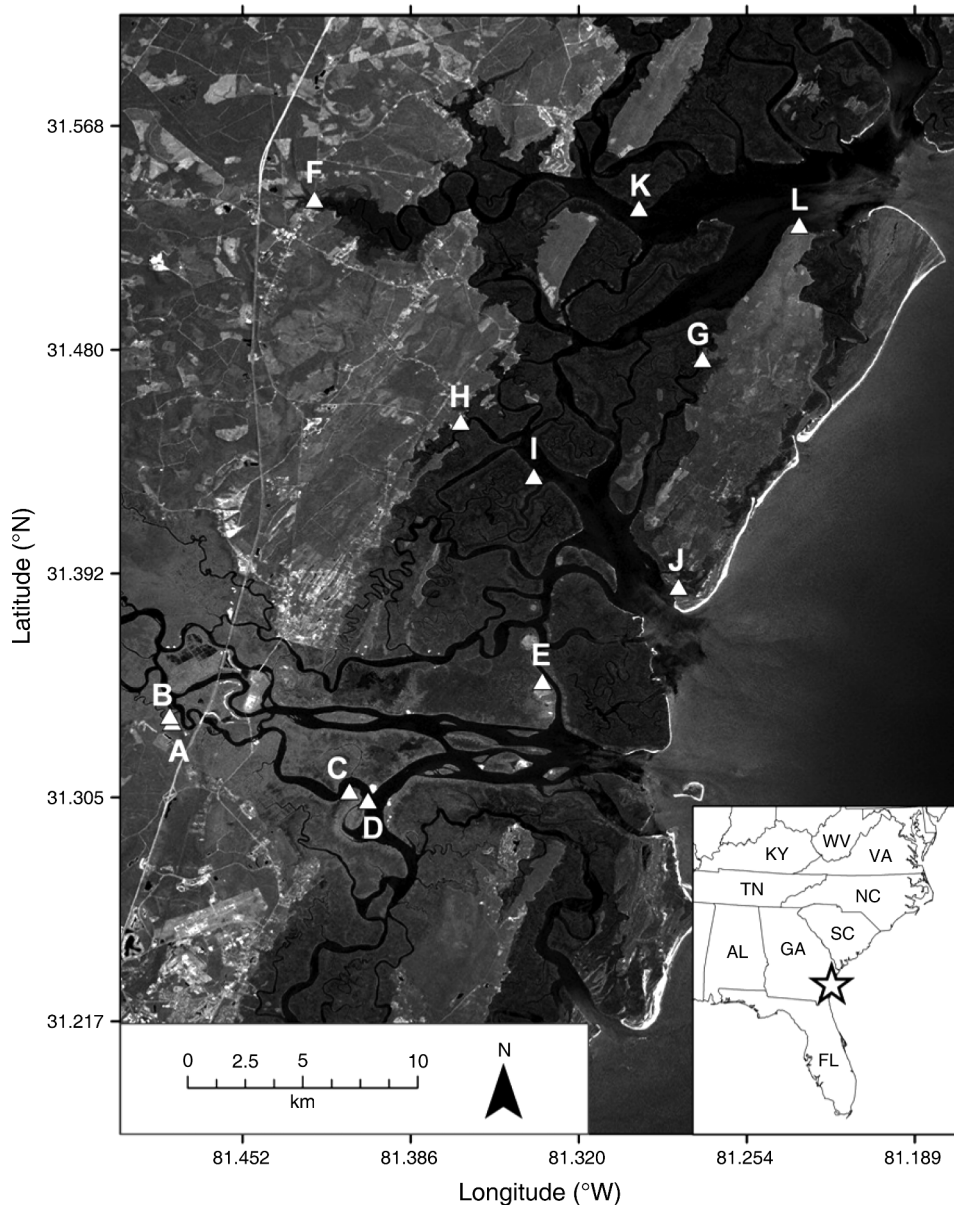


FIG. 1. Locations of the field sites in and near the Altamaha River estuary, Georgia, USA. Labels designate salinity zones: A, freshwater-1; B, freshwater-2; C, brackish-1; D, brackish-2; E, salt-1-1; F, salt-1-2; G, salt-2-1; H, salt-2-2; I, salt-3-1; J, salt-3-2; K, salt-4-1; L, salt-4-2.

Field transplant experiment

At each site, we established four removal plots (3×3 m) and four control plots. The plots were located on the marsh platform of each site, parallel to the riverbank, with treatments interspersed. The removal plots were created by applying a systemic herbicide (glyphosate) in August 2006, seven months before the experiment started, and maintained by clipping any new shoots that grew into the plots every month during the course of the experiments.

We transplanted eight plant species into these plots. We collected *Zizaniopsis*, *Pontederia*, and *Cicuta* from

freshwater marshes; *Juncus* and *Schoenoplectus* from brackish marshes; and *Spartina*, *Batis*, and *Sarcocornia* from salt marshes. For each species, healthy individuals within a narrow range of size were collected with associated soil blocks ($10 \times 10 \times 10$ cm for small species; up to $30 \times 30 \times 30$ cm for the largest species) at the beginning of each growing season (March) from a single location with a salinity regime typical of the distribution of that species. Thus, all the *Zizaniopsis* plants were collected from a single freshwater site; all the *Juncus* plants from a single brackish site; all the *Batis* from a single salt marsh site, and so on. One individual

plant of each species was randomly assigned into each plot at each site (total $n = 12 \text{ sites} \times 2 \text{ treatments} \times 4 \text{ replicates} = 96$ plants of each species). We transplanted *Zizaniopsis*, *Juncus*, and *Spartina* in 2007; *Pontederia*, *Schoenoplectus*, and *Batis* in 2008; and *Cicuta* and *Sarcocornia* in 2009, dividing the work over three years to make the experiments logistically tractable. The individuals of the two to three different species in each plot were placed 1–2 m apart from each other within the plot to minimize any interactions between them. We monitored transplant survival and maintained the plots after 2 months and then monthly during the course of the experiment. At the end of the growing season (October), all aboveground live plant material was harvested, dried for 3 d at 60°C, and weighed.

Data analysis

Analyses were performed with JMP8 statistical software (SAS Institute 2009). Many transplanted plants died during the experiment, so we first analyzed survival time (in months). We used generalized linear models (GLMs) with a log link function to test the effects of “salinity zone,” “neighbor treatment,” and “study site nested in salinity zone” on survival time, assuming a Poisson error (as in Engels and Jensen 2010). Then, we analyzed the effects of the same factors on the aboveground biomass of the transplants that survived in two or more salinity zones using split-plot ANOVAs (as in Quinn and Keough 2002, Crain et al. 2004; study site nested in salinity zone as random factor). Post hoc multiple comparisons were performed using Tukey’s hsd tests.

In order to examine the effects of salinity, flooding, and their interaction on the growth of transplants in the absence of competitors, we conducted multiple linear regression analyses, with the aboveground biomass of the surviving transplants in each plot of the without-neighbor treatment as the response variable, and the corresponding plot-level soil salinity and flooding (proportion of time that the plot was flooded) as the independent variables. This analysis was conducted for the five species that survived in two or more salinity zones (with data from at least 16 plots for each species).

In split-plot ANOVAs and multiple linear regression analyses, biomass data were \log_{10} -transformed to meet the assumptions of normality of residuals and homogeneity of variances. Data were analyzed separately for each plant species. Because the freshwater species *Zizaniopsis*, *Pontederia*, and *Cicuta* only survived in freshwater marshes (Figs. 2 and 3), we could not perform split-plot ANOVAs for these species, and so t tests were instead used to examine the effect of neighbor treatment on the aboveground biomass for these species.

To quantitatively evaluate the nature and strength of biotic interactions across the estuarine gradient, we calculated relative neighbor interaction intensity (RII) using the formula $\text{RII} = (B_{+N} - B_{-N}) / (B_{+N} + B_{-N})$, where B_{+N} and B_{-N} are plant biomass in the presence(+) and absence(–) of neighbors, respectively (Armas et al.

2004). Negative RII values indicate competition; positive RII values indicate facilitation. To calculate RII, adjacent control and experimental plots were paired within each site.

RESULTS

Survival time

All three freshwater species died completely within two months after they were transplanted into salt marshes, regardless of neighbor treatment (Fig. 2A–C). Freshwater species survived longer in brackish marshes, but all individuals still died by the end of the experiment. In contrast, freshwater species survived well in freshwater marshes. GLM analyses indicated a strong effect of salinity on survival time of the freshwater species, but no effect of neighbor or the salinity \times neighbor interaction (Table 1).

The two brackish marsh species had different survival patterns (Fig. 2D, E). *Juncus* survived well overall, but with a decrease in survival at the high-salinity sites, both with and without neighbors (Table 1). *Schoenoplectus* died within two months in the two saltiest zones (salt-3 and salt-4), with or without neighbors present. In the two salt-marsh zones with intermediate salinities (salt-1 and salt-2), *Schoenoplectus* had longer survival times, but eventually also died. In contrast, all *Schoenoplectus* transplants survived in freshwater sites in both with- and without-neighbor treatments (Table 1).

Salt-marsh species survived well in all salt marshes both with and without neighbors, and also survived well when transplanted into freshwater and brackish marshes if neighbors were removed (Fig. 2F–H). When neighboring vegetation was present in freshwater and brackish marshes, however, the survival time of *Spartina* and *Sarcocornia* decreased, leading to a significant interaction between salinity and neighbors (Table 1). The survival of *Batis* was not significantly affected by salinity, neighbors, or their interaction (Table 1).

Aboveground biomass of surviving transplants

Biomass of the freshwater plants *Zizaniopsis*, *Pontederia*, and *Cicuta* was strongly suppressed by neighbors in freshwater marshes (the only habitat where these species survived) (Fig. 3A–C; *Zizaniopsis*, $t_{14} = 10.5$, $P < 0.001$; *Pontederia*, $t_{12} = 11.8$, $P < 0.001$; *Cicuta*, $t_{10} = 4.4$, $P = 0.001$). The two brackish marsh plants, *Juncus* and *Schoenoplectus*, performed best in the lower-salinity marshes when neighbors were removed, but were also suppressed by neighbors in these marshes (Fig. 3D, E).

The three salt marsh plants displayed different growth patterns (Fig. 3F–H). With neighbors removed, *Spartina* grew as well (Tukey’s hsd test, $P > 0.05$) in freshwater marshes, and better (Tukey’s hsd test, $P < 0.05$) in brackish marshes, than in salt marshes. When neighbors were present, however, *Spartina* biomass was strongly suppressed at freshwater and brackish sites (Tukey’s hsd test, $P < 0.05$). The effect of neighbors on *Spartina*

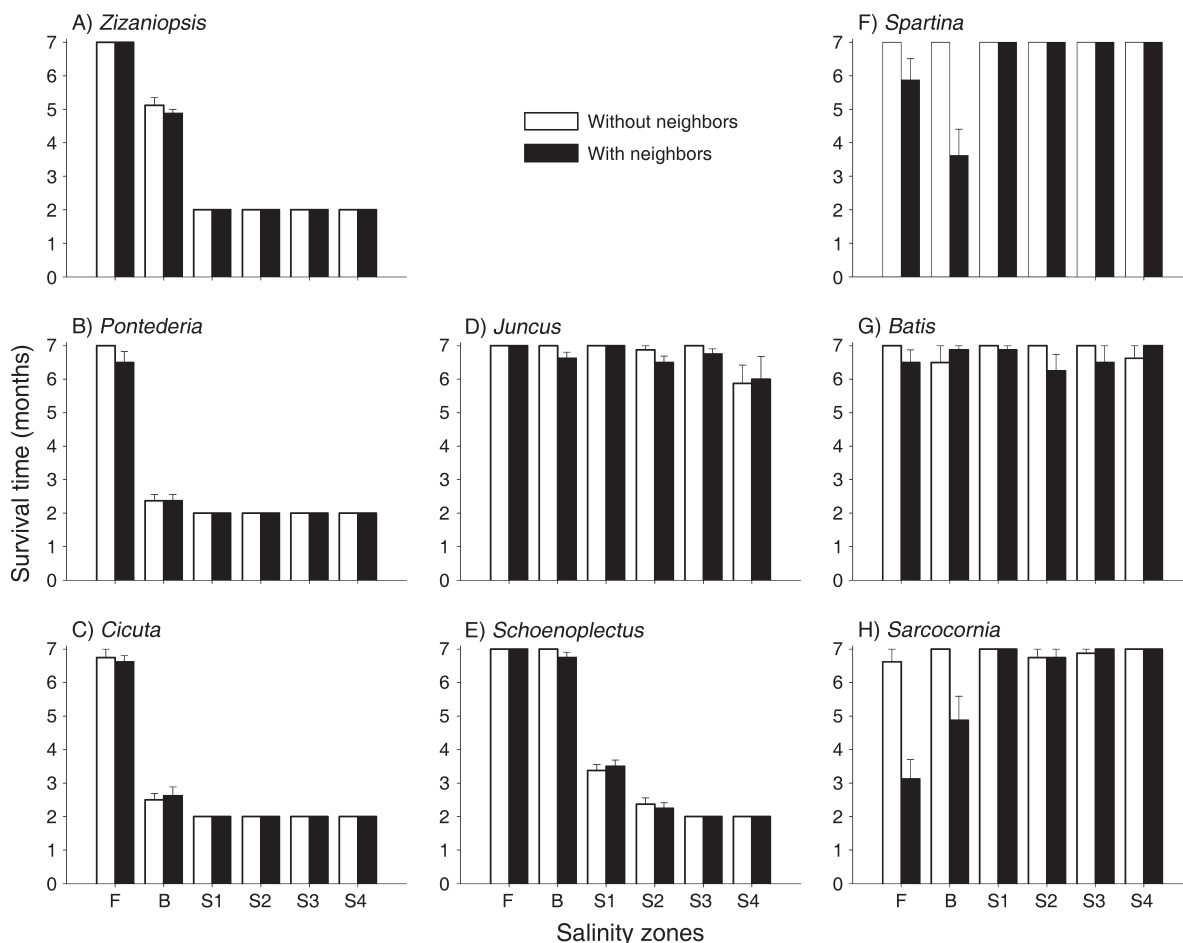


FIG. 2. Survival time of plants transplanted into different salinity zones. Data are means \pm SE. Abbreviations: F, freshwater; B, brackish; S1, salt-1; S2, salt-2; S3, salt-3; S4, salt-4. Plant species in the left-hand column are freshwater marsh species; those in the middle column are brackish marsh species; and those in the right-hand column are salt marsh species. In the without-neighbors treatment, the local marsh vegetation was removed; in the with-neighbors treatment, the local marsh vegetation was left intact.

growth was stronger when salinity was lower (significant salinity \times neighbor interaction; Appendix A: Table A1). Results for *Batis* were similar to those for *Spartina*. In contrast, *Sarcocornia* achieved the highest biomass levels in salt marshes and performed poorly in freshwater and brackish marshes even in the absence of neighbors (Fig. 3H). Neighbors suppressed *Sarcocornia* biomass at all sites, but most strongly at the lower-salinity sites (significant salinity \times neighbor interaction; Appendix A: Table A1).

Multiple regression analyses

In the absence of competition, the biomass of *Juncus* and *Schoenoplectus* was negatively correlated with salinity, but unrelated to flooding (Appendix A: Table A2). The biomass of *Spartina* was negatively correlated with both salinity and flooding, and with their interaction, with the effect of flooding stronger at low vs. high salinity sites. The biomass of *Batis* was negatively correlated with salinity, with flooding marginally significant and the

interaction between salinity and flooding significant. For *Batis*, the effect of flooding was negative at lower salinities, but positive at higher salinities (Appendix A: Table A3). The biomass of *Sarcocornia* was positively correlated with salinity and unrelated to flooding.

Relative neighbor interaction intensity (RII) across estuarine gradients

For the five species that survived in two or more salinity zones, the relative neighbor interaction intensity index (RII) was negatively correlated with marsh productivity (Fig. 4). Although salinity also explained a large amount of the variation in RII (Appendix D: Fig. D1) and flooding explained a small amount of the variation in RII (Appendix D: Fig. D2), marsh productivity was the best single predictor of RII.

DISCUSSION

The competition-to-stress hypothesis for plant distributions across estuarine landscapes was too limited to

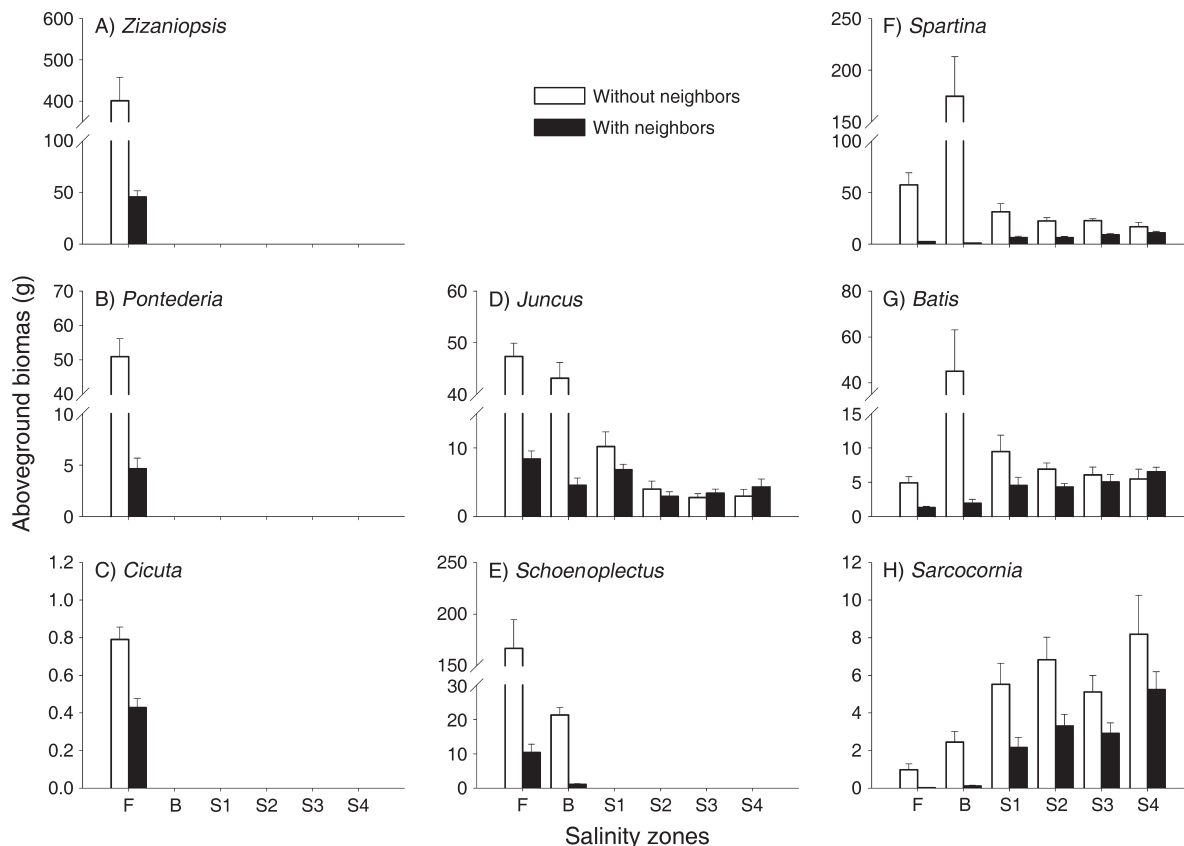


FIG. 3. Aboveground biomass of surviving transplants in different salinity zones. Data are means + SE. Abbreviations: F, freshwater; B, brackish; S1, salt-1; S2, salt-2; S3, salt-3; S4, salt-4. Plant species in the left-hand column are freshwater marsh species; those in the middle column are brackish marsh species; and those in the right-hand column are salt marsh species.

fully explain our results. Although our results were partially consistent with this hypothesis, some important differences emerged that indicated that this hypothesis was an oversimplification of the processes mediating plant distributions along estuarine gradients.

The competition-to-stress hypothesis states that, across estuarine landscapes, plants are excluded from regions of higher salinity than where they normally occur by abiotic stress, and that plants are excluded from regions of lower salinity than where they normally occur by competition (Crain et al. 2004, Engels and Jensen 2010). Many of our results fit this paradigm. Freshwater and brackish marsh plants died when transplanted into higher salinity habitats. In contrast, with one exception, salt marsh plants performed well in freshwater and brackish marshes if neighbors were absent, but were suppressed by competition in these habitats. Four additional results of our study, however, do not fit the competition-to-stress hypothesis.

First, in the absence of neighbors, the salt marsh species *Spartina* and *Batis* achieved the highest aboveground biomass at brackish rather than freshwater sites, inconsistent with the idea that the least abiotic stress is found at sites with the lowest salinities. There is some evidence that *Spartina alterniflora* may have a physio-

logical requirement for sulfur for optimal growth (Stribling 1997). The content of dissolved sulfur is much lower in freshwater than in seawater (Odum 1988), and thus growth of *Spartina* might have been limited by sulfate availability in the freshwater sites (Stribling 1997). This is consistent with data showing that some *Spartina* species experience photoinhibition at very low salinities (Castillo et al. 2005), which might also contribute to the lower aboveground biomass of *Spartina alterniflora* at freshwater sites.

In the case of *Batis*, which is a high-marsh plant (Pennings and Richards 1998), the relatively modest growth performance at the freshwater sites might also be explained by the relatively high flooding frequency of these sites (Appendix C: Fig. C3). The strong performance of *Spartina* and *Batis* at brackish sites could be explained by higher nutrient availability at these sites. Although we did not measure nutrients, phosphorus accumulation in soil is generally greatest in brackish marshes (Loomis and Craft 2010), and periodic pulses of salt water at low-salinity sites can increase nutrient release from sediments (Weston et al. 2006).

Aboveground biomass of *Sarcocornia* deviated even more strongly from the expected pattern of increasing biomass at lower-salinity sites. Instead, *Sarcocornia*

TABLE 1. Summary of generalized linear models (GLMs) examining the effects of salinity, site (nested within salinity), neighbor treatment, and the interaction between salinity and neighbors on the survival time (months) of transplanted plants in tidal marshes of the Altamaha River estuary, Georgia, USA.

Species and source of variation	df	Likelihood ratio χ^2	<i>P</i>
<i>Zizaniopsis</i> (freshwater)			
Salinity	5	7303.09	< 0.01
Site (salinity)	6	0.00	1.00
Neighbor	1	0.32	0.57
Salinity \times neighbor	5	2.78	0.73
<i>Pontederia</i> (freshwater)			
Salinity	5	3687.06	< 0.01
Site (salinity)	6	50.42	< 0.01
Neighbor	1	0.41	0.52
Salinity \times neighbor	5	4.21	0.52
<i>Cicuta</i> (freshwater)			
Salinity	5	2804.62	< 0.01
Site (salinity)	6	43.41	< 0.01
Neighbor	1	0.05	0.82
Salinity \times neighbor	5	1.21	0.94
<i>Juncus</i> (brackish)			
Salinity	5	22.77	< 0.01
Site (salinity)	6	16.00	0.01
Neighbor	1	0.77	0.38
Salinity \times neighbor	5	1.49	0.91
<i>Schoenoplectus</i> (brackish)			
Salinity	5	3154.68	< 0.01
Site (salinity)	6	8.51	0.20
Neighbor	1	0.17	0.68
Salinity \times neighbor	5	2.04	0.84
<i>Spartina</i> (salt)			
Salinity	5	58.14	< 0.01
Site (salinity)	6	17.57	< 0.01
Neighbor	1	21.09	< 0.01
Salinity \times neighbor	5	53.05	< 0.01
<i>Batis</i> (salt)			
Salinity	5	1.36	0.93
Site (salinity)	6	7.29	0.29
Neighbor	1	1.15	0.28
Salinity \times neighbor	5	6.17	0.29
<i>Sarcocornia</i> (salt)			
Salinity	5	78.22	< 0.01
Site (salinity)	6	12.07	0.06
Neighbor	1	30.30	< 0.01
Salinity \times neighbor	5	63.22	< 0.01

Note: Significant *P* values (*P* < 0.05) are in bold.

biomass in the without-neighbor treatment increased toward the higher salinity sites. Laboratory studies have shown that a number of salt marsh plants have a salt requirement for optimal growth. For example, Partridge and Wilson (1987) examined the salt tolerance of 31 halophytic species in New Zealand, and they found that eight species required salt to achieve maximum growth. Similarly, a number of studies with *Salicornia* species have found stimulation of growth at higher salinities (Webb 1966, Ungar et al. 1979, Cooper 1982, Keiffer et al. 1994, Khan et al. 2001, Crain et al. 2004, Redondo-Gómez et al. 2006).

These results indicate that it is an oversimplification to state that abiotic stress decreases as salinity drops. Rather, some halophytes may find freshwater marshes

stressful, and will perform best in brackish or saline conditions. Such differences in the response to environmental gradients among different plant species must be considered carefully when exploring the mechanisms mediating plant distributions, because they indicate that there is not a single “universal” abiotic gradient that applies in the same way to all plant species (Körner 2003, Liancourt et al. 2005).

Second, the competition-to-stress hypothesis states that competition and abiotic stress act to limit plant species distributions at opposite ends of the abiotic gradient in estuaries. As mentioned previously, the low salinities in freshwater and brackish marshes might be stressful to *Sarcocornia* and substantially decreased its biomass; meanwhile, *Sarcocornia* also experienced

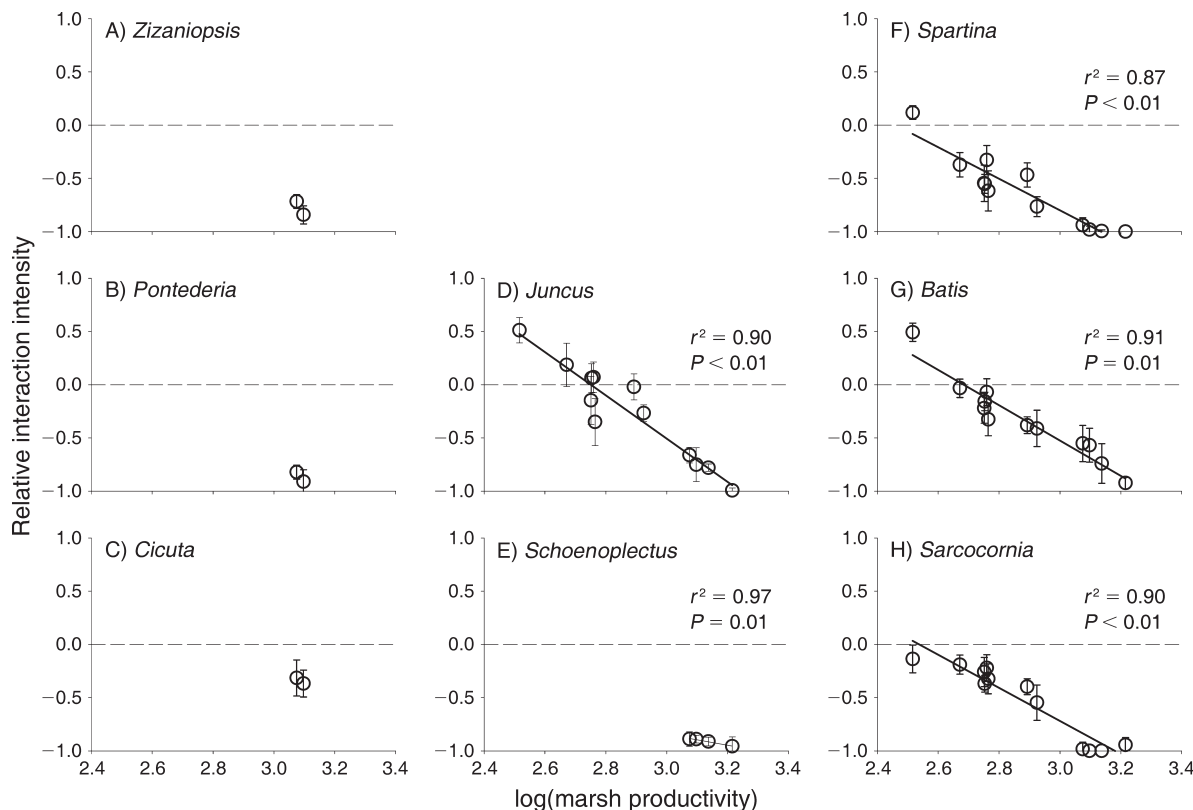


FIG. 4. Relative neighbor interaction intensity (RII) for the transplants along the marsh productivity (\log_{10} -transformed) gradient. Marsh productivity (originally measured in g/m^2) of each experimental site was measured as the aboveground biomass of ambient marsh vegetation. Data are means with 95% CI. Linear regressions are based on the average values for each site. Plant species in the left-hand column are freshwater marsh species; those in the middle column are brackish marsh species; and those in the right-hand column are salt marsh species.

strong competition from local vegetation in freshwater and brackish marshes. Thus, the upstream distribution limit of *Sarcocornia* seems to be set by the combination of both abiotic (low salinity) and biotic (intense competition) factors. This mechanism did not emerge in previous studies on the plant distribution patterns along estuarine gradients (Crain et al. 2004, Engels and Jensen 2010).

Third, the competition-to-stress hypothesis states that competition is greatest at the upstream, lowest-salinity sites. We found instead that the relative neighbor competition intensity (RII) was highest for most species at brackish rather than freshwater sites. The brackish marsh sites in our study tended to have the highest productivity of all the sites (Wieski et al. 2010), and in general plants with more biomass would be expected to have a higher competitive ability (Gaudet and Keddy 1988, Keddy et al. 2002). Correlation analyses indicated that marsh productivity was a better predictor of relative neighbor interaction intensity (RII) than either salinity or flooding. These results suggest that in tidal marsh plant communities it may be more informative to examine biotic interactions across a gradient of productivity than across a gradient of salinity.

Fourth, we observed positive RII values for three out of four species that survived in the sites with the harshest environmental conditions (i.e., highest salinity and lowest productivity; Fig. 4), indicating that facilitation, in addition to competition, plays a role in mediating the distributions of tidal marsh plants along estuarine landscapes. The stress-gradient hypothesis (Bertness and Callaway 1994) predicts that the frequency of positive and negative species interactions varies across environmental gradients, with facilitation being more common under harsh environmental conditions, and competition prevailing where the physical environment is relatively benign. Previous studies have shown that facilitation is important in mediating plant distributions across elevation within single salt marsh sites (Bertness and Hacker 1994, Castellanos et al. 1994, Hacker and Bertness 1995, Bertness and Leonard 1997, Figueroa et al. 2003); however, previous studies of horizontal distribution patterns along the estuary found little or no evidence for facilitation (Crain et al. 2004, Engels and Jensen 2010). The difference between our results and those of Crain et al. (2004) and Engels and Jensen (2010) is likely due to previous studies being conducted at high latitudes, where salt marsh soils are in general less saline

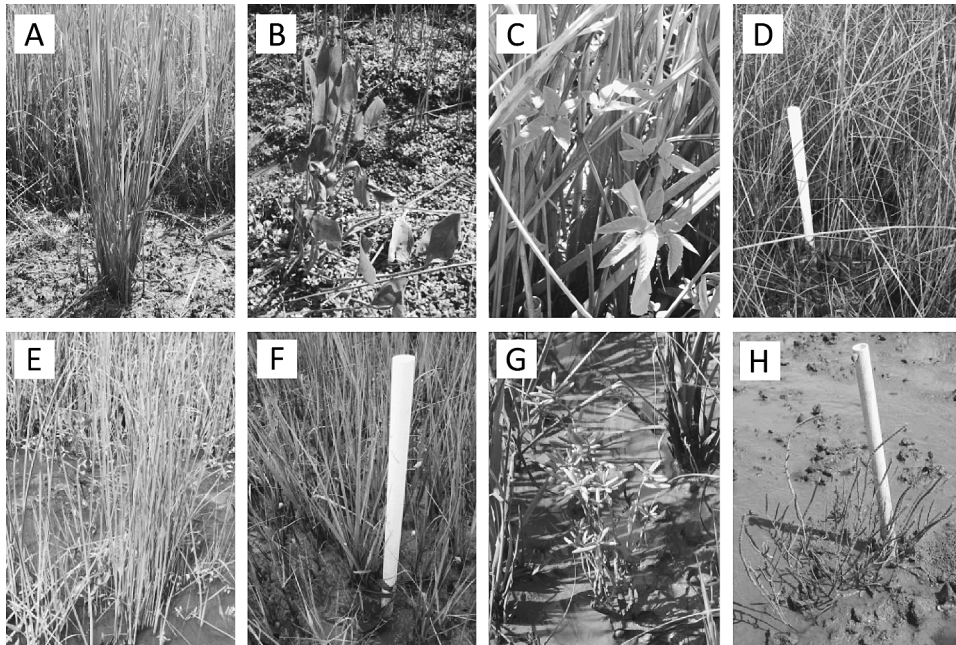


PLATE 1. Photographs of plant species in the transplant experiments. (A) *Zizaniopsis miliacea*, (B) *Pontederia cordata*, (C) *Cicuta maculata*, (D) *Juncus roemerianus*, (E) *Schoenoplectus americanus*, (F) *Spartina alterniflora*, (G) *Batis maritima*, and (H) *Sarcocornia* sp. See Appendix B: Fig. B2 for a color version of this plate. Photo credits: H. Guo.

than at lower latitudes due to less intense solar radiation (Pennings and Bertness 1999, Bertness and Pennings 2000).

The results from our study illustrate the complexity of natural gradients in mediating plant distributions across estuarine landscapes because multiple factors, both abiotic and biotic, may vary in different ways across the landscape, and different plant species may also respond to these factors differently. The competition-to-stress hypothesis oversimplifies these complex processes in estuarine ecosystems. To fully understand the mechanisms driving plant distributions along estuarine gradients, it is necessary to also understand how different abiotic variables vary and interact, and how different plants respond to these gradients. Similar complexities are likely to occur in other systems. We cannot assume that any one abiotic variable is a good surrogate of all abiotic variables and their integrated influence (Parker et al. 1999, Lortie and Callaway 2006, Kawai and Tokeshi 2007), and we cannot assume that all species respond to environmental gradients in the same way (Körner 2003, Liancourt et al. 2005, Maestre et al. 2009). The challenge facing ecologists is to balance the desire for simplification against the need to ramify details and exceptions, and to identify the appropriate level of simplification needed to produce robust, general theories.

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LITERATURE CITED

- Armas, C., R. Ordiales, and F. I. Pugnaire. 2004. Measuring plant interactions: a new comparative index. *Ecology* 85:2682–2686.
- Bertness, M. D. 1991a. Interspecific interactions among high marsh perennials in a New England salt marsh. *Ecology* 72:125–137.
- Bertness, M. D. 1991b. Zonation of *Spartina patens* and *Spartina alterniflora* in New England salt marsh. *Ecology* 72:138–148.
- Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. *Trends in Ecology and Evolution* 9:191–193.
- Bertness, M. D., L. Gough, and S. W. Shumway. 1992. Salt tolerances and the distribution of fugitive salt marsh plants. *Ecology* 73:1842–1851.
- Bertness, M. D., and S. D. Hacker. 1994. Physical stress and positive associations among marsh plants. *American Naturalist* 144:363–372.
- Bertness, M. D., and G. H. Leonard. 1997. The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* 78:1976–1989.
- Bertness, M. D., and S. C. Pennings. 2000. Spatial variation in process and pattern in salt marsh plant communities in eastern North America. Pages 39–57 in M. P. Weinstein and D. A. Kreeger, editors. *Concepts and controversies in tidal marsh ecology*. Kluwer Academic, New York, New York, USA.

- Brooker, R., Z. Kikvidze, F. I. Pugnaire, R. M. Callaway, P. Choler, C. J. Lortie, and R. Michalet. 2005. The importance of importance. *Oikos* 109:63–70.
- Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18:119–125.
- Callaway, R. 1995. Positive interactions among plants. *Botanical Review* 61:306–349.
- Castellanos, E. M., M. E. Figueroa, and A. J. Davy. 1994. Nucleation and facilitation in saltmarsh succession: interactions between *Spartina maritima* and *Arthrocnemum perenne*. *Journal of Ecology* 82:239–248.
- Castillo, J., A. Rubio-Casal, S. Redondo, A. Álvarez-López, T. Luque, C. Luque, F. Nieva, E. Castellanos, and M. Figueroa. 2005. Short-term responses to salinity of an invasive cordgrass. *Biological Invasions* 7:29–35.
- Chapman, V. J. 1974. Salt marshes and salt deserts of the world. Pages 3–19 in R. J. Reimold and W. H. Queen, editors. *Ecology of halophytes*. Academic Press, New York, New York, USA.
- Cooper, A. 1982. The effects of salinity and waterlogging on the growth and cation uptake of salt marsh plants. *New Phytologist* 90:263–275.
- Costa, C. S. B., J. C. Marangoni, and A. M. G. Azevedo. 2003. Plant zonation in irregularly flooded salt marshes: relative importance of stress tolerance and biological interactions. *Journal of Ecology* 91:951–965.
- Crain, C. M., B. R. Silliman, S. L. Bertness, and M. D. Bertness. 2004. Physical and biotic drivers of plant distribution across estuarine salinity gradients. *Ecology* 85:2539–2549.
- Engels, J. G., and K. Jensen. 2010. Role of biotic interactions and physical factors in determining the distribution of marsh species along an estuarine salinity gradient. *Oikos* 119:679–685.
- Farina, J. M., B. R. Silliman, and M. D. Bertness. 2009. Can conservation biologists rely on established community structure rules to manage novel systems?...Not in salt marshes. *Ecological Applications* 19:413–422.
- Figueroa, M. E., J. M. Castillo, S. Redondo, T. Luque, E. M. Castellanos, F. J. Nieva, C. J. Luque, A. E. Rubio-Casal, and A. J. Davy. 2003. Facilitated invasion by hybridization of *Sarcocornia* species in a salt-marsh succession. *Journal of Ecology* 91:616–626.
- Flora of North America. 2003. *Flora of North America*. Volume 4. Editorial Committee, editor. Oxford University Press, New York, New York, USA.
- Gaudet, C. L., and P. A. Keddy. 1988. A comparative approach to predicting competitive ability from plant traits. *Nature* 334:242–243.
- Grace, J. B. 1989. Effects of water depth on *Typha latifolia* and *Typha domingensis*. *American Journal of Botany* 76:762–768.
- Grace, J. B. 1993. The effects of habitat productivity on competition intensity. *Trends in Ecology and Evolution* 8:229–230.
- Grace, J. B., and R. G. Wetzel. 1981. Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. *American Naturalist* 118:463–474.
- Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242:344–347.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:1169–1194.
- Hacker, S. D., and M. D. Bertness. 1995. Morphological and physiological consequences of a positive plant interaction. *Ecology* 76:2165–2175.
- Harpole, W. S., and D. Tilman. 2007. Grassland species loss resulting from reduced niche dimension. *Nature* 446:791–793.
- Kawai, T., and M. Tokeshi. 2007. Testing the facilitation–competition paradigm under the stress-gradient hypothesis: decoupling multiple stress factors. *Proceedings of the Royal Society B* 274:2503–2508.
- Keddy, P. A. 1989. Effects of competition from shrubs on herbaceous wetland plants: a 4-year field experiment. *Canadian Journal of Botany* 67:708–716.
- Keddy, P., K. Nielsen, E. Weiher, and R. Lawson. 2002. Relative competitive performance of 63 species of terrestrial herbaceous plants. *Journal of Vegetation Science* 13:5–16.
- Keddy, P., L. TwolanStrutt, and B. Shipley. 1997. Experimental evidence that interspecific competitive asymmetry increases with soil productivity. *Oikos* 80:253–256.
- Keiffer, C. H., B. C. McCarthy, and I. A. Ungar. 1994. Effect of salinity and waterlogging on growth and survival of *Salicornia europaea* L., an inland halophyte. *Ohio Journal of Science* 94:70–73.
- Khan, M. A., B. Gul, and D. J. Weber. 2001. Effect of salinity on the growth and ion content of *Salicornia rubra*. *Communications in Soil Science and Plant Analysis* 32:2965–2977.
- Körner, C. 2003. Limitation and stress—always or never? *Journal of Vegetation Science* 14:141–143.
- le Roux, P. C. and M. A. McGeoch. 2010. Interaction intensity and importance along two stress gradients: adding shape to the stress-gradient hypothesis. *Oecologia* 162:733–745.
- Liancourt, P., R. M. Callaway, and R. Michalet. 2005. Stress tolerance and competitive-response ability determine the outcome of biotic interactions. *Ecology* 86:1611–1618.
- Loomis, M. J., and C. B. Craft. 2010. Carbon sequestration and nutrient (nitrogen, phosphorus) accumulation in river-dominated tidal marshes, Georgia, USA. *Soil Science Society of America Journal* 74:1028–1036.
- Lortie, C. J., and R. M. Callaway. 2006. Re-analysis of meta-analysis: support for the stress-gradient hypothesis. *Journal of Ecology* 94:7–16.
- Maestre, F. T., R. M. Callaway, F. Valladares, and C. J. Lortie. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology* 97:199–205.
- Maestre, F. T., F. Valladares, and J. F. Reynolds. 2006. The stress-gradient hypothesis does not fit all relationships between plant–plant interactions and abiotic stress: further insights from arid environments. *Journal of Ecology* 94:17–22.
- Nicholls, R. J., and A. Cazenave. 2010. Sea-level rise and its impact on coastal zones. *Science* 328:1517–1520.
- Odum, W. E. 1988. Comparative ecology of tidal freshwater and salt marshes. *Annual Review of Ecology and Systematics* 19:147–176.
- Parker, E. D., Jr., et al. 1999. Stress in ecological systems. *Oikos* 86:179–184.
- Partridge, T. R., and J. B. Wilson. 1987. Salt tolerance of salt marsh plants of Otago, New Zealand. *New Zealand Journal of Botany* 25:559–566.
- Pearson, R. G. 2006. Climate change and the migration capacity of species. *Trends in Ecology and Evolution* 21:111–113.
- Pennings, S. C., and M. D. Bertness. 1999. Using latitudinal variation to examine effects of climate on coastal salt marsh pattern and process. *Current Topics in Wetland Biogeochemistry* 3:100–111.
- Pennings, S. C., and M. D. Bertness. 2001. Salt marsh communities. Pages 289–316 in M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. *Marine community ecology*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Pennings, S. C., and R. M. Callaway. 1992. Salt marsh plant zonation: the relative importance of competition and physical factors. *Ecology* 73:681–690.
- Pennings, S. C., M. B. Grant, and M. D. Bertness. 2005. Plant zonation in low-latitude salt marshes: disentangling the roles

- of flooding, salinity and competition. *Journal of Ecology* 93:159–167.
- Pennings, S. C., and D. J. Moore. 2001. Zonation of shrubs in western Atlantic salt marshes. *Oecologia* 126:587–594.
- Pennings, S. C., and C. L. Richards. 1998. Effects of wrack burial in salt-stressed habitats: *Batis maritima* in a southwest Atlantic salt marsh. *Ecography* 21:630–638.
- Pennings, S. C., E. R. Selig, L. T. Houser, and M. D. Bertness. 2003. Geographic variation in positive and negative interactions among salt marsh plants. *Ecology* 84:1527–1538.
- Petchey, O. L., P. T. McPhearson, T. M. Casey, and P. J. Morin. 1999. Environmental warming alters food-web structure and ecosystem function. *Nature* 402:69–72.
- Pimm, S. L., G. J. Russell, J. L. Gittleman, and T. M. Brooks. 1995. The future of biodiversity. *Science* 269:347–350.
- Quinn, G. P., and J. R. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, UK.
- Redondo-Gómez, S., C. Wharmby, J. M. Castillo, E. Mateos-Naranjo, C. J. Luque, A. De Cires, T. Luque, A. J. Davy, and M. Enrique Figueroa. 2006. Growth and photosynthetic responses to salinity in an extreme halophyte, *Sarcocornia fruticosa*. *Physiologia Plantarum* 128:116–124.
- SAS Institute. 2009. JMP statistical software package. Version 8. SAS Institute, Cary, North Carolina, USA.
- Simpson, R. L., R. E. Good, M. A. Leck, and D. F. Whigham. 1983. The ecology of freshwater tidal wetlands. *BioScience* 33:255–259.
- Snow, A. A., and S. W. Vince. 1984. Plant zonation in an Alaskan salt marsh. II. An experimental study of the role of edaphic conditions. *Journal of Ecology* 72:669–684.
- Stribling, J. M. 1997. The relative importance of sulfate availability in the growth of *Spartina alterniflora* and *Spartina cynosuroides*. *Aquatic Botany* 56:131–143.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.
- Tilman, D. 1987. On the meaning of competition and the mechanisms of competitive superiority. *Functional Ecology* 1:304–315.
- Ungar, I. A., D. K. Benner, and D. C. McGraw. 1979. Distribution and growth of *Salicornia europaea* on an inland salt pan. *Ecology* 60:329–336.
- USDA. 2010. The PLANTS database. National Plant Data Center, Baton Rouge, Louisiana, USA. <http://plants.usda.gov>
- Webb, K. L. 1966. NaCl effects on growth and transpiration in *Salicornia bigelovii*, a salt-marsh halophyte. *Plant and Soil* 24:261–268.
- Weston, N. B., R. E. Dixon, and S. B. Joye. 2006. Ramifications of increased salinity in tidal freshwater sediments: geochemistry and microbial pathways of organic matter mineralization. *Journal of Geophysical Research Biogeosciences* 111:G01009.
- Wieski, K., H. Guo, C. B. Craft, and S. C. Pennings. 2010. Ecosystem functions of tidal fresh, brackish, and salt marshes on the Georgia Coast. *Estuaries and Coasts* 33:161–169.

SUPPLEMENTAL MATERIAL

Appendix A

ANOVA table, multiple regression, and correlation results for analyses of aboveground biomass (*Ecological Archives* E093-009-A1).

Appendix B

Color figure showing site locations and study species (*Ecological Archives* E093-009-A2).

Appendix C

Site elevations, relationship between flooding and salinity, and productivity (*Ecological Archives* E093-009-A3).

Appendix D

Relationship between relative interaction intensity (RII) and salinity or flooding (*Ecological Archives* E093-009-A4).