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Latitudinal and climate-driven variation in the strength and nature of biological interactions in New England salt marshes

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Abstract We examined the linkage between climate and interspecific plant interactions in New England salt marshes. Because harsh edaphic conditions in marshes can be ameliorated by neighboring plants, plant neighbors can have net competitive or facilitative interactions, depending on ambient physical stresses. In particular, high soil salinities, which are largely controlled by solar radiation and the evaporation of marsh porewater, can be ameliorated by plant neighbors under stressful conditions leading to facilitative interactions. Under less stressful edaphic conditions, these same neighbors may be competitors. In this paper, we use this mechanistic understanding of marsh plant interactions to examine the hypothesis that latitudinal and inter-annual variation in climate can influence the nature and strength of marsh plant species interactions. We quantified the relationship between climate and species interactions by transplanting marsh plants into ambient vegetation and unvegetated bare patches at sites north and south of Cape Cod, a major biogeographic barrier on the east coast of North America. We hypothesized that the cooler climate north of Cape Cod would lead to fewer positive interactions among marsh plants. We found both latitudinal and inter-annual variation in the neighbor relations of marsh plants that paralleled latitudinal differences in temperature and salinity. South of Cape Cod, plant neighbor interactions tended to be more facilitative, whereas north of Cape Cod, plant neighbor interactions were more competitive. At all sites, soil salinity increased and plant neighbor interactions were more facilitative in warmer versus cooler years. Our results show that interspecific interactions can be strikingly linked to climate, but also reveal that because the sensitivity of specific species interactions to climatic variation is highly variable, predicting how entire communities will respond to climate change will be difficult, even in relatively simple, well-studied systems.

Keywords Competition · Facilitation · Climate change · Community organization · Plant ecology

Introduction

Understanding how variation in climate can influence the structure and dynamics of natural communities is necessary to accurately predict how climate change will impact natural communities and ecosystems. Most climate change models predict that global warming driven by anthropogenic production of greenhouse gases will lead to temperature increases of at least 5°C over the next century (Kattenberg 1995). Most efforts to predict how this will impact natural ecosystems, however, have been restricted to examining how photosynthetic and respiratory processes and the distribution of ecosystem types will be influenced by temperature increases of this magnitude (Melillo 1995). Relatively few studies have examined how species interactions will be affected by climate change (Karieva et al. 1993). If temperature increases associated with climate change affect species interactions, this also could lead to predictable shifts in the structure and dynamics of natural communities. Yet, with very few exceptions (Davis et al. 1998; Bertness et al. 1999; Leonard 2000), only a few studies have explored the link between climate and species interactions in systems where we have a mechanistic understanding of the processes that generate community pattern.

A promising approach to exploring how variation in climate can influence the structure and organization of natural communities is to examine natural latitudinal variation in communities. Historically, ecologists have learned a great deal about the organization of natural communities by exploring latitudinal patterns in communities (Fischer 1960; MacArthur 1972; Paine 1966; Vermeij 1978; Menge and Lubchenco 1981). Most of the interest in latitudinal variation in the forces structuring natural communities, however, has focused on variation in biological processes such as competition for resources and consumer pressure, rather than the more conspicuous

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and easily measured latitudinal gradients in physical parameters, such as temperature. Examining linkages between temperature, solar radiation and community structure may be more conducive to gaining an understanding of how changes in climate may affect process and pattern in natural communities. Nonetheless, while it is widely recognized that variation in physical stress can influence the intensity and nature of biotic interactions (Menge and Sutherland 1987; Dunson and Travis 1991; Bertness and Callaway 1994), few studies have examined the link between climate and the intensity and nature of biotic interactions

Salt marsh plant communities are good candidate systems in which to explore the potential effects of climatic warming. They are relatively simple systems, dominated by a limited number of plant species usually found in conspicuous vegetation zones parallel to the shoreline. We also already know quite a bit about the role played by physical and biotic forces in shaping marsh plant communities. The striking elevational plant zonation in marshes is caused by physical stress at low elevations and plant competition at high elevations. Competitively subordinate plants are excluded to lower marsh elevations where they are exposed to anoxic soil conditions that the competitive dominants cannot tolerate. Conversely, the competitively superior plants dominate higher elevations and are limited from lower elevations by anoxic soil conditions [see Pennings and Bertness (2001) for a thorough discussion of salt marsh plant zonation]. Global warming may influence the elevational zonation of marshes because sea-level rise will increase soil waterlogging and anoxia in low marsh habitats (Warren and Niering 1993; Donnelly and Bertness 2001). Climatic warming can have another important effect at higher marsh elevations. At higher elevations, marsh plants are potentially exposed to limiting hypersaline soil conditions that are the result of the evaporation of marsh porewater (Bertness et al. 1992). At these elevations in New England marshes, hot summer weather conditions lead to increased evaporation and elevated soil salinities. At lower elevations, higher soil salinities do not occur because frequent tidal flooding routinely flushes salt accumulations from the marsh, whereas at higher marsh elevations, rain and runoff limit the development of hypersaline soil conditions (Bertness et al. 1992). At lower latitudes exposed to higher solar radiation for longer periods of time, such as on the coasts of Georgia and South Carolina, salt accumulation at intermediate marsh elevations results in characteristic salt pans where plant production and densities are suppressed by high salinities (Pennings and Bertness 1999).

Elevated salinities at intermediate marsh elevations, however, can also have important, but more subtle effects on the way plants interact. At intermediate marsh elevations in southern New England, plant neighbors potentially have strong positive effects on one another by shading the substrate and preventing the development of limiting hypersaline soil conditions. These salt stress-ameliorating positive neighbor interactions have been

shown to result in: (1) facilitated secondary succession (Bertness and Shumway 1993), (2) the coexistence of forbs with low salt tolerance with more salt tolerant marsh turfs (Bertness and Hacker 1994; Hacker and Bertness 1999), and (3) the maintenance of insect food chains that are dependent on facilitator-dependent forbs (Hacker and Bertness 1996). In spite of the potential for climatic variation to play an important role in mediating the strength of positive interactions [see Bertness and Pennings (2000) and Pennings and Bertness (2001) for discussion], few studies [see Holzapfel and Mahall (1999) for exception] have explored the linkage between climate and species interactions in any system.

In this paper we utilize our mechanistic understanding of interactions in New England marsh plant species to explore the link between climate and the nature of the species interactions of high marsh plants. In particular, we ask the question, "Does latitudinal and inter-annual variation in climate lead to latitudinal and inter-annual variation in the potential accumulation of salt in high marsh habitats and in the frequency of competitive and salt stress ameliorating facilitative interactions among high marsh plants?" More specifically, we examine the hypotheses that: (1) positive, salt stress-ameliorating interspecific interactions among marsh plants are more common at lower than higher latitudes due to higher temperatures, evaporation and potential salt accumulations typical of lower latitudes, and (2) the relative importance and strength of positive salt stress-ameliorating interactions among high marsh plants is closely linked to inter-annual climatic variation, such that the importance of positive interactions among high marsh plants increases in years with high summer temperatures.

Materials and methods

To quantify variation in the nature of plant interactions between marshes north and south of Cape Cod, we set up parallel experiments to quantify interaction strengths at study sites in Maine and Rhode Island. In southern Maine, we worked at two sites in the Wells National Estuarine Research Reserve, Little River Marsh (43°18'N, 70°34'W) and Drakes Island Marsh (43°19'N, 70°33'W). In Rhode Island we worked at Rumstick Cove (41°44'N, 71°18'W), a site where we have done considerable previous work (Bertness et al. 1992; Bertness and Hacker 1994), and Nag Creek (41°38'N, 71°20'W) at the Narragansett Bay National Estuarine Research Reserve on Prudence Island. All sites are normally exposed to open water salinities of 27–30 parts per thousand (ppt), and have salt marshes with plant zonation patterns typically found in the region. Logistic difficulties prevented us from working at more than four sites. At these sites, however, we worked with a large number of the local marsh plants and were able to replicate some of our experiments annually for 4 years.

In June of 1996, we established ten 4×3-m experimental garden plots at each site, parallel to the shoreline and on the high marsh border at the interface between the *Juncus gerardi* Loisel. and *Spartina patens* Muhl. zones. At each site, half of the plots were designated as vegetated controls and the other half as vegetation removal plots. The vegetation removal plots were then trenched around their perimeter to 25 cm with a straight-edge garden shovel, and then treated with a systemic herbicide (Roundup; Monsanto) known to rapidly degrade and have limited long-term effects on vegetation. This herbicide quickly (within 1–2 weeks)

kills all above- and belowground vegetation and we have used it extensively for creating unvegetated substrate in salt marshes (e.g. Bertness 1991; Bertness and Shumway 1993; Hacker and Bertness 1999). After the plants in the vegetation removal plots died, standing dead vegetation was removed with a gasoline powered, high-speed line trimmer. Plant colonization and growth in experimental bare patches are identical to bare patches created by natural processes (Bertness and Shumway 1993). We created experimental bare patches (June 1996) nearly 1 year before they were used (April 1997) in our study to further minimize any potential artifacts of either the herbicide or the artificial removal of aboveground biomass on transplant performance. We maintained all vegetation removal plots free of vegetation through August 2000 by trimming back invading vegetation as needed.

To examine the hypothesis that the nature of interspecific interactions among marsh plants varies with latitude, north and south of Cape Cod as a function of climate, we transplanted plants at each site into the experimental gardens. When neighbor interactions are largely competitive, transplants were predicted to have maximum performance in unvegetated gardens, released from the competition of neighbors, whereas, when neighbors largely buffer one another from potentially limiting physical stresses, transplants were predicted to have maximum performance in vegetated gardens where neighbors are present (see Bertness and Hacker 1994; Hacker and Bertness 1999). Our experiment allows us to estimate net neighbor interactions, but does not allow us to tease apart the underlying negative and positive components of interspecific plant interactions as has been elegantly done in some recent experiments (Holzapfel and Mahall 1999). Separating the potentially independent positive and negative components of interactions yields much more information than our approach of quantifying net interaction strength. Nonetheless, quantifying changes in net interaction strength with latitude and inter-annual variation in climate is an obvious first step in exploring climate-driven variation in interactions. Not all salt marsh plant species would be predicted to exhibit positive, salt stress-ameliorating neighbor interactions. In particular, these types of positive neighbor interactions would be predicted to occur with species that are sensitive to salt stress, but not with salt tolerant species. For our experiments we used all of the common plants in New England marshes including both salt sensitive and salt tolerant species, with the a priori prediction that salt sensitive, but not salt tolerant species should exhibit positive salt-ameliorating interactions under potentially hypersaline conditions (Hacker and Bertness 1999).

The plant species used can be divided into three groups of ecologically similar taxa or functional groups: matrix species, salt tolerant fugitives and salt sensitive fugitives. The perennial turfs, *Spartina alterniflora* Loisel., *Spartina patens* and *Juncus gerardi*, are grouped together as matrix species. In New England salt marshes, these species are typically the numerically abundant plants that dominate the marsh landscape as dense clonal turfs, which create a background matrix in which the rest of the community lives (Miller and Egler 1950; Bertness and Ellison 1987). Of the matrix species, *J. gerardi* lives on the terrestrial border of the high marsh and is the most sensitive to salt stress, while *S. alterniflora* dominates low marsh habitats and is a stress tolerant species that can tolerate both anoxic waterlogged soils and high soil salinities (Bertness et al. 1992). The remaining species are usually restricted by the competitively dominant matrix species to physically stressful habitats, such as disturbance-generated bare space, or occur at low densities within the vegetation matrix of clonal dominant species (Bertness and Ellison 1987; Bertness et al. 1992; Brewer et al. 1998; Rand 2000). These species will be referred to as fugitive species (sensu Bertness et al. 1992), and subdivided into salt tolerant and salt sensitive fugitives. The salt tolerant fugitives, *Distichlis spicata* L., *Salicornia europaea* L. and *Limonium nashii* Small, are usually found restricted to hypersaline marsh habitats such as recovering bare patches or salt pans (Bertness and Ellison 1987; Bertness et al. 1992; Penning and Bertness 2001). The salt sensitive marsh fugitives (*Atriplex patula* L., *Solidago sempervirens* L. and *Iva frutescens* L.), in contrast, lack physiological mechanisms to deal with hypersaline soils, and are typically restricted to physically benign marsh

habitats (Rand 2000). Exceptions to these groupings are common. The spike grass, *D. spicata*, for example, can be found in physically disturbed or physiologically stressful New England marshes, thus dominating marsh landscapes as a matrix species. The marsh elder, *I. frutescens*, is frequently found in southern New England marshes as a zonal dominant at the terrestrial border of the marsh (Bertness and Hacker 1994). Despite the exceptions, the functional groups are ecologically meaningful and facilitate discussion and interpretation of the results.

All transplants were made in the early spring just as the plants either emerged from overwintering rhizomes or seeds (April–May in Rhode Island, May in Maine). Since all experimental plants were transplanted and were compared only to one another, we did not need transplant controls. In Rhode Island marshes, we used the following clonal turfs for transplantation; *Spartina alterniflora*, *Spartina patens*, *D. spicata*, *J. gerardi*, while the following solitary plants were used as transplants; *Salicornia europaea*, *A. patula*, *Solidago sempervirens*, *L. nashii* and *I. frutescens*. These plants represent the most abundant and common species in these marshes (Bertness 1999). In Maine, we used the same suite of plants for transplantation except for *D. spicata* and *I. frutescens* because they were too rare. In addition, we did not transplant *A. patula* in 1998 because it was too rare at the Rhode Island study sites to make transplantation practical. For the clonal turfs, we used 7.5-cm-diameter circular cores (10–15 cm deep) as transplant material. For solitary plants, we either used 2- to 3-week-old seedlings (*Salicornia europaea*, *A. patula*, and *I. frutescens*) or recently emerged ramets (*Solidago sempervirens* and *L. nashii*). For transplantation, we removed cores with a standard corer or ramet units with a sharp knife, taking care to include as much intact root material as possible from habitats at each site where the transplant was to be used. Transplants were planted (2 replicates per species per plot) in the experimental gardens within an hour of collection and marked with numbered flags. For each species, the transplants were separated by at least 1.5 m in each plot. Transplants that were not healthy after a week (less than ten of the total transplants) due to transplantation shock were replaced. Transplants were then left undisturbed for the remainder of their normal growing season until flowering was observed. After flowering was observed for each species, the aboveground biomass of each transplant was harvested, dried and weighed. We performed these transplants in both 1997 and 1998 to assess inter-annual variation in plant interactions.

To examine variation in transplant performance within and among species, we calculated the percent of maximum biomass achieved at each site and in each year for each individual transplant. For each species, we identified the transplant at each site and in each year with the greatest biomass and we calculated the percentage of the maximum biomass attained by each of the other transplants. We normalized the data in this way because our primary objective was to test the hypothesis that the relative influence of neighbors on transplant performance varied among regions and years. By using this metric of performance, inter-annual and site variation in transplant performance not associated with the neighbor treatments was minimized. Moreover, since the final dry weight of the transplants varied by as much as 3 orders of magnitude between species (the clonal turfs could weigh as much as 10 g while the forbs could weigh as little as 0.1 g), expressing the transplant data as a percentage of maximum growth by species also made it much easier to examine interspecific differences in the results.

Herbivore damage to the transplants was rare both on the perennial turfs (*Spartina alterniflora*, *Spartina patens*, *D. spicata*, and *J. gerardi*) and the forbs (*L. nashii*, *I. frutescens*, *Salicornia europaea*, *A. patula* and *Solidago sempervirens*). While herbivory on the perennial turfs is rare in New England marshes (Ellison 1987), herbivory can be common on some of the forbs, especially *Salicornia europaea*, *A. patula* and *Solidago sempervirens* (Ellison 1987; Rand 1999). The herbivores of these forbs, however, leave distinctive damage on grazed plants and their impact is very patchy in time and space (Rand 1999). Weekly examination of the transplants during our experiments revealed that herbivore damage to the forb transplants was extremely rare, and little, if any, of the overall variation in the performance of transplants in our experi-

ments appeared to be the result of herbivores (personal observations). This was in marked contrast to spatial and temporal variation in the edaphic conditions in the plots, which had clear and unmistakable effects on the performance and health of the transplants. During hot summer weather, not only did the bare patches become dry and covered with a superficial white layer of salt, but the salt sensitive plants in the patches wilted and often died, while those in the nearby vegetation matrix remained green and healthy [see Hacker and Bertness (1999) for data on plant responses to the edaphic conditions in bare patches].

The results of our 1997 and 1998 transplants suggested that climatic variation among years was as important a determinant of the nature of marsh plant species interactions in this system as latitude. Thus, in 1999 and 2000 we transplanted *Spartina patens* and *J. gerardi* cores into the bare and vegetated plots to more thoroughly examine inter-annual variation in plant performance among years, sites and treatments. We chose these two species to explore longer-term variation in plant interaction strengths because they are the high marsh matrix species that commonly dominate New England marsh landscapes, and they both showed inter-annual variation in interaction strength in the first 2 years of our work. These transplants were performed and monitored as outlined above for the initial 2 years of our study.

To quantify differences in substrate salinity among sites, vegetation treatments and years, we monitored soil salinity in all vegetated and unvegetated plots weekly. Soil salinity was monitored by cutting a 2×2×2-cm plug of sediment from a central location of each plot with a knife and squeezing the pore water on a salinity refractometer (see Bertness et al. 1992). We monitored soil salinities at all sites and in all vegetation treatments from the last week of May until the transplants were harvested at the end of the first week of August in all 4 years of this experiment.

To quantify climatic variation among sites, vegetation treatments and years, temperature data loggers were installed in vegetated and unvegetated plots at all sites (2 units per treatment per site). The temperature probes of the data loggers were attached to the sediment surface to measure sediment surface temperature. These data loggers were deployed each year (1997–2000) during the last week of May just as transplantation was being completed and were set to take soil surface temperature every 5 min for the entire growing season of the transplants. When the transplants were harvested each year, the data loggers were returned to the laboratory and the data downloaded.

Statistical analyses

Soil salinity, substrate temperature and plant performance data were analyzed with three-way ANOVAs that considered region (Maine and Rhode Island) and neighborhood treatment (with and without competition) as fixed effects and year as a random effect. Because there were two non-independent transplants for a given

experimental plot for each region×treatment×year combination, it was necessary to add a nested element to our statistical model of plant performance. Hence, individual transplants were nested within each replicate garden for the various region×treatment×year experimental combinations. This term was declared a random effect in our model and was therefore used as the error term for *F*-ratios generated by the JMP statistical package (version 3.2.2, SAS Institute Cary, N.C.). This approach avoids pseudoreplication caused by the use of non-independent replicates as the error term in statistical models. Residuals of all data were examined for heteroscedasticity, and data were arc sine transformed, if necessary, to meet the assumptions of ANOVA. In the few cases where mild heteroscedasticity was detected, an analysis was run on both transformed and untransformed data. In no case did these different analyses produce meaningfully different results, so we present the results from analyses on untransformed data. All post hoc comparisons were performed using the linear contrast feature of JMP.

Results and discussion

Substrate salinities

Weekly soil salinity data from the experimental plots revealed a significant three-way interaction between neighbor treatment, region and year (Fig. 1, Table 1), indicating that the presence of neighbors differentially influenced soil salinity among years and regions. Soil salinity was consistently higher in bare plots (55.5 ± 1.8 ppt pooled across regions and years) than in vegetated plots (38.6 ± 0.9 ppt pooled across regions and years). This has previously been shown to be the simple product of plants shading the surface and limiting surface heating and the evaporation of pore water (Bertness et al. 1992). Typically, salinities in unvegetated plots were 5–10 ppt higher than in vegetated plots, but bare patch salinities could be as much as 30–50 ppt higher than in adjacent vegetated habitats. This variability was due to variation in both tides and local weather conditions (personal observations). During monthly spring tides, the high marsh is covered daily by tides and salt accumulation in high marsh habitats is flushed away. During these spring tides, soil salinities across the entire marsh in vegetated and bare substrate are relatively similar and close to the ambient salinity of the water in the adjacent water column. During the rest of the lunar month

Fig. 1 Weekly substrate salinity data from the experimental plots (1997–2000) from the last week of May through the first week of August when the transplants were in the field. For both Rhode Island and Maine the data represent means of the pooled results from two sites in each region. SEs are not shown since they are smaller than the symbols. See Table 1 for statistics

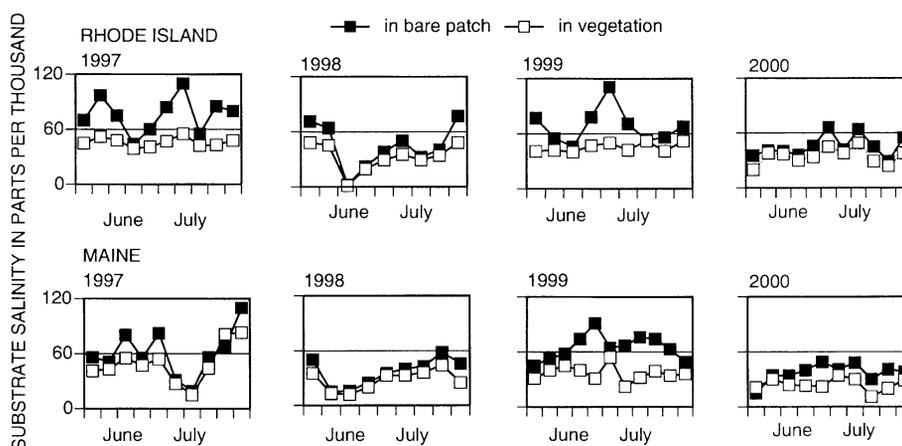
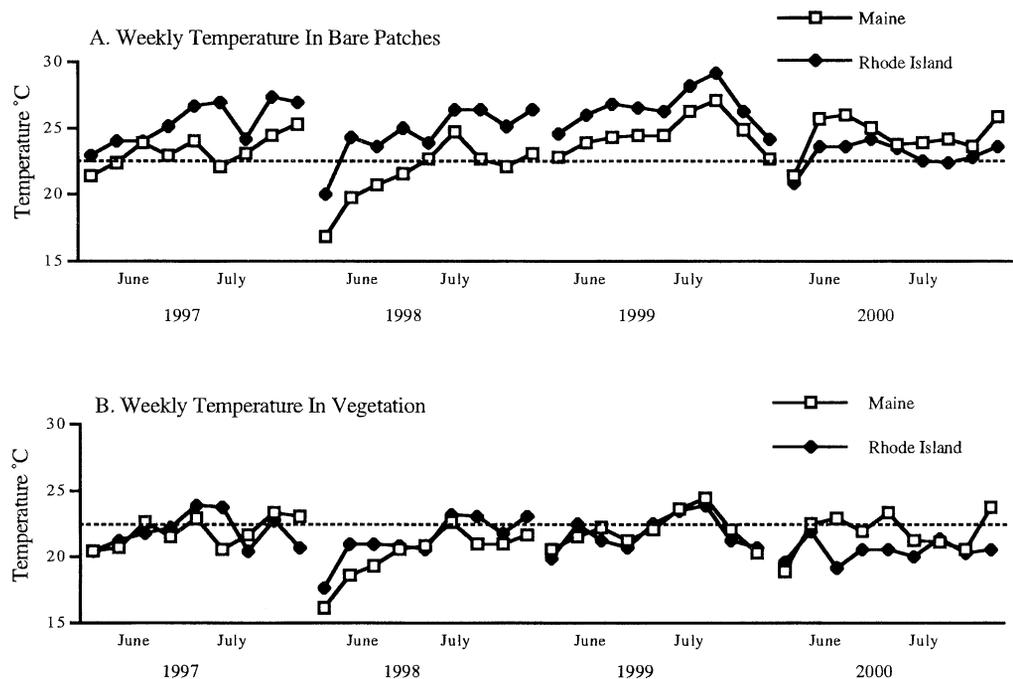


Table 1 Summary of the *P*-values from the ANOVA on the 4-year data sets (1997–2000) for substrate salinities (see Fig. 1), substrate temperatures (see Fig. 2) and *Spartina patens* and *Juncus gerardi* transplant performance (percent maximum biomass attained calcu-

lated by site and year, see Fig. 4). Within each region [Maine (*ME*) and Rhode Island (*RI*)] data from the study sites were pooled for analysis. Significant effects are highlighted in *italics*. See Materials and methods for further details of the analysis. *NA* Not applicable

	Region (ME or RI)	Neighbor× treatment (with or w/o neighbors)	Year	Region× treatment	Region× year	Treatment× year	Region× treatment× year	Replicate (R, T, Y)
Substrate salinity	0.06	<i>0.0001</i>	<i>0.0001</i>	0.09	<i>0.0001</i>	<i>0.0001</i>	<i>0.003</i>	NA
Substrate temperature	<i>0.0001</i>	<i>0.0001</i>	<i>0.0001</i>	<i>0.001</i>	<i>0.0001</i>	0.31	<i>0.01</i>	NA
<i>Spartina patens</i> transplants	<i>0.0138</i>	0.2766	<i>0.0005</i>	0.0622	0.5146	<i>0.0025</i>	<i>0.0225</i>	0.0515
<i>Juncus gerardi</i> transplants	0.8744	<i>0.0001</i>	0.1950	<i>0.0001</i>	0.0868	0.1879	<i>0.0274</i>	0.2818

Fig. 2 Weekly mean substrate surface temperature from experimental plots (1997–2000) from the first of June through the first week of August. For both Rhode Island and Maine the data represent means of the pooled results from two sites in each region. SEs are not shown since they are smaller than the symbols. See Table 1 for statistics



when neap tides prevail and the high marsh is not regularly covered with tidal water, evaporation of marsh sediment pore water leads to increasing soil salinity. Marsh soil salinities are also impacted by rain, but heavy sustained rains over many days are usually needed to markedly lower marsh salinities (personal observations).

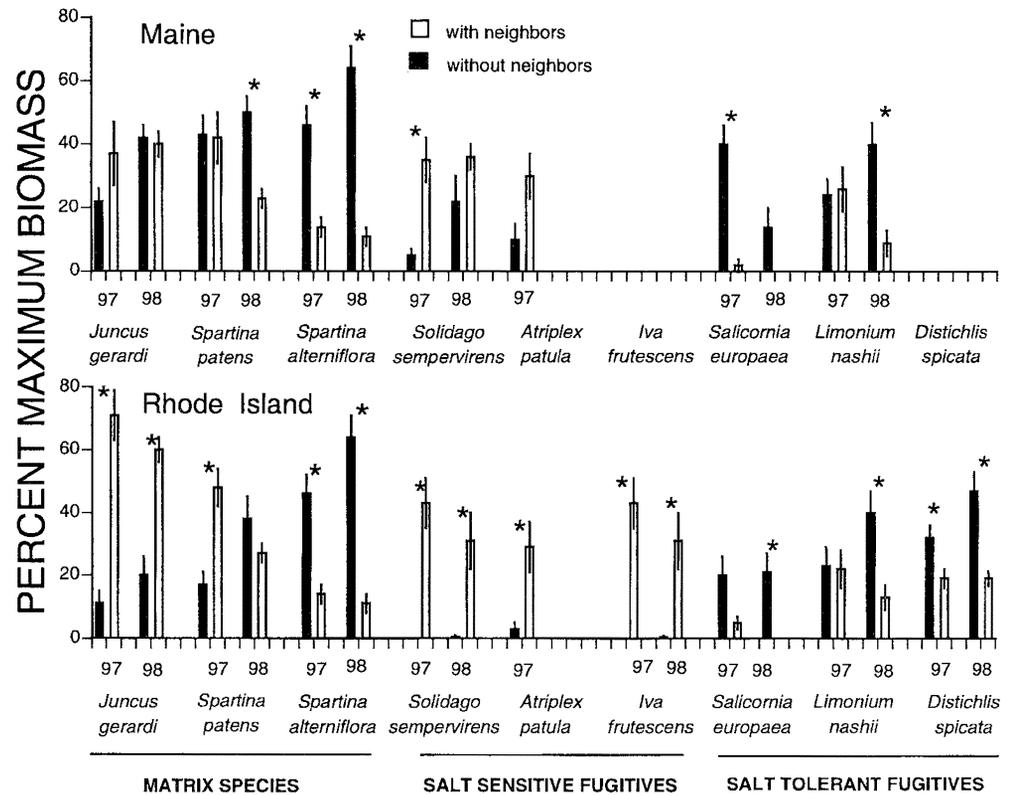
Soil salinity also varied markedly among regions and years (Fig. 1, Table 1). Soil salinities at the Rhode Island study sites in any given week were typically 5–10 ppt higher than at Maine study sites (Fig. 1). Pooling all 4 years of data in bare patches, substrate salinities at Rhode Island study sites (58.7 ± 1.6 ppt) were just over 5 ppt higher than in Maine (52.3 ± 1.2 ppt). Possibly of more importance to the plants in each region, however, is not the average soil salinity, but the occasional extreme salinities they experience. Average weekly salinity in unvegetated bare patches in Rhode Island exceeded 60 ppt and 100 ppt twice as often in Rhode Island marshes than Maine study sites (Fig. 1). Yearly differences in soil salinity were also apparent (Fig. 1). In both Maine and Rhode Island soil salinities were markedly higher in 1997 (bare patch, 74.4 ± 1.8 ppt; vegetation, 53.2 ± 1.2 ppt) and

1999 (bare patch, 67.6 ± 1.9 ppt; vegetation, 42.6 ± 1.1 ppt) than in 1998 (bare patch, 39.1 ± 1.3 ppt; vegetation, 29.6 ± 0.8 ppt) and 2000 (bare patch, 42.3 ± 1.4 ppt; vegetation, 30.6 ± 0.6 ppt). Average weekly soil salinities in 1997 and 1999 were 5–10 ppt higher than in similar habitats in 1998 and 2000, and in experimental bare patches without vegetation, soil salinities over 60 ppt in both Rhode Island and Maine were almost entirely restricted to 1997 and 1999 (Fig. 1).

Substrate temperatures

Soil temperatures from the experimental plots also revealed strong neighbor, regional and inter-annual variation (Fig. 2, Table 1). Daily mean soil surface temperatures in unvegetated plots ($23.4 \pm 0.6^\circ\text{C}$ Maine, $24.7 \pm 0.6^\circ\text{C}$ Rhode Island, pooled over years) were typically 2–3°C higher than in vegetated plots ($21.5 \pm 0.4^\circ\text{C}$ Maine, $21.3 \pm 0.3^\circ\text{C}$ Rhode Island, pooled over years), indicating the importance of plant shading in ameliorating soil surface radiation and heating (Bertness et al. 1992).

Fig. 3 Results of the 1997 and 1998 transplants in plots with and without neighbors with the numerically dominant salt marsh plants in Rhode Island and Maine. For both Rhode Island and Maine the data represent the pooled results from two sites in each region. Results are expressed as the percent maximum biomass attained at each site and in each year. The data presented are means \pm SE. See Table 2 for statistics. An asterisk over bars with and without neighbors indicates a significant ($P < 0.05$, Scheffe test) difference between neighbor treatments



Soil surface temperatures also varied markedly among regions and years (Fig. 2, Table 1). Soil surface temperatures at our Maine study sites were generally 2–3°C lower than at Rhode Island study sites (Fig. 2). Inter-annual differences in soil surface temperatures were also apparent (Fig. 2). In both Maine and Rhode Island soil surface temperatures were higher in 1997 and 1999 than in 1998 and 2000 (Fig. 2). These inter-annual differences were most pronounced in plots without vegetation. In plots without vegetation, substrate surface temperatures were generally higher in 1999 (25.8 \pm 0.25°C in Rhode Island; 24.0 \pm 0.24°C in Maine) and 1997 (25.3 \pm 0.25°C in Rhode Island; 23.2 \pm 0.30°C in Maine), and lower in 1998 (24.6 \pm 0.29°C in Rhode Island; 21.6 \pm 0.30°C in Maine) and 2000 (23.2 \pm 0.23°C in Rhode Island; 24.5 \pm 0.28°C in Maine).

Together, the soil temperature and salinity data reveal three clear patterns: (1) both high soil surface temperatures and salinities are strongly ameliorated by the presence of vegetation, (2) both soil surface temperatures and salinities are generally higher at sites south of Cape Cod than at sites north of Cape Cod, and (3) inter-annually, soil temperatures and salinities were higher in 1997 and 1999 than in 1998 and 2000.

Transplant experiment

To clarify interpretation of the transplant results we discuss the transplant species in terms of the three functional groups of: matrix species, salt tolerant fugitives and

salt sensitive fugitives. Salt sensitive matrix species and fugitives are predicted to benefit from neighbor buffering of potential salt stress, whereas salt tolerant matrix and fugitive species are not expected to be as strongly influenced by neighbor amelioration of potential salt stress. Moreover, based on the temperature and salinity data (Figs. 1, 2), neighbor amelioration of physical stress are predicted to be more common south than north of Cape Cod and more common and stronger in 1997 and 1999 than in 1998 and 2000 due to regional and inter-annual differences in temperature and salinity.

Matrix species transplants

Of the matrix species, the cordgrass, *Spartina alterniflora*, which typically dominates low marsh habitats, had the most straightforward response to being transplanted to the high marsh with and without neighbors (Fig. 3, Table 2). The influence of neighbors on cordgrass performance differed significantly among years ($P < 0.01$ treatment \times year effect). *S. alterniflora* grew best in bare patches without neighbors in both Maine and Rhode Island, but the suppression of cordgrass performance by high marsh neighbors was more pronounced in 1998 than 1997 in both regions (Fig. 3, Table 2). Since 1998 was physically milder than 1997, this result is consistent with competitive interactions among marsh plants being stronger under more benign physical conditions. Cordgrass is an extremely stress tolerant plant capable of dealing with both low soil oxygen levels (King et al. 1982) and high

Table 2 Summary of the *P*-values from the ANOVA on the 1997 and 1998 transplant data (Fig. 3). For each species (except *Atriplex*, *Distichlis*, and *Iva*) the data are the result of a three-way (region×treatment×year) ANOVA on percent maximum biomass attained at each site and year. For *Distichlis* and *Iva*, transplants

were only performed in RI. For *Atriplex*, transplants were only performed in 1997. Within each region (ME and RI) data from the study sites were pooled for analysis. Significant effects are highlighted in *italics*. See Materials and methods for further details of the analysis. For abbreviations, see Table 1

Species	Region (ME or RI)	Neighbor treatment (with or without neighbors)	Year (1997 or 1998)	Region× treatment	Region× year	Treatment× year	Region× treatment× year	Replicates (R, T, Y)
Matrix species								
<i>Spartina patens</i>	0.1008	0.2116	0.9423	<i>0.0025</i>	0.4474	<i>0.0017</i>	0.1632	<i>0.0137</i>
<i>Juncus gerardi</i>	0.5443	<i>0.0001</i>	0.9362	<i>0.0001</i>	0.6572	0.1903	0.5628	0.1210
<i>Spartina alterniflora</i>	0.4925	<i>0.0001</i>	0.3934	0.1018	0.3626	<i>0.0174</i>	0.8867	0.3466
Salt sensitive fugitive species								
<i>Atriplex patula</i>	0.2645	<i>0.0107</i>		0.7285				0.0775
<i>Solidago sempervirens</i>	0.3929	<i>0.0001</i>	0.6986	0.1465	0.1999	0.1675	0.7369	<i>0.0011</i>
<i>Iva frutescens</i>		<i>0.0001</i>	0.4097			0.3835		0.9232
Salt tolerant fugitive species								
<i>Limonium nashii</i>	0.9738	<i>0.0089</i>	0.9689	0.9829	0.7616	<i>0.0105</i>	0.7841	<i>0.0382</i>
<i>Salicornia europaea</i>	0.2864	<i>0.0001</i>	<i>0.0473</i>	0.4092	<i>0.0243</i>	0.1037	<i>0.0438</i>	0.3814
<i>Distichlis spicata</i>		<i>0.0001</i>	<i>0.0150</i>			<i>0.0120</i>		0.9131

soil salinities (Flowers et al. 1977), and would not be predicted to benefit greatly from the presence of neighbors even under very stressful conditions. *S. alterniflora* is the only stress tolerant dominant matrix species, and in New England marshes it is typically competitively excluded from high marsh habitats by the high marsh matrix species (*Spartina patens* and *J. gerardi*, Bertness 1991). Our results reaffirm that cordgrass is at a competitive disadvantage in the high marsh, but suggest that in physically harsh years it may not be as strongly competitively depressed as it is in more physically benign years.

The less stress tolerant high marsh species, *Spartina patens* and *J. gerardi*, responded very differently to transplantation. *Spartina patens* transplant performance varied significantly between Maine and Rhode Island study sites ($P < 0.002$ region×treatment interaction) and among years ($P < 0.001$ treatment×year interaction). In Maine, *S. patens* transplant growth was similar with and without neighbors in 1997, but in 1998, *S. patens* grew twice as much without than with neighbors (Fig. 3). Thus, in Maine net interactions with neighbors for marsh hay transplants were neutral in 1997, when soil temperatures and salinities were high, and competitive in 1998 when temperatures and salinities were lower. In Rhode Island, *S. patens* transplant performance was nearly 3 times better with than without neighbors in 1997 when physical conditions were stressful, but higher without neighbors in 1998 under less physically stressful conditions (Fig. 3). Thus, in Rhode Island the net relationship between marsh hay and high marsh neighbors was positive in 1997 and neutral or competitive in 1998. The influence of neighbors on *J. gerardi* varied significantly between Maine and Rhode Island study sites ($P < 0.0001$ neighbor treatment×region interaction, Fig. 3, Table 2). In Maine, *J. gerardi* grew best with neighbors in 1997 (a physically harsh year), but not in 1998 (a physically benign year), when *J. gerardi* growth

was similar with and without neighbors (Fig. 3). In contrast, in Rhode Island *J. gerardi* grew much better with neighbors than without neighbors in both years.

Together, the transplant data for the high marsh matrix species (*S. patens* and *J. gerardi*) suggest that neighbor interactions in the high marsh are highly variable among regions and years. In general, the results suggest that for the numerically dominant high marsh matrix plants, neighbors more commonly and strongly facilitate each other's performance in Rhode Island than in Maine, but that the effects of neighbors on high marsh plant performance also varies among years (Fig. 3). Among years, high marsh matrix species were generally more strongly facilitated by neighbors in 1997 than 1998 (Fig. 3).

Salt sensitive fugitive species transplants

Salt sensitive fugitives were strongly facilitated by matrix species neighbors in both Rhode Island and Maine (Fig. 3, Table 2). For the marsh goldenrod, *Solidago sempervirens*, neighbors had a strong positive effect on the transplants ($P < 0.0001$) in both regions and years (Fig. 3, Table 2). *Atriplex patula* also benefited from neighbors in both regions, but since we were only able to perform transplants with this species in 1997, we could not quantify inter-annual variation. In Rhode Island, *A. patula* grew nearly 10 times better with than without neighbors in 1997, while in Maine neighbors tripled *A. patula* performance in 1997 (Fig. 3, Table 2). However, the interaction between neighbor treatment and region was not significant. *Iva frutescens* was only transplanted in Rhode Island and showed strong facilitation by matrix vegetation neighbors (Fig. 3). In sum, salt sensitive fugitives were strongly facilitated by neighbors in both Maine and Rhode Island.

Salt tolerant fugitive species transplants

In contrast to the salt sensitive fugitives, the salt tolerant fugitives, in general, were competitively suppressed by matrix species (Fig. 3, Table 2). For *Salicornia europaea*, there was a significant interaction between neighbor treatment, region and year on transplant performance ($P < 0.04$, Fig. 3, Table 2). In both Maine and Rhode Island, *S. europaea* grew well in unvegetated patches without neighbors, but few *S. europaea* survived with neighbors, and those that did were extremely stunted by neighboring matrix vegetation. *S. europaea*, however, did better with neighbors in 1997 than in 1998 leading to the significant three-way interaction (Fig. 3). This suggests that competition from the matrix plants was less severe in 1997 due to harsher physical conditions. Similar results were found with *Limonium nashii* (Fig. 3). Neighbors affected *L. nashii* transplants significantly differently between years ($P < 0.01$ neighbor treatment \times year interaction). *L. nashii* transplant performance with and without neighbors did not differ in either Maine or Rhode Island in 1997 (a physically harsh year), while in 1998 (a physically benign year) *L. nashii* performance was 2–3 times higher without neighbors than with neighbors in both regions (Fig. 3, Table 2). This again suggests that competitive dominance by the matrix species was greater in 1998 than 1997, reflecting inter-annual variation in soil temperatures and salinities. *Distichlis spicata* was only transplanted in Rhode Island, and its performance was significantly suppressed by neighbors more in 1998 than 1997 (Fig. 3, Table 2). While the salt tolerant fugitives all performed best without neighbors, revealing competitive suppression in dense matrix vegetation, for all species (*D. spicata*, *Salicornia europaea* and *L. nashii*) competitive suppression was generally more severe in 1998, a physically mild year, than 1997 a physically harsh year revealing inter-annual variation in the strength of plant competition (Fig. 3).

In summary, our transplant experiments revealed strong regional and annual differences in the relationship between marsh plant neighbors. In particular, the numerically dominant high marsh matrix species (*Spartina patens* and *Juncus gerardi*) were facilitated by their neighbors in Rhode Island marshes south of Cape Cod, but neighbor competitive suppression of transplant growth was more common in Maine marshes north of Cape Cod. This suggests that regional climatic variation leads to differences in the nature of interspecific plant interactions in marshes north and south of Cape Cod (Fig. 3, Table 2). Consistent differences in the response of transplants to neighbors in 1997 and 1998, however, suggest that interactions among marsh plants are also sensitive to year to year variation in climate. In particular, the data suggest that positive interactions driven by neighbor stress amelioration were stronger in 1997 when soil temperatures and salinities were high, and weaker in 1998 when these physical stresses were more benign.

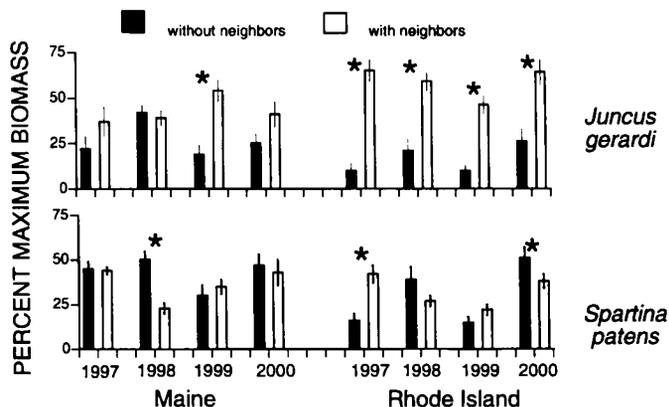


Fig. 4 Results of the 1997, 1998, 1999 and 2000 transplants of *Spartina patens* and *Juncus gerardi* into plots with and without neighbors. As in Fig. 3, for both Rhode Island and Maine the data represent the pooled results from two sites in each region, and the results are expressed as the percent maximum biomass attained at each site and in each year to enhance making comparisons among species. The data presented are means \pm SE. See Table 2 for statistics. An asterisk over bars with and without neighbors indicate a significant ($P < 0.05$, Scheffe test) difference between neighbor treatment

Long-term transplant data for high marsh matrix species

We examined inter-annual variation in the nature and intensity of high marsh matrix species interactions more thoroughly by transplanting the high marsh matrix species, *Juncus gerardi* and *Spartina patens*, in 1999 and 2000. This gave us a 4-year data set to examine inter-annual variation in neighbor interactions.

For *J. gerardi*, the influence of neighbors on transplant performance varied significantly between Maine and Rhode Island ($P < 0.0001$ neighbor treatment \times region interaction) and there was a significant three-way interaction among neighbor treatment, region and year ($P < 0.02$) indicating that the regional variation in the effect of neighbors on *J. gerardi* transplants varied significantly among years (Fig. 4, Table 1). *J. gerardi* transplants grew 2–8 times better in the presence of neighbors than when neighbors were removed in Rhode Island (Fig. 4), whereas in Maine, *J. gerardi* transplants grew significantly better when neighbors were present only in 1999, the hottest year we ran these experiments (Fig. 4).

Similar results were found for the marsh hay, *Spartina patens*. For *S. patens*, the influence of neighbors on transplant performance varied significantly between Maine and Rhode Island ($P < 0.0001$ neighbor treatment \times region interaction) and there was a significant three-way interaction among neighbor treatment, region and year ($P < 0.02$) indicating that the regional variation in the effect of neighbor on *S. patens* transplants varied significantly among years (Fig. 4, Table 1). *S. patens* transplants in Rhode Island were significantly facilitated by the presence of neighbors in only 1997 (Fig. 4) In the coolest years we ran these transplants (1998 and 2000), *S. patens* transplants tended to be competitively suppressed by the matrix species, but these results were not statistically sig-

nificant. In contrast, *S. patens* transplants in Maine did not show any evidence of facilitation by matrix neighbors (Fig. 4). Thus, our 4-year data set shows that the regional differences in the nature and intensity of neighbor interactions among marsh plants north and south of Cape Cod are influenced by inter-annual variation in climate. Regionally, the data show that positive neighbor relations are stronger and more prevalent south of Cape Cod than north of Cape Cod mirroring regional variation in climate and the potential for the development of hypersaline soil conditions (Fig. 4). Inter-annually, in both Maine and Rhode Island the data show that neighbor interactions were almost always more strongly positive in physically stressful years (1997 and 1999) than in physically benign years (1998 and 2000, Fig. 4).

Latitude, climatic variation and marsh plant interactions

Together, our data make a convincing case that the nature and intensity of salt marsh plant species interactions in New England are under the direct influence of latitudinal and inter-annual variation in climate. While linkage between climate and species interactions is often assumed in natural systems, it has rarely been examined (Karieva et al. 1993). Understanding the linkages between climate and species interactions, however, is critical to accurately predicting the impacts of global climate change on natural ecosystems. Yet very few studies have addressed this question experimentally (Davis et al. 1998; Bertness et al. 1999; Leonard 2000).

Our data illustrate how strongly species interactions can be linked to climatic variation, but also point to the difficulties of using climate data to predict changes in species interactions and particularly illustrate the problems of extrapolating this information to predict climate-driven shifts in the organization of natural communities. While our data show clear climate-driven signals in the species interactions of marsh plants, all species did not respond similarly to changes in climate. As a result, even for this well-studied system of salt marsh plants, it is tenuous, at best to make extrapolations of how climate change will influence plant community structure. Our data suggest that climatic warming in New England marshes will generally shift the interactions among many common high marsh matrix plants from competitive to more facilitative, but say little about how important these types of changes in marsh vegetation dynamics will be in influencing marsh ecosystems in contrast to the increased success of more salt tolerant plants, selection for more salt tolerant plants (Pennings and Bertness 1999) and the simultaneous effects of increased sea-level rise and the flooding of marshes (Warren and Niering 1993; Donnelly and Bertness 2001). Thus, our results warn that predicting how climate change will influence the structure and organization of natural communities will be extremely difficult and complex, even in well-studied model systems, and will seriously test our basic understanding of these systems.

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