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Zonation of shrubs in western Atlantic salt marshes

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Abstract We explored the generality of the processes mediating shrub zonation in western Atlantic salt marshes by comparing the results of our experiments in Georgia, USA with previous studies from Rhode Island, USA. The shrub *Borrichia frutescens* dominates the terrestrial border of many Georgia salt marshes. Within the shrub zone, physical stress increased at lower elevations, shrubs at lower elevations were stunted, and experimentally reducing physical stress reduced shrub stunting. Below the shrub zone, physical stress increased further, and the grass *Spartina alterniflora* dominated. Transplant and neighbor-removal experiments indicated that the lower border of the shrub zone was set more by physical stress than by competition, but that the upper border of the grass zone was set primarily by competition with shrubs. Laboratory experiments indicated that *S. alterniflora* seedlings survived best and shrub seedlings worst in the flooded, salty treatment that mimicked low-marsh conditions. These processes are similar to those maintaining zonation patterns between the shrub *Iva frutescens* and the rush *Juncus gerardi* in Rhode Island salt marshes. However, markedly different processes appear to occur further to the north, where woody shrubs are absent from coastal marshes, and further to the south, where woody plants (mangroves) dominate coastal wetlands.

Keywords Competition · Generality · Physical stress · Salt marsh · Zonation

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Introduction

Ecological field studies are haunted by questions of generality (Diamond 1986; Keddy 1989a). Although the danger of over-generalizing limited experimental results into paradigms is well known (Underwood and Denley 1984), most field experiments are so labor-intensive that they are never repeated. The problem with assessing the generality of field studies is complicated by evidence that experimental results often change as a function of abiotic conditions (Moloney 1990; Dunson and Travis 1991; Goldberg and Barton 1992; Bertness and Hacker 1994; Thrush et al. 2000). Here, we repeat in Georgia a suite of experiments that were originally conducted in Rhode Island, to see if similar results would obtain despite a markedly different climate.

We focused on patterns of shrub zonation in coastal salt marshes. Because salt marshes display distinct plant zonation patterns across compact physical gradients (Chapman 1960; Ranwell 1972), they are attractive systems for experimentally examining the relative roles of physical factors and biotic interactions in determining vegetation patterns. Recent studies of the zonation patterns of salt marsh vegetation, mostly conducted at high latitudes, have suggested that lower limits of zones are set primarily by tolerance to physical stress, and upper limits by competition (Snow and Vince 1984; Bertness and Ellison 1987; Bertness 1991a, b; Bertness et al. 1992). Studies of southern marsh communities, however, often note important differences in pattern and process compared to northern marshes (Pennings and Callaway 1992; Nomann and Pennings 1998; Pennings and Richards 1998). Thus, it is unclear how far we can safely generalize our current understanding of salt marsh plant zonation patterns (Pennings and Bertness 1999, 2000; Bertness and Pennings 2000).

Typically, temperate western Atlantic salt marshes from Florida to Cape Cod are dominated by grasses and rushes, with a border of shrubs at the landward margin. In southern New England, the shrub *Iva frutescens* forms a distinct zone at the landward margin of coastal marshes

Table 1 Hypotheses about zonation of shrubs and monocotyledons in salt marshes on the east coast of the United States

Hypothesis	RI result (reference)	GA result (source)
Size gradients within the shrub zone		
Physical stress increases at lower elevations	Yes [a,b,c]	Yes (Fig. 2, Table 2)
Shrubs are stunted at lower elevations	Yes [a,b]	Yes (Fig. 2, Table 2)
Reducing physical stress reduces stunting	Yes [a,c]	Yes (Fig. 3)
Shrub zonation patterns		
Shrub zone is less stressful than lower plant zones	Yes [a,b,d]	Yes (Fig. 4, Table 3)
Shrub zone lower border is set primarily by physical stress	Yes [a,d]	Yes (Figs. 5, 6)
Grass/rush zone upper border is set primarily by competition	Yes [b]	Yes (Figs. 5, 6)
Relative stress tolerance of shrubs versus grasses and rushes		
Shrubs are less tolerant of physical stress than are grasses and rushes	Yes [a]	Yes (Fig. 7, Table 4)

[a] Bertness et al. (1992)
[b] Bertness and Hacker (1994)
[c] Hacker and Bertness (1995)
[d] Hacker and Bertness (1999)

(Bertness et al. 1992; Bertness and Yeh 1994). In southeastern marshes, a similar shrub zone is dominated by *Borrichia frutescens*, with *Iva frutescens* occurring as scattered individuals. The factors controlling the zonal distribution of marsh shrubs have been studied only in Rhode Island, with three general results (Table 1). First, marked gradients in shrub size within the shrub zone are caused by increasing physical stress at lower elevations. Second, the lower limit of the shrub zone is primarily set by physical stress, but the upper limit of the grass/rush zone is primarily set by competition with shrubs. Third, in the laboratory, shrubs are less tolerant of physical stress than are grasses and rushes. Whether these results from New England provide a general explanation for zonation of salt marsh shrubs at other locations is not known.

Here, we examine the factors determining the zonation of the shrub *Borrichia frutescens* and the grass *Spartina alterniflora* in Georgia salt marshes. We tested a series of hypotheses based on previous results from Rhode Island, using a combination of observations, field experiments and laboratory experiments. Our results suggest that the mechanisms determining zonation patterns of salt marsh shrubs are similar between Rhode Island and Georgia.

Materials and methods

Study sites

Research was conducted on Sapelo Island, Ga. (Fig. 1 A). The marshes around Sapelo Island are typical of southeastern coastal salt marshes (Weigert and Freeman 1990). The terrestrial border of the high marsh is dominated by *Borrichia frutescens* and/or *Juncus roemerianus*. "Salt meadow" species, *Batis maritima, Distichlis spicata* and *Salicornia virginica,* may occur at medium to high elevations associated with hypersaline soils. The cordgrass *Spartina alterniflora* dominates lower elevations of the marsh. We refer to these plants by their generic names hereafter.

Not all plant species occur at every site. For simplicity, we focused on five sites dominated by *Borrichia* and *Spartina* (Fig. 1B). At most of these sites, *Borrichia* and *Spartina* directly bordered each other (Fig. 1C). At the East Lighthouse site, a band of *Distichlis* about 20 m wide occurred between the *Borrichia* and

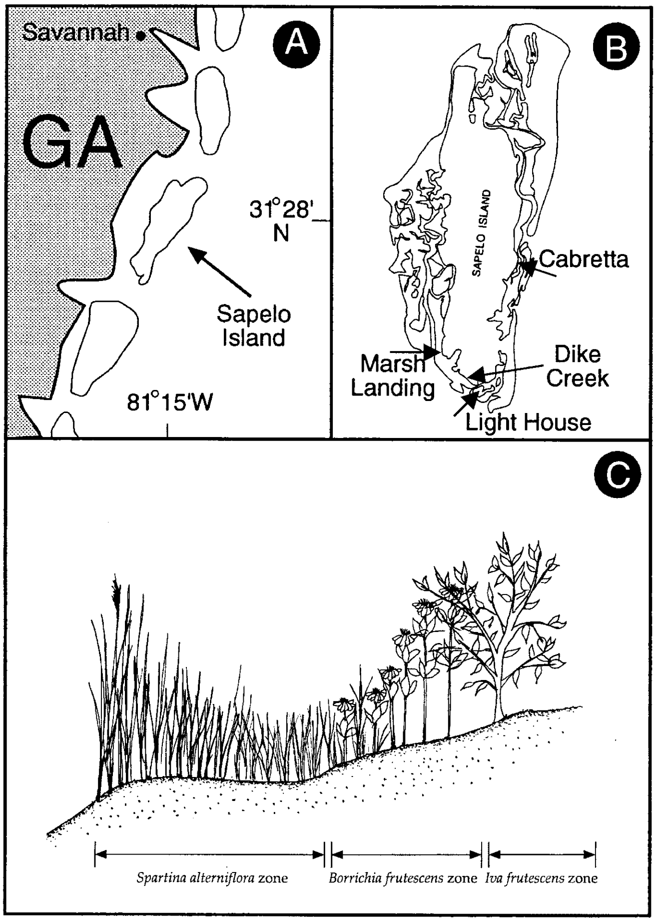

Fig. 1 **A** Location of Sapelo Island, Ga. **B** Location of study sites (East and West Lighthouse sites are indicated together by a *single arrow*). **C** Typical zonation pattern at sites lacking *Juncus roemerianus* and salt meadow species. Horizontal extent of zones differs considerably between sites, but values of 100–400 m for the *Spartina* zone, 5–20 m for the *Borrichia* zone, and 0.5–2 m for the *Iva* zone are typical

Spartina zones. At the Marsh landing site, *Borrichia* stands also occurred on small hummocks scattered throughout the salt pan (Antlfinger 1981).

Variation in physical stress and plant size within the shrub zone

We documented variation in physical stress and plant size (height and number of leaves) within the shrub zone at three sites: West Lighthouse, Cabretta and Marsh Landing (Fig. 1B). At the first two sites we sampled *Borrichia* plants at 24 evenly spaced locations along a transect through the shrub zone. At Marsh Landing, we sampled the center and edge of ten hummocks dominated by *Borrichia*. Sampling was done at low tide in the summer of 1994. Soil redox potential (an indicator of oxygen availability) at 8 cm depth was determined with an Orion redox meter. Water content of surface (top 5 cm) soils was determined gravimetrically, and soil salinity determined by rehydrating dried soils in a known volume of deionized water, stirring, and reading the salinity of the supernatant after 2 days with a refractometer. Readings were corrected to the volume of water originally present in the soil sample. To evaluate water table depth, 3–4 pits were dug at the low and high extents of the *Borrichia* zone at Lighthouse and Cabretta, and the depth of the water table below the soil surface measured on the following day.

To determine if improved drainage would increase growth of stunted *Borrichia* plants, we dug 30-cm-deep drainage ditches from a creek at the Dike Creek site to stunted *Borrichia* plants located 2–3 m away from the creek bank. Ditches were located about 30 cm from experimental plants and >3 m from control plants. Plants were individually tagged (*n* =18/treatment) and measured (height, number of leaves), and ditches dug on 11 April 1995. Ditches were maintained weekly until final data were collected, 16 months later, on 15 August 1996.

Borrichia–Spartina zonation

To explore the importance of competition and physical factors in determining the zonation pattern of *Borrichia* and *Spartina*, we transplanted both species into their own and the other species' zones at the West Lighthouse marsh. Single culms of *Spartina* and single stems of *Borrichia* were transplanted between the middle of the *Spartina* zone and the middle of the *Borrichia* zone (about 130 m inland and 20 cm higher than the *Spartina* zone) on 27 April 1994. In each case, 8 replicates were transplanted back into the original zone, and 16 into the other species' zone. Half of the latter 16 were assigned to a neighbors-removal treatment. Neighbors were removed by periodic clipping at the soil surface inside a 0.5×0.5 m plot centered on the target plant.

To monitor water table depth, we dug eight pits in each zone to a depth of 80 cm. The depth of the water table was measured at low tide at 1- to 2-week intervals between 5 May and 25 August 1994 (*n*=15 dates). We also measured the salinity of surface (top 5 cm) soils, redox, and percolation rates adjacent to transplanted plants on up to four dates between May 1994 and July 1995. Methods were as described above for soil salinity and redox (*n*=7–8/zone/date). Percolation rates (ml/min) were determined by inserting bottomless graduated cylinders 2 cm into the soil, filling with water, and observing how much water drained per unit time (*n*=5–8/zone/date). Plant survival was scored after 26 months, on 6 June 1996, and plants were harvested, dried at 60°C and weighed.

To ensure that the results of this experiment were not biased by artifacts of the transplantation process, we conducted a parallel experiment that took advantage of the fact that occasional *Borrichia* and *Spartina* plants occurred at low densities in the other species' zone. We located 24 isolated *Spartina* culms in the *Borrichia* zone, and 26 isolated *Borrichia* stems in the upper end of the *Spartina* zone. In each case, half of the plants were assigned to control and half to neighbor-removal treatments. Neighbors were removed by periodic clipping at the soil surface inside a 0.5×0.5 m plot centered on the target plant, starting on 17 February 1995. Plants were harvested on 17 June 1996, after 16 months, dried at 60°C and weighed.

We similarly located twenty 0.5×0.5 m plots containing low densities of stunted *Borrichia* stems in the *Distichlis* zone at the East Lighthouse site, and assigned 10 plots each to control and *Distichlis*-removal treatments. Neighbors were removed on 8 April 1994, and treatments maintained by periodic clipping. On 10 December 1995, 20 months later, all *Borrichia* plants in each plot were harvested, dried at 60°C and weighed.

Relative stress tolerance of *Borrichia* and *Spartina*

To compare the influence of salinity and flooding on the survival and growth of seedlings of *Borrichia* and *Spartina*, we conducted a "greenhouse" experiment using an outdoor table shielded by a clear plastic roof to protect plants from rainfall. Seedlings of each species were germinated from seeds in a 1:1:1 mixture of potting soil, vermiculite, and marsh soil and watered with fresh water for 1 week. Once treatments were initiated on 19 April 1995, pots were watered 3 times per week with fresh water or with sea water (salinity ca. 25 ppt). Pots were either saturated with water and then allowed to drain (drained treatment) or were maintained with the water level flush with the soil surface (flooded treatment). Initial sample sizes ranged from 9 to 20 plants/species per treatment, depending upon availability of seedlings. Survival was scored after 2 months, on 19 June 1995, and aboveground biomass was dried at 60° and weighed.

Results

Variation in physical stress and plant size within the shrub zone

The shrub zone spanned ca. 30 cm in elevation at Lighthouse and Cabretta (Fig. 2). At Marsh Landing, the centers of hummocks dominated by shrubs were 15±2 (SE) cm higher than their edges. Redox potential increased with elevation at all three sites (Fig. 2A, Table 2). Soil salinity decreased with increasing elevation at Lighthouse and Marsh Landing, but not at Cabretta (Fig. 2B, Table 2). The water table was almost twice as deep at the upper end of the shrub zone as in the lower end [Lighthouse: –36± 2 (SE) cm vs –18±1, *P*=0.0001; Cabretta: –79±3 vs –47±0.4, *P*=0.007]. *Borrichia* height and leaf number increased with increasing elevation at all sites (Fig. 2C, D, Table 2).

Improving soil drainage improved growth of stunted *Borrichia*. Due to seasonal changes in leaf number, all plants had fewer leaves at the end than at the start of the experiment; however, plants adjacent to experimental ditches grew taller and lost fewer leaves than did control plants (Fig. 3).

Borrichia–Spartina zonation

Soils were generally more favorable for plant growth in the *Borrichia* zone than in the *Spartina* zone. The water table was deeper in the *Borrichia* zone than the *Spartina* zone on all dates and overall (*Spartina* average –19 cm±1.7 (SE); *Borrichia* –41 cm±1.6, Fig. 4 A, Ta-

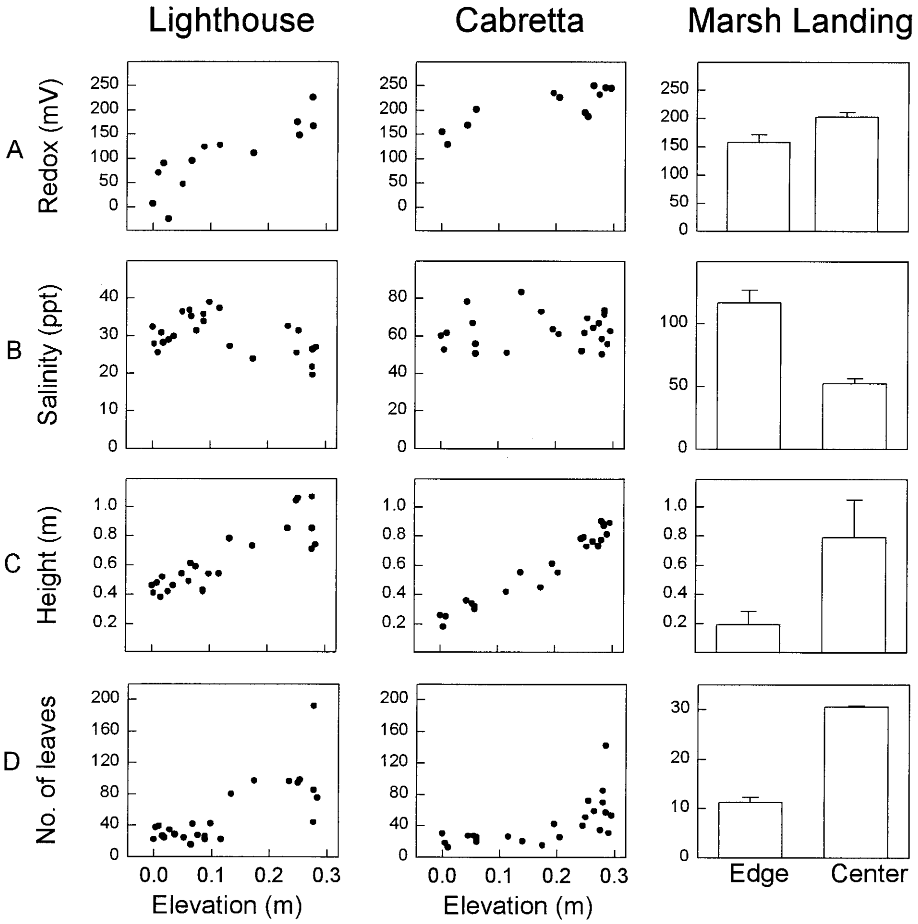

Fig. 2 Variation in physical stress and plant size on transects through the *Borrichia* zone at West Lighthouse and Cabretta, and at the edge and center of *Borrichia*-dominated hummocks in the salt pan at Marsh Landing. Elevation of the lowest *Borrichia* plant at each site was arbitrarily set to zero. At marsh landing, center plants were 0.15±0.06 (SD) m higher in elevation than edge plants. *Bar graphs* present means±1 SE; statistical tests are reported in Table 2

Table 2 Physical stress and plant size in the *Borrichia* zone at three sites (data shown in Fig. 2). At the Lighthouse and Cabretta sites, all variables are regressed against elevation. At the Marsh Landing site, variables are compared with *t*-tests between the edge and center of hummocks dominated by *Borrichia*

Variable	Lighthouse		Cabretta		Marsh Landing	
Physical stress						
Redox	r^2=0.70	*P*=0.0002	r^2=0.65	*P*=0.001	*t*=2.95	*P*=0.02
Salinity	r^2=0.17	*P*=0.026	r^2=0.04	*P*=0.18	*t*=6.12	*P*=0.0002
Plant size						
Height	r^2=0.74	*P*<0.0001	r^2=0.95	*P*<0.0001	*t*=25.72	*P*<0.0001
Number of leaves	r^2=0.54	*P*<0.0001	r^2=0.38	*P*=0.0008	*t*=7.70	*P*<0.0001

ble 3). Soil salinities were higher in the *Borrichia* zone than in the *Spartina* zone on one date, but redox levels and percolation rates were higher in the *Borrichia* zone on most dates (Fig. 4B–D, Table 3). Most edaphic variables differed between sampling dates (probably as a function of variation in tidal flooding and rainfall), and the magnitude of the differences between zones also often differed between dates.

Results of the transplant experiment suggested that competition strongly affected the upper limit of *Spartina*. *Spartina* plants transplanted to the *Borrichia* zone survived well if neighbors were removed but died if *Borrichia* neighbors were present (Fig. 5 A). In contrast, *Borrichia* plants transplanted to the *Spartina* zone survived poorly regardless of whether or not neighbors were present (Fig. 5A), although the two surviving plants

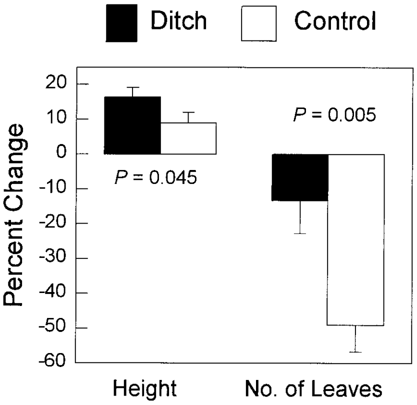

Fig. 3 Effect of improving drainage by ditching on performance of stunted *Borrichia*. Data (percent change in height and number of leaves) are means±1 SE

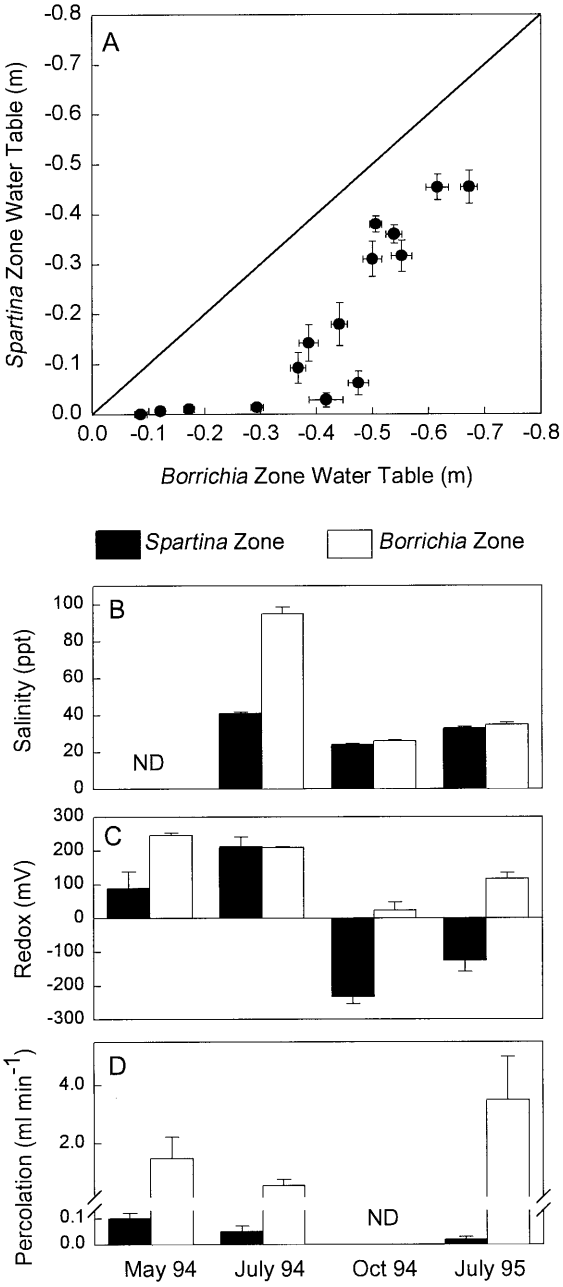

Fig. 4A–D *Borrichia* and *Spartina* transplant experiment, physical stress. **A** Water table levels in pits in the *Borrichia* and *Spartina* zones on 15 dates (*error bars* not shown if smaller than *circles*; *diagonal line* has slope=1); **B** Salinity; **C** Redox; **D** Percolation rates. Data are means±1 SE; *ND* no data; statistical tests are reported in Table 3

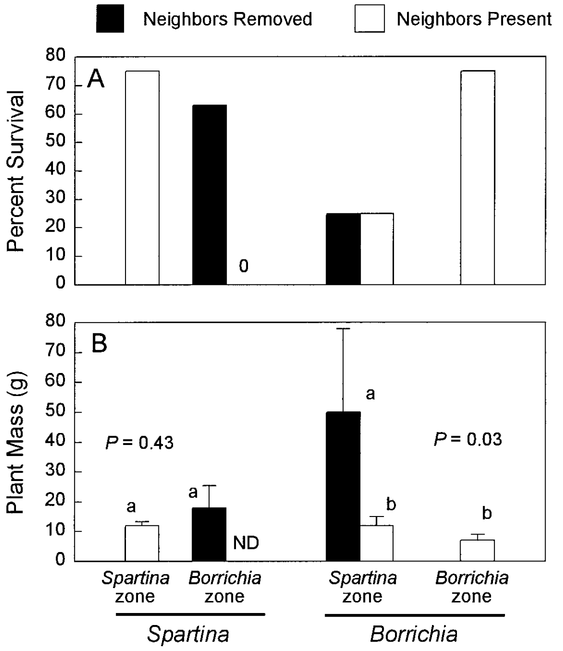

Fig. 5 *Borrichia* and *Spartina* transplant experiment, plant responses. *Spartina* plants transplanted to the *Borrichia* zone with neighbors present had zero survival. Mass data are means±1 SE; *ND* no data (because of zero survival); letters indicate means that are not significantly different (ANOVA followed by Ryan-Einot-Gabriel-Welsch multiple range tests)

without neighbors did grow larger than plants in the other two treatments (Fig. 5B), indicating that competition affected growth of the few surviving plants.

The neighbor-removal experiments similarly suggested that competition affected the upper limit of *Spartina*, but had little effect on the lower limit of *Borrichia*. Removing *Borrichia* neighbors from around *Spartina* in the *Borrichia* zone led to significant increases in *Spartina* survival and mass (Fig. 6A, B). In contrast, removing *Spartina* neighbors from around *Borrichia* in the *Spartina* zone did not significantly affect *Borrichia* survival or mass (Fig. 6A, B). Similarly, removing *Distichlis* neighbors from around stunted *Borrichia* had no effect on *Borrichia* mass (Fig. 6C).

Relative stress tolerance of *Borrichia* and *Spartina*

Survival of *Borrichia* seedlings in the greenhouse was significantly affected by physical stress, but survival of *Spartina* seedlings was not (Fig. 7A). *Borrichia* seedlings experienced 100% mortality in the sea-flood treat-

Table 3 Summary of ANOVA results for edaphic variables from the transplant experiment. Data shown in Fig. 4

Source	Water table depth		Soil water salinity		Soil redox potential		Percolation rates	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Zone	830.35	<0.0001	228.81	<0.0001	72.65	<0.0001	5.10	0.032
Date	126.68	<0.0001	420.62	<0.0001	58.94	<0.0001	1.58	0.22
Zone x date	9.71	<0.0001	178.00	<0.0001	9.41	<0.0001	1.68	0.20

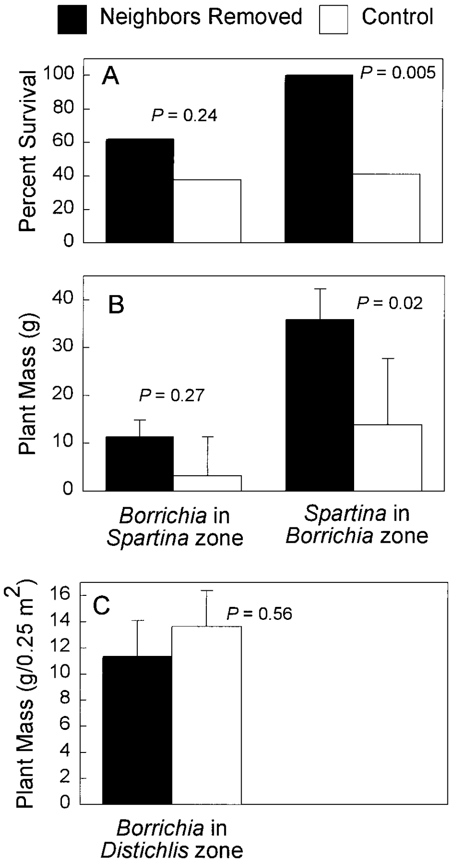

Fig. 6 Neighbor removal experiments, plant survival and final mass. Mass data are means±1 SE

ment, but survived well in other treatments ($X^2_3=30.55$, $P<0.0001$). In contrast, seedlings of *Spartina* showed a trend towards surviving best in the sea-flood treatment, with moderate survival in other treatments ($X^2_3=6.78$, $P=0.08$). Biomass of surviving seedlings of both species was reduced in a similar manner by salinity and flooding (Fig. 7B, Table 4).

Discussion

Our results suggest that the processes controlling shrub zonation in Georgia salt marshes are similar to those controlling shrub zonation in Rhode Island salt marshes, some 10° of latitude to the north (Table 1). In both cases, shrubs are stunted at lower, more stressful elevations, the lower limit of the shrub zone is set primarily by physical stress, and the upper limit of the grass or rush zone is primarily set by competition from shrubs.

Size gradients within the shrub zone

In Georgia, lower elevations within the shrub zone experienced increased physical stress from both flooding and salinity. *Borrichia* at low elevations within the shrub zone were less than 1/4 the size of shrubs at high elevations, and reducing physical stress improved growth of stunted *Borrichia*. Similarly, *Iva* shrubs in Rhode Island marshes are stunted at lower elevations within their zone where they experience increased flooding and salinity, and growth of stunted shrubs is affected by experimental manipulations of soil drainage (Bertness et al. 1992; Bertness and Hacker 1994; Hacker and Bertness 1995, 1999).

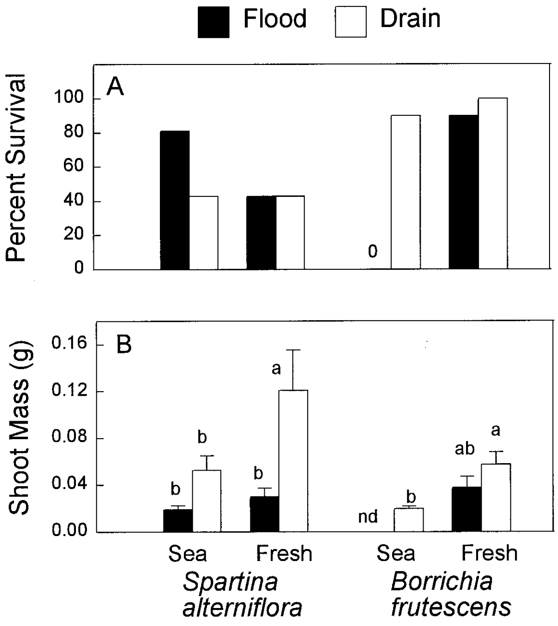

Fig. 7 Greenhouse experiment. Responses of *Spartina* and *Borrichia* seedlings to salt and flooding treatments. Mass data are means ±1 SE; *nd* = no data because of zero survival; letters indicate means that are not significantly different (ANOVA followed by Ryan-Einot-Gabriel-Welsch multiple range tests); statistical tests reported in Table 4

Table 4 Summary of ANOVA results for greenhouse experiment (data shown in Fig. 7). Data for *Spartina* was analyzed using 2-way ANOVA. Data for *Borrichia* was analyzed using 1-way ANOVA (followed by Ryan-Einot-Gabriel-Welsch Multiple Range Tests) because of zero survival in the salt-flooded treatment

Source	Shoot mass	
	F	*P*
Spartina		
Salt	6.20	0.02
Flooding	15.24	0.0005
Salt × flooding	3.20	0.084
Borrichia		
Treatment	5.08	0.01

Factors controlling the zonation of *Spartina* and *Borrichia*

In Georgia, the lower limit of the *Borrichia* zone is primarily set by physical stress. The *Spartina* zone had a higher water table, lower redox levels, and reduced percolation rates relative to the *Borrichia* zone, indicating regularly-flooded, oxygen-poor, poorly-drained soils. Most *Borrichia* died when transplanted into the *Spartina* zone. This mortality was probably caused by flooding more than by salinity, because *Borrichia* can tolerate extremely salty soils (Antlfinger and Dunn 1979, 1983; Antlfinger 1981) and in any case salinities were rarely higher in the *Spartina* zone than in the *Borrichia* zone. In lower marsh zones dominated by grasses (*Spartina* or *Distichlis*), the presence of neighbors rarely had significant effects on *Borrichia* survival or growth, suggesting that neighbor effects were small and inconsistent compared to edaphic effects. Similarly, the lower level of the *Iva* zone in Rhode Island marshes is primarily set by physical stress rather than competition (Bertness et al. 1992; Hacker and Bertness 1999).

In contrast, our results suggest that the upper limit of the *Spartina* zone in Georgia was primarily set by competition from *Borrichia*. *Spartina* plants survived and grew well in the *Borrichia* zone if *Borrichia* neighbors were removed, but not if *Borrichia* was present. Similar results were obtained with grasses and rushes in Rhode Island: growth of plants transplanted to higher elevations than they normally occupied was excellent if neighbors were removed, but poor if neighbors were present (Bertness and Ellison 1987; Bertness 1991a; Bertness and Hacker 1994).

Relative stress tolerance of shrubs versus grasses and rushes

At our study sites, *Spartina* occupied lower, more regularly flooded marsh zones with higher water tables and lower redox potentials than did shrubs. In the greenhouse experiment, *Spartina* survived best in the sea water-flooded treatment, but *Borrichia* experienced 100% mortality under these conditions. These results agree with the general paradigm that *Spartina alterniflora* is able to tolerate flooding with sea water better than most or all other marsh plants (Mendelssohn 1979; Gleason and Zieman 1981; Bertness 1991a). Moreover, just as in Georgia *Borrichia* is less tolerant of flooding than *Spartina*, so in Rhode Island the shrub *Iva* is less tolerant of flooding than are grasses and rushes from lower marsh elevations (Bertness et al. 1992).

How general are these results?

The similarities between our results in Georgia and previous results with *Iva* in Rhode Island (Table 1) suggest that the factors controlling the zonation of shrubs in western Atlantic salt marshes may be somewhat general. Similar processes may also occur in freshwater wetlands, where woody shrubs are competitively dominant but less stress tolerant than herbaceous vegetation (Keddy and Reznicek 1986; Keddy 1989b). These generalities, however, probably apply only within a certain range of latitude. From central Florida south through the tropics, woody plants (mangroves) dominate intertidal wetlands. North of Cape Cod, woody shrubs are largely absent from salt marshes (Ganong 1903; Jacobson and Jacobson 1989). Thus, the generalizations discussed here likely apply only from central Florida to Cape Cod, where a small number of woody shrub species such as *Iva*, *Borrichia* and *Baccharis* spp. dominate the terrestrial borders of salt marshes, and different generalities may apply at lower and higher latitudes.

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References

Antlfinger AE (1981) The genetic base of microdifferentiation in natural and experimental populations of *Borrichia frutescens* in relation to salinity. Evolution 35:1056–1068

Antlfinger AE, Dunn EL (1979) Seasonal patterns of CO_2 and water vapor exchange of three salt marsh succulents. Oecologia 43:249–260

Antlfinger AE, Dunn EL (1983) Water use and salt balance in three salt marsh succulents. Am J Bot 70:561–567

Bertness MD (1991a) Interspecific interactions among high marsh perennials in a New England salt marsh. Ecology 72:125–137

Bertness MD (1991b) Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. Ecology 72:138–148

Bertness MD, Ellison AM (1987) Determinants of pattern in a New England salt marsh plant community. Ecol Monogr 57:129–147

Bertness MD, Hacker SD (1994) Physical stress and positive associations among marsh plants. Am Nat 144:363–372

Bertness MD, Pennings SC (2000) Spatial variation in process and pattern in salt marsh plant communities. In: Kreeger DA, Weinstein MA (eds) Concepts and controversies in tidal marsh ecology. Kluwer, Dordrecht (in press)

Bertness MD, Yeh SM (1994) Cooperative and competitive interactions in the recruitment of marsh elders. Ecology 75:2416–2429

Bertness MD, Wikler K, Chatkupt T (1992) Flood tolerance and the distribution of *Iva frutescens* across New England salt marshes. Oecologia 91:171–178

Chapman, VJ (1960) Salt marshes and salt deserts of the world. Leonard Hill, London

Diamond J (1986) Laboratory experiments, field experiments, and natural experiments. In: Diamond J, Case TJ (eds) Community ecology. Harper and Row, New York, pp 3–22

Dunson WA, Travis J (1991) The role of abiotic factors in community organization. Am Nat 138:1067–1091

Ganong WF (1903) The vegetation of the Bay of Fundy salt and diked marshes: an ecological study. Bot Gaz 36:161–186, 280–302, 350–367, 429–455

Gleason ML, Zieman JC (1981) Influence of tidal inundation on internal oxygen supply of *Spartina alterniflora* and *Spartina patens*. Estuarine Coastal Shelf Sci 13:47–57

Goldberg DE, Barton AM (1992) Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. Am Nat 139:771–801

Hacker SD, Bertness MD (1995) Morphological and physiological consequences of a positive plant interaction. Ecology 76: 2165–2175

Hacker SD, Bertness MD (1999) Experimental evidence for factors maintaining plant species diversity in a New England salt marsh. Ecology 80:2064–2073

Jacobson GL Jr, Jacobson HA (1989) An inventory of distribution and variation in salt marshes from different settings along the Maine coast. Maine Geological Survey, Neotectonic of Maine

Keddy PA (1989a) Competition. Chapman and Hall, London

Keddy PA (1989b) Effects of competition from shrubs on herbaceous wetland plants: a 4-year field experiment. Can J Bot 67:708–716

Keddy PA, Reznicek AA (1986) Great Lakes vegetation dynamics: the role of fluctuating water levels and buried seeds. J Great Lakes Res 12:25–36

Mendelssohn IA (1979) The influence of nitrogen level, form and application method on the growth response of *Spartina alterniflora* in North Carolina. Estuaries 2:106–112

Moloney KA (1990) Shifting demographic control of a perennial bunchgrass along a natural habitat gradient. Ecology 71: 1133–1143

Nomann BE, Pennings SC (1998) Fiddler crab-vegetation interactions in hypersaline habitats. J Exp Mar Biol Ecol 225:53–68

Pennings SC, Bertness MD (1999) Using latitudinal variation to examine effects of climate on coastal salt marsh pattern and process. Curr Top Wetl Biogeochem 3:100–111

Pennings SC, Bertness MD (2000) Salt marshes. In: Bertness, MD, Gaines SD, Hay ME (eds) Marine community ecology. Sinauer, Sunderland (in press)

Pennings SC, Callaway RM (1992) Salt marsh plant zonation: the relative importance of competition and physical factors. Ecology 73:681–690

Pennings SC, Richards CL (1998) Effects of wrack burial in salt-stressed habitats: *Batis maritima* in a southwest Atlantic salt marsh. Ecography 21:630–638

Ranwell DS (1972) Ecology of salt marshes and sand dunes. Chapman and Hall, London

Snow A, Vince S (1984) Plant zonation in an Alaskan salt marsh. II. An experimental study of the role of edaphic conditions. J Ecol 72:669–684

Thrush SF, Hewitt JE, Cummings VD, Green MO, Funnell GA, Wilkinson MR (2000) The generality of field experiments: interactions between local and broad-scale processes. Ecology 81:399–415

Underwood AJ Denley EJ (1984) Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. In: Strong D, Simberloff D, Abele L, Thistle A (eds) Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, pp 151–180

Wiegert RG, Freeman BJ (1990) Tidal salt marshes of the southeast Atlantic coast: a community profile. US Fish Wildl Serv Biol Rep 85(7.29)