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Source: *Ecology*, Vol. 84, No. 6 (Jun., 2003), pp. 1527-1538

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/3107973>

Accessed: 11/08/2011 13:02

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## GEOGRAPHIC VARIATION IN POSITIVE AND NEGATIVE INTERACTIONS AMONG SALT MARSH PLANTS

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**Abstract.** A pressing problem for ecologists is determining whether our understanding of communities, often developed from work at fine scales, can explain processes across broader scales. Here, we explore whether models of positive interactions developed in southern New England can be applied to geographic scales. Salt marsh plants may interact positively by ameliorating harsh physical conditions such as salinity stress. Because marsh porewater salinities are higher in low- vs. high-latitude marshes, we tested the hypothesis that positive interactions are increasingly important at low latitudes. Previous work supported this hypothesis at the regional scale: within New England, positive interactions were rare in Maine but common in Rhode Island. We conducted parallel experiments in Georgia and Alabama to determine whether similar results would be obtained in a geographic comparison. Nine species of salt marsh plants were transplanted into control plots or plots with neighboring vegetation removed, in three marsh zones, at two sites each in Georgia and Alabama. Removing neighbors increased porewater salinities; nevertheless, plants usually performed best in neighbor-removal treatments, indicating that most interactions were competitive rather than facilitative.

Several mechanisms might explain these results. For widely distributed species, southern individuals may be more salt tolerant than northern conspecifics. We tested this hypothesis by comparing the salt tolerance of northern and southern conspecifics of three species in a common garden experiment. In two species, southern plants were more salt tolerant than northern conspecifics. Although this pattern may explain the rarity of facilitation in the south for some species, it cannot explain our overall results because few species were studied in both geographic regions. The most likely explanation for our results is that northern marsh floras are dominated by salt-sensitive species that are likely to be facilitated by neighbors, whereas southern marsh floras are dominated by salt-tolerant species that are unlikely to benefit substantially from neighbor amelioration of soil salinities.

These results illustrate the difficulties inherent in extrapolating results from even well understood systems to different geographic locations or scales. Intraspecific adaptations and community composition are often likely to vary geographically, complicating our efforts to construct geographically robust generalities about community structure and processes.

*Key words:* biogeography; competition; facilitation; latitude; positive interactions; salt marsh.

### INTRODUCTION

Most ecological field experiments are done at single sites, for one or two years, in small plots (Kareiva and Andersen 1988, Tilman 1989). This creates a predicament for ecologists, who are interested in generalizing their experimental results to multiple sites and to larger spatial scales (Goldberg 1990, Brown 1995). On the one hand, the dangers of overextrapolating experimental results are well known (Underwood and Denly

1984). On the other hand, we do not have the time or resources to individually study every species or community; instead, we must develop general principles for ecology to progress as a science (Keddy 1989, Peters 1991).

One obstacle to constructing such generalities is that the nature of interactions among species may change with abiotic conditions (Dunson and Travis 1991). In principle, a full understanding of the relationship between ecological processes and relevant abiotic variables could overcome this obstacle. In practice, however, modeling such relationships may prove complicated because their nature may differ depending on the scale at which they are examined. At the local scale, where gene flow is high, individuals in a population may be adapted to local abiotic conditions and display sharply altered performance if conditions shift away from optimum. At broad, geographic scales, however, where gene flow among populations is low, each local

Manuscript received 6 May 2002; revised 16 September 2002; accepted 24 October 2002. Corresponding Editor: D. Ayres.

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population may be adapted to the conditions prevailing at that site. Thus, at this scale, the relationship between performance and abiotic conditions may be muted or absent. The problem is further exacerbated when comparing communities across large geographic scales, because the species making up the community may differ in each location (Brown 1995). Such assemblage shifts could still permit generalities if the communities were convergent in important properties; however, if the properties of each local assemblage were driven by idiosyncratic traits of its particular component species, community behavior might be unpredictable (Brown 1995, Kelt et al. 1996, Ben-Moshe et al. 2001).

Here we focus on these issues of scale and species composition for plant communities in coastal salt marshes. Salt marshes have been well studied by community ecologists because they are simple, easily manipulated systems in which strong biological interactions operate over compact gradients of physical stress (Pennings and Bertness 2001). Studies of salt marsh plant communities have contributed to our understanding of zonation, secondary succession, competition, and positive interactions. Much of our knowledge about salt marsh plant communities, however, comes from studies conducted at a few sites in Rhode Island, USA (Bertness 1992). How far can we extrapolate results from these studies to other geographic locations or scales?

Some paradigms about salt marsh plant communities appear to generalize well across broad geographic regions. For example, the zonation patterns of dominant salt marsh plants are created by trade-offs between stress tolerance and competitive ability in marshes in a wide variety of geographic locations, although the details of the trade-offs may differ in each location (Pennings and Bertness 2001). In particular, along the Atlantic coast of the United States, the processes constraining a zone of shrubs to the terrestrial border of the marsh are similar between Rhode Island and Georgia marshes (although different species of shrubs occur in each region). These processes change at higher latitudes where the shrub zone is absent, and at lower latitudes where woody plants (mangroves) dominate the entire marsh (Pennings and Moore 2001).

Other predictions about salt marsh plant communities may require consideration of how the physical environment of salt marshes differs geographically. Pennings and Bertness (1999) predicted that, because of latitudinal variation in salt marsh salinity regimes, the processes generating plant community structure should differ across latitude in several ways. In this paper we focus on one of their predictions, that positive interactions among plants should be stronger and more common in low- vs. high-latitude marshes.

After decades of focusing on competition, community ecologists have recently renewed an interest in the role of positive interactions in shaping communities (Bertness 1989, 1991, Bertness and Hacker 1994, Cal-

away 1994, 1995, 1997, 1998, Hacker and Bertness 1995, 1999, Callaway and King 1996, Greenlee and Callaway 1996, Hacker and Gaines 1997, Holzapfel and Mahall 1999, Levine 2000). One type of positive interaction occurs when organisms benefit each other by ameliorating desiccation, severe temperatures or salinities, or other stressful abiotic factors. Models of stress-mediated positive interactions typically predict that they will be most important under conditions of increasing abiotic stress (Bertness and Callaway 1994, Bertness and Leonard 1997, Callaway and Walker 1997, Bruno and Bertness 2001).

Salt marshes have proven to be useful natural systems for studying positive interactions among plants (Bertness 1991, Bertness and Yeh 1994, Callaway 1994, Hacker and Gaines 1997, Hacker and Bertness 1999, Callaway and Pennings 2000). Salt marsh plants experience physical stress due to the anoxic, saline nature of salt marsh soils (Bertness and Hacker 1994, Hacker and Bertness 1995, Pennings and Bertness 2001). Stress due to flooding and salinity varies predictably across the marsh landscape as a function of elevation and disturbance (Bertness and Ellison 1987, Brewer et al. 1997, Pennings and Bertness 2001). Under conditions of high salt stress, plants may interact positively by shading the soil and reducing porewater salinities (Bertness 1991, Bertness and Shumway 1993, Callaway 1994). These positive interactions have been studied thoroughly in New England marshes, where plant interactions vary from negative to positive as a function of (1) elevation, which affects the potential for hypersaline conditions to develop (Bertness and Shumway 1993, Bertness and Hacker 1994, Brewer et al. 1997, Hacker and Bertness 1999), (2) size of the disturbance, which affects how much salinities are elevated above ambient levels (Shumway and Bertness 1994), and (3) the salinity tolerance of different plant species (Bertness et al. 1992, Hacker and Bertness 1999).

The intensity of physical stress in salt marshes also varies with climate. Low-latitude salt marshes have higher soil salinities than do marshes at high latitudes (Pennings and Bertness 1999, 2001). Based on this observation, Pennings and Bertness (1999) predicted that positive interactions would be increasingly common and important in marshes at lower latitudes. Bertness and Ewanchuk (2002) recently tested this hypothesis at the regional scale by comparing plant interactions in New England marshes south (Rhode Island) and north (Maine) of Cape Cod. Soil salinities were 5–10 psu (ppt) higher in Rhode Island than Maine marshes, and positive interactions were more common in Rhode Island than in Maine. The nature of plant interactions also varied within each region as a function of annual variation in climate. In dry, hot years, soil salinities were high and interactions tended to be positive. In wet, cool years, soil salinities were lower and interactions tended to be negative.

These results support the hypothesis (Pennings and Bertness 1999) that positive interactions among salt marsh plants will increase with a hotter climate. This result, however, comes with the caveat that Bertness and Ewanchuk (2002) compared marshes with essentially identical floras across relatively small geographic distances. Thus, research is still needed to determine whether similar results would be obtained when comparing marshes with different floras across broad geographic scales, where local adaptation and assemblage shifts may increasingly alter predictions developed based on results from single sites in New England.

In this paper, we study plant interactions in southern (Georgia and Alabama) coastal salt marshes, and compare our results with those obtained from northern (Rhode Island and Maine) sites in order to determine whether patterns found at the regional level can be extrapolated to larger geographical scales. In particular, we used methods identical to those of Bertness and Ewanchuk (2002), in order to test the hypothesis that positive interactions will become more important at lower latitudes. Because Georgia and Alabama marshes have markedly different tidal regimes, we also explore whether the nature of plant interactions is conditional upon tidal regime in southern marshes.

#### METHODS

We conducted parallel experiments to compare plant interactions in Maine, Rhode Island, Georgia, and Alabama. Results from Maine and Rhode Island have been reported previously (Bertness and Ewanchuk 2002). The hydrological regime at all four study sites is dominated by tidal input of ocean water with salinities of 25–33 psu. Temperatures during the growing season average 6°–12°C higher at the southern sites than at the northern sites (based on May–September National Weather Service temperature data for Portland, Maine [110 years], Providence, Rhode Island [110 years], Brunswick, Georgia [97 years] and Fairhope, Alabama [77 years]). In Georgia, we worked at two sites within the Sapelo Island National Estuarine Research Reserve (31°27' N; 81°15' W), Airport Marsh and Lighthouse Marsh (descriptions in Nomann and Pennings 1998, Pennings and Richards 1998). In Alabama, we worked along the eastern side and the southern tip of Point aux Pins (30°22' N; 88°18' W). Georgia sites experience two tidal cycles each day with a large (~3 m) amplitude, whereas lunar tides in Alabama have a small (<40 cm) amplitude and actual flooding cycles of the marsh are irregular and weather-driven (Stout 1984, Wiegert and Freeman 1990). All sites have vegetation patterns typical of their respective regions (Stout 1984, Wiegert and Freeman 1990).

In June of 1996, we established 10 4 × 3 m experimental garden plots in each of three vegetation zones at each site. Plots were located within a zone dominated by *Juncus roemerianus*, at the border between *Juncus roemerianus* and a mixed species zone called the

“meadow,” and at the border between the meadow and the *Spartina alterniflora* zone. These three zones (henceforth referred to as the *Juncus*, *Juncus*/meadow and meadow/*Spartina* zones) span the breadth of the high marsh at each site (Stout 1984, Wiegert and Freeman 1990). Positive interactions driven by reduction of high salinities do not occur in regularly flooded, low marsh habitats because regular flushing by the tides prevents hypersaline conditions from developing, nor at the terrestrial border of the marsh where salt input is minimal (Bertness and Shumway 1993, Pennings and Bertness 2001).

The three marsh zones differed by only a few centimeters in elevation, but contained markedly different plant communities (Table 1). The vegetation was 3–4 times taller in zones dominated by *Juncus* than at the meadow/*Spartina* border, and blocked a correspondingly higher proportion of the light. The vegetation was similar in height, biomass, and species composition at the Georgia and Alabama sites, except that the meadow/*Spartina* border was dominated by *Distichlis spicata* in Alabama, but by a mixture of *Spartina alterniflora*, *Batis maritima*, and *Salicornia virginica* in Georgia (Table 1).

At each zone in each site, half of the plots were designated as vegetated controls and half as vegetation removal plots. All plots were trenched with a shovel around their perimeters to a depth of 25 cm. Vegetation removal plots were treated with a short-lived systemic herbicide (Roundup, Monsanto Corporation, St. Louis, Missouri) to kill all above and belowground vegetation. Standing dead material was removed with a line trimmer, and removal plots were subsequently maintained free of vegetation through October 1999 by trimming back invading vegetation as needed.

To test the hypothesis that the nature of interactions among marsh plants varies with elevation and geographic region, we transplanted several species of plants into the experimental plots. In habitats where neighbor interactions are largely competitive, transplants would be expected to perform best in the vegetation removal plots where they would be released from competitive effects of neighbors. Conversely, in habitats where neighbor interactions are largely facilitative, transplants would be expected to perform best in the vegetated control plots where neighbors would buffer each other from hypersaline conditions. This design estimates net neighbor interactions, but does not tease apart the negative and positive components of interspecific interactions (Holzapfel and Mahall 1999). Transplants were conducted in March of 1997, 1998, and 1999, before plants began rapid growth typical of the summer months. We worked with nine species of plants that were common at all four sites. These species represented the majority of the species and biomass at each site (this is not fully reflected in Table 1 because the experiments were limited to the marsh zones likely to become most hypersaline), and included plants that

TABLE 1. Characteristics of vegetation zones studied.

Zone†	Elevation‡ (cm), n = 32/zone	Canopy height (cm), n = 20/zone	Percent light transmission,§ n = 18/zone	Plant biomass   (g/0.0625 m <sup>2</sup> ), n = 16/zone	
				<i>Juncus roemerianus</i>	<i>Spartina alterniflora</i>
Georgia					
J	-0.3 ± 1.0	123 ± 5	7 ± 1	125.2 ± 10.2	3.6 ± 1.9
JM	6.8 ± 0.8	107 ± 5	16 ± 2	28.2 ± 3.6	1.1 ± 0.8
MS	0 ± 0.3	35 ± 1	37 ± 3	0 ± 0	17.2 ± 2.8
Alabama					
J	...	127 ± 4	...	94.8 ± 8.2	0 ± 0
JM	...	112 ± 3	...	31.7 ± 4.9	2.3 ± 0.8
MS	...	30 ± 3	...	0 ± 0	3.2 ± 1.4

Note: All data are means ± 1 SE.

† J, *Juncus*; JM, *Juncus*/meadow; MS, meadow/*Spartina*.

‡ Elevation was measured using a total station. Elevation of meadow/*Spartina* zone was set to zero. Elevation was not measured in Alabama for logistic reasons.

§ Percentage of light (PAR) at the soil surface compared with above the plant canopy (not measured in Alabama for logistic reasons).

|| Several other plant species (including *Limonium carolinianum* and *Solidago sempervirens*) were present at low abundance in these zones but not recorded in these particular quadrats.

form large continuous clones (*Batis maritima*, *Borrichia frutescens*, *Distichlis spicata*, *Juncus roemerianus*, and *Spartina alterniflora*), and clonal and solitary species that live as isolated "individuals" (*Aster tenuifolius*, *Limonium carolinianum*, *Salicornia bigelovii*, *Solidago sempervirens*). Three were conspecific (*D. spicata*, *S. sempervirens*, *S. alterniflora*) and two congeneric (*J. roemerianus*, *L. carolinianum*) with the species used in parallel experiments in New England (Bertness and Ewanchuk 2002). The size of the transplants was scaled to represent a functional, independent ramet of each species, and ranged from large culms of *J. roemerianus* or *S. alterniflora* (several leaves or shoots, soil blocks of 25 × 25 × 25 cm) to small seedlings of *S. bigelovii* (~1 cm tall, soil blocks of 5 × 5 × 5 cm). Transplants were planted (two replicates per species per plot) into the central portion of each garden within an hour of collection, and marked with numbered flags. Transplants that were not healthy after 2 wk (<10% of the total) were replaced. Plots were fenced to exclude deer. Some plants experienced modest grasshopper herbivory, but this appeared to explain relatively little of the variation in transplant performance among zones or treatments (S. C. Pennings, *personal observations*).

In each year, transplants were followed until the end of the growing season in October, when aboveground biomass was harvested, dried, and weighed. Plants that died during the experiment were included in analyses with biomass equal to 0, and the two replicate individuals of each species in each plot were treated as subsamples (their masses were averaged to yield a single data point/plot). We worked with all species in 1997 and 1998, and with four species (*A. tenuifolius*, *B. frutescens*, *J. roemerianus*, *L. carolinianum*) in 1999. Because differences among sites within each state and among years were minor, data for each state are presented pooled across sites and years for clarity and brevity. Data were ln(mass + 0.01 g) transformed and

analyzed using ANOVA, with neighbor manipulation, marsh zone, and state all treated as fixed effects.

To supplement biomass data, we measured gas exchange of three plant species (*D. spicata*, *J. roemerianus*, *S. alterniflora*) in June of 1997 and 1998. Instantaneous measurements of gas exchange were taken with an ADC Corporation, Model LCA4 (Dynamax Incorporated, Houston, Texas) open gas exchange system and a portable light source (1.5 mmol·m<sup>-2</sup>·s<sup>-1</sup>) at low tide on cloudless days between 1000 and 1500 hours. For logistical reasons, photosynthetic rates were measured only in Georgia. Because differences among sites within Georgia and among years were minor, data are presented pooled across sites and years for clarity and brevity. Data were analyzed using ANOVA, with neighbor manipulation and marsh zone treated as fixed effects.

To quantify edaphic differences among treatments, we monitored soil water content and pore water salinity approximately monthly during each growing season (April–September). Cores (5 cm deep) were collected during neap tide cycles and weighed, then dried and reweighed to determine water content. Dried soil was mixed with a known volume of deionized water. The salinity of the supernatant was measured with a refractometer after 48 h, and the salinity of the original pore water was calculated based on the initial water content of the core. Edaphic data were collected only in Georgia because the unpredictable tidal regime in Alabama made it difficult to routinely time our visits to coincide with low tides. Data from each plot were averaged over time to yield a single value/plot. Because differences between sites in Georgia were minor, data are presented pooled across sites for clarity and brevity.

Our results indicated that, despite higher soil salinities in the south than in the north, facilitative interactions were rarer in the south than in the north. One possible explanation for this result would be that south-

TABLE 1. Extended.

Plant biomass  (g/0.0625 m <sup>2</sup> ), n = 16/zone					
<i>Distichlis spicata</i>	<i>Batis maritima</i>	<i>Salicornia bigelovii</i>	<i>Aster tenuifolius</i>	<i>Borrchia frutescens</i>	Total
0 ± 0	0.5 ± 0.5	0 ± 0	0 ± 0	0.2 ± 0.2	129.6 ± 10.0
0 ± 0	13.6 ± 2.1	0.5 ± 0.2	0.03 ± 0.03	1.5 ± 0.7	45.0 ± 4.2
2.9 ± 1.2	4.7 ± 1.6	4.7 ± 1.4	0 ± 0	0 ± 0	29.5 ± 2.3
0.04 ± 0.04	0 ± 0	0 ± 0	0 ± 0	0 ± 0	94.8 ± 8.2
4.8 ± 0.8	0 ± 0	0 ± 0	0 ± 0	0 ± 0	39.0 ± 4.6
21.6 ± 2.5	0 ± 0	0 ± 0	0 ± 0	0 ± 0	24.8 ± 1.7

ern plants were more salt tolerant than northern conspecifics. To test this hypothesis, we compared the salinity tolerances of three species of marsh plants by growing northern and southern individuals across a range of salinities in a common greenhouse experiment. Seeds of *Aster tenuifolius* and *Distichlis spicata* and culms of *Spartina alterniflora* were collected from up to 19 sites/geographic region in New England (Maine and Rhode Island) and the South Atlantic Bight (northern Florida, Georgia, South Carolina). Porewater salinities from these sites in August 1999 indicated that vegetated, high marsh zones at southern sites were 50% more saline than comparable zones at northern sites (southern meadow zone, 66 ± 5 psu, mean ± 1 SE; northern *Spartina patens*/*Juncus gerardi* border, 43 ± 2 psu).

Culms of *S. alterniflora* were collected in the summer of 1997 and clonally propagated in the greenhouse for one year. New ramets were used in experiments beginning in the spring of 1998 to minimize carryover effects of previous environmental conditions. Seeds of *Aster* and *Distichlis* were collected in the fall of 1998 and germinated in the spring of 1999. Isolated ramets and seedlings were grown for one month before salinity treatments (0, 15, 30, 60, and 90 psu) were applied by watering with artificial seawater twice a day. Plants assigned to higher salinity treatments were started at 30 psu and gradually brought up to their final salinities over 10 d to avoid treatment shock. Salinity levels were monitored daily and adjusted as needed.

Plants were grown under experimental conditions for 42 (*Spartina* ramets) or 72 (*Aster* and *Distichlis* seedlings) d and then harvested, dried, and weighed. Gas exchange of greenhouse plants was measured before harvest using an ADC LCA4 open gas exchange system and ambient light, on cloudless days between 1000 and 1500 hours. Within each salinity treatment and geographic region, one plant from each of four (*Aster*, *Distichlis*) or eight (*Spartina*) collection sites was randomly selected for measurement of gas exchange. Data were analyzed using ANOVA, with salinity and geographic region treated as fixed effects. For biomass analyses, plants that died during the experiment were included with biomass equal to 0.

## RESULTS

Soil salinities in vegetated plots were lowest in the *Juncus* zone and highest in the meadow/*Spartina* zone (Fig. 1A). Soil salinities increased 20–40 psu when vegetation was removed by clipping. A significant interaction between clipping and zone indicated that the buffering effect of vegetation on salinity was lowest in the meadow/*Spartina* zone, where plant biomass was

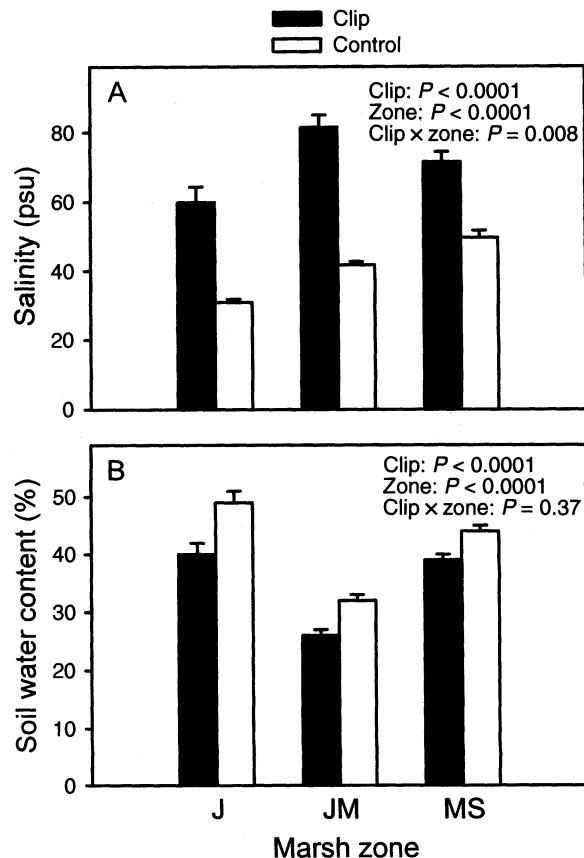


FIG. 1. Edaphic conditions in experimental garden plots in Georgia marshes. Data are means + 1 SE. (A) soil salinity, and (B) soil water content (percentage of total mass of soil core composed of water). Abbreviations: J, *Juncus*; JM, *Juncus*/meadow; MS, meadow/*Spartina*.

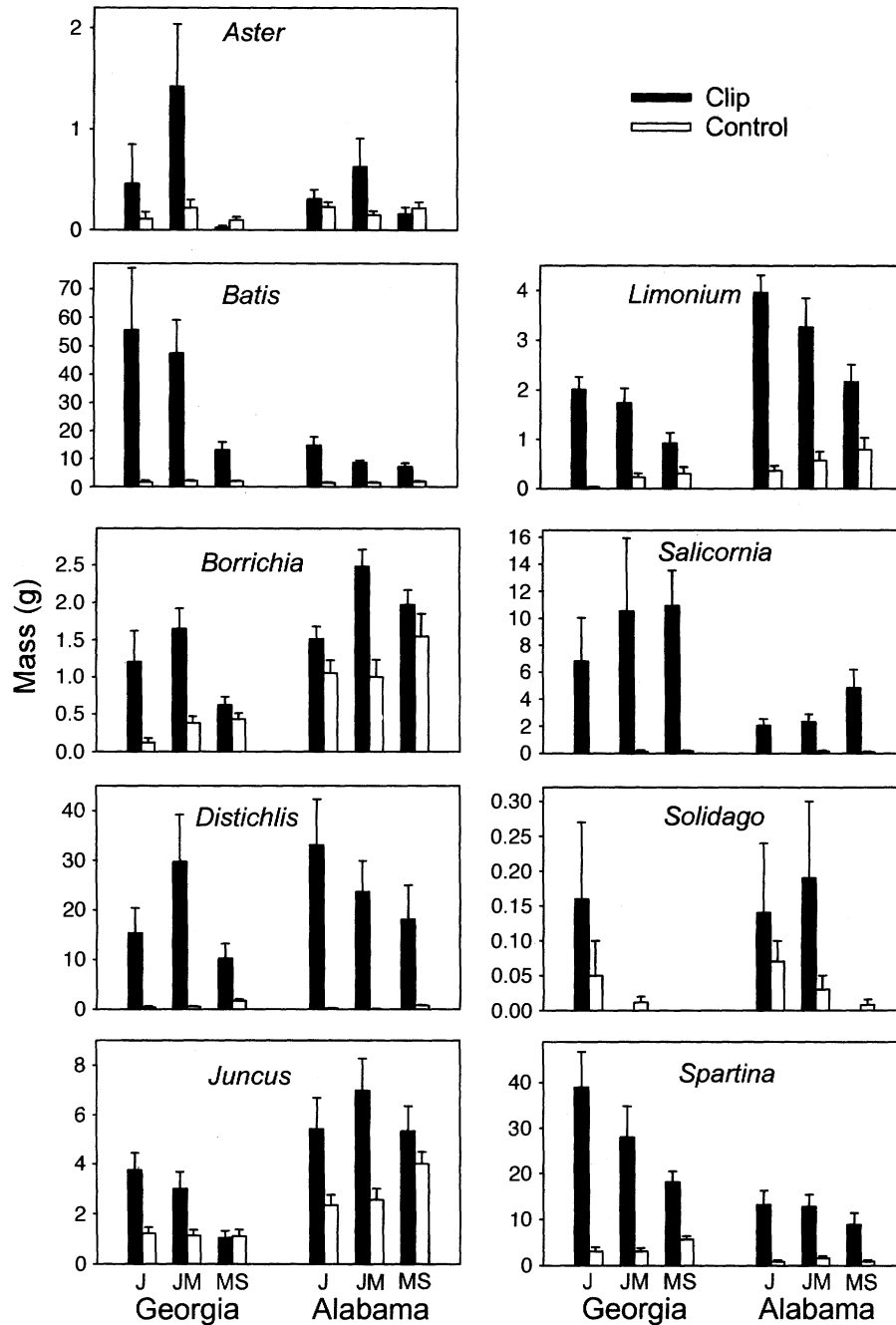


FIG. 2. Final biomass of transplanted plants with and without neighbors in Georgia and Alabama. Data are means + 1 SE. Abbreviations are as in Fig. 1.

least (Table 1). Clipped plots also experienced greater peak salinities, with values exceeding 100 psu in every zone (range of monthly salinity means in clipped plots: J: 35–117 psu; JM: 59–116; JS: 55–103; control plots: J: 28–38; JM: 37–48; JS: 38–73). Soil water content was lowest in the *Juncus*/meadow zone (Fig. 1B), perhaps because it was slightly higher in elevation (Table 1) and thus better drained than the other two zones.

Soil water content was slightly reduced in the vegetation removal plots.

In the absence of neighbors, transplants of most plant species attained their greatest biomass in the *Juncus* or *Juncus*/meadow zones (Fig. 2, Table 2), paralleling background patterns of plant biomass (Table 1). The only exception to this pattern was *Salicornia bigelovii*, probably the most salt-tolerant plant studied, which

TABLE 2. Summary of ANOVA results ( $P$  values) for transplant experiment.

Effect	<i>Aster</i>	<i>Batis</i>	<i>Borrchia</i>	<i>Distichlis</i>	<i>Juncus</i>	<i>Limonium</i>	<i>Salicornia</i>	<i>Solidago</i>	<i>Spartina</i>
Neighbors	0.61	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.02</b>	<b>0.0001</b>	<b>0.0001</b>	0.96	<b>0.0001</b>
Zone	<b>0.02</b>	<b>0.04</b>	<b>0.0004</b>	<b>0.0002</b>	0.07	0.28	<b>0.0005</b>	<b>0.003</b>	0.54
N × Z	<b>0.02</b>	<b>0.0001</b>	<b>0.01</b>	<b>0.0001</b>	<b>0.02</b>	<b>0.0001</b>	0.14	0.90	<b>0.054</b>
State	<b>0.03</b>	0.87	<b>0.0001</b>	0.97	<b>0.0001</b>	<b>0.0001</b>	0.07	<b>0.002</b>	<b>0.0001</b>
State × N	0.83	<b>0.001</b>	0.23	<b>0.0003</b>	0.75	0.12	0.08	0.99	0.26
State × Z	<b>0.002</b>	<b>0.0006</b>	0.07	0.71	0.44	0.46	0.12	0.17	<b>0.04</b>
S × N × Z	0.52	<b>0.02</b>	0.08	0.50	0.38	0.50	0.78	0.29	0.27

Note: Data were pooled across years and  $\ln(\text{mass} + 0.01 \text{ g})$ -transformed before analysis. Significant results are indicated in bold.

grew best in the meadow/*Spartina* zone. Many plants also showed differences in biomass between states (Table 2), with some species such as *Aster* and *Spartina* growing best in Georgia, and others such as *Juncus* and *Limonium* growing best in Alabama. These state-to-state differences in average growth rates likely resulted from tidal, edaphic, or climatic differences favoring different species in different states. These differences

are peripheral to the focus of this paper, and will not be discussed further.

Most plant species attained much greater biomass in the vegetation removal treatments than in the control treatments (Fig. 2, Table 2), indicating that interactions between marsh plants in both Georgia and Alabama were overwhelmingly competitive. There were indications, however, that interactions were neutral to facilitative for some species in some marsh zones. The effect of neighbors on *Aster* differed among marsh zones (Table 2), with positive effects of neighbors in the meadow/*Spartina* zone and negative effects in the other two zones. Similarly, neighbors tended to facilitate *Solidago* at lower elevations and to compete with it at higher elevations, but this trend was not significant due to high variability in growth of *Solidago*. More generally, there was a significant neighbor × zone interaction for seven of the nine species studied (Table 2), reflecting weaker competitive effects in the meadow/*Spartina* zone and stronger competitive effects in the other two zones (Fig. 2).

Photosynthetic rates of *Distichlis*, *Juncus*, and *Spartina* at constant light levels were higher for plants grown in clipped vs. control plots (Fig. 3), indicating a weakened physiological state of plants experiencing competition. These short-term measurements did not display consistent zone or zone × neighbor effects.

Photosynthetic rates of seedlings of *Aster* and *Distichlis* and clonal fragments of *Spartina* in the greenhouse were reduced at high salinities, but did not differ by geographic origin of plants (Fig. 4). In contrast to *Aster* and *Distichlis*, photosynthesis of *Spartina* appeared to increase at intermediate salinities. Biomass of all three species was reduced at high salinities, and southern clones of *Aster* and *Distichlis* grew larger than northern clones (Fig. 5). Significant region by salinity interactions for *Aster* ( $P < 0.0001$ ) and *Distichlis* ( $P = 0.054$ , marginally significant), indicated that clones from the south performed disproportionately better in the higher salinity treatments.

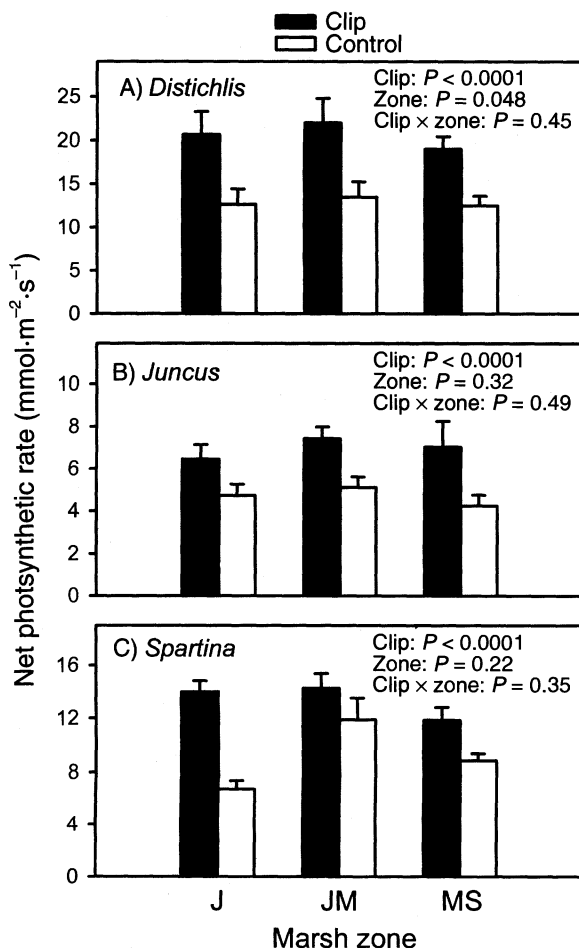


FIG. 3. Photosynthetic rates of transplanted plants with and without neighbors in Georgia. Data are means + 1 SE. Abbreviations are as in Fig. 1.

## DISCUSSION

Previous results from southern New England indicated that positive interactions between plants are predictable and important in structuring salt marsh plant



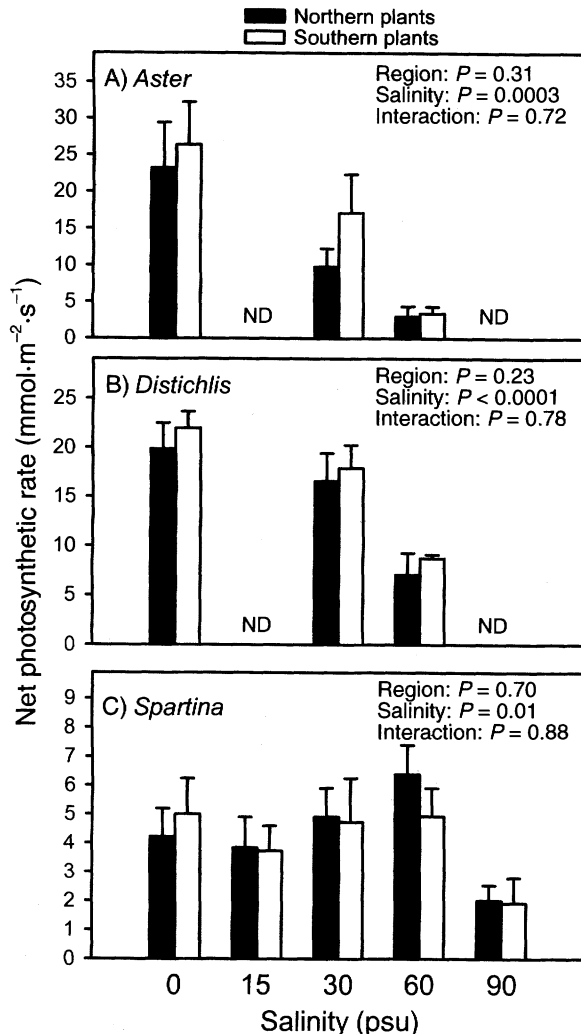


FIG. 4. Photosynthetic rates of clonal fragments (*Spartina*) or seedlings (*Aster*, *Distichlis*) grown under different salinity treatments in a common greenhouse. Data are means + 1 SE. "ND" indicates not done.

communities. In particular, positive interactions are common in large disturbed patches and in marsh zones where edaphic conditions favor salt accumulation when vegetation is removed (Bertness and Shumway 1993, Bertness and Hacker 1994, Bertness and Yeh 1994, Shumway and Bertness 1994, Brewer et al. 1997, Hacker and Bertness 1999). Moreover, the strength of positive interactions varies as a function of climate among years and with latitude within New England (Bertness and Ewanchuk 2002). Because southern marshes are hotter and more saline than northern ones, we hypothesized that positive interactions would be even more important in southern USA marshes.

In striking contrast to our prediction, we found that interactions between salt marsh plants in Georgia and Alabama were almost always strongly competitive.

With two partial exceptions, competitive interactions were the rule among all nine plant species studied, across three marsh zones, and at four sites located in two states with markedly different tidal regimes. Thus, in the southern marshes that we studied, competitive interactions appear to dominate among most of the common plant species that occur in higher marsh zones.

In two species we did find occasional instances of positive interactions. These exceptions are consistent with previous studies from Rhode Island. First, they occurred with relatively salt-sensitive species, *Aster* and *Solidago*. Second, they occurred in the most stressful marsh zones. Across most of the plant species we studied, growth in clipped plots was worst in the meadow/*Spartina* zone, indicating that this zone was potentially the most stressful to plants. As expected, positive interactions involving *Aster* and *Solidago* occurred primarily (three of four cases) in this highly stressful zone. In the fourth case (*Solidago* in Georgia), the positive

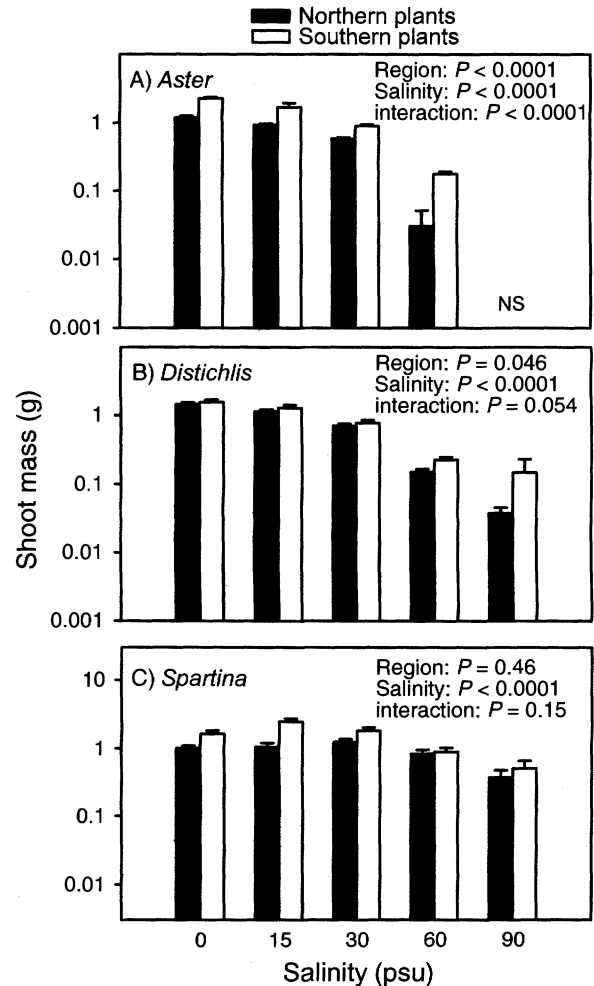


FIG. 5. Final biomass of northern and southern plants grown in the greenhouse under a range of salinity treatments. Data are means + 1 SE. NS indicates that there were no surviving plants.

interaction occurred in the next most stressful zone (*Juncus*/meadow) because no individuals survived in the meadow/*Spartina* zone. Although other species did not display positive effects, the negative effects of neighbors tended to be strongest in the *Juncus* and *Juncus*/meadow zones and weakest in the meadow/*Spartina* zone. Thus, both the species involved in positive interactions and the zones in which these interactions occurred were consistent with results of previous studies; however, the low overall frequency of positive interactions was unexpected.

Our failure to find many positive interactions did not occur because the surrounding vegetation failed to affect edaphic conditions. As has been shown in numerous salt marsh studies (Bertness 1991, Iacobelli and Jefferies 1991, Bertness et al. 1992, Bertness and Hacker 1994, Bertness and Yeh 1994, Hacker and Bertness 1995, 1999, Brewer et al. 1997), the removal of vegetation strongly elevated soil salinities. This effect occurred in all three vegetation zones, indicating the potential for positive interactions to occur across the high marsh. Moreover, soil salinities in experimental plots were similar to or greater than those in parallel experiments in New England (Bertness and Ewanchuk 2002), where positive interactions were common. Because many factors differ between northern and southern marshes, several hypotheses might explain why our experiments did not find a greater incidence of positive interactions at these southern sites. We will discuss what we believe to be the three most reasonable ones.

First, a selection-driven gradient in intraspecific salt tolerance across latitude may make southern plants less sensitive to salt stress. Our common garden experiments indicated latitudinal differences in salt tolerance for the high marsh plants *Aster* and *Distichlis*, but not for *Spartina alterniflora*. Because *S. alterniflora* occurs in low marsh zones, which rarely become hypersaline, it may experience less of a latitudinal gradient in selection for salt tolerance than do high marsh plants. Population-level variation in salinity tolerance does exist in *S. alterniflora*, but indicators of this variation are subtle (Hester et al. 1998, 2001). If latitudinal variation in salinity tolerance also occurs in *Solidago*, this could explain why background vegetation strongly facilitated *Solidago* in northern but not southern experiments. In general, however, latitudinal variation in salt tolerance alone cannot explain our results, because (1) only three species were included in field experiments in both geographic regions (most species were studied in only one geographic region because they were absent or rare in the other, see below), and (2) only one of these three species (*Solidago*) behaved differently in the two geographic regions. The two other species that were included in both northern and southern field experiments (*Distichlis*, *S. alterniflora*) displayed competitive release in both regions.

Second, southern floras may be less sensitive than northern floras to salt stress. In other words, latitudinal

variation in salinity may lead to a shift in the species that make up the plant community, such that the southern flora is highly tolerant to the prevailing edaphic conditions. In general, the most salt-sensitive plant species found at our northern sites are not common in the south, but are replaced by more salt-tolerant species that are rare in the north (Pennings and Bertness 1999). In particular, the five species that commonly benefit from neighbors in New England are absent (*J. gerardi*) or rare (*Atriplex*, *Iva frutescens*, *S. patens*, *Solidago*) at our southern sites, where they occur primarily as peripheral species at the terrestrial border of the marsh. Because these species were so rare in the south, only one (*Solidago*) was included in our experiments. At the same time, the most salt-tolerant southern species (*Batis maritima*, *Borrchia frutescens*, *Salicornia bigelovii*) are rare or absent in the north, and were not included in northern experiments. Thus, a likely explanation for our results is that northern marsh floras are dominated by salt-sensitive species that are likely to be facilitated by neighbors, whereas southern marsh floras are dominated by salt-tolerant species that are unlikely to benefit substantially from neighbor amelioration of soil salinities.

Third, competition may have been stronger in southern vs. northern sites, overwhelming latitudinal differences in positive interactions. Because the effects of plants on neighbors are a combination of positive and negative components (Callaway and Walker 1997, Holzapfel and Mahall 1999), changes in net effects could result from changes in the strength of either positive or negative components. The plant communities in the *Juncus* and *Juncus*/meadow zones were taller and/or had more biomass than comparable plant communities in New England (Emery et al. 2001). Thus, it is possible that competitive interactions among plants were also more intense, at least in marsh zones containing *Juncus roemerianus*. If so, the negative component of plant interactions may have overwhelmed the positive component, even if positive effects were stronger in the south than in the north. This hypothesis, however, cannot explain the fact that interactions were still mostly negative in the meadow/*Spartina* zone, which did not differ dramatically in canopy height or biomass from northern marshes.

Regardless of the mechanism involved, our results highlight the difficulties inherent in generalizing the results of ecological studies, even within specific systems. The interactions that we studied (positive and negative interactions among salt marsh plants) are well understood in southern New England marshes (Bertness 1991, Bertness and Shumway 1993, Bertness and Hacker 1994, Bertness and Yeh 1994, Shumway and Bertness 1994, Hacker and Bertness 1995, 1996, 1999, Hacker and Gaines 1997). We generated logical hypotheses about how these results should generalize across latitude, and these predictions were confirmed in regional comparisons within New England at sites

with similar floras (Bertness and Ewanchuk 2002). In contrast, when we attempted to generalize our results to southern marshes, our predictions failed. We argue that this was likely due to shifts in the composition of the plant community: southern plant communities were far more tolerant of prevailing high salinities than we predicted based on studies from New England. Similar assemblage shifts are likely to routinely complicate efforts to compare geographically distant communities (Kelt et al. 1996).

Ecologists have long been curious about how ecological interactions vary across broad spatial scales (Menge 1976, Vermeij 1977, 1978, Jeanne 1979, Lubchenco 1980, Bertness et al. 1981, Menge and Lubchenco 1981, Gaines and Lubchenco 1982, Fawcett 1984, Hay 1984, Steinberg 1992, Bryant et al. 1994, Bolser and Hay 1996, Connolly et al. 2001, Pennings and Moore 2001, Pennings et al. 2001, Hughes et al. 2002). Nevertheless, we know relatively little about the generality of field studies, because ecological field experiments are rarely repeated due to logistical constraints and/or the perception that repeating studies is uninteresting. This lack of attention to generality represents an important weakness in ecology (Strong et al. 1984, Underwood and Denley 1984, Keddy 1989). Understanding generality across broad spatial scales is central to the success of ecology as a predictive science (Goldberg 1990, Reader et al. 1994), and without it, ecological studies may be little more than a collection of special cases, limited to the time and place in which they were done (Peters 1991).

For several reasons, however, successfully extrapolating from single studies to other sites or scales presents a daunting challenge. The results of ecological field experiments often change depending on the abiotic and biotic environment (Moloney 1990, Dunson and Travis 1991, Goldberg and Barton 1992, Travis 1996, Thompson 1999). Even if the extrinsic factors affecting ecological outcomes are well understood, however, ecological predictions may fail due to the intervention of evolutionary processes. As our results illustrate, it can be difficult to extrapolate even well-understood ecological interactions to larger geographic regions, because selection on individuals and species may change the way that populations and communities respond to environmental constraints. Although these issues are daunting, they are not insoluble. Improving our understanding of how ecological and evolutionary processes interact to structure communities at broad spatial scales is a vital goal, and will greatly assist in developing ecology into a truly predictive science.

#### ACKNOWLEDGMENTS

Many people helped with the field work; we particularly thank T. Buck, S. Franks, M.-B. Grant, F. Jackson, B. No-mann, C. Miller, D. Moore, B. Pister, K. Reinhart, C. Richards, E. Siska, and L. Stanton for their assistance. We thank the National Institute for Global Climate Change of the De-

partment of Energy and NSF (Georgia Coastal Ecosystems LTER, OCE 99-82133) for funding. We thank two anonymous reviewers for their helpful comments on the manuscript. This is contribution number 908 from the University of Georgia Marine Institute.

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