



Interspecific Interactions among High Marsh Perennials in a New England Salt Marsh

Mark D. Bertness

Ecology, Vol. 72, No. 1. (Feb., 1991), pp. 125-137.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28199102%2972%3A1%3C125%3AIIAHMP%3E2.0.CO%3B2-O>

Ecology is currently published by The Ecological Society of America.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

INTERSPECIFIC INTERACTIONS AMONG HIGH MARSH PERENNIALS IN A NEW ENGLAND SALT MARSH¹

MARK D. BERTNESS

Graduate Program in Ecology and Evolutionary Biology, Brown University,
Providence, Rhode Island 02912 USA

Abstract. High marsh habitats in New England exhibit conspicuous zonation of vascular plants. *Spartina patens* and *Juncus gerardi* dominate the seaward and terrestrial borders of the high marsh, respectively, whereas *Distichlis spicata* is common in disturbed habitats. In this paper I examine the role of interspecific interactions among these marsh perennials in maintaining marsh plant zonation.

Removal and transplant experiments were performed to examine species interactions in dense stands. In both types of experiments *J. gerardi* competitively dominated *S. patens* and *D. spicata*, while *S. patens* competitively dominated *D. spicata*. Each of these perennials showed maximum growth when transplanted into the *J. gerardi* zone without neighbors. *J. gerardi* appears to dominate the terrestrial border of the marsh by competitively excluding *S. patens* to lower marsh levels, while *D. spicata* is competitively restricted to disturbed habitats by both *J. gerardi* and *S. patens*.

Species interactions during the colonization of bare patches were strikingly different than those found in dense vegetation. Colonization of bare patches by both *S. patens* and *D. spicata* facilitated the colonization of *J. gerardi*, the competitive dominant in dense vegetation. Bare patches in the high marsh are typically hypersaline due to increased surface evaporation in the absence of plant cover. Patch colonization by competitive subordinates, which are relatively salt tolerant, appears to reduce substrate salinity by passively shading the substrate and, as a by-product, facilitate the invasion of a superior competitor.

While interspecific competition in dense vegetation dictates the zonation of New England perennials in the high marsh, secondary succession in this assemblage may commonly be driven by facilitations. This scenario may not be uncommon among assemblages in harsh physical environments where plants or sessile animals ameliorate their physical environment.

Key words: facilitation; halophytes; plant competition; salt marsh ecology; secondary succession; zonation.

INTRODUCTION

Understanding the processes that generate distribution patterns in natural communities is one of the primary goals of plant ecology (Harper 1977, Tilman 1988). Recently, a growing number of experimental studies have provided evidence for the widely held notion that competitive processes are important determinants of plant community patterns (Putwain and Harper 1970, Fowler 1981, Grace and Wetzel 1981, Silander and Antonovics 1982, Keddy 1984, Platt and Weis 1985, Tilman 1988). Other work, however, has shown that competitive processes are unimportant in structuring certain plant assemblages (Fowler 1986), and that facilitation may be critical in still other plant assemblages (Niering et al. 1963, Wood and Del Moral 1987). Disturbance (Pickett and White 1985), physiological stress (Bazzaz 1979), and consumer pressure (Atsatt and O'Dowd 1976, Louda 1982) also clearly influence plant distribution and may influence the role of interspecific interactions in plant communities. Un-

derstanding how these processes interact to generate pattern in natural communities presents a major challenge, which is best explored with manipulative field studies.

Salt marshes are ideal for examining plant community patterns. Marsh species are typically found in distinct zones (Chapman 1974), and the physiological problems faced by marsh plants have been identified. Soil oxygen levels (Howes et al. 1981, Mendelssohn et al. 1981), flooding (Gleason 1980), nutrient limitation (Valiela and Teal 1974), and soil drainage (Mendelssohn and Seneca 1980, King et al. 1982) have been suggested as major determinants of marsh plant success, but experimental studies (Silander and Antonovics 1982, Snow and Vince 1984, Bertness and Ellison 1987) have repeatedly hinted that biotic interactions may also be important in structuring these communities.

The zonation of marsh plants in New England is striking (Johnson and York 1915, Miller and Egler 1950, Nixon 1982). *Spartina alterniflora* dominates low marsh habitats that are covered daily by tides. The seaward border of the high marsh is typically dominated by

¹ Manuscript received 18 September 1989; revised 5 March 1990; accepted 8 March 1990.

Spartina patens, while the terrestrial border is generally dominated by the rush *Juncus gerardi*. *Distichlis spicata* is also found in the high marsh, either in low abundance mixed with the numerical dominants or in discrete patches. These species are perennials that generally colonize free space vegetatively rather than by seeds (Mooring et al. 1971, Barber 1981). The annual succulent *Salicornia europaea* is also common in the high marsh but is restricted almost exclusively to high marsh disturbance-generated bare space (Ellison 1987).

Two lines of evidence suggest that interspecific competition plays a major role in dictating the distribution of species in this community (Bertness and Ellison 1987): (1) the secondary succession of disturbance-generated bare space, and (2) the performance of marsh perennial transplants across the tidal gradient. Disturbance-generated bare patches are initially colonized by *S. europaea* seedlings and *D. spicata* vegetative runners in both the *S. patens* and *J. gerardi* zones. Within 3–4 yr, however, these early colonizers are displaced by the high marsh numerical dominants, suggesting that *S. patens* and *J. gerardi* are the competitive dominants in their respective habitats (Bertness and Ellison 1987). Moreover, transplant studies have shown that each of the high marsh perennials grows best in the absence of interspecific competition in the *J. gerardi* zone (Bertness and Ellison 1987), clearly suggesting that physiological tolerances alone are insufficient to explain the pronounced zonation across New England salt marshes.

In this paper I examine interspecific interactions among these high marsh perennials to test the hypothesis that competitive relations dictate species distributions across the high marsh habitat. Controlled species removals in natural sympatric stands and transplants into the *S. patens* and *J. gerardi* zones with and without neighbors are used to test the role of interspecific competition in dense vegetation. Interspecific interactions during the colonization of disturbance-generated bare patches are also experimentally quantified. These three approaches together test the role of interspecific interactions in shaping the high marsh plant communities of New England. In a companion paper (Bertness 1990) I examine the role of interspecific interactions in dictating the zonation of *Spartina* spp. on the high marsh/low marsh border.

METHODS

All field work was carried out at Rumstick Cove, Barrington, Rhode Island (Bertness 1984, 1988).

Species removal experiments

Interspecific interactions in natural areas of sympatry were examined with reciprocal species removals. In March 1985, prior to spring emergence, 15 × 15 cm quadrats were marked in high marsh areas supporting *Spartina patens*/*Juncus gerardi* mixtures ($n =$

30), *S. patens*/*Distichlis spicata* mixtures ($n = 30$), and *J. gerardi*/*D. spicata* mixtures ($n = 30$). Quadrats in each mixture were grouped in sets of three separated by <0.5 m, and 10 sets of quadrats for each species pair were placed over a 200 m² area. Within each set of three plots, a control and single-species removal plots for each of the two species present were randomly assigned. Every 10–14 d from March through September the aboveground portion of the species targeted for removal was removed with scissors. In August, the center of each quadrat (10 × 10 cm) was harvested, tillers were sorted to species, counted, and measured (length), and the aboveground biomass of each species was dried and weighed.

Turf transplant experiments

To further examine competitive relations in dense stands, transplants were established in March 1986 and followed for three growing seasons. Large (35 × 35 × 35 cm, length × width × depth) blocks of substrate were excavated from monospecific stands and implanted in identically sized (35 × 35 × 35 cm) holes in the *S. patens* and *J. gerardi* zones. For *D. spicata*, blocks were transplanted either into direct contact with surrounding vegetation (with competition) or into areas where surrounding vegetation was removed every other week (without competition) by weeding a 25 cm wide strip around the perimeter of each transplant ($n = 8$ per zone per treatment). Manipulated and unmanipulated transplant controls were also followed in the area where the original *D. spicata* transplants were obtained. Eight blocks were excavated and randomly moved among locations for manipulated controls and eight areas were simply marked and followed as unmanipulated controls. Similarly, for *S. patens* and *J. gerardi*, manipulated ($n = 8$) and unmanipulated ($n = 8$) controls were followed. Finally, *S. patens* blocks were transplanted into the *J. gerardi* zone with ($n = 8$) and without ($n = 8$) surrounding vegetation. *J. gerardi* blocks were also transplanted into the *S. patens* zone with ($n = 8$) and without ($n = 8$) surrounding vegetation. Transplants were not made into *D. spicata* backgrounds since large *D. spicata* monocultures were not available at the study site. Intraspecific controls with cleared borders were not attempted due to the difficulty of differentiating between transplanted and ambient vegetation. However, tests of the effect of intraspecific competition on transplants of these species have found intraspecific effects to be negligible and not significant (Bertness 1990).

Transplants were maintained and monitored from April 1986 to September 1988. In August of each growing season a separate corner (10 × 10 cm) of each replicate was harvested, tillers were sorted to species and counted, 10–15 random tillers of each species present were measured (height), and then the tillers were dried and weighed. Vegetative colonization into substrates bordering the transplants was also monitored.

In August 1987 and 1988, the maximum distance that transplant tillers had invaded surrounding substrate was measured and transplant tiller density counts were made in randomly placed 10 × 10 cm quadrats immediately adjacent to the initial transplant borders.

Colonization of artificial bare patches

Interspecific interactions during the secondary succession of bare space were examined in paired mixtures of the high marsh perennials. Bare patches for this work were generated by foliar application of a short-lived systemic herbicide (Roundup, Monsanto) 9–12 mo before the experiment began. The colonization of herbicide-generated bare patches did not differ qualitatively or quantitatively from the closure of natural bare patches (Bertness and Ellison 1987) and seedlings transplanted into herbicide-generated and natural patches had identical survivorship and growth (M. D. Bertness, *personal observation*).

Three types of bare patches were created in June–July 1985: (1) 30 in mixed *J. gerardi*/*S. patens* vegetation, (2) 30 in the *J. gerardi* zone in mixtures of *J. gerardi* and *D. spicata*, and (3) 30 in the *S. patens* zone in *S. patens*/*D. spicata* mixtures. All patches (0.5 × 0.5 m) were generated by severing rhizome connections between the patch area and surrounding vegetation (to a depth of 30 cm), and applying herbicide 3 times at 2-wk intervals. A 50 × 50 cm grid of 100 individual 5 × 5 cm cells was then placed over each patch to facilitate monitoring spatial patterns of patch recolonization. The following spring all remaining above-ground vegetation was removed from each patch, and the patches in each set were randomly divided into three equal groups. One group was maintained as controls, while the remaining two groups were designated as removal patches for each of the two species in each mixture. Every other week for the following three growing seasons removal patches were maintained by manual weeding. To quantify the abundance of perennials around the patches, in August of 1986 and 1988, a 100-cm² quadrat was haphazardly placed immediately outside each patch on three sides, and tillers were identified to species and counted. Tiller densities did not differ among years or treatments in each patch set ($P > .25$, ANOVA, each case).

Patch recolonization was quantified by annually monitoring seedlings and invading vegetative tillers. Monthly (April–July) seedling counts were made in all of the 0.25-m² patches, and most seedlings were individually marked. In all 3 yr seedling densities were extremely low. *S. patens* and *D. spicata* seedling densities were <0.1 seedlings/patch in each year and <50% of these seedlings survived their first growing season. For *J. gerardi*, <0.1 seedlings/patch were found in the *S. patens*/*J. gerardi* patches and none of these seedlings survived, while in the *D. spicata*/*J. gerardi* patches *J. gerardi* seedling densities were higher but did not affect patch closure rates. Vegetative growth was responsible

for >95% of the recolonization of all patches. Vegetative invasion of the plots was quantified in August (1986–1988) by identifying and counting tillers in each of the 100 cells in each plot. The patch invasion experiment was analyzed with repeated-measurement MANOVA on cell frequency counts and tiller density data, followed by corrected ANOVA to test within-year patterns (SAS 1985).

The only abundant annual at the site, *Salicornia europaea*, was left at natural densities in all patches. *S. europaea* is rapidly overgrown and competitively displaced by each of the marsh perennials (Ellison 1987), and its effect on perennial patch invasion is negligible (M. D. Bertness, *personal observation*).

Bare patch edaphic conditions

Edaphic conditions were quantified in all experimental patches and adjacent vegetation. Substrate redox potential and acidity were measured with electrodes inserted directly into the substrate (Howes et al. 1981). Substrate water content was measured by wet weighing cores (3 × 10 cm, diameter × length), drying them, and determining percent water content. Pore water salinities were determined with a refractometer (± 1 g/kg) on water samples collected with pore water sampling tubes with input ports at a depth of 5 cm (Bertness and Ellison 1987). Each of these measurements was made in all experimental patches and adjacent vegetation in August 1985.

To test the hypothesis that high salinities in bare patches limited plant success, marsh perennials were transplanted into bare patches of different sizes, because patch salinities increase with increasing patch size (see *Results*). Ten 0.25 m², 0.5 m², and 1 m² bare patches were generated in the *S. patens* and *J. gerardi* zones in June 1985 using herbicide. In June of 1986 and 1987, two seedlings or size-standardized tillers of four locally common marsh perennials were transplanted into each of these patches and adjacent undisturbed vegetation. *S. alterniflora* and *J. gerardi* seedlings (<2 wk old) collected near the patches were used for this work. For *S. patens* and *D. spicata*, seedlings are rare at the study site (Bertness et al. 1987) so isolated tillers were used as transplant material. For both species, pairs of tillers and a 2 cm length of attached rhizome were isolated from nearby plants for transplants. All transplants were collected and transplanted within 1 h, and those that did not appear healthy after 1 wk were discarded and replaced. The following August, after 3 mo, all transplants were scored for survival.

In June 1987, *J. gerardi* seedlings and *S. patens* tillers were also transplanted into the species removal patches in *S. patens*/*J. gerardi* mixtures. Two transplants of each species were made in each patch, marked, and scored for survivorship the following August. This manipulation tested the influence of patch colonization on transplant survival.

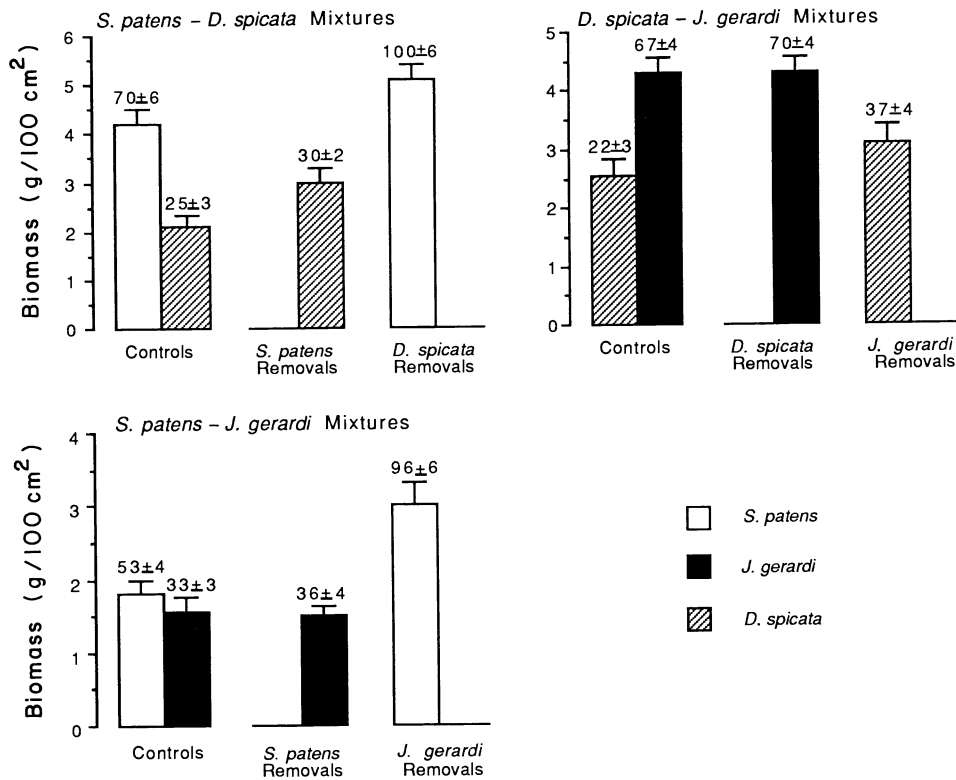


FIG. 1. Results of single-season species removal experiments in dense two-species mixtures of the high marsh perennials. For each mixture 30 plots were followed and equally divided among treatments. All plots were established in March and harvested the following August. Results are expressed as dry aboveground biomass per 100 cm² ($\bar{X} \pm 1$ SE). Tiller density data (tillers/100 cm²) are also presented for each species and treatment ($\bar{X} \pm 1$ SE) above biomass bars.

TABLE 1. Tiller heights from the species removal experiment in natural two-species mixtures of the high marsh perennials (means ± 1 SE).*

Treatment	Tiller height (cm)		
	<i>Spartina patens</i>	<i>Juncus gerardi</i>	<i>Distichlis spicata</i>
<i>D. spicata</i> / <i>S. patens</i> mixture			
Controls	27.4 \pm 0.4	...	24.6 \pm 0.4
<i>S. patens</i> removed	20.1 \pm 0.4
<i>D. spicata</i> removed	23.9 \pm 0.4
<i>D. spicata</i> / <i>J. gerardi</i> mixture			
Controls	...	31.7 \pm 0.4	34.4 \pm 0.5
<i>D. spicata</i> removed	...	26.5 \pm 0.3	...
<i>J. gerardi</i> removed	23.7 \pm 0.4
<i>S. patens</i> / <i>J. gerardi</i> mixture			
Controls	20.9 \pm 0.3	19.7 \pm 0.3	...
<i>S. patens</i> removed	...	16.6 \pm 0.2	...
<i>J. gerardi</i> removed	17.8 \pm 0.3

* All values are based on sample sizes ranging from 80 to 200 random tillers from each mixture. For each species in each mixture tillers were taller in sympatry than when competitors were removed ($P < .05$, ANOVA each case).

RESULTS

Species removal experiments

Tiller removals in *S. patens*/*D. spicata* mixtures revealed reciprocal competitive effects, but with *S. patens* inhibiting *D. spicata* more than *D. spicata* inhibited *S. patens* (Fig. 1). *S. patens* removal increased *D. spicata* biomass by 38% ($P < .01$, ANOVA) and tiller density by 20% ($P < .05$, ANOVA), whereas *D. spicata* removal increased *S. patens* biomass by 19% ($P < .05$, ANOVA) and tiller density by 30% ($P < .01$, ANOVA). For both species, tillers were taller in sympatry (controls) than in plots where the other species had been removed (Table 1).

In contrast to the reciprocal competitive effects found in *S. patens*/*D. spicata* mixtures, both *S. patens* and *D. spicata* were negatively affected by *J. gerardi*, while *J. gerardi* was not markedly influenced by sympatry (Fig. 1). *D. spicata* aboveground biomass increased by 28% ($P < .05$, ANOVA) and tiller production increased by 68% ($P < .01$, ANOVA) when *J. gerardi* was removed from sympatric areas. The effect of *J. gerardi* on *S. patens* was even more pronounced (Fig. 1). *J. gerardi* removal increased *S. patens* production by 67% ($P < .01$, ANOVA) and nearly doubled *S. patens* tiller density ($P < .01$, ANOVA). *D. spicata* and *S. patens*

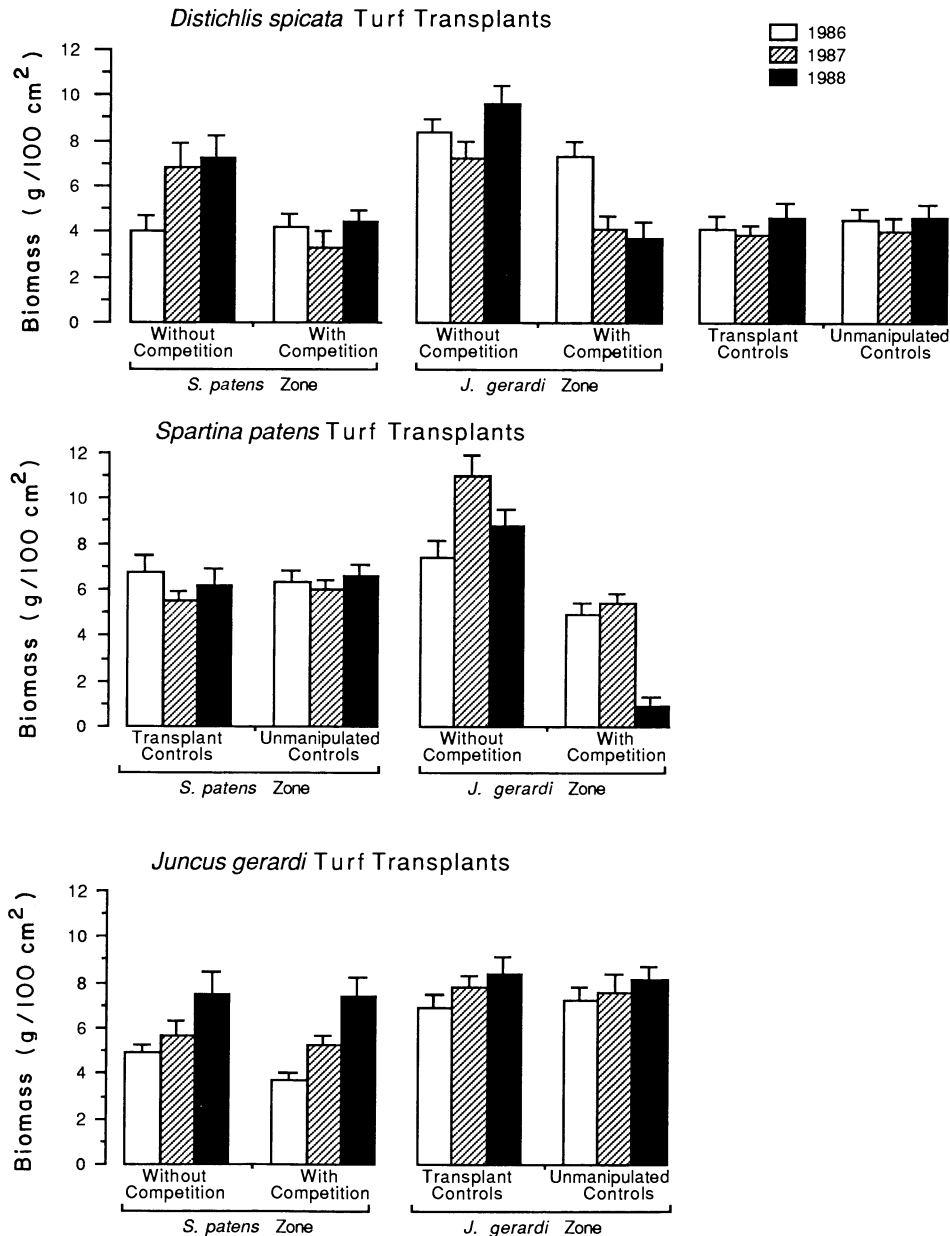


FIG. 2. Results of turf transplant experiments where monoculture turfs of each of the high marsh perennials were transplanted into the *Spartina patens* and *Juncus gerardi* zones in direct contact with surrounding vegetation (With Competition) or with the surrounding vegetation removed from a 25-cm strip around the perimeter of each transplant (Without Competition). All treatments were replicated 8 times. Results are expressed as dry aboveground biomass per 100 cm² ($\bar{X} + 1 \text{ SE}$). Tiller density patterns were very similar (M. D. Bertness, *personal observation*). Transplant controls were turfs removed from original locations and then transplanted back into the same area. Unmanipulated controls were simply marked areas near where the transplant material was obtained.

tillers were also taller in sympatry with *J. gerardi* than when *J. gerardi* tillers were removed (Table 1).

Neither the aboveground biomass or tiller production of *J. gerardi* was influenced by the removal of *S. patens* or *D. spicata* in sympatric areas (Fig. 1, $P > .05$, ANOVA, each case). The only effect of removal of sympatric grasses on *J. gerardi* was on tiller height. *J. gerardi* tillers were taller in sympatry than when competitors were removed (Table 1).

Transplant experiments

Distichlis spicata monocultures transplanted into *S. patens* and *J. gerardi* monocultures were strongly suppressed by competitors but grew vigorously in the absence of competitors (Fig. 2). After 3 yr, *D. spicata* transplanted into the *S. patens* zone with neighbors had 64% less biomass ($P < .01$, ANOVA) than similar transplants without neighbors. Moreover, extension of

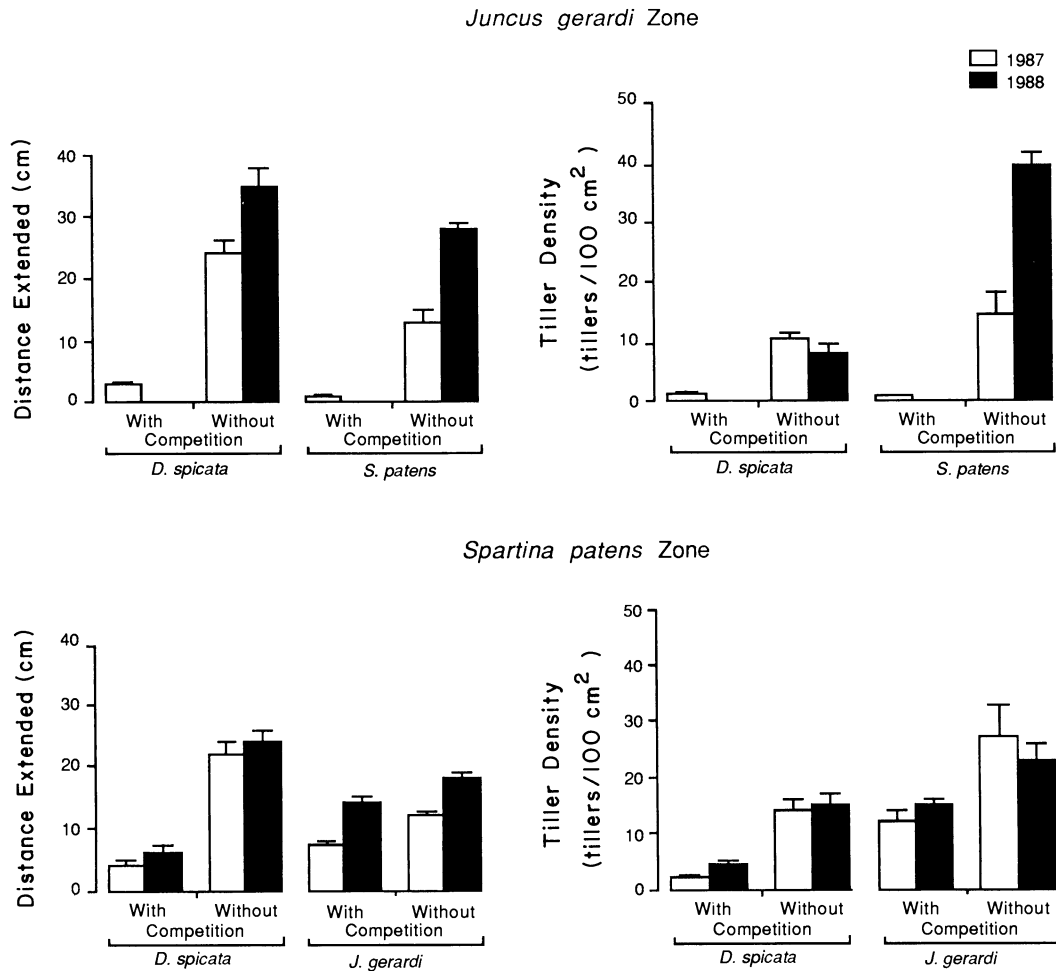


FIG. 3. Tiller expansion and density in substrate immediately adjacent to monoculture turfs transplanted into the *Juncus gerardi* and *S. patens* zones in direct contact with vegetation (With Competition) or into a 25-cm cleared border around each transplant (Without Competition). Tiller movement was assessed by measuring the maximum distance that transplant tillers had invaded surrounding substrate ($\bar{X} + 1$ SE). Tiller density was quantified by counting tillers in 100-cm² frames immediately adjacent to each transplant ($\bar{X} + 1$ SE).

transplanted *D. spicata* into adjacent substrate was strongly influenced by neighbors (Fig. 3). After 3 yr, *D. spicata* spread vegetatively 4 times as far into cleared substrate as into surrounding *S. patens* ($P < .001$, ANOVA) and *D. spicata* tiller densities adjacent to transplants with cleared borders were nearly 4 times as great as in transplants bordered by *S. patens* ($P < .001$, ANOVA).

Distichlis spicata transplants into *J. gerardi* vegetation were even more strongly suppressed by neighbors (Fig. 2). After 3 yr, *D. spicata* transplanted into *J. gerardi* vegetation had less than a third of the biomass ($P < .001$, ANOVA) of transplants without immediate *J. gerardi* neighbors. In addition, *D. spicata* vigorously invaded substrate in the *J. gerardi* zone without neighbors, but, after 3 yr had not successfully colonized *J. gerardi* vegetation (Fig. 3). Without neighbors, growth of *D. spicata* transplants was greater in the *J. gerardi* zone than in the *S. patens* zone (Fig. 2).

Spartina patens transplanted into *J. gerardi* vegetation was also severely suppressed (Fig. 2). After 3 yr, *S. patens* transplanted into the *J. gerardi* zone with neighbors had <10% of the biomass of transplants without neighbors ($P < .001$, ANOVA). In contrast, *S. patens* transplanted into the *J. gerardi* zone with cleared borders were over 30% more productive than *S. patens* transplants in the *S. patens* zone ($P < .05$, ANOVA, Fig. 2). *S. patens* transplanted into the *J. gerardi* zone without neighbors also vigorously expanded into the surrounding substrate, while transplants with *J. gerardi* neighbors did not expand (Fig. 3).

In contrast to the negative effects found when *D. spicata* and *S. patens* were transplanted into foreign vegetation, *J. gerardi* thrived when transplanted into *S. patens* vegetation (Fig. 2). After 3 yr, *J. gerardi* transplanted into the *S. patens* zone with and without neighbors had similar biomass ($P < .50$, ANOVA). More-

over, *J. gerardi* also vigorously invaded dense *S. patens* vegetation (Fig. 3).

These results provide strong support for the hypothesis that in dense vegetation *J. gerardi* is competitively dominant to both *S. patens* and *D. spicata*, and that, of the high marsh perennials, it is the only one capable of pre-emptive competitive dominance.

Species interactions during secondary succession

Examination of species interactions in the colonization of bare patches bordered by *S. patens*/*D. spicata* mixtures gave results consistent with the dominance relationships found in dense vegetation (Fig. 4). Removal of *D. spicata* from recovering patches significantly increased *S. patens* cover and total tiller density ($P < .001$, MANOVA). Neither of these effects varied statistically among years ($P < .10$, treatment \times year interaction, MANOVA, both cases), but the data (Fig. 4) suggest a diminished effect of *D. spicata* on *S. patens* over time. Removal of *S. patens* from patches bordered by *S. patens*/*D. spicata* mixtures (Fig. 4) significantly increased *D. spicata* recruitment into patches (frequency and tiller density, $P < .01$, MANOVA), and this effect differed between years (treatment \times year interaction, $P < .05$, MANOVA, both cases). In the 1st yr of patch colonization, removal of *S. patens* tended ($P < .10$, ANOVA) to increase *D. spicata* cover but did not influence *D. spicata* tiller density ($P > .25$, ANOVA) (Fig. 4). After 3 yr of recovery *S. patens* reduced *D. spicata* cover by nearly 50% ($P < .05$, ANOVA) and tiller densities by $>75\%$ ($P < .05$, ANOVA).

Patches bordered by *J. gerardi* did not respond as would be predicted by the competitive relationships found in dense vegetation. Whereas *J. gerardi* is competitively dominant to *S. patens* and *D. spicata* in dense vegetation (Figs. 1 and 2), during secondary succession *S. patens* and *D. spicata* facilitated *J. gerardi* recolonization. In patches bordered by *S. patens* and *J. gerardi*, removal of *J. gerardi* did not ($P > .05$, MANOVA) influence *S. patens* cover (Fig. 4), but did influence *S. patens* tiller density ($P < .01$, MANOVA), and this effect varied over time ($P < .05$, MANOVA interaction). *J. gerardi* removal did not influence *S. patens* tiller density in the 1st yr ($P > .25$, ANOVA), but by the 3rd yr, *J. gerardi* removal had resulted in a 34% ($P < .05$, ANOVA) increase in *S. patens* tiller densities (Fig. 4). Conversely, *S. patens* removal dramatically decreased the cover ($P < .01$, MANOVA) and tiller density ($P < .01$, MANOVA) of *J. gerardi* (Fig. 4). After 3 yr, *S. patens* removal had decreased *J. gerardi* cover by 60% and tiller density by 70%.

Similar facilitation effects were found in patches bordered by *D. spicata*/*J. gerardi* mixtures (Fig. 4). Removal of *J. gerardi* significantly influenced the cover ($P < .01$, MANOVA) and tiller density ($P < .001$, MANOVA) of colonizing *D. spicata*, and both of these responses varied over time (treatment \times year interaction, $P < .01$, MANOVA). In the 1st and 2nd yr, *J.*

gerardi removal did not affect *D. spicata* cover ($P > .05$, ANOVA) or tiller density ($P > .05$, ANOVA). By the 3rd yr of patch recovery (Fig. 4), however, colonizing *J. gerardi* reduced *D. spicata* cover by 45% ($P < .05$, ANOVA) and tiller density by $>70\%$ ($P < .01$, ANOVA). Removal of *D. spicata* influenced the cover ($P < .05$, MANOVA) but not the tiller density ($P > .10$, MANOVA) of colonizing *J. gerardi*. Removal of *D. spicata* decreased the rate at which *J. gerardi* colonized patches (Fig. 4).

These results suggest that the competitive dominant in dense vegetation is limited from invading bare space in the absence of its competitors, and that edaphic conditions, modified by plant cover, may limit *J. gerardi* invasion into bare space.

Bare patch edaphic conditions

Examination of bare patch edaphic conditions revealed no significant differences between bare patches and adjacent vegetation in substrate redox ($P > .25$, ANOVA, for each patch set), pH ($P > .50$, ANOVA, for each patch set), or water content ($P > .25$, ANOVA, for each patch set). Substrate salinities, however, were consistently higher in bare patches than in adjacent vegetated substrate. Elevated salinities in unvegetated marsh substrate are common (Pethick 1978, Boston 1983). Substrate salinities in the size series of patches in the *S. patens* and *J. gerardi* zones illustrate two patterns in bare patch salinities at the study site. Substrate salinities increase with increasing patch size (Table 2), reflecting increased exposure to direct solar radiation and surface heating as patch size increases. In addition, while substrate salinities in vegetation decrease with marsh elevation (Bertness and Ellison 1987), bare patch salinities increase with increasing marsh elevation (Table 2), reflecting that frequent tidal flooding buffers bare patches from evaporative salinity increases.

Among the patches used to examine interspecific interactions during patch closure, initial substrate salinities (August 1985) were highest in patches bordered by *J. gerardi* and *S. patens* (26 ± 2 g/kg, $n = 30$, adjacent vegetation 18 ± 2 g/kg, $n = 30$), intermediate in patches bordered by *S. patens* and *D. spicata* (18 ± 1 g/kg, $n = 48$, adjacent vegetation 14 ± 2 g/kg, $n = 30$), and lowest in patches bordered by *J. gerardi* and *D. spicata* (16 ± 2 g/kg, $n = 30$, adjacent vegetation 10 ± 2 g/kg, $n = 30$). In August 1987, after two seasons of recolonization, salinities were measured to assess the effects of species removal treatments on patch salinities. In patches bordered by *J. gerardi* and *S. patens*, *S. patens* removal patches were more saline (25 ± 3 g/kg) than either control (19 ± 2 g/kg) or *J. gerardi* removal (20 ± 1 g/kg) patches ($P < .01$, ANOVA). In patches bordered by *J. gerardi* and *D. spicata*, *D. spicata* removal patches tended to be more saline (14 ± 2 g/kg) than either *J. gerardi* removal (11 ± 2 g/kg) or control patches ($P < .10$, ANOVA). In contrast, in

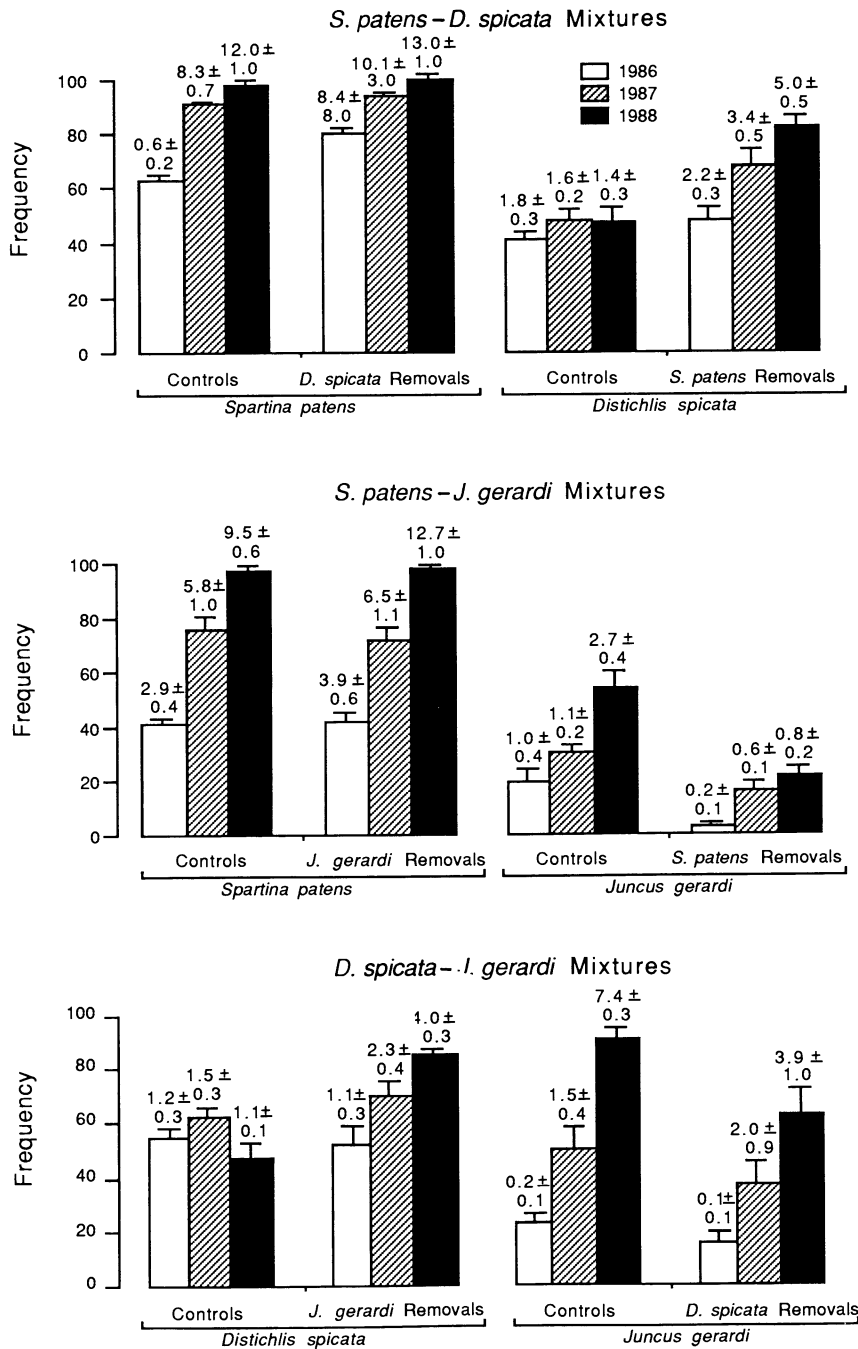


FIG. 4. Colonization of manipulated bare patches (0.25 m²) in two-species mixtures of the high marsh perennials. For each mixture 30 plots were equally divided among the three treatments and maintained and monitored for 3 yr. Data are presented as the number of the 100 5 × 5 cm cells in each plot that contained a given species ($\bar{X} \pm 1$ SE). Tiller densities (tillers per 100-cm² plot, $\bar{X} \pm$ SE) are given above the frequency bars. Data are from September 1986–1988.

patches bordered by *S. patens* and *D. spicata* where interspecific facilitations were not found, salinities were similar ($P > .50$, ANOVA) among treatments (16 ± 2 g/kg, $n = 30$). These patterns suggest that since plant invasion ameliorates hypersaline patch conditions, patch salinities decline as patches are recolonized. They also demonstrate interspecific differences in the ame-

lioration of hypersaline patch conditions. *S. patens* and *D. spicata* (but not *J. gerardi*) both rapidly invade high marsh bare space and in the process appear to ameliorate patch edaphic conditions.

Seedling and tiller transplants of marsh perennials into patches of different sizes yielded straightforward results (Fig. 5). Substrate salinities of the patches (Table

TABLE 2. Substrate salinities (g/kg) of the size series of artificial bare patches and adjacent vegetation in August 1987. Vegetation salinities were taken 10–25 cm from the borders of all bare patches. All salinities ($\bar{X} \pm se$) are from a depth of 5 cm.

	Large patches (1 m ²)	Medium patches (0.25 m ²)	Small patches (0.06 m ²)	In dense vegetation
<i>Spartina patens</i> zone	27 ± 2 n = 10	22 ± 1 n = 10	20 ± 1 n = 10	21 ± 2 n = 30
<i>Juncus gerardi</i> zone	33 ± 1 n = 10	25 ± 1 n = 10	18 ± 2 n = 10	17 ± 2 n = 30

2) increased with patch size. For all four species in both zones ($P < .01$, G test), transplant survivorship increased with decreasing patch size and substrate salinity, but then sharply declined in dense vegetation. These

results strongly suggest that high substrate salinities limit marsh plant success in hypersaline bare patches.

Transplant survivorship in experimental patches (in 1987) bordered by *J. gerardi* and *S. patens* (Fig. 4) indicated that plant success in recovering patches was significantly influenced by the presence of vegetative colonizers. The survivorship of *J. gerardi* seedlings and *S. patens* tillers was higher ($P < .05$, G test) in control (*J. gerardi* 65%, $n = 20$; *S. patens* 64%, $n = 22$) and *J. gerardi* removal (*J. gerardi* 55%, $n = 20$, *S. patens* 67%, $n = 22$) plots than in *S. patens* removal plots (*J. gerardi* 0%, $n = 20$; *S. patens* 10%, $n = 21$). In contrast to *J. gerardi* removal and control plots, *S. patens* removal plots had low plant frequency (Fig. 4) and nearly twice as high substrate salinity. These results strongly suggest that colonization by *S. patens* facilitated transplant success.

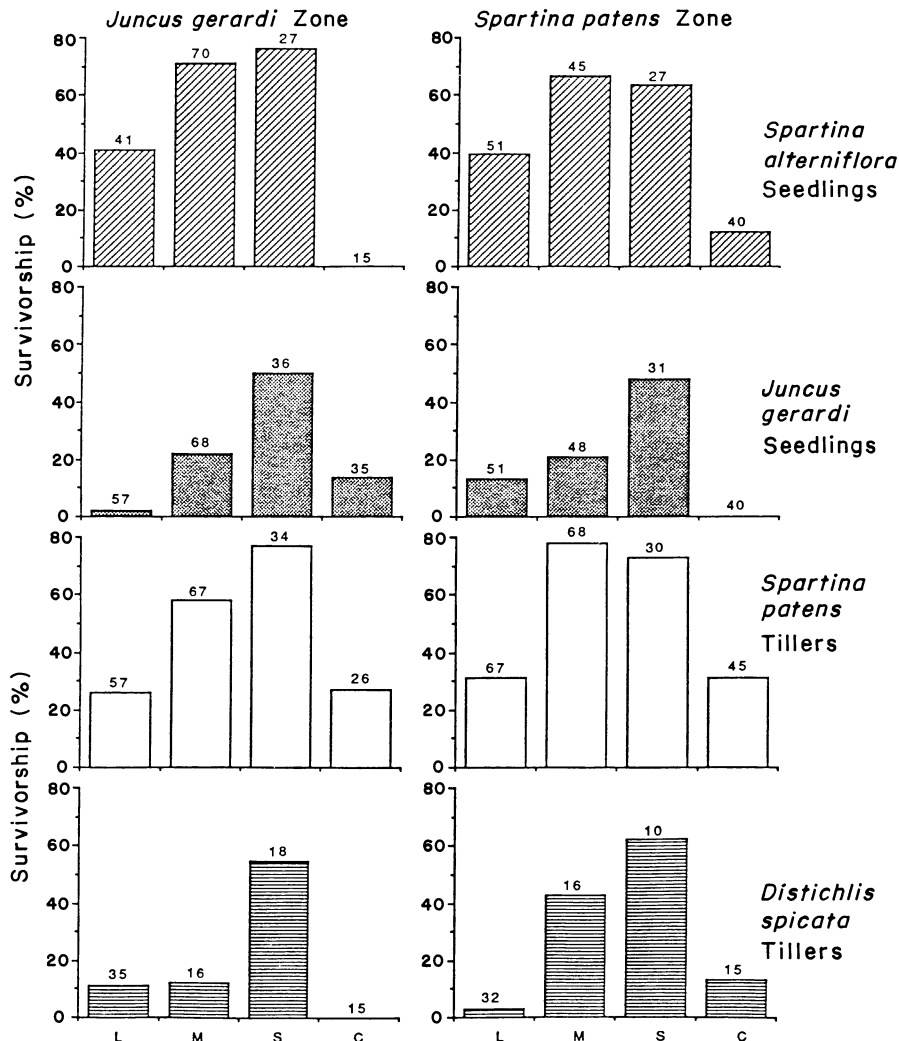


FIG. 5. Results of seedling and tiller transplants of marsh perennials into three sizes of artificial bare patches (L = large, 1 m²; M = medium, 0.5 m²; S = small, 0.25 m²) and dense vegetation (C=control) in the *S. patens* and *J. gerardi* zones. Substrate salinities of the patches are given in Table 2. Data from 1986 and 1987 were similar and were pooled. Sample sizes are given above the bars.

DISCUSSION

Results presented in this paper suggest that the distinct zonation of high marsh perennial plants across New England salt marshes is driven strongly by interspecific competition, but that interspecific facilitation may be important in the secondary succession of disturbance-generated bare space.

*Interspecific competition and marsh
plant zonation*

New England salt marsh plants are typically zoned in distinct bands correlated with major breaking points in the degree of tidal flooding across marsh habitats (Nixon 1982). *Spartina alterniflora* dominates the low marsh habitat, but is restricted to the low marsh by the competitive dominance of *Spartina patens* on the seaward border of the high marsh (Bertness 1990). Conversely, *S. patens* is incapable of persisting in the frequently flooded low marsh habitat (Gleason 1980, Bertness and Ellison 1987, Bertness 1988, 1989).

Plant distributions across the high marsh also appear to be strongly dictated by interspecific competition. When competitors were removed, the performance of each of the high marsh perennials increased with marsh elevation or decreased exposure to tidal flooding (Fig. 2), suggesting that *J. gerardi* dominates the most favorable high marsh habitat. Experiments examining the competitive abilities of marsh perennials in dense vegetation (Figs. 1–3) showed strong competitive dominance by *J. gerardi*. On natural borders *J. gerardi* limited the success of other perennials, but was not markedly affected by sympatry. The competitive dominance of *J. gerardi* appears to be the product of its early growing season (Bertness and Ellison 1987). Unlike *S. patens* and *D. spicata*, which emerge from rhizomes in early May, *J. gerardi* aboveground growth commences in late February. Consequently, *J. gerardi* emerges without interspecific shading, while emergent *D. spicata* and *S. patens* can be severely shaded (by >50%) by existing *J. gerardi* tillers. Apparently as a result, *J. gerardi* pre-emptively and actively displaces *S. patens* and *D. spicata* from the terrestrial border of the high marsh. *J. gerardi* appears to be restricted to the terrestrial border of the marsh by increased physical disturbance and flooding on the seaward border of the high marsh habitat (Bertness and Ellison 1987).

Distichlis spicata is found throughout high marsh habitats at low densities mixed with the high marsh dominants and at higher densities in discrete patches (Miller and Eglar 1950). It is more resistant to wrack burial than other marsh perennials and rapidly invades disturbance-generated bare space vegetatively, which leads to its dominance in disturbed high marsh areas (Bertness and Ellison 1987). *D. spicata*, however, is competitively subordinate to both *S. patens* and *J. gerardi* (Figs. 1–3), and over time is competitively displaced in low disturbance habitats. The competitive

dominance of *S. patens* and *J. gerardi* over *D. spicata* reflects differences in growth morphologies (Bertness and Ellison 1987). *S. patens* and *J. gerardi* have dense turf morphologies, while *D. spicata* expands vegetatively on long adventitious runners and never forms dense turfs. As a result, *D. spicata* is a rapid vegetative invader, but loses competitive encounters with perennials with turf morphologies. Similar consequences of growth morphologies on the competitive ability of clonal organisms have been documented in other vascular plant (Lovett Doust 1981, Schmid and Harper 1985) and sessile marine invertebrate (Jackson 1985) assemblages.

Secondary succession of high marsh bare space

While competitive dominance appears to strongly dictate marsh plant zonation, interspecific interactions during secondary succession have a distinctly different character. In New England marshes bare space is commonly generated when floating plant debris (wrack) is deposited by tides, killing underlying vegetation (Reidenbaugh and Banta 1980, Hartman et al. 1983). High marsh bare patches are initially invaded by *Salicornia europaea* and *D. spicata*. *S. europaea* invades bare patches by seeds but is rapidly displaced by the vegetative colonization of perennials (Bertness and Ellison 1987, Ellison 1987). Sexual recruitment of marsh perennials is limited by flower and seed predation, which dramatically reduce seed set (Bertness et al. 1987) and high patch salinities, which limit germination and seedling survivorship (Zedler 1982, S. Shumway, *personal communication*). *D. spicata* invades bare patches with adventitious runners and often initially dominates recovering patches, but is displaced from recovering patches by *S. patens* or *J. gerardi* in 2–4 yr (Bertness and Ellison 1987). Experimental examination of patch closure confirms that competitive interactions dictate the outcome of patch secondary succession, but also that interspecific facilitation may play an important role in patch recovery.

While interspecific interactions during the closure of bare patches bordered by *S. patens*/*D. spicata* mixtures were exclusively competitive, both *S. patens* and *D. spicata* invasion into patches facilitated *J. gerardi* colonization (Fig. 4). The mechanistic basis for the facilitation of *J. gerardi* by its competitive subordinates is likely a product of the differential abilities of marsh perennials to invade hypersaline bare space and the ameliorating effect of vegetation on substrate salinity. Bare substrate is exposed to direct radiation and heating producing increased evaporation and elevated salinities in contrast to substrate shaded by dense vegetation (Table 2; Pethick 1978, Boston 1983). High soil salinities are widely known to inhibit vascular plant success (Chapman 1974).

A number of lines of evidence suggest that hypersaline conditions limit the colonization of high marsh

perennials into bare patches. Tillers and seedlings transplanted into patches showed decreased survivorship with increasing patch size and salinity (Fig. 5). This result is most parsimoniously explained as a response to high patch salinities. *S. patens* and *D. spicata* tillers transplanted into hypersaline patches reveal severe water stress in contrast to tillers transplanted into low salinity patches or dense vegetation (S. Shumway, *personal communication*). In addition, *S. patens* tillers and *J. gerardi* seedlings transplanted into patches of similar size but with different salinities and vegetation cover showed increasing survival with increased vegetation cover and decreased salinity. Finally, work in progress (S. Shumway and M. D. Bertness, *personal observation*) has shown that artificially decreasing bare patch salinities in the *J. gerardi* zone increases *J. gerardi* seedling abundance by over three orders of magnitude.

I hypothesize that the interspecific facilitation of *J. gerardi* during secondary succession is the product of the differential ability of these marsh plants to vegetatively invade and ameliorate hypersaline bare space, and a strong inverse relationship between plant colonization ability and competitive dominance. Available evidence (Bertness and Ellison 1987) suggests that *D. spicata* is the most tolerant and *J. gerardi* the least tolerant perennial to stressful physical conditions. *S. patens* and *D. spicata* are able to rapidly invade hypersaline bare space vegetatively, and for both of these perennials, ramets invading hypersaline soils are supported by water transport from sister ramets in surrounding vegetation that is not under osmotic stress (S. Shumway, *personal communication*, also see Salzman 1985). In contrast, *J. gerardi* does not appear to support water stressed ramets, is severely limited by hypersaline conditions (Fig. 4), but is capable of vigorously invading dense vegetation and competitively excluding *S. patens* and *D. spicata* in benign habitats (Fig. 3).

If this mechanism for marsh plant facilitation is correct, interactions during marsh patch secondary succession may differ markedly under disparate environmental conditions. Substrate salinities of bare patches vary widely within marshes. Large patches are generally more saline than small patches, suggesting that the occurrence of secondary succession facilitation may increase with patch size. Similarly, local variation in patch salinities due to differences in tidal flooding, small scale topographic features, which influence drainage and annual variation in rainfall, may all influence patch salinities and potentially the relative importance of facilitative and competitive interactions in marsh secondary succession.

Is facilitation rare in natural assemblages?

In contrast to competitive phenomena, facilitation has received little experimental attention, ostensibly as a reaction to the uncritical acceptance of facilitation

mechanisms early in this century and the preoccupation of ecologists over the last two decades with competitive processes (Connell 1983, Strong et al. 1984). Historically, facilitation was thought to be important in secondary succession (Clements et al. 1926, Odum 1969). Little experimental evidence supported this contention, but whether this reflects a paucity of facilitation in nature or the conspicuous lack of rigorous experiments designed to examine them is unclear (Connell and Slatyer 1977). It is clearly true that facilitation hypotheses have not been given the attention and bias accorded to competitive mechanisms since field experimentation has become a common tool in understanding the dynamics of natural communities. A number of recent field studies with sessile invertebrates, algae, and vascular plants (Menge 1976, Hay 1981, 1986, Taylor and Littler 1982, Turner 1983, Bertness and Grosholz 1985, Wood and Del Moral 1987, Bertness 1988, Pfister and Hay 1988) have found facilitation to be important in physically and biologically stressful habitats. Critical reassessment of the role of facilitation in natural assemblages unshackled by negative bias may find it to be a predictable and pervasive force in the dynamics of communities in harsh environments.

ACKNOWLEDGMENTS

I thank Aaron Ellison, Rachel Ballard, Scott Shumway, Erich Stephens, Mary Memmott and Steve Gaines for field assistance and comments on this work and am particularly grateful to Beth Farnsworth whose efforts were indispensable in getting this project started. Mark Hay, John Sutherland, and two anonymous reviewers considerably improved the manuscript. This work was supported by grants (BSR-8516992 and BSR-8906354) from the National Science Foundation.

LITERATURE CITED

- Atstatt, P. R., and D. J. O'Dowd. 1976. Plant defense guilds. *Science* **193**:24–29.
- Barber, M. C. 1981. Below-ground interactions among salt marsh plants. Dissertation. Johns Hopkins University, Baltimore, Maryland, USA.
- Bazzaz, F. A. 1979. The physiological ecology of plant succession. *Annual Review of Ecology and Systematics* **10**: 351–371.
- Bertness, M. D. 1984. Ribbed mussels and the productivity of *Spartina alterniflora* in a New England salt marsh. *Ecology* **65**:1794–1807.
- . 1988. Peat accumulation and the success of marsh plants. *Ecology* **69**:703–713.
- . 1989. Intraspecific competition and facilitation in a Northern acorn barnacle population. *Ecology* **70**:257–268.
- . 1990. Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. *Ecology* **72**:138–148.
- Bertness, M. D., and A. M. Ellison. 1987. Determinants of pattern in a New England salt marsh plant community. *Ecological Monographs* **57**:129–147.
- Bertness, M. D., and T. Grosholz. 1985. Population dynamics of the ribbed mussel, *Guekensia demissa*: the costs and benefits of a clumped distribution. *Oecologia* (Berlin) **67**:192–204.
- Bertness, M. D., C. Wise, and A. M. Ellison. 1987. Con-

- sumer pressure and seed set in New England marsh perennials. *Oecologia* (Berlin) **71**:191–200.
- Boston, K. G. 1983. The development of salt pans on tidal marshes, with particular reference to south-eastern Australia. *Journal of Biogeography* **10**:1–10.
- Chapman, V. J. 1974. Salt marshes and salt deserts of the world. J. Cramer, Lehre, Germany.
- Clements, F. E., J. Weaver, and H. Hanson. 1926. Plant competition: an analysis of the development of vegetation. Carnegie Institute, Washington, D.C., USA.
- Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* **122**:661–696.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111**:1119–1144.
- Ellison, A. M. 1987. Effects of competition, disturbance, and herbivory in *Salicornia europaea*. *Ecology* **68**:576–586.
- Fowler, N. 1981. Competition and coexistence in a North Carolina grassland. II. The effects of the experimental removal of species. *Journal of Ecology* **69**:843–854.
- . 1986. The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics* **17**:89–110.
- Gleason, M. L. 1980. Influence of tidal inundation on internal oxygen supply of *Spartina alterniflora* and *Spartina patens*. Dissertation. University of Virginia, Charlottesville, Virginia, USA.
- Grace, J. B., and R. Wetzel. 1981. Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. *American Naturalist* **118**:463–474.
- Harper, J. L. 1977. Population biology of plants. Academic Press, London, England.
- Hartman, J., H. Caswell, and I. Valiela. 1983. Effects of wrack accumulation on salt marsh vegetation. Pages 99–102 in Proceedings of the 17th European Marine Biology Symposium. Oceanologica Acta, Brest, France.
- Hay, M. E. 1981. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. *Ecology* **62**:739–750.
- . 1986. Associational defenses and the maintenance of species diversity: turning competitors into accomplices. *American Naturalist* **128**:617–641.
- Howes, B. L., R. W. Howarth, J. M. Teal, and I. Valiela. 1981. Oxidation-reduction potentials in salt marshes: spatial patterns and interactions with primary production. *Limnology and Oceanography* **26**:350–360.
- Jackson, J. B. C. 1985. Distribution and ecology of clonal and aclonal benthic invertebrates. Pages 197–256 in J. B. C. Jackson et al., editors. Population biology and evolution of clonal organisms. Yale University Press, New Haven, Connecticut, USA.
- Jackson, J. B. C., L. W. Buss, and R. Cook, editors. 1985. Population biology and evolution of clonal organisms. Yale University Press, New Haven, Connecticut, USA.
- Keddy, P. A. 1984. Plant zonation on lakeshores in Nova Scotia: a test of the resource specialization hypothesis. *Journal of Ecology* **72**:797–808.
- King, G. M., M. J. Klug, R. G. Wiegert, and A. G. Chalmers. 1982. Relation of soil water movement and sulfide concentration to *Spartina alterniflora* production in a Georgia salt marsh. *Science* **218**:61–63.
- Louda, S. M. 1982. Distributional ecology: variation in plant recruitment over a gradient in relation to insect predation. *Ecological Monographs* **52**:25–41.
- Lovett Doust, L. 1981. Population dynamics and local specialization in a clonal perennial, *Ranunculus repens*. *Journal of Ecology* **69**:743–755.
- Mendelssohn, I. A., K. L. McKee, and W. H. Patrick. 1981. Oxygen deficiency in *Spartina alterniflora* roots: metabolic adaptation to anoxia. *Science* **214**:439–441.
- Mendelssohn, I. A., and E. D. Seneca. 1980. The influence of soil drainage on the growth of salt marsh cordgrass, *Spartina alterniflora* in North Carolina. *Estuarine and Coastal Marine Science* **11**:27–40.
- Menge, B. A. 1976. Organization of a New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecological Monographs* **46**:355–393.
- Miller, W. B., and F. E. Egler. 1950. Vegetation of the Wequetequock-Lawcatuck tidal marshes, Connecticut. *Ecological Monographs* **20**:143–172.
- Mooring, M. T., A. W. Cooper, and E. D. Seneca. 1971. Seed germination response and evidence for height ecophenes in *Spartina alterniflora* from North Carolina. *American Journal of Botany* **58**:48–55.
- Niering, W. A., R. H. Whittaker, and C. W. Lowe. 1963. The saguaro: a population in relation to environment. *Science* **142**:15–23.
- Nixon, S. W. 1982. The ecology of New England high salt marshes: a community profile. United States Department of the Interior, Washington, D.C., USA.
- Odum, E. P. 1969. The strategy of ecosystem development. *Science* **164**:262–269.
- Pethick, J. S. 1974. The distribution of salt pans on tidal salt marshes. *Journal of Biogeography* **1**:57–62.
- Pfister, C. A., and M. E. Hay. 1988. Associational plant refuges: convergent patterns in marine and terrestrial communities result from differing mechanisms. *Oecologia* (Berlin) **77**:118–129.
- Pickett, S., and P. White, editors. 1985. Natural disturbance: the patch dynamic perspective. Academic Press, New York, New York, USA.
- Platt, W. J., and I. M. Weis. 1985. An experimental study of competition among fugitive prairie plants. *Ecology* **66**:708–720.
- Putwain, P. D., and J. L. Harper. 1970. Studies in the dynamics of plant populations. III. The influence of associated species on populations of *Rumex acetosa* and *R. acetosella* in grassland. *Journal of Ecology* **58**:251–264.
- Reidenbaugh, T. G., and W. C. Banta. 1980. Origin and effects of tidal wrack in a Virginia salt marsh. *Gulf Research Reports* **6**:393–401.
- Salzman, A. 1985. Habitat selection in a clonal plant. *Science* **25**:603–604.
- SAS. 1985. SAS user's guide: statistics. Version 5. SAS Institute, Cary, North Carolina, USA.
- Schmid, J., and J. L. Harper. 1985. Clonal growth in grassland perennials. I. Density and pattern dependent competition between plants with different growth forms. *Journal of Ecology* **73**:793–808.
- Silander, J. A., and J. Antonovics. 1982. Analysis of interspecific interactions in a coastal plant community—a perturbation approach. *Nature* **298**:557–560.
- Snow, A., and S. Vince. 1984. Plant zonation in an Alaskan salt marsh. II. An experimental study of the role of edaphic conditions. *Journal of Ecology* **72**:669–684.
- Strong, D., D. Simberloff, L. G. Abele, and A. Thistle, editors. 1984. Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, New Jersey, USA.
- Taylor, P. R., and M. M. Littler. 1982. The roles of compensatory mortality, physical disturbance, and substrate retention in the development and organization of a sand-influenced rocky intertidal community. *Ecology* **63**:135–146.
- Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey, USA.

- Turner, T. 1983. Facilitation as a successional mechanism in a rocky intertidal community. *American Naturalist* **121**: 729-738.
- Valiela, I., and J. M. Teal. 1974. Nutrient limitation salt marsh vegetation. Pages 547-563 in R. J. Reimold and W. H. Queen, editors. *Ecology of halophytes*. Academic Press, New York, New York, USA.
- Wood, D. M., and R. Del Moral. 1987. Mechanisms of early primary succession in subalpine habitats on Mount St. Helens. *Ecology* **68**:780-790.
- Zedler, J. B. 1982. The ecology of southern California coastal salt marshes. United States Department of Interior **FWS-OBS-81-54**.