

PHYSICAL AND BIOTIC DRIVERS OF PLANT DISTRIBUTION ACROSS ESTUARINE SALINITY GRADIENTS

CAITLIN MULLAN CRAIN,¹ BRIAN R. SILLIMAN, SARAH L. BERTNESS, AND MARK D. BERTNESS

Department of Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island 02912 USA

Abstract. Although it has long been recognized that marsh plant community composition shifts across estuarine salinity gradients, the mechanisms responsible for this species zonation have never been experimentally examined. In southern New England marshes of the United States, we investigated the relative importance of physical and biotic factors in generating estuarine species distribution patterns. Greenhouse studies revealed that all of the common plants in this system grow better in fresh water than in full-strength salt water. To test the hypothesis that the spatial segregation of these plants is driven by differential tolerance to salt stress and plant competition, we performed transplant experiments with 10 common plants in the system. When freshwater marsh plants were transplanted to salt marshes, they did poorly and generally died with or without neighbors present. In contrast, when saltmarsh plants were transplanted to freshwater marshes, they thrived in the absence of neighbors, growing better than they did in salt marshes, but when neighbors were present, they were strongly suppressed. These results suggest that the spatial segregation of plants across estuarine salinity gradients is driven by competitively superior freshwater marsh plants displacing salt-tolerant plants to physically harsh saltmarsh habitats, whereas freshwater marsh plants are limited from living in salt marshes by physical factors (e.g., high salinities). These results contribute to our understanding of the organization and assembly of tidal marsh plant communities and have important implications for understanding how marsh plant communities will respond to human modification of estuarine hydrology and climate change.

Key words: *biotic drivers; brackish marsh; estuary; New England; physical drivers; plant distribution; Rhode Island; salinity gradient; salt marsh; trade-offs; zonation.*

INTRODUCTION

Understanding the mechanisms that generate the spatial distributions of organisms at local, regional, and global spatial scales is one of the major goals of ecology. Shoreline habitats, where organisms often inhabit distinct zones across steep environmental gradients, have been especially valuable in elucidating the mechanisms that generate spatial distributions of species in natural communities (e.g., Connell 1961, Paine 1966). Rocky intertidal habitats, in particular, have been model systems for examining the causes of zonation patterns. Although early studies attributed species distributions to the abiotic gradient alone (e.g., Stephenson and Stephenson 1949), experimental ecologists have since discovered that high intertidal borders are set by physical stress, but low intertidal borders are set by biotic factors, typically interspecific competition and predation (Little and Kitching 1996, Raffaelli and Hawkins 1996, Bertness 1999). The more general rule, that predators and dominant competitors often displace other organisms from physically benign habitats, restricting them to living in physically harsh habitats, has also been applied to rocky shores to explain latitudinal and

biogeographic patterns in organism distribution patterns (Vermeij 1978, Wethey 1984, Leonard 2000).

Experimental ecology provided equal benefits to our understanding of species distributions in salt marshes. Distinct zonation of species, once thought to be driven exclusively by physical factors (e.g., Pomeroy and Wiegert 1981), is now understood to be additionally influenced by interspecific competition (Vince and Snow 1984, Bertness and Ellison 1987, Bertness 1991a, b). In general, for terrestrially derived marsh plants, the lower intertidal borders are set by physical factors, whereas the high intertidal borders are set by competition (but see Pennings and Callaway [1992] for a common exception to this generalization). Considerably less work has been done to understand the often sharply delimited distributions of plant species in freshwater marshes, but the work that has been done (Grace and Wetzel 1981, Wilson and Keddy 1986) again suggests that dominant competitors typically displace competitively subordinate plants from physically benign habitats, restricting them to living in physically harsh habitats.

Although researchers have examined vertical zonation patterns in saltmarsh and freshwater marsh habitats, the mechanisms responsible for the horizontal zonation of plants at the landscape scale, along estuarine salinity gradients, have not been addressed experimentally. It is well known that plant species composition

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¹ E-mail: Caitlin_Crain@Brown.edu

shifts predictably along estuarine salinity gradients, with salt-tolerant halophytic plants dominating salt marshes and nonhalophytic wetland plants dominating tidal freshwater habitats (Simpson et al. 1983, Odum and Hoover 1988, Mitsch and Gosselink 2000). Typically, it is assumed that plant salt tolerances dictate the distribution of plants along these gradients (Odum 1988, Odum and Hoover 1988, Latham et al. 1994). This idea, however, is based on plant salt tolerances established in the lab, correlated with marsh salinity patterns, but it has not been experimentally verified in the field. In addition, laboratory studies have suggested that salt tolerance and competitive ability are inversely related (Barbour 1978, LaPeyre et al. 2001), but application of this evidence to estuarine field distributions has not been experimentally examined. Based on our understanding of factors driving zonation patterns along vertical intertidal gradients, we hypothesize that biotic interactions play an important role in driving plant distribution patterns across horizontal estuarine salinity gradients; specifically, that interspecific competition may limit upriver distribution of saltmarsh plants.

Understanding plant segregation along salinity gradients is not simply a major gap in our knowledge of tidal wetlands; it is also crucial for both the conservation and restoration of coastal marsh systems. Without a mechanistic understanding of the processes that drive macrophyte distributions, we will not be able to predict accurately how wetland plant communities will respond to increasingly intense anthropogenic modification of coastal hydrologic regimes (e.g., freshwater diversions, sea level rise, and tidal restrictions).

In this paper, we document field distributions, quantify salt tolerances, and experimentally examine factors controlling the distributional limits of common marsh plants across southern New England estuarine salinity gradients.

METHODS

Study sites

Fieldwork for this study was carried out in marshes in Narragansett Bay, Rhode Island, USA. For saltmarsh sites, we worked at four marshes at the Narragansett Bay National Estuary Research Reserve on Prudence Island. These marshes have zones of dominant vegetation typical of southern New England salt marshes (Nixon 1982) that are exposed to full-strength sea water: 27–33 ppt (parts per thousand, micrograms NaCl per gram of water). For low-salinity tidal marsh sites, we worked on two tidal rivers, Barrington and Palmer, which drain into northern Narragansett Bay. Tidal freshwater sites were located in the uppermost tidal reaches of each river, where vegetation is typical of freshwater marshes (narrow-leafed cattail, *Typha angustifolia* L.; salt marsh bulrush, *Scirpus robustus* Pursh). Soil salinities at these sites varied from 0 to 10

ppt salt during our study. Intermediate salinity or brackish water marshes on each of the two rivers had a mixture of plants typically found in southern New England salt marshes (salt marsh hay, *Spartina patens* Ait (Muhl); spike grass, *Distichlis spicata* (L.) Greene) and plants typically found in New England freshwater marshes (*Typha angustifolia* and *Scirpus robustus*). The brackish water sites were ~1 km downriver from the freshwater sites; during our study, they had soil salinities ranging from 15 to 25 ppt. Salinity was measured weekly throughout the growing season by squeezing porewater from 2 × 2 × 2 cm blocks of substrate onto a hand-held NaCl refractometer (± g/kg). For the purpose of this study we call these tidal marshes salt, brackish, and fresh.

Estuarine marsh survey

In August 2001, we surveyed two representative marshes of each type, salt, brackish, and fresh, along each of the two rivers to quantify the distribution of wetland plants across the estuarine salinity gradient (four marshes per salinity in total). In each marsh, we ran 10 transect lines perpendicular to the main river channel and placed quadrats at 1-m intervals in the low marsh (defined as the area covered daily by the tide) and 2-m intervals in the mid marsh (low marsh border to upland edge, averaging 40 m total). Percent cover of all species within each 0.25-m² quadrat was measured by dividing the quadrat into 100 equal units, noting species presence in each unit and summing values for total percent cover of each species. Mean coverage of each species in the low and mid elevation for each of the 40 replicate transects was used to calculate marsh composition at each salinity.

To document species diversity patterns across salinity gradients, we examined vegetation within the *Spartina patens* zone, a dominant community type common to all the marshes studied, that also varies in species composition across salinity. Within this zone, we quantified percent cover, using the same method as just described, of all species in 50 randomly placed quadrats in the same four salt, brackish, and fresh marshes.

Greenhouse salt tolerance tests

We quantified interspecific differences in the salt tolerances of nine common marsh plants in the system. For these tests, plants of each species were collected from a single location in Narragansett Bay where that species was abundant, and then were reared in a greenhouse under a wide range of salinities. This technique does not take into consideration genetic, maternal, or acclimation effects on the salt tolerances of these plants (Hester et al. 1996), but does provide basic information on salt tolerance between species. The plants we tested were *Spartina patens*, *Typha angustifolia*, *Scirpus robustus*, *Salicornia europaea* L., *Juncus gerardii* Loiseleur, *Limonium nashii* Small, *Distichlis spicata*, *Solidago sempervirens* L., and *Potentilla anserina* L. For

the clonal turfs, we haphazardly collected young ramets from the field sites and transplanted size-standardized ramet units ($6 \times 6 \times 8$ cm for *Spartina patens*, *Juncus gerardii*, and *Distichlis spicata*, and $10 \times 10 \times 15$ cm for *Typha angustifolia* and *Scirpus robustus*) into pots in the greenhouse. For the remaining solitary plants, size-standardized juveniles (averaging $8 \times 8 \times 8$ cm) were collected and transplanted into greenhouse pots. We collected 100 replicates per species and grew the plants in the greenhouse for two weeks with fresh water to allow for acclimation to indoor conditions before exposing them to salinity treatments. We discarded plants that exhibited any transplanting stress and then randomly assigned eight replicate plants of each species to the following salinity treatments: 0, 10, 20, 30, 40, 50, 60, 70, 80, 90, and 100 ppt salt for a total of 88 replicates per species. For plants receiving high-salinity treatments, we gradually increased water salinity to avoid shock. When the experiment began, we brought all plants with salinity treatments >0 ppt to 10 ppt and maintained them there for three days; all plants with salinity treatments >10 ppt were then increased to 20 ppt. This process was repeated until all salinity treatments were in force. Soil salinity in the treatments was measured and adjusted daily. The experiment began in May 2002; the salinity treatments were in force by 1 June and were maintained for eight weeks.

To quantify the response of plants to salinity treatments over time, we scored the condition of every replicate weekly. Plants were given a score of 0, 25, 50, 75, or 100 based on percentage of green (live) plant tissue. After the eighth week, the experiment was terminated and aboveground biomass of all replicates was harvested, dried, and weighed. To examine variation in salt tolerance within and among species, we calculated the percentage of maximum biomass achieved for each replicate. For each species, we identified the replicate with the greatest biomass at the end of the salt tolerance trials and then calculated the percentage of the maximum biomass attained by each of the other replicates of that species. We normalized the data in this way because the final dry mass of the replicates varied by as much as three orders of magnitude between species (the clonal turfs weighed as much as 10 g, whereas the forbs weighed as little as 0.1 g). Expressing the transplant data as a percentage of maximum growth by species made it much easier to examine interspecific differences in salt tolerances.

Field transplant studies

We ran two separate field transplant studies to examine the roles of physical stress and interspecific competition in generating the distribution of marsh plants across southern New England estuarine salinity gradients. The first was a two-year experiment using dominant clonal turfs from both saltmarsh and freshwater marsh habitats. The second was a one-season experi-

ment using smaller transplants of many common plants in the system at marshes of different salinities: fresh, brackish, and salt. Combined, we studied transplants of 10 common species in the system.

Dominant turf transplant experiment.—For our large-scale clonal turf experiment, we conducted reciprocal transplants between saltwater and freshwater marshes at equivalent tidal elevations with neighboring native vegetation present and removed (with and without competition, respectively). The mid-elevation salt marsh dominant *Spartina patens* was exchanged with a mid-elevation dominant of low-salinity marshes, *Typha angustifolia*. In low marsh elevations, the salt marsh dominant *Spartina alterniflora* was exchanged with both *Typha angustifolia* and *Scirpus robustus*, two species that occur in areas of patchy dominance in low-elevation freshwater marshes. Within each species zone, we cut 24 blocks of substrate ($30 \times 30 \times 30$ cm) containing healthy emerging tillers of each of the target transplant species. These blocks were distributed evenly among three salinity treatments: for example, *Spartina patens* was transplanted to a fresh marsh *Typha angustifolia* zone (out fresh), salt marsh *Spartina patens* zone of origin (native), and another salt marsh *Spartina patens* zone as a transplantation control (out salt). Of the transplants, half were planted within created bare patches (no competition, $n = 4$) or vegetated patches (with competition, $n = 4$). We created bare patches (5×5 m) by removing all aboveground vegetation with a gasoline-powered weed-whacker and raking away the aboveground plant material. These large clearings were then covered with a commercial-grade weed cloth that limited the vegetative regrowth of the turf plants and effectively removed belowground root competition, but was water permeable (as in Bertness and Hacker 1994). Transplant blocks were planted flush with the substrate. This design was repeated with plants from each of the five dominant zones and was replicated at four marshes of each salinity. Plants were transplanted in April 2001 and were maintained until September 2002, when we harvested, dried, and weighed the aboveground biomass in the central 10×10 cm of each transplant.

Individual transplant experiment.—We carried out a second transplant experiment to expand the number of plant species included in our study. We created 3×3 m bare patches and 3×3 m control patches within *Spartina patens*-dominated mid-elevation marshes at four saltmarsh sites at Prudence Island and two brackish and freshwater marsh sites along each of the two rivers (for a total of four replicates of each marsh salinity within Narragansett Bay). Bare areas were treated with herbicide in the previous growing season to remove belowground competition from roots and were subsequently treated as in the transplant experiment just described. In April and May 2002, we transplanted the nine plant species used in our salt tolerance studies (using identical transplant units as in the greenhouse

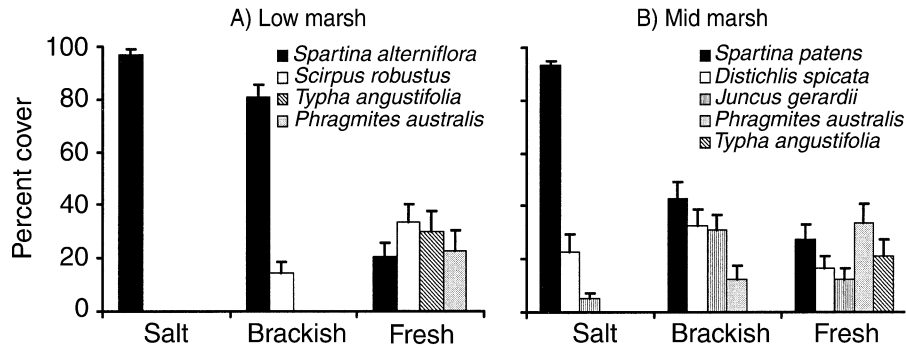


FIG. 1. Percent cover of dominant species in (A) low-elevation and (B) mid-elevation tidal salt, brackish, and fresh marshes. Data are shown as mean + 1 SE for 40 transects.

experiment) into each of these plots (four replicates per species per plot; total $n = 96$). During the first week after transplanting, plants were watered with fresh water to reduce transplant shock and any plants that died during this acclimation period due to transplanting were replaced. We monitored and maintained these transplants for three months, and in early August we harvested, dried, and weighed all of the transplants.

Statistical analysis

Biomass data from both the turf and individual transplant experiments were $\log_{10}(x + 1)$ -transformed when necessary to increase homogeneity of variance and normality and therefore meet the assumptions of ANOVA. Data were analyzed with JMP statistical software (SAS Institute 2001) and planned comparisons were performed using the linear-contrast feature of JMP. Turf and individual transplant experiments were analyzed as split-plot ANOVAs (as in Quinn and Keough 2002), where salinity was the between-plot factor, marsh was nested within salinity, and neighbor was the within-plot treatment. Salinity and neighbor were fixed factors, whereas marsh was a random factor. This analysis accounted for the spatial dependency of environmental variables being investigated as experimental treatments. In our case, salinity was segregated spatially and thus could be applied only on the whole-plot (marsh) level, with neighbor treatment applied within marshes.

RESULTS

Estuarine marsh survey

Marsh coverage by dominant clonal turfs varied dramatically across the estuarine salinity gradient (Fig. 1). In salt marshes, monospecific stands of *Spartina alterniflora* and *Spartina patens* covered nearly 100% of the low- and mid-elevation marsh, respectively. At low tidal levels, *Spartina alterniflora* remained dominant in brackish marshes, although it was interrupted by dense patches of *Scirpus robustus*, whereas in fresh marshes, *Spartina alterniflora* was rarely dominant and was replaced by monotypic patches of *Scirpus robustus*,

Typha angustifolia, and *Phragmites australis*. A similar pattern held in the mid-elevation marsh. *Spartina patens* dominated >96% of the mid zone in salt marshes, but was penetrated in brackish marshes by high abundance (20–30% coverage) of *Juncus gerardii* and *Distichlis spicata* and in fresh marshes by additional stands of *Typha angustifolia*, and *Phragmites australis*. This shift in dominant space holders in the varying salinity marshes is evidence of species zonation along the estuarine salinity gradient.

A second major pattern in plant community composition apparent in our field surveys was the significant increase in species diversity, both evenness and richness, as salinity decreased. Within the *Spartina patens* zone, low-salinity marshes had a higher abundance of grasses and forbs found rarely in salt marshes, in addition to a number of unique forbs, sedges, and grasses not found in salt marshes (Table 1). Within the *Spartina patens* zone, diversity, as assessed by the Shannon-Weiner Index (H'), was significantly influenced by salinity (one-way ANOVA, $F_{2,297} = 91.04$, $P < 0.0001$) and increased from salt ($H' = 0.12 \pm 0.013$) to brackish ($H' = 0.22 \pm 0.015$) to fresh ($H' = 0.39 \pm 0.016$) marshes.

In salt marshes, *Spartina patens* dominated in nearly monotypic stands penetrated only occasionally (2–15%) by the disturbance-generated guerrilla runner *Distichlis spicata*, patchy *Spartina alterniflora*, and low-density halophytic fugitive forbs *Limonium nashii* and *Salicornia europaea*. Although similar in appearance, the *Spartina patens* zone of a brackish marsh contained low densities (<5%) of an additional group of species more typical of low-salinity marshes, including *Scirpus robustus*, *Phragmites australis*, *Typha angustifolia*, *Solidago sempervirens*, and a greater abundance of *Juncus gerardii* than occurs in salt marshes, where it was restricted to the more physically benign high marsh. Finally, in the fresh marsh, the *Spartina patens* zone was peppered with a high abundance of forbs (*Solidago sempervirens*, *Potentilla anserina*, *Aster tenuifolius* L., *Rumex crispus* L., *Pluchea purpurascens* Swartz DC.), lone invaders from neighboring

TABLE 1. Composition of the *Spartina patens* zone in marshes of varying salinity, from two rivers draining into Narragansett Bay, Rhode Island, USA.

Species	Percent cover (mean \pm 1 SE) [†]		
	Salt	Brackish	Fresh
<i>Spartina patens</i>	98.6 \pm 0.04	89.8 \pm 0.15	80.3 \pm 0.12
<i>Distichlis spicata</i>	14.9 \pm 0.15	12.6 \pm 0.14	12.2 \pm 0.12
<i>Spartina alterniflora</i>	8.9 \pm 0.13	2.12 \pm 0.086	1.39 \pm 0.04
<i>Limonium nashii</i>	0.388 \pm 0.009	0.0	0.0
<i>Salicornia europaea</i>	1.79 \pm 0.03	0.402 \pm 0.02	0.0
<i>Juncus gerardii</i>	0.255 \pm 0.02	3.95 \pm 0.10	2.49 \pm 0.04
<i>Scirpus robustus</i>	0.0	2.32 \pm 0.05	2.85 \pm 0.03
<i>Phragmites australis</i>	0.0	1.88 \pm 0.07	5.66 \pm 0.06
<i>Typha angustifolia</i>	0.0	0.138 \pm 0.005	4.39 \pm 0.06
<i>Iva frutescens</i>	0.0	0.638 \pm 0.02	0.409 \pm 0.01
<i>Solidago sempervirens</i>	0.0	0.672 \pm 0.03	7.96 \pm 0.06
<i>Potentilla anserina</i>	0.0	0.0	4.12 \pm 0.04
<i>Aster tenuifolius</i>	0.0	0.0	1.30 \pm 0.01
<i>Festuca rubra</i>	0.0	0.0	5.61 \pm 0.05
<i>Rumex crispus</i>	0.0	0.0	0.257 \pm 0.01
<i>Panicum virgatum</i>	0.0	0.0	0.603 \pm 0.02
<i>Agrostis stolonifera</i>	0.0	0.0	6.8 \pm 0.05
<i>Carex hormathodes</i>	0.0	0.0	2.7 \pm 0.03
<i>Calystegia sepium</i>	0.0	0.0	0.8 \pm 0.01
<i>Eleocharis</i> sp.	0.0	0.0	1.1 \pm 0.02
<i>Pluchea purpurascens</i>	0.0	0.0	0.906 \pm 0.02

[†] Sample size is 200 quadrats.

zones (*Typha angustifolia*, *Scirpus robustus*, *Phragmites australis*), and patches of clonal graminoids in low abundance (*Juncus gerardii*, *Distichlis spicata*, *Festuca rubra* L., *Panicum virgatum* L.).

Greenhouse salt tolerance tests

Our greenhouse salt tolerance tests showed that the plants found in saltmarsh habitats were, in general, much more salt tolerant than plants found in freshwater marshes (Fig. 2). Of the saltmarsh plants, *Salicornia europaea* was the most salt tolerant, growing better at low salinities than in freshwater and growing well at salinities as high as 80 ppt. All of the other saltmarsh plants grew best in fresh water and their growth decreased markedly with increasing salinity. *Limonium nashii* and *Distichlis spicata* were also tolerant of high salinities; each of these salt marsh species survived eight weeks in the greenhouse exposed to salinities as high as 70 ppt. *Spartina patens* and *Juncus gerardii*, both dominant saltmarsh plants with distributions that extend well into brackish marshes, were the least salt tolerant saltmarsh plants. *Spartina patens* did not survive at salinities >60 ppt and *Juncus gerardii* did not survive at salinities >50 ppt. Of the freshwater marsh plants, *Potentilla anserina* was the least salt tolerant, not surviving at salinities >20 ppt. *Typha angustifolia* did not persist above 30 ppt; *Scirpus robustus* and *Solidago sempervirens* did not survive above 40 ppt. For saltmarsh species, survival at the highest salinities reached (70–80 ppt) generally meant severely stunted growth, but plants maintained >70% live green tissue. Conversely, freshwater marsh species growing at the highest salinities reached (20–40 ppt) had <25% live

tissue. Population persistence by freshwater marsh species at these salinities is doubtful, as suggested by field transplant studies, so survival at extreme salinities in the greenhouse may mean different things for saltmarsh and freshwater marsh species. Together these data show that although plants characteristic of salt marshes were capable of living across a wide range of salinities, plants characteristic of freshwater marshes could survive only at lower salinities.

Field transplant studies

Dominant turf transplant experiment.—Transplants of marsh dominants showed that all species grew best in fresh marshes when neighbors were removed, but that growth of saltmarsh species was severely suppressed (~90%) in the fresh marsh when neighbors were included (Fig. 3, Table 2). Additionally, fresh marsh species did not survive the physical conditions of the salt marsh regardless of neighbor treatment (Fig. 3, Table 2). Results from transplant controls (transplants to a second marsh with the same salinity as the marsh of origin) for each of the five species tested were not significantly different from native marsh controls. This confirms that results were due to experimental treatments and not to transplanting per se. Transplant controls were thus removed from the analysis for simplicity.

Low- and mid-elevation *Typha angustifolia* blocks transplanted to equivalent elevations in salt marshes were almost entirely dead within two months of transplanting and were completely absent after two growing seasons. *Scirpus robustus* transplanted to the salt marsh persisted slightly longer, but was effectively gone with-

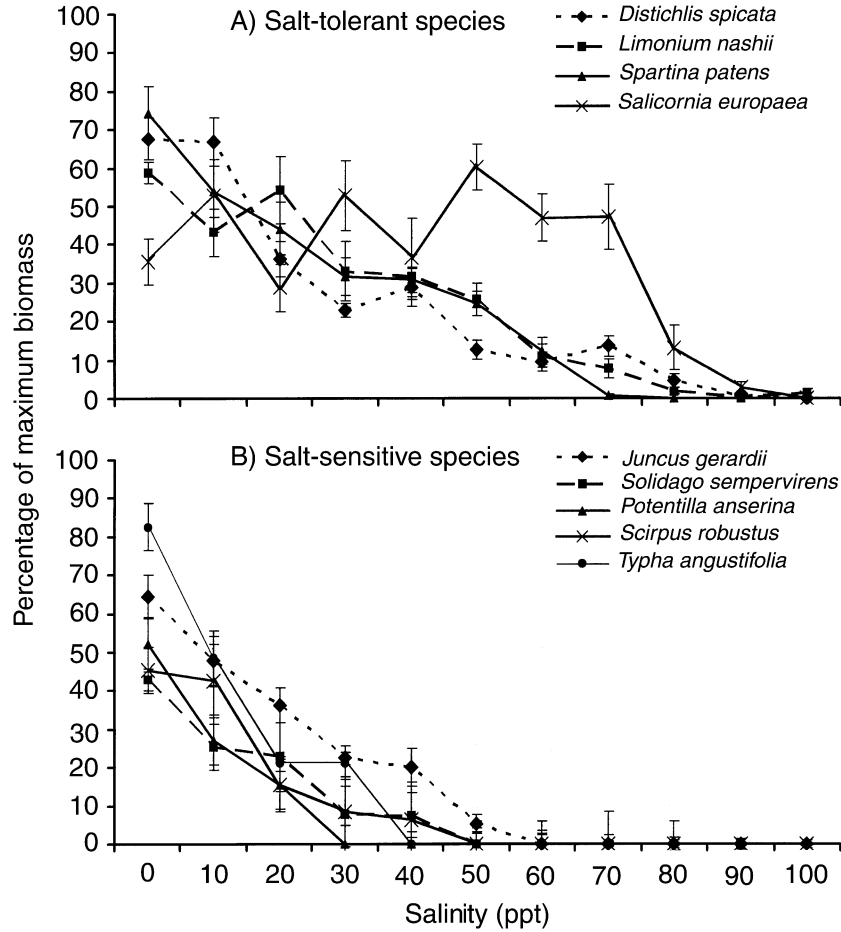


FIG. 2. Standardized biomass at varying salinities (parts per thousand; micrograms NaCl per gram water) of common coastal marsh species that are relatively (A) salt tolerant and (B) salt sensitive, based on greenhouse performance and field distributions. Data are shown as mean \pm 1 SE for $n = 8$ individuals per species.

in the first summer. Conversely, *Spartina patens* transplanted to the freshwater marsh with neighbors removed grew as well or better than in the no-neighbor saltmarsh treatments (linear contrast, $F_{1,6} = 3.9$, $P = 0.09$), but was almost entirely absent (90% suppressed) when neighbors were included (linear contrast, fresh marsh transplants with and without neighbors, $F_{1,6} = 62.8$, $P = 0.0002$). Based on allometric regressions after the first growing season, *Spartina patens* within freshwater *Typha angustifolia* stands etiolated, gaining nearly twice the height per biomass as *Spartina patens* in saltmarsh treatments (C. M. Crain, B. R. Siliman, S. L. Bertness, and M. D. Bertness, unpublished data). These tall, weak transplants were buried over the winter by dead *Typha angustifolia* wrack so that most transplants were dead by the second growing season. *Spartina alterniflora* followed a similar pattern when transplanted into the low-elevation fresh marsh; it achieved high biomass when neighbors were experimentally removed and was almost completely suppressed in neighbor-intact treatments (93% and 90%

suppressed in *Typha angustifolia* and *Scirpus robustus* stands, respectively).

Individual transplant experiment.—Results from transplants of individuals of nine species into common gardens along the salinity gradient provided further evidence that all species grew optimally in the freshest marshes with neighboring vegetation removed, but that competitive suppression by surrounding vegetation was strongest in these marshes (Table 3, Fig. 4). Similar to results from the turf transplant experiment, the interaction term (salinity \times neighbor) in the individual transplant experiment was highly significant for eight of the nine species investigated (Table 3), showing that the effect of neighbors on plant performance varied with salinity. Competitive release was much more important in fresh marshes than in salt marshes, where the stressful physical environment limited growth even in neighbor removals. Competitive release in saltmarsh treatments was only exhibited by the most salt-tolerant species in the study: *Limonium nashii*, *Salicornia europaea*, and *Distichlis spicata* (Fig. 4).

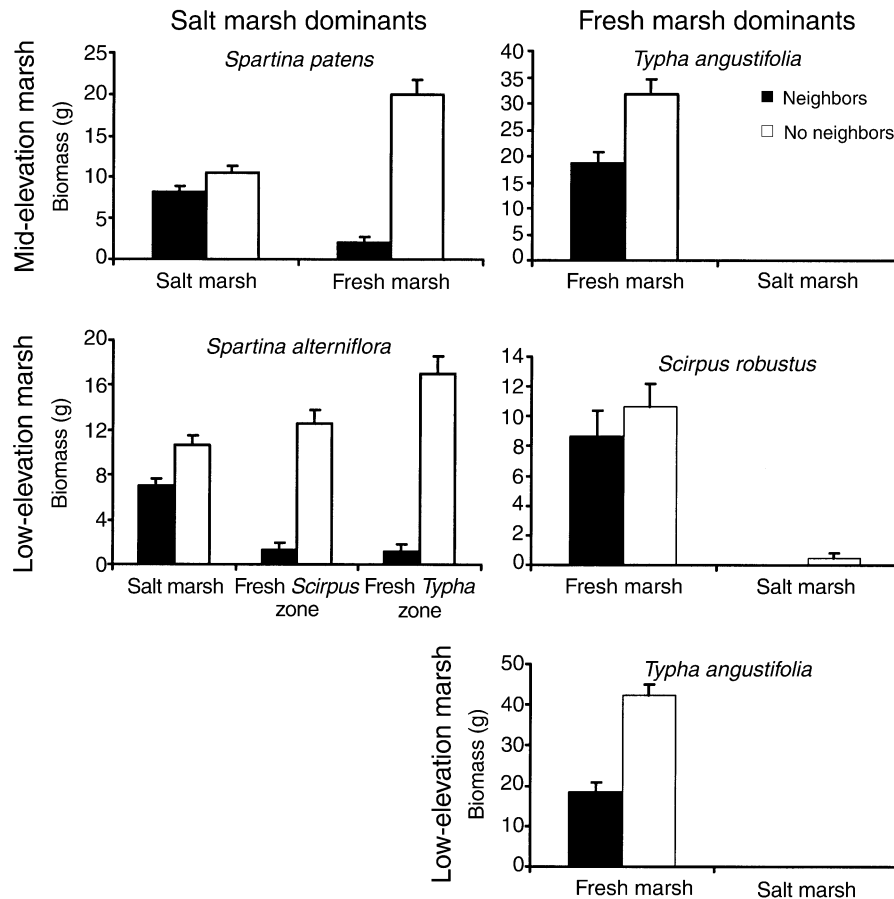


FIG. 3. Aboveground biomass harvested after two growing seasons from the central 10×10 cm of large turf transplants of five dominant species in salt and freshwater tidal marshes. Data are shown as mean + 1 SE for 16 replicates per treatment.

DISCUSSION

Our work demonstrates that biotic interactions, in addition to physical factors, play a key role in driving plant distribution patterns along estuarine salinity gradients, contrary to the generally accepted notion that marsh plants are found in habitats where they grow best. Instead, our results suggest that freshwater marsh plants are restricted from saltmarsh habitats by physical factors, but are competitive dominants in low-salinity marshes. Salt-tolerant species are thereby displaced from fresh marshes, where they grow best in the absence of competition, to salt marshes, where they are able to persist in competitive refuge.

Salt tolerance and species distributions

Results from our greenhouse study confirmed previous findings (e.g., Barbour and Davis 1970, Bertness et al. 1992) that coastal plants have varying responses to salinity (generally evidenced by variation in the maximum salinity at which survival is possible), but they also overwhelmingly grow best in fresh water. For example, in a survey of salt tolerance of 31 coastal plants in New Zealand, Partridge and Wilson (1987)

found that all but one species reached its maximum growth at salinities below 10 ppt and that 23 species grew best in totally fresh water. In our greenhouse study, none of the species tested required salt to survive and all but *Salicornia europaea* grew best and reached maximum biomass in entirely fresh water.

Field surveys of Narragansett Bay showed that the species most able to tolerate high salt levels in the greenhouse corresponded to the plants found in the most seaward and high-salt environments of the Bay. Field surveys also illustrated that concurrent with decreasing salinity in upriver marshes comes both a shift in identity of dominant plant species and an increase in species diversity within dominant zones. Greenhouse results suggested that saltmarsh species do not grow optimally in salty environments, so salt tolerance does not explain the limits to upriver distribution of these species. A study by Wilson et al. (1996), using nine common riverbank species, found that downstream distributional limits of these plants were good predictors of salinity tolerance (explaining 64% of the variation in tolerance), whereas upstream distributions were not significantly related to salt tolerance. The Wilson et al.

TABLE 2. Statistical summary of the dominant turf transplant experiment showing results of split-plot ANOVA testing effects of salinity (S), marsh nested in salinity (M(S)), neighbor (N), and salinity \times neighbor interaction on above-ground biomass of the five dominant species tested.

Species and Source of Variation	df	F	P
<i>Spartina patens</i>			
S	1, 6	3.76	0.1005
M(S)	6, 50	3.59	0.0049
N	1, 50	111	<0.0001
S \times N	1, 50	76.8	<0.0001
Mid <i>Typha angustifolia</i>			
S	1, 6	990.8	<0.0001
M(S)	6, 53	1.937	0.0921
N	1, 53	13.9	0.0005
S \times N	1, 53	13.9	0.0005
<i>Spartina alterniflora</i>			
S	1, 10	20.5	0.0011
M(S)	10, 82	1.77	0.0783
N	1, 82	138	<0.0001
S \times N	1, 82	72.2	<0.0001
<i>Scirpus robustus</i>			
S	1, 6	219	<0.0001
M(S)	6, 53	1.75	0.1286
N	1, 53	2.23	0.1411
S \times N	1, 53	0.11	0.7424
Low <i>Typha angustifolia</i>			
S	1, 6	4225	<0.0001
M(S)	6, 53	0.72	0.6345
N	1, 53	48.8	<0.0001
S \times N	1, 53	48.8	<0.0001

(1996) study and results from our greenhouse study suggest that tolerance to salinity stress may be important in determining a species' downstream distributional limit, but it does not sufficiently explain a species' upriver distributional limit.

Seaward distribution of estuarine vegetation

Field experiments corroborated the untested assumption that coast-ward distribution of estuarine vegetation is limited by tolerance to physiological stressors in high-salinity marshes. In the turf transplant experiment, freshwater marsh dominants *Typha angustifolia* and *Scirpus robustus* had substantially decreased photosynthetic rates (C. M. Crain, B. R. Silliman, S. L. Bertness, and M. D. Bertness, unpublished data) within two weeks of transplanting to equivalent tidal elevations in salt marshes and were dead within two months. Similar results were found for smaller units of four salt-sensitive species (*Scirpus robustus*, *Typha angustifolia*, *Solidago sempervirens*, and *Potentilla anserina*) when transplanted to salt marshes. In both of these experiments, plant performance in saltmarsh treatments was not influenced by neighboring vegetation, because transplants died regardless of neighbor treatment. Therefore, physiological tolerance rather than biotic interactions is responsible for limiting the seaward limits of these species. Of the species tested, the perennial

TABLE 3. Results of split-plot ANOVA testing effects of salinity (S), marsh nested in salinity (M(S)), neighbor (N), and salinity \times neighbor interaction on above-ground biomass of individual transplants of nine common coastal species transplanted to salt, brackish, and fresh tidal marshes.

Species and Source of Variation	df	F	P
<i>Distichlis spicata</i>			
S	2, 9	5.62	0.03
M(S)	9, 81	1.70	0.10
N	1, 81	156.65	<0.0001
S \times N	2, 81	13.35	<0.0001
<i>Juncus gerardii</i>			
S	2, 9	14.16	<0.01
M(S)	9, 81	2.31	0.02
N	1, 81	35.05	<0.0001
S \times N	2, 81	15.37	<0.0001
<i>Limonium nashii</i>			
S	2, 9	4.34	0.05
M(S)	9, 80	0.56	0.83
N	1, 80	52.48	<0.0001
S \times N	2, 80	2.17	0.12
<i>Spartina patens</i>			
S	2, 9	22.73	<0.01
M(S)	9, 79	1.64	0.12
N	1, 79	100.69	<0.0001
S \times N	2, 79	30.21	<0.0001
<i>Potentilla anserina</i>			
S	2, 9	28.14	<0.01
M(S)	9, 80	1.81	0.08
N	1, 80	25.63	<0.0001
S \times N	2, 80	19.37	<0.0001
<i>Salicornia europaea</i>			
S	2, 9	1.44	0.29
M(S)	9, 78	3.13	<0.01
N	1, 78	34.67	<0.0001
S \times N	2, 78	6.72	<0.01
<i>Scirpus robustus</i>			
S	2, 9	18.99	<0.01
M(S)	9, 79	2.01	0.05
N	1, 79	42.87	<0.0001
S \times N	2, 79	12.86	<0.0001
<i>Solidago sempervirens</i>			
S	2, 9	107.41	<0.0001
M(S)	9, 80	0.66	0.74
N	1, 80	55.34	<0.0001
S \times N	2, 80	25.67	<0.0001
<i>Typha angustifolia</i>			
S	2, 9	12.80	<0.01
M(S)	9, 79	3.06	<0.01
N	1, 79	76.32	<0.0001
S \times N	2, 79	20.26	<0.0001

forbs *Solidago sempervirens* and *Potentilla anserina* were least able to tolerate salt; even in transplants to brackish marshes, these two species performed poorly regardless of neighbor treatment, indicating that physiological stress was still limiting their occurrence in these intermediate-salinity marshes.

Although the precise physiological stressor limiting seaward plant distributions was not explicitly tested in this study, our lab data and field monitoring suggest

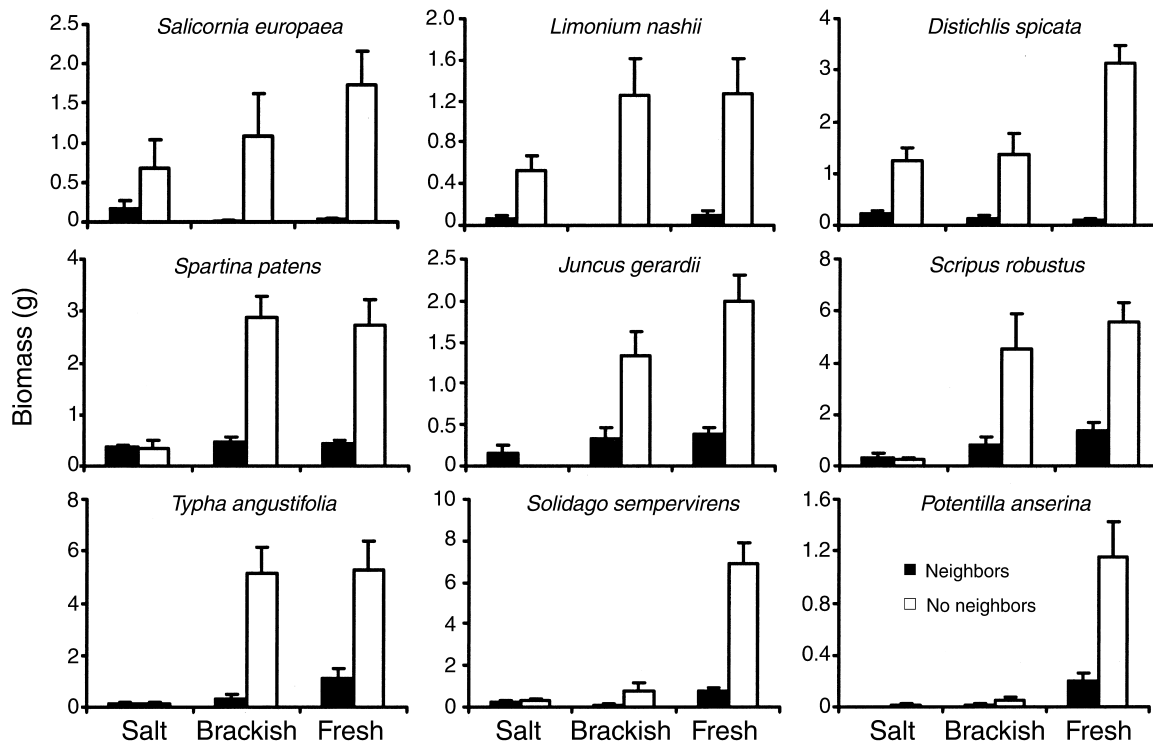


FIG. 4. Aboveground biomass of nine common coastal marsh species transplanted to salt, brackish, and fresh tidal marshes with and without neighboring vegetation. Data are shown as mean + 1 SE for 16 individuals per treatment. Graphs are grouped with more salt-tolerant species in the upper left and more salt-sensitive species in the lower right.

that salinity is likely to be one major component. Salinity tolerance matches closely with downriver distribution limits and salinity is a known stressor to terrestrially derived angiosperms (Adam 1990, Bertness 1999). Other stressors that potentially contribute to physiological limitations include sulfides and waterlogging, and these may vary across salinity gradients despite similar tidal regimes. In brackish and tidal freshwater marshes, soils become more porous and less waterlogged (C. M. Crain, *personal observation*), organic matter increases (Latham et al. 1991), and redox potentials increase (*unpublished data*). Additionally, pore-water sulfide concentrations that are quite high in salt marshes (e.g., King et al. 1982) and toxic to plants (Bradley and Dunn 1989, Koch et al. 1990) are lower in brackish and tidal freshwater marshes (C. M. Crain, *unpublished data*). Waterlogging and sulfide levels could work synergistically or interactively with salinity in limiting seaward plant distributions, but these specific mechanisms remain to be tested.

Upriver distribution of estuarine vegetation

Transplant studies confirmed the results from the greenhouse that, in the absence of competition from neighboring vegetation, all 10 species tested grew best in the freshest marshes. Transplant experiments also demonstrated that competitive suppression of all species was strongest in the fresh marsh, and that for salt-

marsh species, the suppression was complete. Together, these results indicate that upriver distribution of estuarine vegetation is restricted by competitive interactions with other plant species.

In the study of marsh dominants, large turf blocks of *Spartina alterniflora* and *Spartina patens* transplanted into fresh marshes survived and thrived in the absence of neighboring vegetation, gaining biomass far exceeding that of control transplants into native salt marshes. However, the same turf blocks transplanted at equivalent tidal elevations into stands of *Scirpus robustus* and *Typha angustifolia*, freshwater marsh dominants, were entirely suppressed after two growing seasons. These results indicate that competitive exclusion by freshwater marsh dominants restricts saltmarsh species from living in fresh marshes where they could potentially perform better. The specific mechanism of competitive exclusion, be it for belowground nutrients or water, or for aboveground light resources, was not explicitly tested. However, the high aboveground biomass achieved by both *Typha angustifolia* and *Scirpus robustus* stands bestows an apparent light-capturing advantage on these species. Additionally, nutrients may be less of a limiting factor in low-salinity marshes. Although the limiting belowground resource in oligohaline marshes has not been investigated, substantial evidence shows nitrogen limitation in saltmarsh systems (Valiela and Teal 1974, Morris 1991). Experi-

mental evidence demonstrates that nitrogen uptake ability by plants increases in less saline environments (Morris 1984, Bradley and Morris 1991) so available nutrients may be more accessible to plants in these marshes, relieving competition for belowground resources.

The individual transplants showed that, for all nine species, the intensity of competition, or the difference between biomass achieved in the absence of competitors minus that achieved with competitors present, increases dramatically as salinity decreases. Despite the short duration of this experiment, competitive suppression of the salt-tolerant species *Salicornia europaea*, *Limonium nashii*, and *Distichlis spicata* was nearly complete, indicating that these species are generally restricted from these marshes by competitive displacement. Thus, competition with neighboring vegetation in the relatively more benign physical conditions of low-salinity marshes plays a dominant role in structuring the vegetative community. The paradox of greater plant diversity where competitive intensities are highest remains to be investigated.

Generality and conservation implications

Experimental studies have established that trade-offs in competitive ability and stress tolerance along vertical stress gradients result in species zonation in salt marshes (Vince and Snow 1984, Bertness and Ellison 1987, Bertness 1991a, b), freshwater marshes (Grace and Wetzel 1981), and rocky shores (Little and Kitching 1996, Raffaelli and Hawkins 1996, Bertness 1999). The current study along a horizontal, landscape-scale, and more diffuse environmental gradient shows that plant distributions are set at the coastal extreme by tolerance to physiological stress and at the inland extreme by competitive ability. This suggests that ecological concepts developed over steep vertical gradients may hold true at larger spatial scales. Together these experimental studies support the general assertion that dominant competitors monopolize more benign habitats and displace inferior competitors to physically stressful environments. Current models of estuarine plant zonation must be modified to reflect the fact that species are not growing in the environmental conditions to which they are maximally adapted, but that saltmarsh species are restricted to high-salinity marshes as refuges from competition.

The mechanistic understanding of estuarine plant distribution patterns developed in this study is critical knowledge for improving the conservation and restoration of the full range of tidal marsh communities. Numerous anthropogenic impacts alter physical conditions (i.e., tidal restrictions, dams, sea level rise, or freshwater diversions) and competitive dynamics (i.e., eutrophication and invasive species) in coastal estuaries, thus influencing the forces that structure plant distribution along this gradient. Understanding estuarine plant response to the interactive effects of altered

physical and biotic environments is only possible with this baseline understanding of the forces that structure native plant distributions.

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