http://www.jstor.org

Plant zonation in low-latitude salt marshes: disentangling the roles of flooding, salinity and competition

STEVEN C. PENNINGS*, MARY-BESTOR GRANT†‡ and
MARK D. BERTNESS‡

University of Georgia Marine Institute, Sapelo Island, GA 31327, USA, and ‡Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912, USA

Summary

1 We investigated the factors producing zonation patterns of the dominant plants in south-eastern USA salt marshes where *Juncus roemerianus* dominates the high marsh, and *Spartina alterniflora* the middle and low marsh.

2 *Juncus* did not occur naturally in the *Spartina* zone and performed poorly when transplanted there, irrespective of whether neighbours were present or removed, indicating that its lower limit was set by physical stress.

3 In contrast, although *Spartina* occurred naturally at low densities in the *Juncus* zone, it performed well if transplanted there only if neighbours were removed, indicating that its upper limit was set by competition.

4 Parallel laboratory and field manipulations of flooding, salinity and competition indicated that the lower limit of *Juncus* was mediated by both flooding and salinity, but not by competition.

5 The general mechanisms producing zonation patterns of vegetation in coastal salt marshes may be universal, as suggested by previous studies, but the importance of particular factors is likely to vary geographically. In particular, salinity stress probably plays a much more important role in mediating plant zonation patterns at lower latitudes.

6 Our results suggest that the nature of ecological interactions is likely to vary geographically because of variation in the physical environment, and this variation must be taken into account in order to successfully generalize the results of field studies across geographical scales.

Key-words: competition, latitude, *Juncus roemerianus*, physical gradient, soil salinity, *Spartina alterniflora*, zonation

Introduction

Salt-marsh plant communities are characterized by striking zonation patterns across elevational gradients (Chapman 1974). Over recent decades, a series of experimental studies (Snow & Vince 1984; Bertness & Ellison 1987; Bertness 1991a,b; Pennings & Callaway 1992) have led to an emerging paradigm about the forces that mediate these patterns. According to this paradigm, there is an inverse relationship between competitive ability and stress tolerance, such that competitively superior plants occupy the least stressful zones of the salt marsh and displace competitively inferior plants to more stressful zones (Bertness 1992; Pennings & Bertness 2001). This paradigm about zonation patterns in salt marshes is consistent with results from non-saline wetlands (Grace & Wetzel 1981; Grace 1989; Keddy 1989) and with general ideas about inherent trade-offs in plants between competitive ability and stress tolerance (Grime 1977; Grime 1988). In marshes that are irregularly flooded, however, this paradigm may not apply because there may not be a consistent gradient in physical stress across the marsh (Costa *et al.* 2003).

Despite the broad success of this paradigm in explaining plant zonation patterns, little attention has been paid in field studies to experimentally disentangling the relative importance of the various physical stresses involved. Salt marshes are physically stressful

*Present address and correspondence: Steven C. Pennings, Department of Biology and Biochemistry, University of Houston, Houston, TX 77204, USA (tel. +1 713 7432989; fax +1 713 7432636; e-mail spennings@uh.edu).
†Present address: 2628 Carriage Place, Birmingham, AL 35223, USA.

habitats for angiosperms because their soils are periodically inundated with seawater and their soils are consequently both waterlogged and salty. Numerous laboratory experiments have shown that both water-logging and salinity are stressful to angiosperms (Ungar 1966; Mahall & Park 1976a,b; Linthurst & Seneca 1981; Pearcy & Ustin 1984; Rozema *et al.* 1985; Callaway *et al.* 1990; Rozema & Van Diggelen 1991; Kuhn & Zedler 1997; Huckle *et al.* 2000; Mendelssohn & Morris 2000; Noe & Zedler 2000; Pennings & Bertness 2001; Noe 2002), but because it is difficult to mimic precisely the complex salinity, flooding and biogeochemical regimes of marsh soils in the laboratory, the relevance of laboratory studies to field patterns is always questionable (Davy & Costa 1992). A handful of studies have experimentally manipulated flooding (Linthurst & Seneca 1980; Wiegert *et al.* 1983; Bertness *et al.* 1992; Hacker & Bertness 1995) or salinity (Hacker & Bertness 1995; Shumway & Bertness 1992; Kuhn & Zedler 1997; Moon & Stiling 2002) in the field, but most of these studies were interested in performance of plants in monocultures, or in plant–herbivore interactions, rather than in plant zonation patterns. We are aware of no studies that have manipulated both flooding and salinity in the field to examine their importance in mediating plant zonation patterns.

Disentangling the role of flooding and salinity in producing zonation patterns is particularly important in low-latitude habitats. In New England, where most experimental studies of plant zonation in salt marshes have been conducted (Bertness & Ellison 1987; Bertness 1991a,b, 1992; Bertness *et al.* 1992), both flooding and salinity increase in severity from the marsh upland border to the water's edge (Pennings & Bertness 1999, 2001). Because most marsh plants can tolerate salinities typical of undisturbed New England marshes, previous studies concluded, albeit without explicit tests, that flooding was the primary stress mediating zonation patterns (Bertness 1991b; Bertness *et al.* 1992). In contrast, in hotter, low-latitude marshes on the east and west coasts of the United States, salinities reach a peak in mid marsh zones (Pennings & Bertness 1999, 2001); consequently, salinity and flooding gradients are not parallel, and workers have speculated that both stresses could play an important role in mediating plant zonation patterns (Pennings & Callaway 1992). Thus, a more general understanding of salt marsh plant zonation patterns may require a better understanding of geographical variation in the roles of different physical factors.

Here, we focus on the zonation of *Spartina alterniflora* Loisel and *Juncus roemerianus* Scheele (henceforth referred to as *Spartina* and *Juncus*) in salt marshes in Georgia, USA. These two plant species comprise the vast majority of the plant biomass in south-eastern USA salt marshes along both the Atlantic and Gulf coasts (Eleuterius 1976a; Stout 1984; Wiegert & Freeman 1990). Interactions between these two species have been experimentally examined in only one study (Stanton

1998). Along the southern Atlantic Coast, *Spartina* typically occupies salty soils at lower marsh elevations, and *Juncus* less salty soils at higher elevations (Wiegert & Freeman 1990), although considerable overlap occurs in these environmental variables (Woerner & Hackney 1997). We asked three questions using a combination of field and glasshouse studies. First, what is the role of competition and physical stress in creating this zonation pattern? Secondly, what is the relative importance of salinity and flooding in excluding *Juncus* from the *Spartina* zone? Thirdly, do field and glasshouse studies provide similar insights into the nature of these interactions?

Methods

STUDY SITE AND ZONATION PATTERNS

Fieldwork was conducted at Sapelo Island, GA (31°27′ N, 81°16′ W). Plant zonation patterns in salt marshes around Sapelo Island are typical of coastal salt marshes throughout the South Atlantic Bight (Wiegert & Freeman 1990). We worked at three sites on the west side of Sapelo Island (north to south: Keenan Field, Airport Marsh, Marsh Landing) in locations where the *Juncus* and *Spartina* zones directly abutted each other, because this zonation pattern is the most typical of the region. At some sites with extremely high soil salinities, this typical zonation pattern is interrupted by unvegetated salt pans and associated 'salt meadow' communities comprised of highly salt-tolerant plants (Wiegert & Freeman 1990); we did not consider these more complicated zonation patterns in this study.

Spartina alterniflora is a C4 grass that grows as upright shoots connected by underground rhizomes. It is highly tolerant of flooding and anoxic soils, and moderately tolerant of high salinities (Mendelssohn & Morris 2000). *Juncus roemerianus* is a C3 rush that grows as horizontal shoots with upright leaves (Eleuterius 1976b). It is thought to be less tolerant of flooding and salinity than *Spartina* (Eleuterius 1976b; Wiegert & Freeman 1990).

To document a typical zonation pattern of *Spartina* and *Juncus*, 1 × 1 m quadrats were centred 1, 2, 4 and 6 m on each side of the border between the two species at Keenan Field (*n* = 8 transects, ≥ 5 m between transects) in October 1996. We counted the number of shoots (*Spartina*) or leaves (*Juncus*) of each species in each quadrat. Data (means ± SE) are presented for visual inspection of the patterns without formal statistical analysis.

COMPETITION EXPERIMENTS

Edge removal experiment

We established 30 0.5 × 0.5 m plots on each side of the border between *Juncus* and *Spartina* at Airport Marsh in March 1994. Plots were located with one side along the border between the two species. Measurements of

each species were made in three conditions: in its own zone, in the other species' zone and in the other species' zone with the other species removed to assess the impact of competition ($n = 10$ individuals treatment^{-1}). In the removal treatment, we removed the zonal dominant by clipping at the soil surface bi-weekly. Because the border was not perfectly abrupt, both species were initially present in the other species' zones. These individuals were not removed in either the control or 'zonal dominant removal' treatments. Treatments were fully interspersed and initial conditions were similar across all replicates of all treatments within each zone. The central 0.25×0.25 m of each plot was harvested in November 1995, and all above-ground live plant material was dried for 3 days at 60 °C and weighed. In this, and all the following experiments, we focused on above-ground biomass because it was very difficult to excavate completely the below-ground portions of these highly clonal plants and to separate accurately the roots from the soils. For similar reasons, most previous studies of salt-marsh plant zonation patterns have also focused primarily on above-ground biomass (Vince & Snow 1984; Scholten & Rozema 1990; Bertness 1991a,b; Pennings & Callaway 1992; Huckle *et al.* 2000). Data on above-ground biomass for each species were compared among treatments with a one-way ANOVA.

Transplant experiment

Individual *Spartina* and *Juncus* culms with associated soil blocks ($20 \times 20 \times 20$ cm) were transplanted into their own and the other species' zone at Airport Marsh in April 1994. We removed the vegetation surrounding half of the transplants into the other species' zone by clipping a 0.25-m radius border around the plant at the soil surface. Clipping treatments were maintained by repeated clipping every 2 weeks as needed. Unmanipulated culms were tagged and left as transplant controls. All treatments were replicated eight times. Measurements with electronic surveying equipment documented that transplanted plants in the *Spartina* zone were located 190 m seawards from the transplanted plants in the *Juncus* zone, and 6 cm lower in elevation. To document edaphic patterns in both zones we measured soil organic content in September 1995 by ashing at 450 °C ($n = 12$ zone^{-1}), and soil pore water salinity in July and October 1994 and September 1995 by rehydrating dried soil samples in a known volume of distilled water, mixing thoroughly, measuring the salinity of the supernatant after 48 hours, and calculating the salinity of the original pore water based on the original gravimetric water content of the individual soil samples ($n = 8$–12 zone^{-1} date^{-1}). Water content of the soil (grand mean 62.2%) varied among dates with a significant date × treatment interaction (data not shown). Above-ground biomass of surviving plants was estimated in October 1994 by summing the length of all the shoots (*Spartina*) or leaves (*Juncus*) within the transplant block. For these species, the total length of shoots or leaves, respectively,

correlates highly with biomass (Pennings & Callaway 2000). Five *Spartina* plants that gradually shrank in size and then died (presumably due to competition) were included in the analysis with total shoot length set to zero. Three *Spartina* plants that were eaten by deer were excluded from the analysis. Proportional data (organic content) were arcsine (square root) transformed before analysis. Edaphic data (organic content, salinity) were compared among zones, or zones and dates, using one- or two-way ANOVA, respectively. Above-ground size (total shoot length) of plants of each species was compared among treatments using a one-way ANOVA.

MEDIATION OF COMPETITION BY EDAPHIC CONDITIONS

Glasshouse experiment

In order to examine the roles of flooding, salinity and competition on performance of *Juncus* and *Spartina*, we grew the two species alone and together in the glasshouse under a variety of edaphic conditions. Plants were collected in May 1995 from an area of Keenan Field where the two species grew highly intermingled. Blocks of soil ($20 \times 20 \times 20$ cm) containing one or both species were excavated from within a small (10×25 m) collection area that appeared to have homogenous soil conditions throughout. Plants were thinned by clipping at the soil surface to four to five shoots of *Spartina* and/or eight to twelve leaves of *Juncus* and potted in 20-L (29 cm wide × 35 cm high) pots lacking drainage holes, using additional soil collected from a single marsh site. Drained and flooded treatments were achieved by drilling small holes in the sides of the pots at the soil surface (flooded) or 10 cm below the soil surface (drained), representative of conditions commonly observed in the *Spartina* and *Juncus* zones, respectively. After filling with water to 5 cm above the soil surface, pots took *c.* 1 hour to drain to the level of the drain holes. Plants were watered three times each week with fresh water or seawater as needed to maintain flooding and salinity treatments. Our aim was to achieve salinities of approximately 10 and 40 p.p.t., representative of conditions commonly encountered in the *Juncus* and *Spartina* zones, respectively (Wiegert & Freeman 1990). Salinities around representative plants from each treatment were checked on every watering date to ensure that salinity treatments were being appropriately maintained. The two flooding treatments were crossed with the two salinity treatments and the two competition treatments (alone, with the other species), for a total of eight treatments, each replicated 10 times for each species. Pots were located outdoors under a plastic roof to shelter them from rain, but were otherwise exposed to ambient temperature, humidity and light. All live above-ground biomass was harvested from each pot in November 1995, dried for 3 days at 60 °C and weighed. Plants did not appear to be 'pot-bound'. Data for each

species were analysed with three-way ANOVA, with flooding, salinity and competition as the three main effects.

Field experiment

In order to further examine the roles of flooding, salinity and competition on the performance of *Juncus* in the field, we transplanted plants into the *Spartina* zone in a fully factorial experiment that manipulated flooding, salinity and competition. In April 1997 we collected culms of *Juncus* and transplanted them into the middle of the *Spartina* zone at Marsh Landing. Single culms were planted inside 20 cm diameter pvc pipe sections. For the elevated treatment, the pipe sections were 12 cm long, and were pressed 4 cm into the soil, so that the plants were elevated 8 cm above ambient. For the not-elevated treatment, plants were planted in a 4 cm long section of pipe that was fully pressed into the soil surface so that plants were level with the ambient soil. In order to manipulate competition, we either left neighbouring vegetation intact (competition) or clipped neighbouring *Spartina* plants, both inside and around the pipe, at the soil surface within a 50-cm radius of the transplant (no-competition). In order to manipulate salinity, plants were either unmanipulated (salt) or were watered twice a week throughout the entire duration of the experiment with fresh water (fresh), which reduced salinity by 5–20 p.p.t. (effectiveness of watering varied with climate and the lunar component of the tidal cycle) without significantly affecting soil water content. Each treatment combination was replicated 15 times. All above-ground biomass within each pvc pipe was harvested in August 1998, dried for 3 days at 60 °C and weighed. Data were analysed with three-way ANOVA, with flooding, salinity and competition as the three main effects.

Results

ZONATION PATTERNS

The zonation pattern we documented at Keenan Field was typical of what we have observed at other sites within Georgia (S. C. Pennings, personal observations). There was an abrupt transition over 1–2 horizontal metres between dominance by *Juncus* and dominance by *Spartina* (Fig. 1). *Spartina* was present in the *Juncus* zone, but only at 10–20% of the density that it attained in its own zone. *Juncus* did not occur at all in the *Spartina* zone.
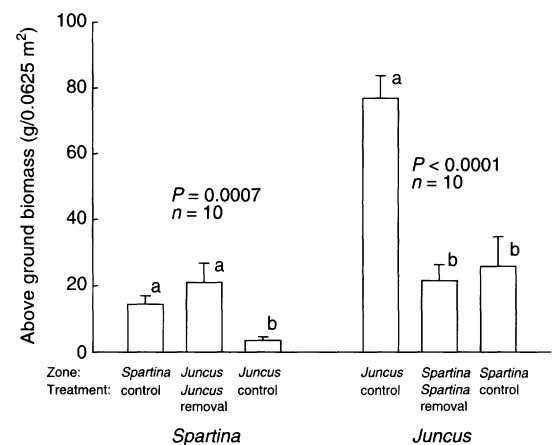
COMPETITION EXPERIMENTS

Edge removal experiment

Above-ground biomass of *Spartina* on its own side of the border was four times greater than just across the border in the *Juncus* zone (Fig. 2, ANOVA, $F_{2,27} = 9.72$,
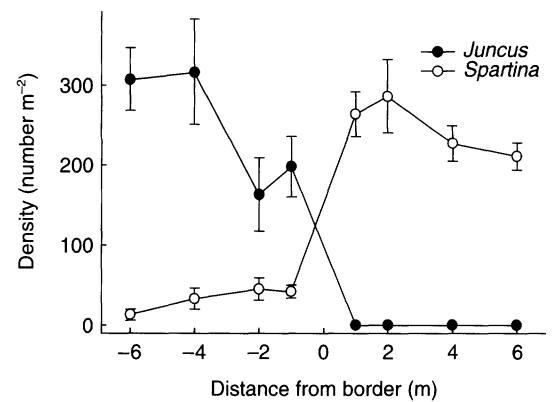
Fig. 1 Zonation pattern of *Spartina alterniflora* and *Juncus roemerianus*. Data (means ± 1 SE) are the number of shoots (*Spartina*) or leaves (*Juncus*) in 1 × 1 m^2 plots centred at 1- or 2-m intervals away from the border between the two species.
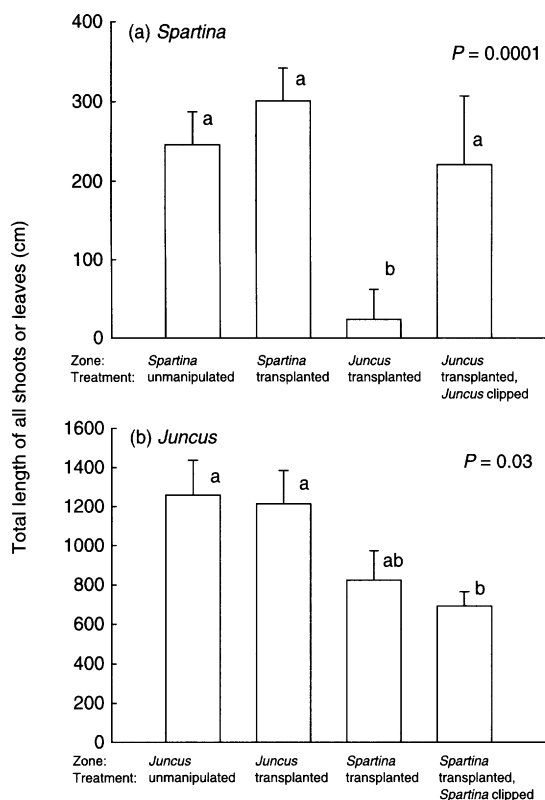

Fig. 2 Impact of competition on the zonation of *Spartina alterniflora* and *Juncus roemerianus*: edge removal experiment. Data (means ± 1 SE) are dry mass of live above-ground biomass of *Spartina* and *Juncus* in unmanipulated control plots in both zones and in neighbour-removal plots in the other species' zone. For each species, *P*-values (ANOVA) and sample sizes are indicated above the groups of bars. Within each species, letters above bars indicate means that are not significantly different from each other (Tukey means comparisons).

$P = 0.0007$). When *Juncus* was removed, however, biomass of *Spartina* increased sixfold in the *Juncus* zone. The absolute above-ground biomass of *Spartina* in these treatments was low compared with values typically reported in the literature because the experiment was conducted in an area of very short 'short-form' *Spartina*. Above-ground biomass of *Juncus* on its own side of the border was three times greater than just across the border in the *Spartina* zone (Fig. 2, ANOVA, $F_{2,27} = 18.69, P < 0.0001$). Removing *Spartina*, however, had no effect on *Juncus* biomass in the *Spartina* zone.

TRANSPLANT EXPERIMENT

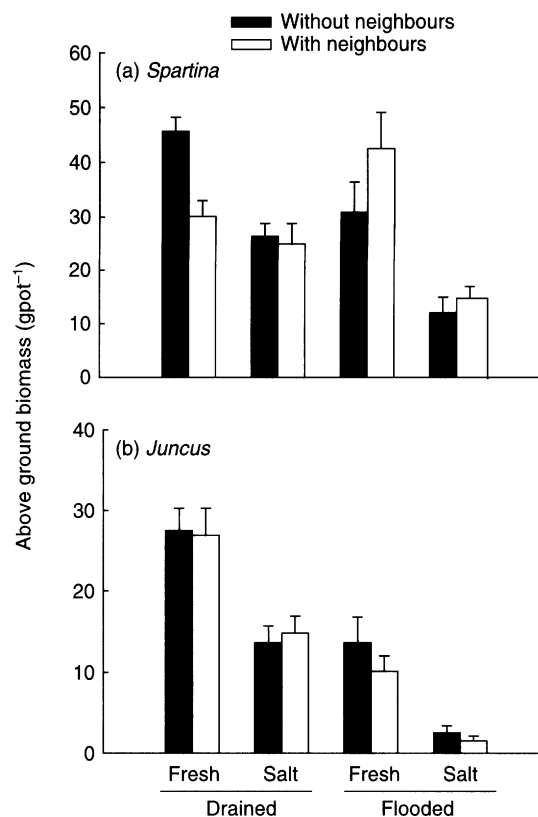Soil organic content was higher in the *Spartina* vs. the *Juncus* zone (19 ± 1% vs. 10 ± 1, ANOVA, $F_{1,22} = 24.75$, $P = 0.0001$). Soil pore water was sometimes hypersaline in the *Spartina* zone, and consistently saltier than

Fig. 3 Impact of competition on the zonation of *Spartina alterniflora* and *Juncus roemerianus*: transplant experiment. Data (means ± 1 SE) are total length of all shoots of *Spartina* (a) and leaves of *Juncus* (b) plants that were unmanipulated, transplanted into their own zone, or transplanted into the other species' zone with neighbours unmanipulated or clipped. Sample sizes were 8, except for *Spartina* transplanted into the *Juncus* zone with *Juncus* neighbours clipped (*n* = 5). Within each species, letters above bars indicate means that are not significantly different from each other (Tukey means comparisons).

Fig. 4 Impact of edaphic conditions on competition between *Spartina alterniflora* and *Juncus roemerianus*: glasshouse experiment. Data (means ± 1 SE) are dry mass of *Spartina* (a) and *Juncus* (b) grown alone and in competition with each other in soil that was watered with 'fresh' (10 p.p.t.) or 'salt' (40 p.p.t.) water, and kept flooded or allowed to drain. *n* = 10 individuals species^{-1} treatment^{-1}. *P*-values are given in Table 1(a, b).

in the *Juncus* zone, where the maximum recorded salinities were only marginally hypersaline. Although the pattern of higher salinities in the *Spartina* zone was consistent, salinity values and the magnitude of the difference between zones varied among dates (*Spartina* zone: July 1994, 67 ± 2 p.p.t.; October 1994, 31 ± 1; September 1995, 39 ± 1; *Juncus* zone: July 1994, 38 ± 2%; October 1994, 23 ± 1%; September 1995, 30 ± 1%; ANOVA: date, $F_{2,54} = 159.16$, $P < 0.0001$; zone, $F_{1,54} = 171.57$, $P < 0.0001$; date × zone, $F_{2,54} = 35.51$, $P < 0.0001$). Similar organic content and salinity differences between the *Spartina* and *Juncus* zones are consistently found in marshes around Sapelo Island (Antlfinger & Dunn 1979; Wiegert & Freeman 1990; Pennings *et al*. 2003).

Transplanted *Spartina* plants performed well in their own zone and in the *Juncus* zone if *Juncus* neighbours were removed, but performed poorly in the *Juncus* zone if neighbours were present (Fig. 3a, ANOVA, $F_{3,25} = 17.40$, $P < 0.0001$). Transplanted *Juncus* plants performed well in their own zone but tended to perform less well in the *Spartina* zone, especially if *Spartina* neighbours were removed (Fig. 3b, ANOVA, $F_{3,28} = 3.59$, $P = 0.03$).

MEDIATION OF COMPETITION BY EDAPHIC CONDITIONS

Glasshouse experiment

In the glasshouse, biomass of *Spartina* was significantly reduced by both increased flooding and increased salinity (Fig. 4a, Table 1a). A significant three-way interaction between flooding, salinity and competition, and associated significant two-way interactions between flooding and salinity, and between flooding and competition (Table 1a), indicated different effects of *Juncus* on *Spartina* in the two low-salinity treatments, reducing *Spartina* biomass, probably by competing for resources, when drained, but increasing it, perhaps by increasing oxygenation of soils, when flooded (Fig. 4a).

In the same experiment, biomass of *Juncus* was, like biomass of *Spartina*, reduced by both increased flooding and increased salinity (Fig. 4b, Table 1b). In contrast to results from *Spartina*, however, neighbours had no effect on biomass of *Juncus*, either alone or in interactions.

Field experiment

Biomass of *Juncus* plants that were transplanted into the *Spartina* zone was greater in the fresh than the salt

Table 1 ANOVA tables for experiments examining mediation of competition by edaphic conditions. Significant *P*-values are highlighted
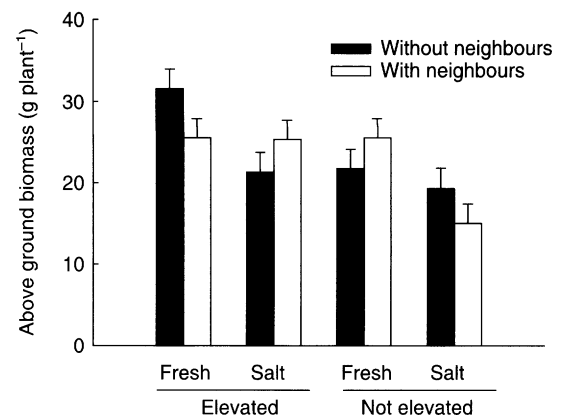
Source	d.f.	SS	F	P
(a) Biomass of *Spartina alterniflora*				
in glasshouse experiment				
Flooding	1	900.4	5.98	**0.017**
Salinity	1	6336.6	42.07	**0.0001**
Competition	1	9.9	0.07	0.79
Flooding × salinity	1	610.5	4.05	**0.048**
Flooding × competition	1	1207.4	8.02	**0.006**
Salinity × competition	1	34.3	0.23	0.63
Three-way interaction	1	664.8	4.41	**0.04**
Residual	72	10844.2		
(b) Biomass of *Juncus roemerianus*				
in glasshouse experiment				
Flooding	1	3782.6	69.59	**0.0001**
Salinity	1	2616.3	48.13	**0.0001**
Competition	1	19.5	0.36	0.55
Flooding × salinity	1	52.3	0.96	0.33
Flooding × competition	1	31.88	0.59	0.45
Salinity × competition	1	23.8	0.44	0.51
Three-way interaction	1	0.7	0.01	0.91
Residual	72	3913.8		
(c) Biomass of *Juncus roemerianus*				
in field experiment				
Flooding	1	1295.6	15.0	**0.0002**
Salinity	1	681.6	7.9	**0.006**
Competition	1	85.2	1.0	0.32
Flooding × salinity	1	5.8	0.1	0.80
Flooding × competition	1	12.5	0.2	0.70
Salinity × competition	1	68.5	0.8	0.37
Three-way interaction	1	373.8	4.3	**0.04**
Residual	111	12097.0		

Fig. 5 Impact of edaphic conditions on competition between *Spartina alterniflora* and *Juncus roemerianus*: field experiment. Data (means ± 1 SE) are dry mass of *Juncus* transplanted into the middle of the *Spartina* zone such that soil level of the transplant was elevated above or flush with ('not elevated') the ambient soil; transplants were watered with freshwater to reduce salinity ('fresh') or not watered ('salt'). *n* = 15 individuals per treatment combination. *P*-values are given in Table 1(c).

treatments, and greater in the elevated than the not-elevated treatments (Fig. 5, Table 1c). A significant interaction between salinity, elevation and competition (Table 1c) indicated that *Spartina* competed with *Juncus* in some treatment combinations but facilitated it in others (Fig. 5).

Discussion

Our general understanding of plant distributions revolves around inherent trade-offs in plants between competitive ability and stress tolerance (Grime 1977; Grime 1988). Similarly, studies focused on freshwater (Grace & Wetzel 1981; Grace 1989; Keddy 1989) and marine (Snow & Vince 1984; Partridge & Wilson 1988; Bertness 1991a,b; Pennings & Callaway 1992) wetlands have identified a trade-off between competitive ability and stress tolerance as the key factor creating plant zonation patterns. In most cases, however, the physical factors creating stress are not explicitly identified. Below, we first discuss how our results are in broad agreement with current paradigms, then discuss how a more explicit focus on physical stress suggests that the factors mediating plant zonation in salt marshes may change geographically.

Our results indicate that the zonation pattern between *Juncus* and *Spartina* in Georgia is maintained

by a trade-off between competitive ability and stress tolerance. Although *Spartina* dominates lower marsh zones, it occurs at low densities in the *Juncus* zone, and performs well when transplanted there if *Juncus* is removed. Thus, the upper limit of *Spartina* appears to be set by competition, not physical stress (but see the discussion of salt pans below). In contrast, *Juncus* almost never occurs as scattered individuals within the *Spartina* zone, and it performs poorly when transplanted there whether *Spartina* is present or removed. Although *Juncus* plants transplanted to the *Spartina* zone did not die in the first growing season, *Juncus* is a slow-growing plant with extensive below-ground reserves, and hence tends to respond slowly to changes in abiotic conditions. The *Juncus* plants transplanted into the *Spartina* zone looked unhealthy, and we are confident that they would eventually have died had the experiment been extended for additional growing seasons. Thus, the lower limit of *Juncus* appears to be set by physical stress, not competition. These differences between *Spartina* and *Juncus* in stress tolerance and competitive ability lead to a general pattern in south-eastern USA marshes wherein *Spartina* dominates lower and middle marsh elevations, which tend to be flooded more often and saltier, and *Juncus* dominates higher marsh elevations, which tend to be flooded less often and lower in salinity (Wiegert & Freeman 1990). In particular, the peak salinities reached in the *Spartina* zone (> 60 p.p.t.) are probably highly stressful for *Juncus*. There is broad overlap in the environmental conditions experienced by each plant, however (Woerner & Hackney 1997), and the details of this zonation pattern vary considerably from site to site (sometimes the *Spartina* zone is larger than the *Juncus* zone and sometimes the reverse, and large patches of *Juncus* occasionally occur within extensive stands of *Spartina*), but this variation probably reflects heterogeneity in the underlying physical

environment (i.e. spatial variation in geology and hydrology creating spatial variation in salinity and flooding) rather than variation in the general mechanisms affecting plant interactions (Buck and Pennings, unpublished data).

Although we have concluded that our results are consistent with general paradigms about zonation of marsh plants (Grace & Wetzel 1981; Grace 1989; Keddy 1989; Bertness 1992; Pennings & Bertness 2001), and about plant distributions in general (Grime 1977; Grime 1988), we now argue that a more explicit examination of physical stress will suggest that the underlying mechanisms driving marsh plant zonation may change geographically. Most of the experimental studies of plant zonation in USA salt marshes have been conducted at high latitudes in New England (Bertness & Ellison 1987; Bertness 1991a,b; Bertness *et al.* 1992). Salt marshes, however, are the dominant intertidal habitat along the entire east coast of the United States. We argue that the details of how these systems work are likely to vary across latitude because of predictable differences in salinity patterns between high and low latitude marshes on the eastern seaboard of the United States (Pennings & Bertness 1999). Previous studies in New England concluded, albeit based on correlations rather than experiments, that flooding was the major physical stress limiting plant distributions in the absence of physical disturbance (Bertness 1991b; Bertness *et al.* 1992). In contrast, studies conducted at lower latitudes (Pennings & Callaway 1992), similarly working with correlative data, have speculated that salinity was an additional important physical stress mediating plant zonation patterns. Salinity might assume a greater role at low latitudes because low-latitude salt marshes on the eastern and western coasts of the United States generally have saltier soils than high-latitude marshes on the same coasts.

In high-latitude marshes on both US coasts, salinity levels in undisturbed vegetation tend to decline from the low to the high marsh, and rarely are much greater than levels found in seawater (Pennings & Bertness 1999). In contrast, in low-latitude marshes on both coasts, salinity levels often increase to a peak in the middle or high marsh because of increased evaporation, which concentrates salts in the soil, and salinities may reach levels several times those found in seawater (Pennings & Bertness 1999, 2001). Our field and laboratory studies consistently indicated that salinity and flooding were both important in excluding *Juncus* from the *Spartina* zone (Figs 4 and 5). Thus we concluded that, in contrast to the conventional wisdom from studies in New England, salinity stress was important in setting the lower distribution limit of *Juncus* in Georgia. Similarly, previous work in a low-latitude marsh in California pointed to the importance of both flooding and salinity in mediating plant zonation patterns (Pennings & Callaway 1992). Although the conventional wisdom that salinity does not play a major role in setting zonation patterns in New England salt marshes is consistent

with a large body of research, experimental manipulations of salinity conducted in parallel in both geographical regions are needed to provide a rigorous test of our proposal that the role of salinity changes geographically. We plan to report the results of such studies in the future. Whether a similar transition occurs across latitude in other geographical regions of the world is an interesting question that begs for further coordinated field studies.

The most extreme evidence of geographical variation in the role of salinity in mediating salt-marsh plant patterns lies in the occurrence of 'salt pans' in low-latitude marshes (Pennings & Bertness 1999, 2001). Salt pans, unvegetated expanses of the marsh that occur where soil salinities exceed levels that plants can tolerate, are a common feature of low-latitude marshes. In contrast, unvegetated areas that occur in New England marshes typically result from disturbance or waterlogging, rather than from high salinities (Pennings & Bertness 2001). Salt pans in south-eastern US marshes are typically surrounded by 'salt meadows', zones of highly salt-tolerant plants, such as *Batis* and *Salicornia* (Wiegert & Freeman 1990). In areas of moderately elevated salinities, salt meadows may occur without salt pans. We avoided sites where the typical zonation pattern of *Spartina* and *Juncus* was interrupted by salt meadows and/or salt pans; however, studies at such sites would probably have indicated an even stronger role for salinity in mediating zonation patterns. In particular, at many such sites, salinity probably plays a role in setting the upper distributional limit of *Spartina*.

The performance of *Juncus* in the various experimental treatments in the field was highly correlated with its performance in the analogous treatments in the glasshouse (Fig. 6). The broad agreement between these two approaches lends an extra level of confidence to our conclusions. It also suggests that, despite potential concerns (Davy & Costa 1992; Davy *et al.* 2000), laboratory studies of wetland systems can be highly informative if field conditions are mimicked well and more than one environmental factor is tested in combination with competition.

One interesting result that occurred in the glasshouse experiment was that *Spartina* performed better under freshwater flooded conditions when *Juncus* was present than when it was absent (Fig. 4). Although we are reluctant to speculate too much about this result because we did not measure redox potentials in this experiment, one interpretation of these results would be that *Juncus* was aerating the soil and thus facilitating *Spartina*. In New England *Juncus gerardii* has been shown to aerate marsh soils and increase performance of coexisting plants under certain conditions (Bertness & Hacker 1994; Hacker & Bertness 1995, 1999). Similar effects might not have occurred in the salt treatments because *Juncus* was more stressed, and might have been overwhelmed in the freshwater drained treatment (best conditions for *Juncus*) by a strong competitive effect of *Juncus* on *Spartina*.
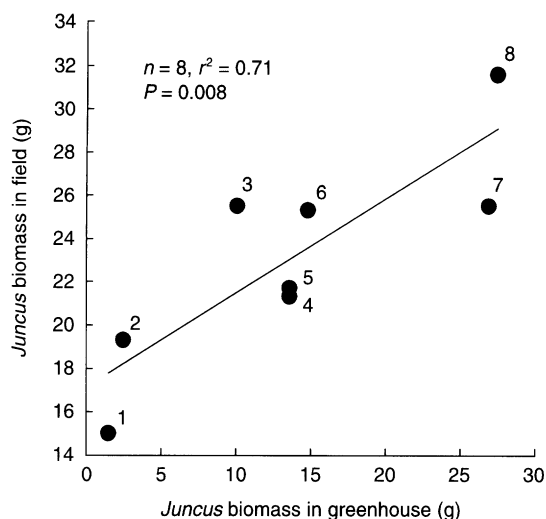
Fig. 6 Relationship between *Juncus roemerianus* performance in different treatments in the glasshouse and in the field. Field and glasshouse treatments were paired as follows. 1: field, not elevated, salt, with neighbours; laboratory, flooded, salt, with neighbours. 2: field, not elevated, salt, without neighbours; laboratory, flooded, salt, without neighbours. 3: field, not elevated, fresh, with neighbours; laboratory, flooded, fresh, with neighbours. 4: field, elevated, salt, without neighbours; laboratory, drained, salt, without neighbours. 5: field, not elevated, fresh, without neighbours; laboratory, flooded, fresh, without neighbours. 6: field, elevated, salt, with neighbours; laboratory, drained, salt, with neighbours. 7: field, elevated, fresh, with neighbours; laboratory, drained, fresh, with neighbours. 8: field, elevated, fresh, without neighbours; laboratory, drained, fresh, without neighbours. Data indicate above-ground biomass.

Field experiments in ecology are highly informative, but are also labour intensive and expensive. Consequently, there is the natural desire to extrapolate their lessons as far as possible. Extrapolation, however, is risky (Underwood & Denley 1984) because ecological interactions may change with changes in abiotic conditions (Dunson & Travis 1991; Pennings *et al.* 2003). Comparing studies of salt-marsh plant communities conducted at low and high latitudes suggests that, in coastal wetlands, the basic trade-off between competition and stress tolerance that creates vegetation pattern is universal. The relative importance of different physical stresses, however, is likely to vary geographically as a function of geographical variation in the physical environment (Pennings & Moore 2001; Bertness & Ewanchuk 2002; Ewanchuk & Bertness 2004).

Acknowledgements

GCE-LTER program) for financial support. This is contribution number 938 from the University of Georgia Marine Institute.

References

Antlfinger, A.E. & Dunn, E.L. (1979) Seasonal patterns of CO_2 and water vapor exchange of three salt marsh succulents. *Oecologia*, **43**, 249–260.

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 a New England salt marsh. *Ecology*, **72**, 138–148.

Bertness, M.D. (1992) The ecology of a New England salt marsh. *American Scientist*, **80**, 260–268.

Bertness, M.D. & Ellison, A.M. (1987) Determinants of pattern in a New England salt marsh plant community. *Ecological Monographs*, **57**, 129–147.

Bertness, M.D. & Ewanchuk, P.J. (2002) Latitudinal and climate-driven variation in the strength and nature of biological interactions in New England salt marshes. *Oecologia*, **132**, 392–401.

Bertness, M.D. & Hacker, S.D. (1994) Physical stress and positive associations among marsh plants. *American Naturalist*, **144**, 363–372.

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

Callaway, R.M., Jones, S., Ferren, W.R. Jr & Parikh, A. (1990) Ecology of a mediterranean-climate estuarine wetland at Carpinteria, California: plant distributions and soil salinity in the upper marsh. *Canadian Journal of Botany*, **68**, 1139–1146.

Chapman, V.J. (1974) Salt marshes and salt deserts of the world. *Ecology of Halophytes* (ed. W.H. Queen), pp. 3–19. Academic Press, New York.

Costa, C.S., Marangoni, J.C. & Azevedo, A.M. (2003) Plant zonation in irregularly flooded salt marshes: relative importance of stress tolerance and biological interactions. *Journal of Ecology*, **91**, 951–965.

Davy, A.J. & Costa, C.S.B. (1992) Development and organization of saltmarsh communities. *Coastal Plant Communities of Latin America* (ed. U. Seeliger), pp. 157–178. Academic Press, San Diego.

Davy, A.J., Costa, C.S.B., Yallop, A.R., Proudfoot, A.M. & Mohamed, M.F. (2000) Biotic interactions in plant communities of saltmarshes. *British Saltmarshes* (ed. T. Harris), pp. 109–127. Forrest Text, Ceredgion.

Dunson, W.A. & Travis, J. (1991) The role of abiotic factors in community organization. *American Naturalist*, **138**, 1067–1091.

Eleuterius, L.N. (1976a) The distribution of *Juncus roemerianus* in the salt marshes of North America. *Chesapeake Science*, **17**, 289–292.

Eleuterius, L.N. (1976b) Vegetative morphology and anatomy of the salt marsh rush, *Juncus roemerianus*. *Gulf Research Reports*, **5**, 1–10.

Ewanchuk, P.J. & Bertness, M.D. (2004) Structure and organization of a northern New England salt marsh plant community. *Journal of Ecology*, **92**, 72–85.

Grace, J.B. (1989) Effects of water depth on *Typha latifolia* and *Typha domingensis*. *American Journal of Botany*, **76**, 762–768.

Grace, J.B. & Wetzel, R.G. (1981) Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. *American Naturalist*, **118**, 463–474.

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.

Grime, J.P. (1988) The C-S-R model of primary plant strategies – origins, implications and tests. *Plant Evolutionary Biology* (ed. S.K. Jain), pp. 371–393. Chapman & Hall, London.

Hacker, S.D. & Bertness, M.D. (1995) Morphological and physiological consequences of a positive plant interaction. *Ecology*, **76**, 2165–2175.

Hacker, S.D. & Bertness, M.D. (1999) Experimental evidence for factors maintaining plant species diversity in a New England salt marsh. *Ecology*, **80**, 2064–2073.

Huckle, J.M., Potter, J.A. & Marrs, R.H. (2000) Influence of environmental factors on the growth and interactions between salt marsh plants: effects of salinity, sediment and waterlogging. *Journal of Ecology*, **88**, 492–505.

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.

Kuhn, N.L. & Zedler, J.B. (1997) Differential effects of salinity and soil saturation on native and exotic plants of a coastal salt marsh. *Estuaries*, **20**, 391–403.

Linthurst, R.A. & Seneca, E.D. (1980) The effects of standing water and drainage potential on the *Spartina alterniflora*-substrate complex in a North Carolina salt marsh. *Estuarine and Coastal Marine Science*, **11**, 41–52.

Linthurst, R.A. & Seneca, E.D. (1981) Aeration, nitrogen and salinity as determinants of *Spartina alterniflora* Loisel. growth response. *Estuaries*, **4**, 53–63.

Mahall, B.E. & Park, R.B. (1976a) The ecotone between *Spartina foliosa* trin. & *Salicornia virginica* L. in salt marshes of northern San Francisco Bay. II. Soil water and salinity. *Journal of Ecology*, **64**, 793–809.

Mahall, B.E. & Park, R.B. (1976b) The ecotone between *Spartina foliosa* trin. & *Salicornia virginica* L. in salt marshes of northern San Francisco bay. III. Soil aeration and tidal immersion. *Journal of Ecology*, **64**, 811–819.

Mendelssohn, I.A. & Morris, J.T. (2000) Eco-physiological controls on the productivity of *Spartina Alterniflora* Loisel. *Concepts and Controversies in Tidal Marsh Ecology* (ed. D.A. Kreeger). Kluwer Academic, Dordrecht.

Moon, D.C. & Stiling, P. (2002) The effects of salinity and nutrients on a tritrophic salt-marsh system. *Ecology*, **83**, 2465–2476.

Noe, G.B. (2002) Temporal variability matters: effects of constant vs. varying moisture and salinity on germination. *Ecological Monographs*, **72**, 427–443.

Noe, G.B. & Zedler, J.B. (2000) Differential effects of four abiotic factors on the germination of salt marsh annuals. *American Journal of Botany*, **87**, 1679–1692.

Partridge, T.R. & Wilson, J.B. (1988) The use of field transplants in determining environmental tolerance in salt marshes of Otago, New Zealand. *New Zealand Journal of Botany*, **26**, 183–192.

Pearcy, R.W. & Ustin, S.L. (1984) Effects of salinity on growth and photosynthesis of three California tidal marsh species. *Oecologia*, **62**, 68–73.

Pennings, S.C. & Bertness, M.D. (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. & Bertness, M.D. (2001) Salt marsh communities.

Marine Community Ecology (ed. M.E. Hay), pp. 289–316. Sinauer Associates, Sunderland.

Pennings, S.C. & Callaway, R.M. (1992) Salt marsh plant zonation: the relative importance of competition and physical factors. *Ecology*, **73**, 681–690.

Pennings, S.C. & Callaway, R.M. (2000) The advantages of clonal integration under different ecological conditions: a community-wide test. *Ecology*, **81**, 709–716.

Pennings, S.C. & Moore, D.J. (2001) Zonation of shrubs in western Atlantic salt marshes. *Oecologia*, **126**, 587–594.

Pennings, S.C., Selig, E.R., Houser, L.T. & Bertness, M.D. (2003) Geographic variation in positive and negative interactions among salt marsh plants. *Ecology*, **84**, 1527–1538.

Rozema, J., Bijwaard, P., Prast, G. & Broekman, R. (1985) Ecophysiological adaptations of coastal halophytes from foredunes and salt marshes. *Vegetatio*, **62**, 499–521.

Rozema, J. & Van Diggelen, J. (1991) A comparative study of growth and photosynthesis of four halophytes in response to salinity. *Acta Oecologica Plantarum*, **12**, 673–681.

Scholten, M. & Rozema, J. (1990) The competitive ability of *Spartina Anglica* on Dutch salt marshes. *Spartina anglica – a Research Review* (ed. P.E.M. Benham), pp. 39–47. Natural Environmental Research Council, London.

Shumway, S.W. & Bertness, M.D. (1992) Salt stress limitation of seedling recruitment in a salt marsh plant community. *Oecologia*, **92**, 490–497.

Snow, A. & Vince, S.W. (1984) Plant zonation in an Alaskan salt marsh. II. An experimental study of the role of edaphic conditions. *Journal of Ecology*, **72**, 669–684.

Stanton, L.E. (1998) *The relative importance of facilitation and competition between* Juncus roemerianus *Scheele and* Spartina Alterniflora *Loisel. in coastal Alabama*. MS thesis. University of South Alabama, Mobile.

Stout, J.P. (1984) *The Ecology of Irregularly Flooded Salt Marshes of the Northeastern Gulf of Mexico: a Community Profile*. U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC.

Underwood, A.J. & Denley, E.J. (1984) Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. *Ecological Communities: Conceptual Issues and the Evidence* (ed. A. Thistle), pp. 151–180. Princeton University Press, Princeton.

Ungar, I.A. (1966) Salt tolerance of plants growing in saline areas of Kansas and Oklahoma. *Ecology*, **47**, 154–155.

Vince, S.W. & Snow, A.A. (1984) Plant zonation in an Alaskan salt marsh. I. Distribution, abundance and environmental factors. *Journal of Ecology*, **72**, 651–667.

Wiegert, R.G., Chalmers, A.G. & Randerson, P.F. (1983) Productivity gradients in salt marshes: the response of *Spartina alterniflora* to experimentally manipulated soil water movement. *Oikos*, **41**, 1–6.

Wiegert, R.G. & Freeman, B.J. (1990) *Tidal Salt Marshes of the Southeast Atlantic Coast: a Community Profile*. U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC.

Woerner, L.S. & Hackney, C.T. (1997) Distribution of *Juncus roemerianus* in North Carolina tidal marshes: the importance of physical and biotic variables. *Wetlands*, **17**, 284–291.