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DETERMINANTS OF PATTERN IN A NEW ENGLAND SALT MARSH PLANT COMMUNITY¹

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Abstract. In New England salt marshes, *Spartina alterniflora* dominates the low-marsh habitat, which is covered daily by tides. The high-marsh habitat, which is not flooded daily, is dominated on its seaward border by *Spartina patens*, and on its terrestrial border by *Juncus gerardi*. Each of these vegetation zones has a characteristic suite of physical factors associated with differences in tidal inundation. In particular, substrate redox increases and salinity decreases with increasing marsh elevation. Although correlations between physical factors and the occurrence of specific marsh plants have been suggested to be causal, a 5-mo transplant experiment suggested that the distribution of perennials across the marsh does not correspond to their potential performance across the marsh in the absence of surrounding vegetation. While the high-marsh perennials appear to be restricted to the high-marsh habitat by harsh physical conditions in the low-marsh habitat, the low-marsh dominant, *S. alterniflora*, is capable of vigorous growth across the entire marsh and appears to be excluded from the high-marsh habitat by the high-marsh perennials.

Throughout the high marsh, two other plant species, *Distichlis spicata* and *Salicornia europaea*, are found associated with areas that have been disturbed recently. Physical disturbance, in the form of mats of dead plant material (wrack) rafted by tides onto the marsh, is most severe in the spring and early summer, and decreases with increasing marsh elevation. Differential plant mortality results from short-term disturbance events. *D. spicata* and *S. alterniflora* are more tolerant of wrack burial than are the other marsh plants, and short-term disturbance increases the relative abundance of these species in the community. Longer lasting disturbance events kill all the underlying vegetation, leaving discrete bare patches throughout the high marsh. *D. spicata* rapidly colonizes these patches with vegetative runners, while *S. alterniflora* and *Sa. europaea* recruit to these patches by seed. The relative abundance of these plants in recently created bare patches exceeds greatly their relative abundance in the surrounding vegetation. Over time, however, these early colonizers are overgrown and displaced in high-marsh patches by *S. patens* and *J. gerardi*, which grow slowly, as dense turfs of roots, rhizomes, and tillers.

Physical disturbance and interspecific competition appear to be major determinants of the spatial pattern of marsh plant communities. These processes will need to be considered in relation to edaphic factors in elucidating the underlying mechanisms of salt marsh plant zonation.

Key words: disturbance; plant community structure; plant competition; plant morphology; salt marsh plants.

INTRODUCTION

A major goal of plant community ecologists is to understand the processes that generate pattern in natural communities. In spite of a long botanical history of interest in community organization questions (see Whittaker 1978 for review) and efforts early in this century to evaluate experimentally the structure of vascular plant communities (see Jackson 1981), most recent work in plant ecology has focused on understanding the dynamics of plant populations (see Harper 1977 for review). Less work has been directed at elucidating how plant populations interact to generate pattern in natural communities, and our understanding of the

organization and dynamics of vascular plant communities has lagged behind our understanding of plant population dynamics (Harper 1977, Silander and Antonovics 1982). Most studies of the spatial organization of vascular plant communities attempt to correlate species distributions with environmental variables (Strain and Billings 1974, Whittaker 1978, Greig-Smith 1982), in spite of the limitation of correlative studies in addressing issues of causation (Connell 1980, 1983). In contrast, while work with marine invertebrate and algal assemblages has often overlooked important population processes (Underwood and Denley 1984), experimental evaluation of marine communities has pointed to the importance of the interactions of competitive (e.g., Connell 1961, Buss 1986), consumer (e.g., Paine 1966, Lubchenco 1978), and disturbance (e.g.,

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Dayton 1971, Sousa 1979) processes with environmental variables in generating community pattern. Our understanding of the organization of natural vascular plant communities is limited by a lack of empirical studies that simultaneously examine the importance and interactions of competitive (e.g., Werner 1979, Grace and Wetzel 1981, Wilson and Keddy 1986), disturbance (e.g., Platt 1975, White 1979, Pickett 1980), consumer (e.g., Atsatt and O'Dowd 1976), and physiological (e.g., Barbour 1978, Cooper 1982) processes in shaping natural plant communities.

Salt marsh communities are ideal for addressing questions of plant-community pattern generation. They are discrete, simple systems dominated by only a handful of plant species (Chapman 1960), and are stable over a time span of hundreds of years (Miller and Egler 1950). The plants of marshes are found in recurring and well-described patterns, zoned on a conspicuous gradient of tidal inundation (Nixon 1982, Zedler 1982, Vince and Snow 1984). This striking plant zonation has attracted the attention of ecologists for over a century, but the mechanisms generating the segregation of marsh plant species are poorly understood (see Nixon 1982 for review).

To date, most work on salt marsh vegetation has focused on the role of physical factors in affecting plant growth and plant zonation. Soil oxygen levels (Howes et al. 1981, Mendelssohn et al. 1981), flooding (Armstrong et al. 1985), nutrient limitation (Valiela and Teal 1974), soil sulfide accumulation (King et al. 1982), and soil drainage (Mendelssohn and Seneca 1980) have all been proposed as major determinants of plant success in marsh habitats. There appears to be general agreement among salt marsh researchers that physical rather than biotic factors are the principal determinants of plant species distributions across marsh habitats (Cooper 1982). Studies in Alaskan salt marshes (Snow and Vince 1984), freshwater plant communities (Grace and Wetzel 1981, Wilson and Keddy 1985), and mangroves (Rabinowitz 1978), however, have shown that plant distributions in marshes do not necessarily correspond to plant physiological tolerances, implying that biotic interactions may be of unrecognized importance in structuring these communities.

The roles of interspecific competition, consumer pressure, and physical disturbance in generating plant spatial patterns have received little attention in salt marshes. Interspecific plant competition has been suggested to be important in marsh communities (Pielou and Routledge 1976, Gray and Scott 1977, Barbour 1978, Snow and Vince 1984, Wilson and Keddy 1985), but has been examined rarely (Grace and Wetzel 1981, Silander and Antonovics 1982, Wilson and Keddy 1986, Ellison 1987). North American marsh plants do not appear to be consumed heavily by herbivores (Smalley 1960, Teal 1962, Denno 1977, Vince et al. 1981), suggesting that consumers do not play a major role in limiting marsh-plant distributions (but see Bert-

ness et al. 1986). The potential importance of physical disturbance in marsh communities has been identified by a number of workers (Redfield 1972, Reidenbaugh and Banta 1980, Hartman et al. 1983). Physical disturbance in high-marsh habitats along the east coast of North America is generally the result of dead plant debris (wrack), rafted by tides, covering and killing underlying vegetation. The importance of this disturbance in generating pattern in marsh plant communities, however, has received little attention.

In this paper, we examine the spatial organization of a New England salt marsh plant community employing observational and experimental methods. We describe the distribution of plants and edaphic factors across the marsh community, report the results of transplant studies to test the hypothesis that plant distributions correspond to their physiological tolerances, and examine the spatial and temporal pattern of wrack disturbance and its impact on plant species abundance in the community. Together, our results suggest how plant physiological tolerances, physical disturbance, and interspecific competition interact to generate the conspicuous zonation pattern of this plant community.

STUDY SITE

These studies were conducted on the marsh at Rumstick Cove, a small, protected embayment of Smith Cove in Barrington, Rhode Island, USA (see Bertness 1984 for description). The vegetation pattern at Rumstick Cove is similar to other southern New England marshes (Nixon 1982). The low-marsh habitat is subject to daily tidal submergence (Nixon 1982), and is dominated by a dense monoculture of *Spartina alterniflora*. The high-marsh habitat is not subject to daily flooding (Nixon 1982), and is dominated on the seaward edge by a distinct band of *Spartina patens* and on the terrestrial edge by a distinct zone of the rush *Juncus gerardi*. These major vegetation zones will be referred to in the text as the *S. alterniflora*, *S. patens*, and *J. gerardi* zones, respectively. In addition to these numerically dominant perennials, the succulent annual *Salicornia europaea* and the perennial grass *Distichlis spicata* are found in discrete patches throughout the high marsh. Other salt marsh species are uncommon and inconspicuous. Above the level of tidal inundation, the marsh vegetation is abruptly replaced by *Iva frutescens* and other woody plants (Nixon 1982).

METHODS

Transect sampling was employed to describe the vegetation pattern of the high-marsh habitat. The low-marsh habitat at the study site is described in detail elsewhere (Bertness 1984, 1985). In June 1984, at two locations in the marsh, beginning on the seaward edge of the high marsh and at 2-m intervals moving up the marsh to the woods (≈ 30 m), we sampled the vegetation along a 20-m transect-line parallel to the shoreline at 2-m intervals. A 0.5×0.5 m quadrat subdivided

into 100 5×5 cm cells was censused at each location. Percent cover of each of the plant species, bare area, and wrack was determined by counting the number of cells of the quadrat containing each of those items. Wrack-cover was operationally defined as dead plant material >2 cm deep, completely covering one cell (25 cm²). Since few bare areas were encountered in random transect samples, we located and sampled 2–10 bare patches at each level sampled with transects. We defined disturbance-generated bare patches as areas with >0.25 m² of substrate devoid of perennial vegetation as a result of being covered by plant debris for a time long enough to kill the underlying vegetation (Reidenbaugh and Banta 1980, Hartman et al. 1983). At the study site, virtually all conspicuous disturbance features observed in the high marsh from 1981–1986 were the product of wrack coverage (M. D. Bertness and A. M. Ellison, *personal observation*). In the low-marsh habitat, ice damage and erosion are important disturbance processes (Bertness 1984). We sampled vegetation associated with high-marsh bare patches by estimating plant cover at 2–3 random locations on the perimeter of each patch.

To describe the above- and belowground structure of the perennial plants on the marsh, we counted and measured tiller heights in random 10×10 cm quadrats in pure stands of each species, and examined root and rhizome distributions in core samples. Ten cores (6.5 cm diameter, 30 cm deep) taken from pure stands of each species were sectioned at 2.5-cm vertical intervals, and each section was washed through a sieve (2-mm mesh), and sorted into roots, rhizomes, and dead plant debris. The components from each core section were dried and weighed (see Bertness 1984 for detailed methods).

To examine the ability of each of the marsh perennials to invade bare space, we located 8–10 natural bare patches >1 m² that were bordered by monospecific stands of each of the marsh perennials. On the perimeter of each of the patches, we installed a 0.5×0.5 m grid of 1-mm nylon fishing line. The grid of 100 individually addressed 5×5 cm cells was supported on oversized plastic frames and fastened to the substrate with plastic pins. In March 1984, the grids were installed on the patches, with 25–30% of one side in perennial vegetation and the remaining grid area on bare substrate. Weekly, from April to September 1984, we counted and identified tillers and seedlings in each of the 100 cells of each grid.

Physical parameters across the marsh habitat

We quantified substrate salinity, redox potential, pH, substrate water content, and the amount of particulate organic material (peat) in the sediment across the marsh habitat. In each marsh vegetation zone, water samples were taken by installing 20 plastic tubes (15 cm long and 2.5 cm diameter), capped at both ends, into the

substrate. Half the tubes had input ports at a depth of 2 cm, and the other half had input ports at 10 cm. Every 2 wk from June through September 1985, water was sampled from the tubes, and the salinity and pH of the sample were determined. Ten to twenty substrate redox-potential measurements were made with standard techniques (Howes et al. 1981, Bertness 1985) at 2 and 10 cm depths in each marsh vegetation zone in July 1984 using an Orion ionalyzer and redox probe. Substrate water content was determined by taking 10 cores (3 cm diameter, 10 cm long) in each marsh zone, during neap tides, weighing them wet, drying them at 30°C for 1 wk, and then reweighing them. The density of macro-organic plant debris (peat) in the substrate was determined for each marsh vegetation zone using the dried peat masses from the cores described earlier for root and rhizome analysis. Substrate hardness across the marsh was measured with a penetrometer as described in Bertness and Miller (1984). In the summer of 1985, we observed tidal flooding across the marsh to determine the tidal heights necessary to flood each vegetation zone. The relative frequency of tidal flooding for each marsh zone was then estimated using predicted tidal heights (NOAA 1985).

Transplant experiments

Transplants were performed to assess the growth potential of each of the four common marsh perennials across the marsh habitat in the absence of foreign vegetation. To minimize disturbance effects, 40 blocks of substrate (15 \times 15 cm, 25 cm deep) containing live rhizomes were removed from monospecific stands of each species and were transplanted directly to each of the different marsh habitats (including controls) in May 1984. In the high marsh, vegetation within 20 cm of each transplant was clipped weekly to minimize interference from surrounding vegetation. In the low marsh, where natural plant-heights are 3–4 times those of the high marsh (Nixon 1982), a 30 m² area was maintained clear of aboveground growth for the transplants. In September 1984, we harvested a 10×10 cm area in the center of each transplant, counted and measured (height) each tiller, and dried and weighed the aboveground biomass of each sample. In comparison to unmanipulated control stands of each species, the transplanting operation reduced aboveground biomass production by 35–45%. We were unable to follow the transplants for more than one season since the low-marsh transplants were destroyed by winter ice in January 1985. Ideally, transplants should be examined for more than one growing season. In spite of this difficulty, the consistency of our results among species and between rhizome and seedling transplants (see Results), suggest that our transplant experiments accurately assessed relative plant success in each marsh zone.

Since ambient substrate was transplanted with the plants in each block, the above transplant experiment

tested whether marsh location affected plant growth with substrate type held constant for each species. To test marsh elevation effects on plant growth in ambient substrate, seedling transplants were made in the summer of 1985. Only *S. alterniflora* seedlings were tested, since they were abundant and were found to tolerate transplantation handling. In May 1985, 25–50 randomly collected *S. alterniflora* seedlings were transplanted within 30 min of collection into 1–8 m² bare patches in each marsh vegetation zone, and individually marked with a colored straw (1.5 mm diameter). In September 1985, the transplanted seedlings were scored for survival and 15 randomly selected survivors from each zone were excavated. We also excavated a sample of unmanipulated *S. alterniflora* seedlings from bare areas in the tall-form *S. alterniflora* zone. The maximum tiller height (cm), number of tillers, number of rhizomes, depth of root penetration, and root and shoot dry weights of each seedling were measured.

Disturbance effects on marsh vegetation

Our examination of physical disturbance effects on marsh vegetation had four objectives: (1) to determine whether marsh perennials differed in resistance to debris-burial mortality; (2) to determine the spatial and temporal pattern of wrack disturbance across the marsh; (3) to examine the effects of short-term wrack burial, not leading to bare patch formation, on marsh vegetation; and (4) to determine whether disturbance-generated bare patches were invaded randomly by marsh plants.

To examine mortality of the marsh perennials under wrack cover, 16 random 50 × 50 cm quadrats in pure stands of each species were covered with a 2–3 cm thick layer of wrack, held in place with fishnet (2-cm mesh) and plastic pins, on 1 June 1984. Quadrats were uncovered briefly each week, and 250 tillers in the center of each replicate were scored as dead or alive.

The distribution of disturbance across the high marsh was quantified in 1985 in two 30 × 30 m transect areas extending to the terrestrial edge of the high marsh. Within each area, a grid of 225 permanent 50 × 50 cm sampling locations was marked at 2-m intervals. Weekly, from March to September, percent cover of wrack was determined in each area using the 50 × 50 cm gridded quadrat described above. Monitoring of debris cover over the spring and summer was timed to coincide with the growing season of the plants and the peak abundance of wrack on the marsh (M. D. Bertness and A. M. Ellison, *personal observation*). Mobile plant debris consisted primarily (>95%) of dead *S. alterniflora*, which had been produced the previous year, decayed over the summer, and was tidally transported out of the marsh basin (see Results: Physical Disturbance Effects on Marsh Vegetation).

To examine the effects of short-term wrack cover not resulting in the generation of bare patches, mixtures of

marsh perennials were covered with debris for 2- and 4-wk periods. We started this experiment the 1st wk of June 1985 to coincide with the time when plants were most likely to be covered by natural wrack in the habitat. Two- and four-week treatments were selected to correspond to the most frequent short-term residence time of debris dictated by bimonthly high tides. Thirty 0.25 × 0.25 m quadrats in *S. alterniflora*–*S. patens* mixes, *S. patens*–*D. spicata* mixes, and *J. gerardi*–*D. spicata* mixes were marked with flags and divided randomly into an equal number of control, 2-wk, and 4-wk cover treatments. Initial tiller counts in each of the mixtures revealed no significant differences in species abundance among treatments. Covered treatments consisted of a 2–5 cm layer of plant debris, and after 2 and 4 wk, wrack was removed from the corresponding treatments in each species mixture. Quadrats were then maintained free of natural wrack cover until late August when the central 10 × 10 cm of each quadrat was harvested. Tillers were sorted to species, counted, measured (height), dried, and weighed.

The influence of disturbance-generated bare space on the relative abundance of marsh plants was examined by following the recolonization and closure of freshly generated bare patches. In May 1983, we located and marked 30 random bare patches in the *S. patens* zone that had resulted from wrack cover during the summer of 1982 (M. D. Bertness and A. M. Ellison, *personal observation*). In the spring of 1984, we marked 30 freshly generated patches in the *J. gerardi* zone. All patches were individually marked with labelled stakes (4 × 4 cm) driven flush with the substrate. Patches where the underlying vegetation had not been entirely killed were not marked. All patches were photographed when initially marked and subsequently in May and September each year through 1985. Patch photographs were then projected, and a planimeter was used to estimate the area of each patch at each date. Patch area was defined as space unoccupied by plant cover. To examine the species composition of plants colonizing the marked patches and of the surrounding vegetation, we censused vegetation within the initial patch boundaries and immediately outside each marked patch in late August of 1983, 1984, and 1985. As many non-overlapping percent-cover estimates as could be made (1–6) inside each patch and 3–6 cover estimates around the perimeter of each patch were made. Tiller counts of each species were made in 10 × 10 cm quadrats inside and immediately outside of the initial patch boundaries. Six to twenty-five random quadrats were censused inside each patch, and 6–10 quadrats were censused at random locations around each patch's perimeter. The number of quadrats censused increased with patch size.

All data were analyzed using standard methods (SAS 1982). Data were transformed when necessary to meet the assumptions of parametric statistics.

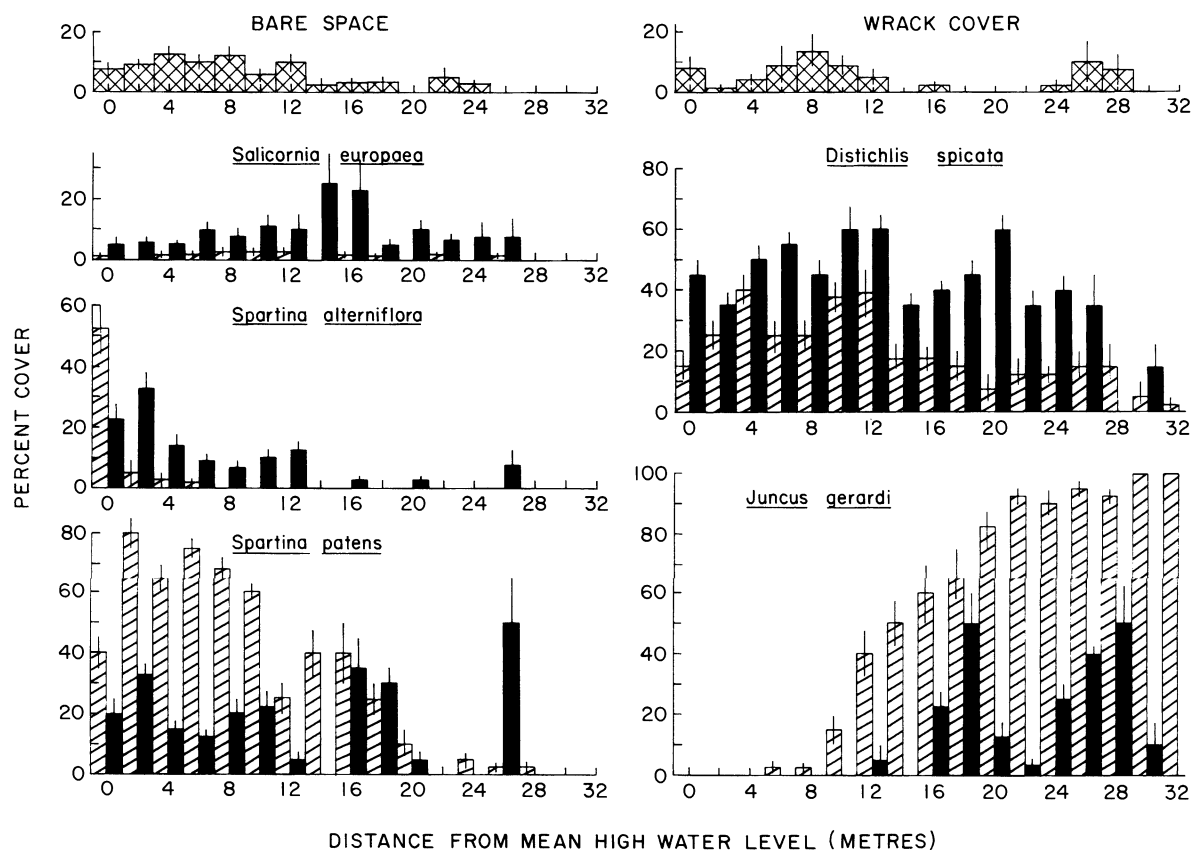


FIG. 1. Summary of the transect survey of high-marsh vegetation at the study area. Data are percent cover estimates from 0.25-m² quadrats (see Methods). Two 255-m² areas of the high marsh were surveyed (June 1984) and the data were pooled. Hatched and crosshatched bars represent random locations, with each bar representing the mean of 20–30 estimates \pm \pm SD. Solid bars are data from the periphery of bare areas at each level and represent the mean of 6–12 estimates \pm \pm SD.

RESULTS

Spatial pattern of the marsh vegetation

Bare substrate accounted for <5% of high-marsh surfaces ($4.6 \pm 0.5\%$) in June and decreased significantly ($P < .001$, ANOVA) with increasing distance from the shoreline (Fig. 1). Maximum abundance of bare space was found on the shoreward edge of the high marsh, where $\approx 10\%$ of space within 8 m from the low marsh was bare (Fig. 1). Bare areas were patchily distributed across the marsh ($cv = 275\%$), and most were discrete patches >0.1 m² apparently generated by wrack burial. Wrack covered $6.03 \pm 0.8\%$ of the high marsh and varied ($P < .001$, ANOVA) with distance from the shoreline. Wrack cover was highest 8–10 m from the seaward edge, and near the terrestrial border of the high marsh (Fig. 1), corresponding to the mean higher high water and maximum high tide levels of the marsh habitat.

S. patens was rare below the mean high water (MHW) line where it would be subject to daily tidal submergence (see Variation in Physical Parameters across the Marsh Habitat); co-occurred with the low-marsh dominant, *S. alterniflora*, at the mean high water line; cov-

ered 70–80% of the substrate in an ≈ 8 m wide zone of thick perennial turf immediately above the mean high water level (the *S. patens* zone); and then rapidly decreased in abundance with increasing distance from the shoreline (Fig. 1).

J. gerardi was rare in the *S. patens* zone (Fig. 1), but from there it increased in abundance with increasing distance from the shoreline, covering $>90\%$ of the terrestrial border of the marsh. In the *J. gerardi* zone, *J. gerardi* abundance was reduced severely in recently disturbed areas (Fig. 1). The interface between the *S. patens* and *J. gerardi* zones was discrete, with few areas supporting mixtures of those species. Generally, where the vegetative turfs of those species met, dense stands abutted one another with minimal mixing. On the interface between the *S. patens* and *J. gerardi* zones (10–16 m from MHW), *S. patens* and *J. gerardi* abundances were negatively correlated ($r = -0.69$, $P < .001$).

D. spicata was found in relatively low abundance in random locations across the high marsh, with its abundance significantly ($P < .001$, ANOVA) influenced by distance from the shoreline (Fig. 1). *D. spicata* was nearly twice as abundant (cover $28.1 \pm 1.9\%$) in the

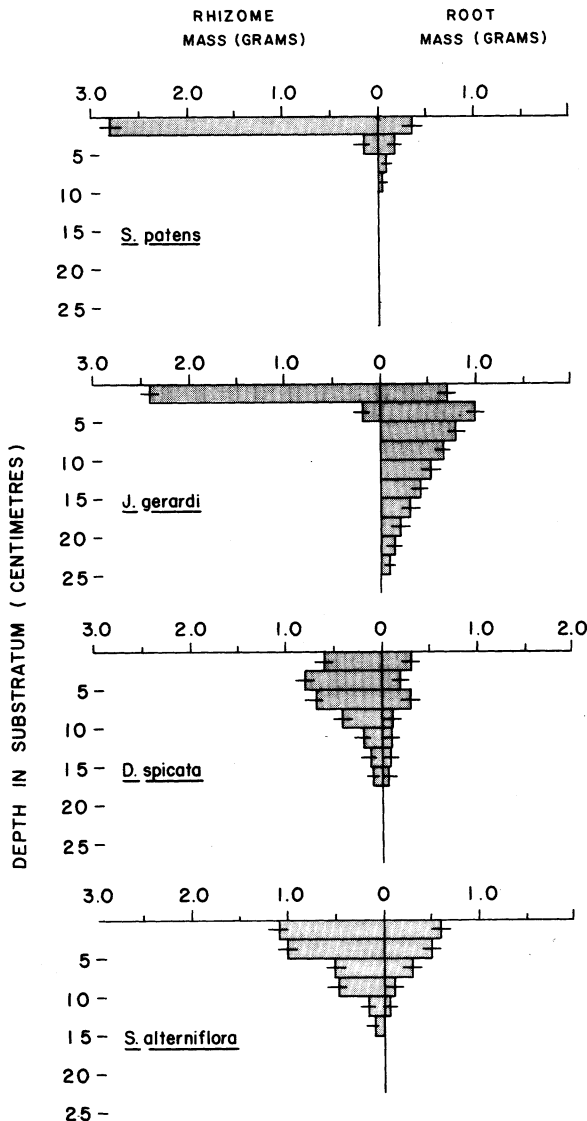


FIG. 2. Distribution of belowground biomass from dense monospecific stands of each of the common marsh perennials. Data are from 6.5 cm diameter cores in each of 10 areas ($\bar{X} \pm$ SD). *Spartina alterniflora*, *S. patens*, and *Juncus gerardi* cores were taken in the marsh vegetation zones dominated by each of these species. *Distichlis spicata* cores were taken in a large (25 m²) dense stand of *D. spicata* in the *S. patens* zone.

S. patens zones as in the *J. gerardi* zone ($15.6 \pm 1.3\%$). Considering the entire high marsh, *D. spicata* was over twice as common ($P < .001$, ANOVA) in recently disturbed areas ($47.6 \pm 2.5\%$) as in random locations ($19.6 \pm 1.0\%$). In the *S. patens* zone, *D. spicata* cover was positively correlated with bare space ($r = 0.51$, $P < .001$) and negatively correlated ($r = -0.45$, $P < .001$) with *S. patens* cover. Similarly, in the *J. gerardi* zone, *D. spicata* cover was positively correlated with bare space ($r = 0.60$, $P < .001$) and negatively correlated with *J. gerardi* cover ($r = -0.59$, $P < .001$).

The low-marsh dominant, *S. alterniflora*, was un-

common in the high marsh (Fig. 1) covering $< 5\%$ ($3.7 \pm 0.6\%$) of available space. Its abundance in the high marsh decreased dramatically ($P < .001$, ANOVA) with distance from the low marsh, and it was found only in bare patches in the *J. gerardi* zone (Fig. 1). In the *S. patens* zone, *S. alterniflora* cover was positively correlated ($r = 0.75$, $P < .001$) with bare space and negatively correlated ($r = -0.64$, $P < .001$) with *S. patens* cover.

The annual *Salicornia europaea* was found predominantly in bare patches throughout the high marsh (Fig. 1). *Sa. europaea* was extremely rare in random locations ($1.2 \pm 0.3\%$ cover) but its relative abundance increased by nearly an order of magnitude ($9.4 \pm 0.6\%$) in bare patches. *Sa. europaea* abundance varied significantly with distance from the shoreline ($P < .01$, ANOVA), peaking near the interface of the *S. patens* and *J. gerardi* zones, and dropping out of the assemblage near the terrestrial border of the marsh. Other annuals, *Limonium nashii*, *Suaeda maritima*, and *Atriplex triangularis*, were rare ($< 1\%$ cover) and occurred exclusively in the high marsh, associated with bare patches.

Tiller densities and heights differed among dense stands of the marsh perennials. Tiller densities were highest in *S. patens* (420 ± 21 tillers/100 cm², $n = 30$) and *J. gerardi* (325 ± 16 tillers/100 cm², $n = 30$), considerably lower in *D. spicata* (92 ± 5 tillers/100 cm², $n = 30$), and lowest in short-form *S. alterniflora* (7.5 ± 0.5 tillers/100 cm², $n = 8$). Tiller heights in dense monospecific stands decreased in the following order: short-form *S. alterniflora* (35.9 ± 1.1 cm, $n = 80$), *D. spicata* (31.9 ± 1.0 cm, $n = 80$), *J. gerardi* (26.2 ± 0.6 cm, $n = 80$), and *S. patens* (23.2 ± 0.5 cm, $n = 80$).

Cores from monospecific stands of each of the marsh perennials (Fig. 2) revealed interspecific differences in belowground space utilization. *S. patens* and *J. gerardi* occupied belowground space in dense superficial turfs of rhizomes primarily ($\approx 90\%$) restricted to the top 2.5 cm of the substrates. Root distributions of the two species differed, however, with roots of *S. patens* confined primarily (85%) to the top 5 cm of the substrate, while *J. gerardi* roots penetrated up to 25 cm into the substrate. In contrast, neither *D. spicata* nor *S. alterniflora* occupied belowground space as dense superficial turfs (Fig. 2). Roots and rhizomes of *D. spicata* penetrated up to 17.5 cm into the substrate, while roots and rhizomes of short-form *S. alterniflora* penetrated 12.5 and 15 cm, respectively, into the substrate. Tall-form *S. alterniflora* roots and rhizomes penetrate up to 30 cm into the substrate (Bertness 1985).

Invasion of the perennials into adjacent bare space further illustrated differences among these species (Table 1). Whereas the four species did not differ in the production of new tillers in bare space ($P > .20$, ANOVA), the spatial distribution of the tillers produced differed markedly among species. In the same period

TABLE 1. Characterization of each of the marsh perennials invading disturbance-generated bare space. Data are from 0.25 m² (0.5 × 0.5 m) areas on the borders of natural bare patches adjacent to pure stands of each species. Different superscript letters indicate significant differences between means ($P < .05$, Scheffé test). Values are $\bar{X} \pm \text{SE}$.

	<i>n</i>	Percent increase in tiller density, May–Sept	Percent increase in cover by vegetative growth, May–Sept	Percent increase in total cover, May–Sept (vegetative & seedlings)	Seedling density	Seedling survivor- ship, May–Sept (%)
<i>Spartina alterniflora</i>	8	314 ± 20 ^a	20.0 ± 2 ^a	21.8 ± 2 ^a	9.7 ± 1.9 ^a	48.7
<i>Distichlis spicata</i>	16	275 ± 40 ^a	29.9 ± 2 ^b	29.9 ± 2 ^b	1.1 ± 0.5 ^b	15.2
<i>Spartina patens</i>	12	311 ± 50 ^a	13.0 ± 1 ^c	13.0 ± 2 ^c	2.1 ± 1.1 ^b	42.1
<i>Juncus gerardi</i>	10	245 ± 40 ^a	12.3 ± 4 ^c	27.3 ± 9 ^b	127 ± 44 ^c	40.9

of time, *S. patens* and *J. gerardi* colonized only about half the space that was colonized by *S. alterniflora* and *D. spicata* with vegetative tiller production. *S. patens* and *J. gerardi* vegetatively invaded adjacent bare space slowly with a dense front of rhizomes, roots, and associated tillers (Fig. 3), and are best characterized as having phalanx growth forms (Lovett Doust 1981). In contrast, *S. alterniflora* and *D. spicata* invaded free space more rapidly with long adventitious rhizomes (Table 1, Fig. 3), and can be characterized as having guerilla (Lovett Doust 1981), or runner, growth forms.

S. alterniflora rhizomes invaded bare space 5–10 cm below the substrate, tillering at 5–20 cm intervals, while *D. spicata* rhizomes were generally superficial runners within 2.5 cm of the surface, often reaching lengths of 30 cm (Fig. 3). These morphological differences among species appeared to be far greater than morphological variation within any of the species (M. D. Bertness and A. M. Ellison, *personal observation*). Consequently, *D. spicata* invaded free space most rapidly, and both *D. spicata* and *S. alterniflora* invaded free space more rapidly than *S. patens* and *J. gerardi* by vegetative

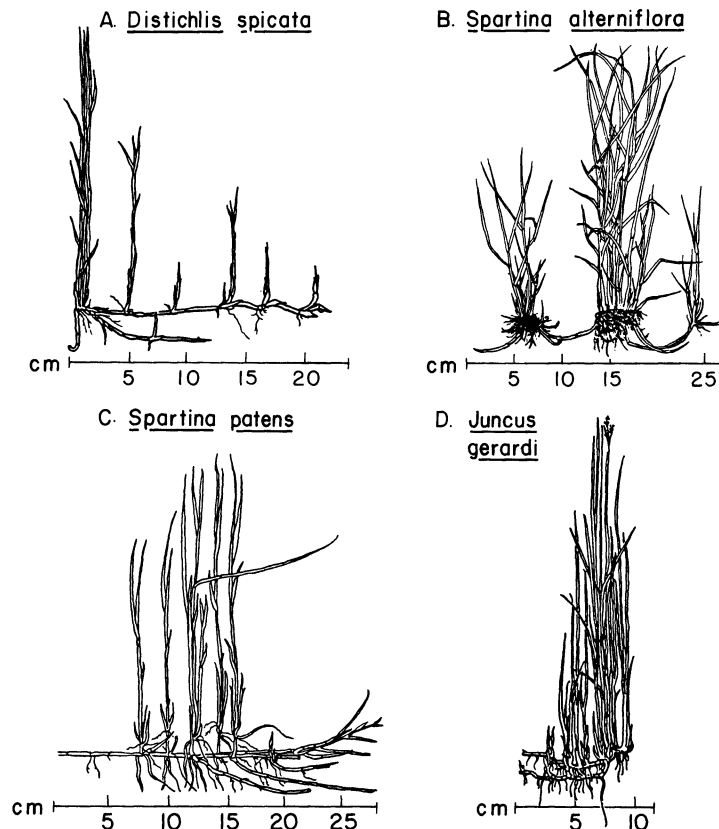


FIG. 3. Morphology of each of the common marsh perennials invading bare space. Sketches were made from plants excavated from the perimeter of naturally occurring bare patches and are composite drawings from 10 excavations of each species.

TABLE 2. Results of physical parameter survey across the marsh habitat by major vegetation zones. Different superscript letters indicate significant differences ($P < .05$, Scheffé test) between zones. Values are $\bar{X} \pm \text{SE}$.

Variable	Substrate depth (cm)	Marsh zone					ANOVA	
		Tall-form <i>Spartina alterniflora</i>	Short-form <i>S. alterniflora</i>	<i>S. patens</i>	<i>Distichlis spicata</i>	<i>Juncus gerardi</i>	Source of variation	P
Redox potential (mV)	2	-157 ± 16 ^a	-189 ± 13 ^a	18 ± 13 ^b	9 ± 11 ^b	59 ± 9 ^c	habitat	<.001
	10	-242 ± 16 ^a	-263 ± 22 ^a	27 ± 12 ^b	6 ± 8 ^b	110 ± 8 ^c	depth	<.04
Salinity (‰)	2	24.4 ± 0.4 ^a	22.1 ± 0.3 ^b	17.0 ± 0.7 ^c	16.0 ± 0.9 ^c	16.6 ± 0.7 ^c	interaction	<.001
	10	24.8 ± 0.3 ^a	23.0 ± 0.4 ^b	19.0 ± 0.4 ^c	19.0 ± 0.7 ^c	23.0 ± 0.7 ^{a,b}	habitat	<.001
pH	2	6.58 ± 0.04 ^a	6.73 ± 0.03 ^b	6.61 ± 0.10 ^c	6.40 ± 0.10 ^c	6.45 ± 0.05 ^c	depth	<.01
	10	6.71 ± 0.08 ^a	6.70 ± 0.04 ^a	6.61 ± 0.10 ^b	6.63 ± 0.03 ^b	6.42 ± 0.04 ^c	interaction	>.45
Substrate hardness (N)		181 ± 11 ^a	279 ± 11 ^b	470 ± 20 ^c	336 ± 22 ^d	337 ± 18 ^d		<.001
Substrate water content (%)		48.4 ± 2.7 ^b	42.7 ± 2.1 ^a	52.0 ± 2.0 ^{b,c}	55.6 ± 1.7 ^c	43.6 ± 2.1 ^a		<.001
Organic debris (g)		6.8 ± 0.6 ^a	9.1 ± 0.6 ^b	16.8 ± 0.6 ^d	13.5 ± 0.7 ^c	6.9 ± 0.6 ^a		<.001
Tidal height above sea level (m)		0.1–1.0	1.0–1.2	1.2–1.3	1.2–1.4	1.3–1.4		
Period covered by tide (d/mo; April–Sept 1985)		30.5 ± 0.2	23.5 ± 1.3	17.3 ± 1.8		8.7 ± 1.1		

growth (Table 1). With the exception of *J. gerardi*, seedlings did not play a major role in the colonizing ability of the perennial species. *J. gerardi* seedlings were >10 times as abundant as *S. alterniflora* seed-

lings, which were nearly 10 times as abundant as *S. patens* and *D. spicata* seedlings (Table 1). Because of those differences in seedling success, the total colonizing ability (vegetative and seedling recruitment) of *J.*

TABLE 3. Results of species transplants across the marsh. Blocks (400 cm²) of rhizomes were transplanted in May 1984 and the central 100 cm² of each was harvested the following September. Mass per tiller was calculated for each block replicate. All values are $\bar{X} \pm \text{SE}$. Different superscript letters indicate significant differences ($P < .05$, Scheffé) between zones.

Species transplanted		Marsh zone		
		Tall-form <i>S. alterniflora</i>	Short-form <i>S. alterniflora</i>	<i>S. patens</i>
Tall-form <i>Spartina alterniflora</i>	biomass (g/100 cm ²)	25.3 ± 0.8 ^a	35.1 ± 2.6 ^b	36.7 ± 2.4 ^b
	tiller height (cm)	66.8 ± 2.4 ^b	77.6 ± 2.5 ^a	76.5 ± 2.5 ^a
	tiller density (no./100 cm ²)	19.3 ± 1.3 ^a	16.9 ± 3.1 ^a	19.5 ± 1.2 ^a
	mass/tiller (g)	1.3 ± 0.1 ^a	2.1 ± 0.3 ^b	2.0 ± 0.2 ^b
Short-form <i>S. alterniflora</i>	biomass (g/100 cm ²)	10.5 ± 1.1 ^a	13.4 ± 1.3 ^{a,b}	15.1 ± 1.7 ^b
	tiller height (cm)	42.9 ± 1.3 ^a	42.8 ± 1.5 ^a	41.6 ± 1.2 ^a
	tiller density (no./100 cm ²)	27.3 ± 3.2 ^a	33.3 ± 2.6 ^a	34.0 ± 1.8 ^a
	mass/tiller (g)	0.3 ± 0.1 ^{b,c}	0.4 ± 0.1 ^c	0.4 ± 0.1 ^c
<i>S. patens</i>	biomass (g/100 cm ²)	0.2 ± 0.2 ^a	6.4 ± 1.3 ^b	9.5 ± 1.0 ^c
	tiller height (cm)	15.9 ± 1.1 ^a	20.0 ± 0.8 ^b	21.1 ± 0.6 ^b
	tiller density (no./100 cm ²)	6.3 ± 5.9 ^a	135.8 ± 26.5 ^b	275.0 ± 23.9 ^{c,d}
	mass/tiller (g)	0.02 ± 0.001 ^a	0.04 ± 0.003 ^b	0.09 ± 0.001 ^c
<i>Distichlis spicata</i>	biomass (g/100 cm ²)	4.2 ± 0.7 ^a	10.6 ± 1.5 ^b	11.8 ± 0.9 ^b
	tiller height (cm)	19.9 ± 0.6 ^a	22.7 ± 0.6 ^b	23.3 ± 0.4 ^{b,c}
	tiller density (no./100 cm ²)	72.6 ± 12.6 ^a	140.8 ± 21.3 ^b	131.8 ± 9.9 ^b
	mass/tiller (g)	0.06 ± 0.003 ^a	0.07 ± 0.002 ^{a,b}	0.9 ± 0.001 ^{c,d}
<i>Juncus gerardi</i>	biomass (g/100 cm ²)	2.0 ± 1.3 ^a	2.6 ± 0.3 ^a	13.0 ± 1.5 ^b
	tiller height (cm)	16.6 ± 0.8 ^a	18.9 ± 0.9 ^a	31.1 ± 1.0 ^{b,c}
	tiller density (no./100 cm ²)	40.2 ± 4.1 ^a	105.1 ± 11.6 ^b	202.3 ± 8.8 ^d
	mass/tiller (g)	0.04 ± 0.02	0.02 ± 0.02	0.07 ± 0.006

gerardi and *D. spicata* were similar, and both colonized bare space more rapidly than *S. alterniflora*, with *S. patens* the slowest colonizer of the perennials (Table 1).

Variation in physical parameters across the marsh habitat

Substrate redox potential generally increased with distance from the shoreline, with the most dramatic change occurring between the low- and high-marsh habitats (Table 2). In the high marsh, redox increased from the *S. patens* to the *J. gerardi* zone, and redox in *D. spicata* areas in the *S. patens* zone did not differ from that in areas covered by *S. patens* (Table 2). In contrast to redox in *S. alterniflora* and *D. spicata* areas, which decreased with substrate depth, *S. patens* and *J. gerardi* zone redox increased with substrate depth (Table 2).

Substrate salinity generally decreased with distance from the shoreline (Table 2), and was significantly higher in the low marsh than in the high marsh. Substrate salinity generally increased with substrate depth, with the relative difference between 2- and 10-cm depths increasing from the low to the high marsh (Table 2). The relatively high salinity found in the *J. gerardi* zone at 10 cm, below most living plant material, will be discussed elsewhere (M. D. Bertness and E. J. Farnsworth, *personal observation*). Variation in substrate pH

was minimal, with the high-marsh tending to be more acidic than low-marsh substrate (Table 2).

Substrate hardness, a measure of peat density and live root material, increased from tall- to short-form *S. alterniflora*, reached a maximum in the *S. patens* zone, and then declined in the *J. gerardi* zone (Table 2). High substrate hardness in the *S. patens* zone resulted from heavy peat accumulation and the dense superficial root mat of *S. patens*. Organic debris density increased from the tall- to short-form *S. alterniflora*, peaked in the *S. patens* zone, and then fell to a level similar to the low marsh in the *J. gerardi* zone (Table 2). Substrate water content was highest in the tall-form *S. alterniflora*, *S. patens*, and *D. spicata* areas, and lower in the *J. gerardi* and short-form *S. alterniflora* zones (Table 2). Lack of a consistent correlation between tidal height and water content most likely reflected decreased drainage efficiency in the high marsh (Bertness 1985).

Tall-form *S. alterniflora* consistently occurred at tide levels less than mean lower high water (MLHW, +1.0 m) that were flooded daily. The short-form *S. alterniflora* zone occurred between MLHW and the mean high water line (MHW, +1.2 m) and was flooded two-thirds of the days each month. The *S. patens* zone extended from MHW to the mean higher high water line (MHHW, +1.3 m) and was flooded just over half of the days each month, while the *J. gerardi* zone was found above the +1.3 m tidal mark and was flooded only by the extreme spring tides of each month (Table 2).

Transplant experiments

Transplants of the marsh perennials showed that the production of each increased from the low- to high-marsh habitats, with maximum production in each species occurring in the *J. gerardi* zone on the terrestrial border of the marsh (Table 3). The biomass response of each species was the product of variation in tiller density, height, and robustness, but the relative contribution of those variables to overall differences in biomass was not consistent among species (Table 3). Biomass of tall-form *S. alterniflora* increased by $\approx 45\%$ in the short-form *S. alterniflora* and *S. patens* zones, and by nearly 90% in the *J. gerardi* zone, relative to its biomass in its natural habitat. Short-form *S. alterniflora* was not as responsive, but showed a similar pattern (Table 3). *S. patens* biomass was severely reduced when transplanted to the low marsh (98 and 33% reductions in the tall- and short-form *S. alterniflora* zones, respectively), but increased by 37% in the *J. gerardi* zone. *D. spicata* biomass was reduced by 54% in the tall-form *S. alterniflora* zone, but had similar biomass in all other marsh zones (Table 3). *J. gerardi* biomass was reduced by $> 80\%$ in the low marsh, while its production did not vary among high-marsh habitats (Table 3).

Transplantation of *S. alterniflora* seedlings yielded

TABLE 3. Continued.

Marsh zone		ANOVA P
<i>D. spicata</i>	<i>J. gerardi</i>	
38.0 \pm 3.0 ^b	47.1 \pm 2.6 ^c	<.001
70.8 \pm 2.7 ^c	79.6 \pm 2.1 ^a	<.001
16.6 \pm 1.5 ^a	24.7 \pm 1.8 ^b	<.05
2.3 \pm 0.2 ^b	1.9 \pm 0.2 ^b	<.01
11.4 \pm 1.0 ^a	18.4 \pm 0.9 ^c	<.001
31.4 \pm 1.1 ^b	37.4 \pm 1.1 ^b	<.001
47.8 \pm 2.9 ^b	34.9 \pm 3.3 ^a	<.001
0.2 \pm 0.1 ^{b,c}	0.6 \pm 0.1 ^a	<.01
9.2 \pm 0.9 ^c	13.0 \pm 0.8 ^d	<.001
22.1 \pm 0.6 ^b	21.4 \pm 0.6 ^b	<.01
232 \pm 21.9 ^c	311.1 \pm 16.7 ^d	<.001
0.04 \pm 0.003 ^{b,c}	0.04 \pm 0.003 ^{b,c}	<.01
9.1 \pm 1.2 ^b	12.3 \pm 1.8 ^b	<.001
22.3 \pm 0.5 ^b	24.8 \pm 0.7 ^c	<.001
110.6 \pm 15.4 ^b	121.7 \pm 15.7 ^b	<.02
0.08 \pm 0.003 ^{b,c}	0.10 \pm 0.004	<.001
11.5 \pm 0.6 ^b	13.5 \pm 1.5 ^b	<.001
29.2 \pm 0.9 ^b	32.8 \pm 1.0 ^c	<.001
176.4 \pm 4.4 ^c	201.7 \pm 13.3	<.001
0.07 \pm 0.003	0.07 \pm 0.007	>.05

TABLE 4. Results of *Spartina alterniflora* seedling transplant experiments. Emergent *S. alterniflora* seedlings were transplanted from the marsh flat in May 1985 and harvested in September 1985. For each variable measured, significant differences ($P < .05$, Scheffé) between zones are indicated by differing superscript letters. All data are $\bar{X} \pm SE$ of individual seedlings.

Marsh zone	Sample size*	Maximum tiller height (cm)	Number of tillers	Number of rhizomes	Root depth (cm)	Aboveground mass (g)
Tall-form <i>S. alterniflora</i>	15c	44.4 \pm 3.9 ^a	4.6 \pm 0.9 ^a	2.2 \pm 0.4 ^a	7.2 \pm 0.7 ^a	0.73 \pm 0.1 ^a
Tall-form <i>S. alterniflora</i>	15t	34.4 \pm 3.0 ^b	3.8 \pm 0.8 ^a	1.9 \pm 0.3 ^a	4.0 \pm 0.4 ^b	0.35 \pm 0.1 ^b
Short-form <i>S. alterniflora</i>	21t	29.0 \pm 1.1 ^c	9.9 \pm 0.6 ^b	4.2 \pm 0.4 ^b	5.9 \pm 0.3 ^c	0.53 \pm 0.03 ^{a,b}
<i>S. patens</i>	25t	31.5 \pm 1.3 ^c	9.0 \pm 0.8 ^b	4.8 \pm 0.4 ^b	5.3 \pm 0.5 ^c	0.89 \pm 0.1 ^a
<i>Juncus gerardi</i>	17t	36.8 \pm 1.4 ^b	14.2 \pm 1.0 ^c	6.8 \pm 0.4 ^c	10.2 \pm 0.8 ^d	1.58 \pm 0.2 ^c

* c = controls, t = transplants.

results consistent with the general results of the rhizome transplants (Table 4). The number of tillers and rhizomes produced, depth of root penetration, and above- and belowground biomass of seedlings each increased markedly with increasing marsh height. Seedling survivorship was also three times as high in the *J. gerardi* zone (Table 4) as in the tall-form *S. alterniflora* zone (also see Metcalfe et al. 1986).

To facilitate comparing species responses to the marsh gradient, relative yield calculations are presented in Fig. 4. All of the transplants showed increased success with increasing tidal height, and species differences in response to the gradient were also apparent. *S. alterniflora* had the best overall performance across the gradient, with its biomass never falling below 50% (Fig. 4). *S. alterniflora* seedlings, however, were much more sensitive to habitat differences than were adult plants. *D. spicata* also performed fairly well across the gra-

dient, with its biomass falling below 70% only in the tall-form *S. alterniflora* zone. In contrast, *S. patens* and *J. gerardi* biomasses were sharply reduced in the low marsh (Fig. 4). This suggests that *S. alterniflora* has the widest tolerance for physical conditions across the marsh, followed by *D. spicata*, with *S. patens* and *J. gerardi* the least tolerant of variation in physical conditions across the marsh.

Physical disturbance effects on marsh vegetation

In March, <1% of the high marsh was covered with wrack (Fig. 5A). At that time, most of the aboveground *S. alterniflora* production from the previous summer was either dead but still standing, or floating in large entangled mats in the low marsh, and was prevented from being rafted onto the high marsh by the barrier of standing dead *S. alterniflora*. As the spring pro-

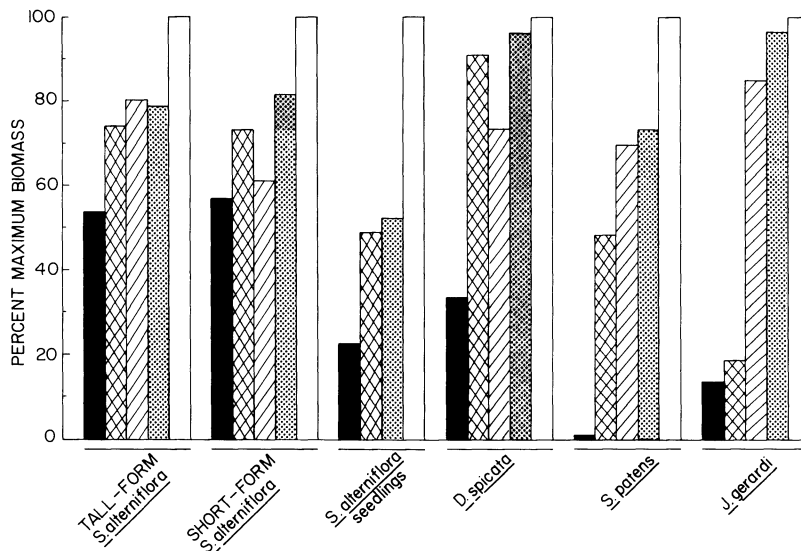


FIG. 4. Relative growth of each of the marsh perennials transplanted to each of the major marsh vegetation zones. Data are the percent mean biomass achieved in each area relative to the maximum biomass recorded for each transplanted species or type. ■ transplants to the tall-form *Spartina alterniflora* zone, ▨ transplants to the short-form *S. alterniflora* zone, ▩ transplants to a *Distichlis spicata* area in the *S. patens* zone, ▪ transplants to the *S. patens* zone, □ transplants to the *Juncus gerardi* zone.

TABLE 4. Continued.

Belowground mass (g)	Total mass	Survivorship	
		%	Total marked
0.35 ± 0.1 ^a	1.08 ± 0.2 ^a	63	62
0.19 ± 0.04 ^a	0.54 ± 0.1 ^b	30	50
0.67 ± 0.06 ^b	1.20 ± 0.1 ^a	80	50
0.39 ± 0.05 ^a	1.28 ± 0.14 ^a	75	75
0.92 ± 0.11 ^c	2.48 ± 0.3 ^c	92	50

gressed, standing dead *S. alterniflora* broke off and the wrack was rafted onto the high marsh by high tides. Wrack abundance on the high marsh peaked in June with 30% cover, and then declined over the remainder of the summer as a result of tidal transport and decay. By December, <1% of the high marsh was covered by wrack. We have observed this temporal pattern of wrack abundance for the last 4 yr (1982–1986). Spatially, wrack was more common at lower levels of the high marsh (Fig. 5B). On the high marsh–low marsh boundary (MHW), 80% of surfaces were covered >2 d over the course of the summer. That compares to 20–44% for the *S. patens* zone (2–14 m above MHW) and only 5–10% for the *J. gerardi* zone (>16 m above MHW). Residence time of wrack on specific locations in the high marsh, however, increased with increasing distance from the shoreline (Fig. 5C). The most commonly observed residence times of wrack across the high marsh were 2 and 4 wk, corresponding to the bimonthly high tide cycle.

Survivorship of the marsh perennials under wrack cover (Fig. 6) revealed interspecific differences ($P < .001$, ANOVA). Survivorship did not differ between *S. patens* and *J. gerardi* ($P > .05$, Scheffé), but *S. alterniflora* and *D. spicata* both survived longer under wrack than either *S. patens* or *J. gerardi* ($P < .001$, Scheffé). All *S. patens* and *J. gerardi* died after being covered for 5 wk, all *S. alterniflora* died by 7 wk, while *D. spicata* persisted under wrack for up to 10 wk.

Covering mixtures of the marsh perennials with wrack for 2- and 4-wk periods in June, to mimic the seasonal timing and modal duration of natural wrack disturbance, reduced the biomass ($P < .001$, ANOVA) and tiller density ($P < .001$, ANOVA) of covered mixtures relative to adjacent controls, and dramatically affected relative species abundance (Fig. 7). Covering *S. alterniflora*–*S. patens* mixtures increased the relative abundance of *S. alterniflora* tillers ($P < .001$, ANOVA) and biomass ($P < .001$, ANOVA) in relation to *S. patens*. In those mixtures, both *S. alterniflora* and *S. patens* tiller densities and biomass were reduced by wrack cover, but the effect was most pronounced on *S. patens* (Fig. 7). In *D. spicata*–*S. patens* mixtures (Fig. 7), wrack

cover increased the relative abundance of *D. spicata* tillers ($P < .001$, ANOVA) and biomass ($P < .001$, ANOVA). Wrack cover significantly reduced ($P < .001$, ANOVA) *S. patens* tiller density and biomass, but did not significantly affect ($P > .05$, ANOVA) *D. spicata* biomass, and significantly increased ($P < .05$, ANOVA) *D. spicata* tiller density by $\approx 70\%$. Similar results

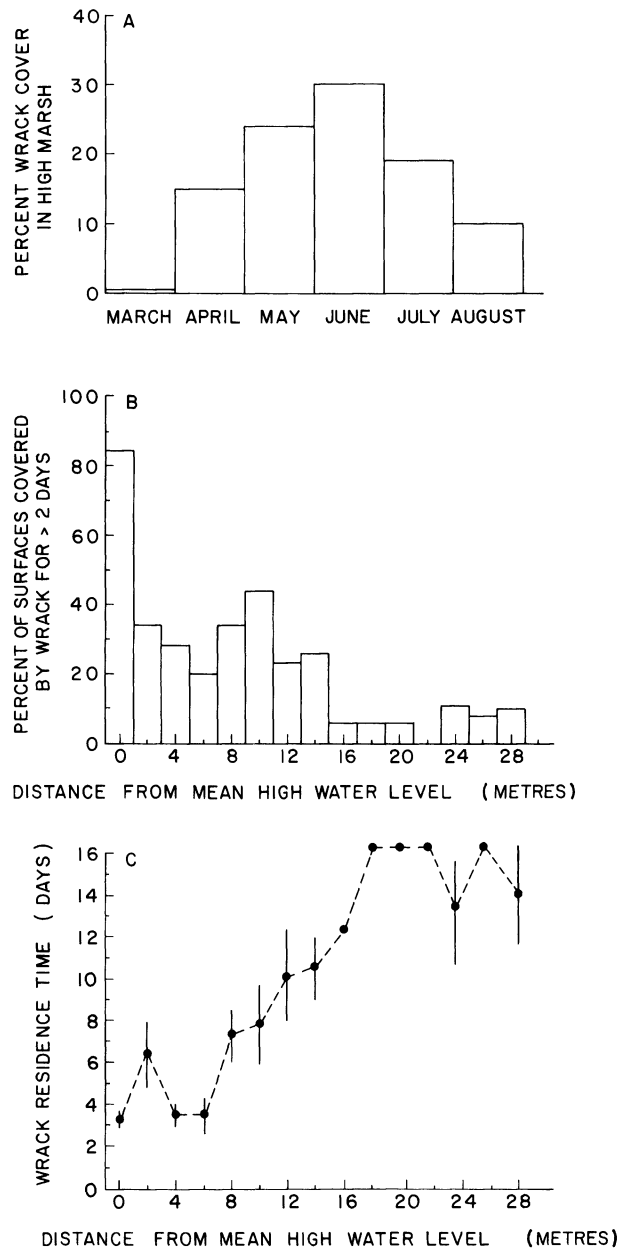


FIG. 5. Spatial and temporal distribution of wrack across the high marsh. (A) Total percent of marked locations ($n = 410$) across the marsh, covered by wrack over time. (B) Percent of marked locations covered by wrack for >2 d as a function of distance from the low marsh (March–August). (C) Residence time ($\bar{X} \pm \text{SE}$) of wrack on marked locations is a function of distance from the low marsh (March–August).

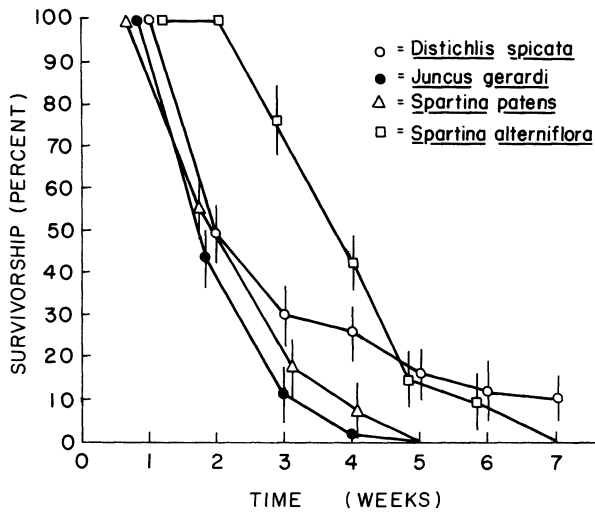


FIG. 6. Survivorship of each of the common marsh perennials under plant debris (wrack) cover. Each point represents the $\bar{X} \pm SE$ of 16 estimates.

were found for *D. spicata*-*J. gerardi* mixtures. Wrack cover significantly increased the relative abundance of *D. spicata* tillers ($P < .001$, ANOVA) and biomass ($P < .001$, ANOVA) in mixtures with *J. gerardi* (Fig. 7). Tiller densities ($P < .001$, ANOVA) and biomass ($P < .001$, ANOVA) of *J. gerardi* were both reduced by wrack cover; *D. spicata* tiller densities significantly increased ($P < .01$, ANOVA), whereas its biomass was not significantly ($P > .05$, ANOVA) affected by wrack cover (Fig. 7).

Bare patch closure and colonization

Closure of marked disturbance-generated bare patches in the *S. patens* and *J. gerardi* zones is given in Fig. 8. All bare patches marked in the *S. patens* zone were colonized completely by perennial vegetation within three growing seasons, while all *J. gerardi* zone patches that were marked closed within 2 yr.

In the *S. patens* zone, *D. spicata* and *Sa. europaea* colonized bare patches rapidly and were more common in patches than in the surrounding vegetation (Fig. 9). *D. spicata* occupied $<8\%$ of available space, with low tiller density (3 tillers/100 cm²) outside of patches. After only 1 yr, however, its cover more than tripled ($P < .001$, ANOVA) and tiller density was nearly 20 times as great ($P < .001$, ANOVA) in the patches (Fig. 9). Essentially all of the *D. spicata* patch invasion resulted from surrounding *D. spicata* sending runners (Fig. 3) into the patches. Two years after patch formation, *D. spicata* cover in patches was $>4\times$ that of the surrounding vegetation, but in the 3rd yr *D. spicata* cover declined by 41% in comparison to the previous year. The drop in *D. spicata* cover and tiller density (Fig. 9) coincided with *S. patens* reinvading the patches. *Sa. europaea* cover in undisturbed vegetation surrounding the *S. patens* zone patches was only 1% with

<1 tiller/100 cm². One year after patch birth *Sa. europaea* cover in patches was >35 times as great ($P < .001$, ANOVA) and individual density increased to >30 ($P < .001$, ANOVA) times that of the surrounding vegetation (Fig. 9). Two years after patch birth, *Sa. europaea* cover increased slightly ($\approx 20\%$) over the 1st yr, but its density more than doubled as a result of localized seed set (Fig. 9; Ellison 1987). Three years after patch birth, as *S. patens* reinvaded, *Sa. europaea* density in the patches remained high, but cover declined markedly (Fig. 9). *S. alterniflora* was entirely absent in the vegetation surrounding the patches, and none of the patches were <5 m from stands of *S. alterniflora*. Two years after patch birth, however, *S. alterniflora* covered $\approx 6\%$ of patch areas with tiller densities of 4.8 ± 0.2 tillers/100 cm². Three years after patch birth, *S. alterniflora* cover in patches remained $\approx 6\%$, but tiller density dropped by a factor of 4 (1.2 ± 0.2 tillers/100 cm²). *S. alterniflora* recruited to the patches as seedlings, from seeds transported from the low marsh by tides (M. D. Bertness and A. M. Ellison,

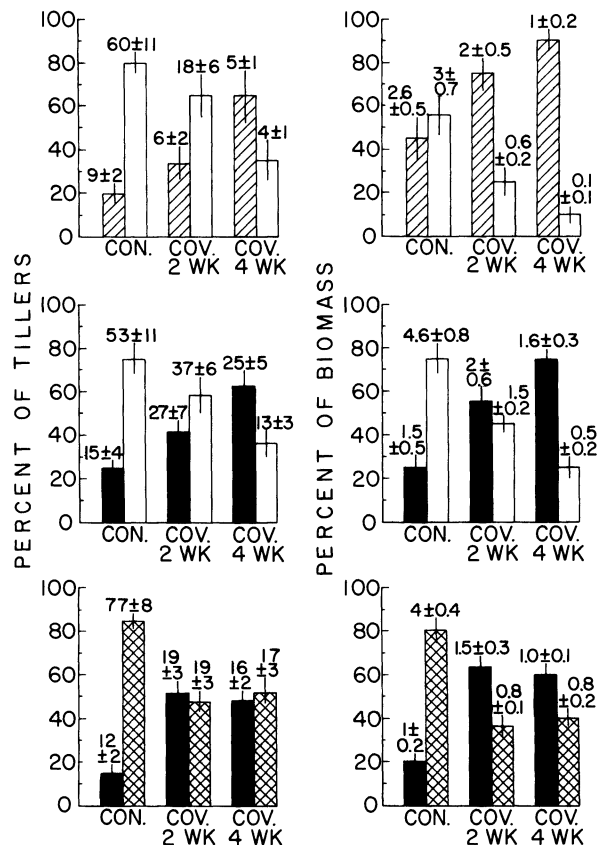


FIG. 7. Relative abundance of marsh perennials in mixtures after short-term wrack cover. Top panels present \square *Spartina patens*- hatched *S. alterniflora* mixtures, middle panels \square *S. patens*- \blacksquare *Distichlis spicata* mixtures, and bottom panels hatched *Juncus gerardi*- \blacksquare *D. spicata* mixtures. Error bars are standard errors of the percentages. Means ($\pm SE$) of tiller number and biomass (in grams) are given above the bars. All data are for 100-cm² areas. CON = control; COV = covered.

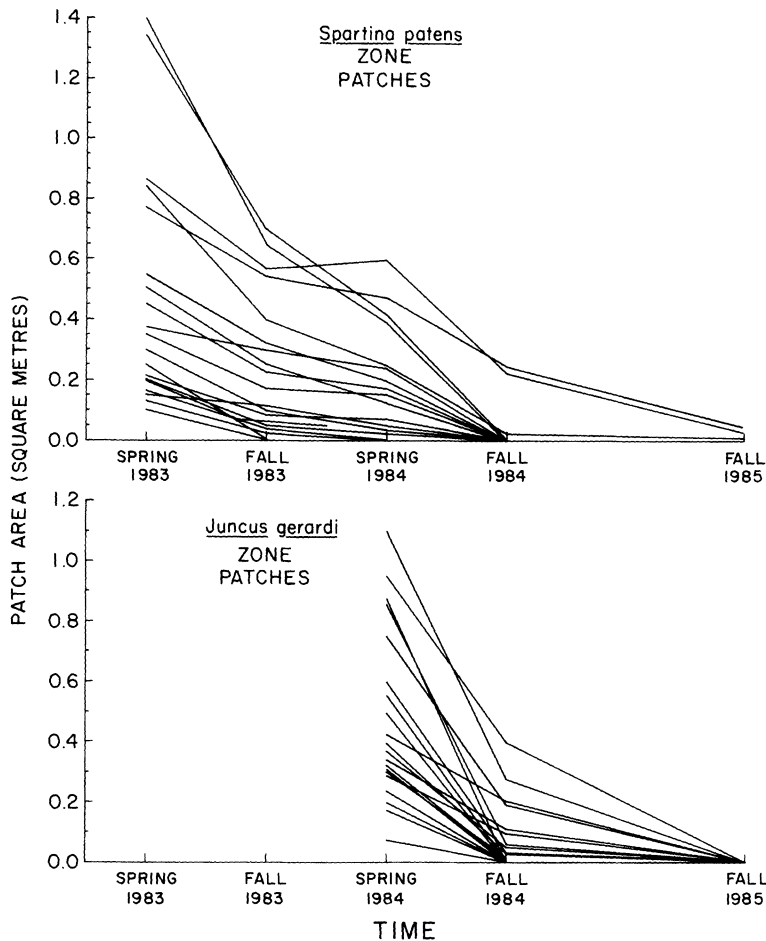


FIG. 8. Closure of disturbance-generated bare patches in the *Spartina patens* and *Juncus gerardi* zones. Patch area was defined as area without live vegetation.

personal observation). *S. patens* reinvaded patches in the *S. patens* zone slowly, primarily as dense fronts of rhizomes and tillers (Fig. 3) on the perimeters of the patches. Less than 0.1% of the *S. patens* tillers invading the patches were produced by seedlings. Three years after patch formation, *S. patens* cover in the patches was >90%, but tiller density was <50% of that found in the surrounding vegetation.

Similar results were found in patches in the *J. gerardi* zone (Fig. 9). *D. spicata* cover and tiller density both were >3 times as great in patches, in comparison to surrounding vegetation ($P < .001$, ANOVA, both cases), after 1 yr. *Sa. europaea* cover and density also increased by over an order of magnitude in patches compared to ambient vegetation ($P < .001$, ANOVA, both cases). *S. alterniflora* was also found in the *J. gerardi* zone patches, but not in the surrounding vegetation. After 2 yr, *S. alterniflora* covered $\approx 1\%$ of patch surfaces with a tiller density of 0.3 ± 0.3 tillers/100 cm². Recruitment of these species into the *J. gerardi* zone patches was identical to that found in the *S. patens* zone: *D. spicata* invaded patches vegetatively with run-

ners, while *Sa. europaea* and *S. alterniflora* recruited via seeds. *J. gerardi* reinvaded patches slowly in relation to its abundance in the surrounding vegetation (Fig. 9). Two years after patch birth, *J. gerardi* cover in the patches was $\approx 60\%$, with tiller densities one-third of those adjacent to the patches. *J. gerardi* invaded the patches vegetatively with dense fronts of rhizomes and associated tillers (Fig. 3) and with seedlings (Table 1). During the 1st yr, 35% of the invading *J. gerardi* tillers were produced by seedling recruits. By the 2nd yr, tillers resulting from seedling and vegetative recruitment could no longer be differentiated.

DISCUSSION

Plant zonation at our study site is similar to that described for other New England marshes (Miller and Eglar 1950, Ayers 1959, Redfield 1972, Nixon 1982). Emergent perennial halophytic vegetation covers >95% of available space in dense monospecific turfs of rhizomes and tillers, with striking zonation and segregation of plant species across the habitat. *Spartina alterniflora* exclusively dominates the low-marsh habitat

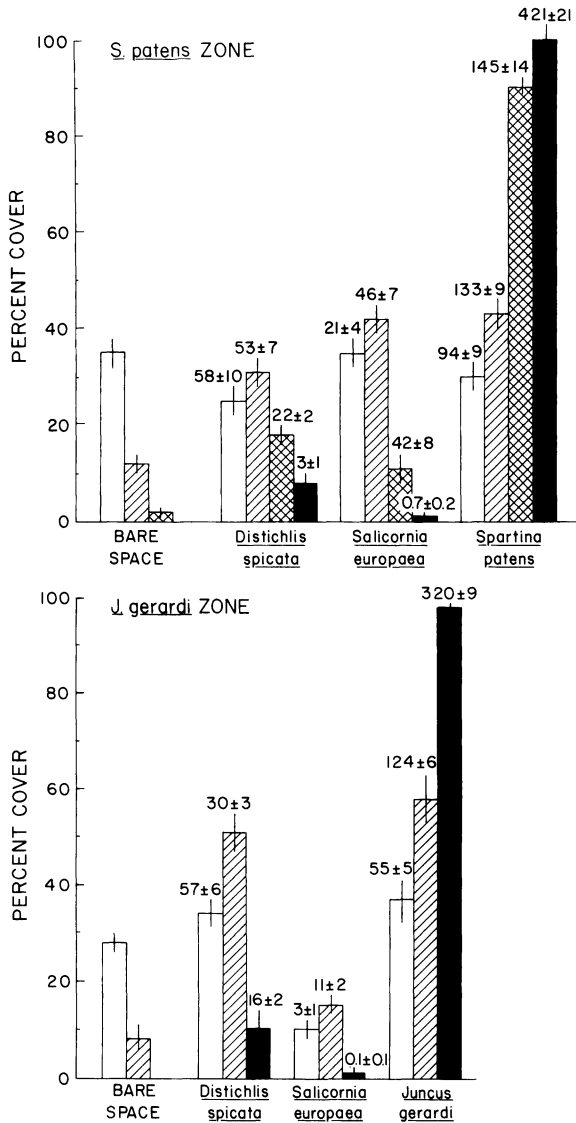


FIG. 9. Disturbance-generated bare patch plant invasion data for bare patches in the *Spartina patens* and *Juncus gerardi* zones (also see Fig. 8). Data are from □ one-year-old, ▨ two-year-old, and ▩ three-year-old patches and ■ areas immediately adjacent to the patches. Error bars are standard errors; no. tillers/100 cm² ($\bar{X} \pm SE$) is given over the bars.

regularly flooded by tides. Immediately above that zone *Spartina patens* dominates the vegetation on the seaward border of the high marsh, while *Juncus gerardi* dominates the terrestrial border of the high marsh. Superimposed on this high marsh zonation, *Distichlis spicata* and *Salicornia europaea* are common in ephemeral patches generated by predictable physical disturbance. With the exception of these patches, the dominant perennials (*S. alterniflora*, *S. patens*, and *J. gerardi*) monopolize most space in their respective zones in dense monocultures that generally do not intermingle. Dense monocultures of each of the dominant pe-

rennials reduce light penetration to the substrate by >90%, which limits seedling success (Metcalfe et al. 1986, Ellison 1987). Each of the marsh perennials primarily colonizes available bare space vegetatively, rather than with seedlings (Table 1). This is especially the case for *S. patens* and *D. spicata*, whose seed production is dramatically reduced by grasshoppers (*Conocephalus spartinae*) feeding on flowers and seeds (Bertness et al. 1986). *S. alterniflora* and *J. gerardi* are not as heavily attacked by consumers, and their seedlings are more common (Table 1; Bertness et al. 1986). *S. alterniflora* seedlings only contribute to the patch colonization of relatively large (> 1 m²) patches (Metcalfe et al. 1986), while *J. gerardi* seedlings appear to contribute to the ability of *J. gerardi* to colonize patches of much smaller size (Table 1). *Sa. europaea*, the solitary annual, relies entirely on seeds to persist, and its seed set is not affected markedly by predators (Ellison 1987). With the exception of *Sa. europaea* and *S. alterniflora* seeds, which disperse commonly in association with floating wrack (Ellison 1987), seed dispersal in these marsh plants is very localized, and marsh sediments do not appear to retain a persistent seed bank (Ellison 1987).

Physical factors and the distribution of the marsh perennials

Most variation in physical factors across the marsh appeared to be due to elevational differences in tidal flooding. Substrate redox generally increased and substrate salinity generally decreased with increasing tidal height and decreased tidal flooding (Table 2). Low substrate redox is characteristic of flooded soils (Ponnamperuna 1972) and has been shown to inhibit plant growth (Howes et al. 1981, Mendelssohn 1981). The growth-inhibiting effect of saline soils is also well known (Linthurst 1980). Tidal flooding most likely influences many other important edaphic factors (Ponnamperuna 1972, Chalmers 1982).

The major vegetation zones of the marsh corresponded well with major differences in flooding frequency across the habitat (Table 2; see Nixon 1982 for discussion). *S. alterniflora* dominated habitats flooded by all but the weakest neap tides, *J. gerardi* dominated habitats flooded by only the highest spring tides, and *S. patens* dominated habitats between those extremes. This tight correspondence between flooding frequency and vegetation zones has been commonly interpreted to reflect differential adaptation of marsh plants to the physical conditions in specific marsh zones (Cooper 1982, Armstrong et al. 1985).

Transplantation of the marsh perennials across the marsh habitat, however, indicated that the performance of each was lowest in the low marsh and highest on the terrestrial border of the marsh, suggesting that they were all adversely affected by tidal flooding (Table 3). This lack of correspondence between plant performance on the marsh tidal gradient and their natural

distribution on the gradient suggests that factors other than environmental variables are important determinants of plant distributions in this salt marsh plant community. Other disparities between the physiological tolerances of marsh plants and their distributions on physical gradients have been reported (Barbour 1978, Snow and Vince 1984, Wilson and Keddy 1985).

A cautionary note, however, needs to be made regarding the results of the transplant experiments reported in this paper (Table 3, Fig. 4). Recently, we have replicated the rhizome transplant experiments reported here with the intention of following them over a number of growing seasons. After 1 yr, this work has yielded results consistent with those presented in this paper for *S. patens*, *J. gerardi*, and *D. spicata*, but not for *S. alterniflora*. Replication of the rhizome transplant experiment with *S. alterniflora* indicated that it performs equally well across the entire marsh and is not adversely affected by tidal submergence in the low-marsh habitat as suggested by the results reported in this paper (Table 3, Fig. 4). Replication of the *S. alterniflora* seedling transplant experiment in 1986, however, showed the same strong pattern of increasing seedling growth with increasing marsh elevation as reported here (Table 4; M. D. Bertness and A. M. Ellison, *personal observations*). The cause of these disparities in our work with *S. alterniflora* are currently being examined and will be presented elsewhere. A conservative interpretation of the available data, however, strongly suggests that *S. alterniflora* is capable of vigorous growth across the entire marsh in the absence of other marsh perennials, which stands in marked contrast to its almost complete restriction to low-marsh habitats in nature (Fig. 1; Nixon 1982).

Physical disturbance effects on the distribution of marsh plants

Physical disturbance appears to play a major role in generating pattern in this marsh community. Most disturbance in this and other New England salt-marsh communities results when floating plant debris, consisting mostly of dead *S. alterniflora* stems, is rafted to the high marsh and stays stationary long enough to cause mortality of underlying vegetation. Seasonal production and tidal transport of this wrack result in predictable temporal and spatial patterns in this disturbance (Fig. 5), which may be important determinants of the influence of wrack on marsh vegetation (Reidenbaugh and Banta 1980, Hartman et al. 1983). Since most wrack present at any given time is the product of *S. alterniflora* production during the previous growing season, and decomposes and is transported off the marsh over time, wrack disturbance is most severe in the spring and early summer and then decreases (Fig. 5A). Plants growing early in the spring and summer may therefore be more affected by the disturbance than plants emerging later in the summer. Wrack disturbance is also heavier at lower levels of the marsh than

on the terrestrial border of the marsh. Frequency of wrack disturbance was 3–4 times greater in the *S. patens* zone than in the *J. gerardi* zone. Lower marsh levels, consequently, appear to be more strongly influenced by disturbance than higher marsh levels.

Marsh perennials differed markedly in ability to withstand periods of wrack burial (Fig. 6). *S. patens* and *J. gerardi* were more susceptible to wrack mortality than were *S. alterniflora* or *D. spicata*. The dichotomy found between the resistance of perennials within phalanx growth morphology (*S. patens* and *J. gerardi*) and those with a guerilla growth morphology (*S. alterniflora* and *D. spicata*) may be indicative of greater physiological integration within genets of guerilla form plants relative to plants with a phalanx growth morphology.

Because of differential mortality of the perennials under wrack, short-term wrack cover affected the species composition of mixed stands of marsh perennials. In the three mixtures examined (Fig. 7), disturbance-resistant species with guerilla growth morphologies were favored over phalanx growth forms when covered by wrack for 2- and 4-wk periods. In *S. patens*–*S. alterniflora* mixes, wrack cover reduced the tiller density and biomass of both species, but the effects were greater on *S. patens*, resulting in a decrease in its relative abundance. Short-term wrack disturbance of *D. spicata*–*S. patens* and *D. spicata*–*J. gerardi* mixes, however, showed that while *S. patens* and *J. gerardi* biomass and tiller densities were reduced when covered, *D. spicata* tiller densities increased and its biomass was not affected by wrack cover. The data suggest that by causing heavy mortality of *S. patens* and *J. gerardi*, wrack cover may increase *D. spicata* performance. This interpretation is supported by results of reciprocal species-removal experiments in *S. patens*–*D. spicata* and *J. gerardi*–*D. spicata* mixes, where removal of *S. patens* and *J. gerardi* resulted in minimal increases in *D. spicata* aboveground biomass, but dramatic increases in *D. spicata* tiller densities and belowground biomass (M. D. Bertness and E. J. Farnsworth, *personal observation*). By differentially causing high mortality of the high-marsh dominants (Fig. 6), short-term disturbance may benefit *D. spicata* by reducing interspecific competition.

The most conspicuous effects of wrack disturbance, however, occur when wrack covers vegetation long enough to kill all underlying vegetation, leaving a discrete bare patch (Reidenbaugh and Banta 1980). Bare patches can result from wrack cover lasting only 8 wk, but more commonly are the result of wrack covering an area for an entire growing season (M. D. Bertness and A. M. Ellison, *personal observation*). Patches resulting from being covered for less than a complete growing season are often sparsely covered with surviving plants or have halos of vegetation revealing partial mortality. The recolonization of such patches is strongly influenced by differential mortality. *D. spicata*

generally dominates the surviving vegetation in and around the patches, and they are rapidly invaded the following year by runners of the surviving *D. spicata*. In our examination of bare patches, we followed only discrete patches that had no surviving vegetation to allow examination of patch invasion independent of the effects of differential mortality in patch birth.

Bare patches closed rapidly, and even the largest patches marked closed completely within 3 yr (Fig. 8). Patches appeared to close more rapidly in the *J. gerardi* zone than in the *S. patens* zone because of the contribution of *J. gerardi* seedlings to patch closure (Table 1) and higher *D. spicata* densities around *J. gerardi* zone patches (Fig. 9). Patches were disproportionately invaded by *Sa. europaea* and *D. spicata*, relative to their abundance in the surrounding vegetation (Fig. 9). *Sa. europaea* colonized patches as seedlings. *Sa. europaea* seeds have hooked hairs on their seed coats, which adhere to wrack, resulting in wrack transport dispersing *Sa. europaea* seeds (Ellison 1987). The disturbance that generates suitable *Sa. europaea* habitats, then, also seeds new bare patches with *Sa. europaea*. Since *Sa. europaea* was rare in vegetation surrounding patches (Fig. 9) and its seeds do not persist >1 yr in the seed bank (Ellison 1987), wrack dispersal most likely was responsible for the rapid arrival of *Sa. europaea* in the patches. Heavier recruitment into *S. patens* zone patches, which are covered frequently by wrack (Figs. 5, 9), supports that suggestion.

D. spicata invasion into patches was almost entirely vegetative (Fig. 9) by means of long adventitious runners (Fig. 3). *D. spicata* tiller densities increased by as much as 20 times in yearling patches in contrast to the surrounding vegetation. *S. alterniflora* recruited to patches even though it was totally absent in the surrounding vegetation. *S. alterniflora* in the patches originated from seeds, most likely transported by wrack containing flower heads (M. D. Bertness and A. M. Ellison, *personal observation*).

The numerically dominant plants in the *S. patens* and *J. gerardi* zones invaded patches slowly relative to their ambient abundance (Fig. 9). Vegetatively, each invaded patches with dense mats of rhizomes and associated tillers (Fig. 3) characteristic of plants with phalanx growth morphologies. *S. patens* invasion was almost entirely (>99%) vegetative, whereas 35% of *J. gerardi* patch invasion was via seedlings. In *S. patens* zone patches, which we followed for 3 yr until *S. patens* covered >90% of initial patch areas, recolonization of *S. patens* coincided with decreased success of *Sa. europaea*, *D. spicata*, and *S. alterniflora* in the patches.

Interspecific competition and the spatial structure of the marsh plant community

While this work has not examined the importance of interspecific competition experimentally, it provides strong inferential evidence that competition is a major determinant of pattern in this salt marsh plant com-

munity, and points to plant growth form as a major determinant of plant competitive dominance. The contention that interspecific competition is an important organizing force in this community is supported by: (1) transplant studies, which suggest that all plant species in the community are adversely affected by tidal submergence; (2) the distribution and rapid recruitment of rare high-marsh plants in areas lacking numerically dominant high-marsh plants; and (3) the rapid closure of disturbance-generated bare patches and relative rarity of early colonists in undisturbed vegetation.

S. alterniflora is found almost exclusively in the low-marsh habitat regularly flooded by tides, but transplants reveal that it grows well across the entire marsh (Table 3). The *S. alterniflora* and *S. patens* zones interface abruptly on a discrete boundary demarcating MHW (Nixon 1982). *S. patens* transplanted below the interface is severely stunted (Table 3) and appears to be intolerant of flooding (Gleason 1980). *S. patens* is almost never found in the low marsh dominated by *S. alterniflora* (Nixon 1982), while *S. alterniflora* is a frequent occupant of disturbance-generated patches in the high marsh (Fig. 1). We suggest that *S. alterniflora* is largely precluded from the high marsh by the dense superficial rhizome and root mat of *S. patens*, which precludes both successful penetration of rhizomes and seedling establishment. Thus, we suggest that *S. alterniflora* is restricted to the low marsh, not because it is the only habitat where it can thrive, but because the low marsh offers it a spatial refuge from competitively superior high-marsh plants. We further suggest that the competitive subordination of *S. alterniflora* is a by-product of its guerrilla growth morphology being competitively inferior to the phalanx growth forms found in the high marsh. Experimental studies in progress support this interpretation (M. D. Bertness, *personal observation*).

The mechanism of the discrete zonation of *S. patens* and *J. gerardi* in the high marsh is less clear. Both have phalanx growth morphologies and show the most vigorous growth on the terrestrial border of the marsh dominated by *J. gerardi*. Two potential explanations may be responsible for *J. gerardi* domination of the highest reaches of New England salt marshes, both based on differences in the growing season of those species. *J. gerardi* growth begins in early March, 2 mo earlier than other marsh perennials, and continues through July, while *S. patens* growth begins in May and continues into September (Bertness et al. 1986). Earlier emergence may give *J. gerardi* a competitive advantage in monopolizing both above- and belowground space, which in combination with its high seed output may lead to *J. gerardi* dominating the terrestrial edge of the marsh. That, however, does not explain the absence of *J. gerardi* in the *S. patens* zone, where it does well when transplanted (Fig. 4). We hypothesize that *J. gerardi* is prevented from invading the *S. patens* zone because its earlier growing season

coincides with heavy wrack disturbance in the *S. patens* zone (Fig. 4).

D. spicata is found primarily associated with disturbed areas in the high marsh. It is the most resistant perennial to mortality under wrack (Fig. 6) and rapidly invades bare areas vegetatively even when extremely rare (Fig. 9). We suggest that *D. spicata* is best described as a disturbance-dependent species whose success is a product of its ability to tolerate and recover from disturbance in marsh habitats. The apparent inability of *D. spicata* to persist in colonized bare areas appears to reflect that its guerrilla growth morphology (Fig. 3) is competitively inferior to the high-marsh phalanx growth forms. Its wider tolerance of physical conditions across the marsh than the other high-marsh plants (Fig. 4), however, may also result in its dominating certain physically marginal high-marsh habitats, such as waterlogged soils (Miller and Egler 1950).

Like *D. spicata*, *Sa. europaea* appears to be disturbance-dependent in this community. It is found almost exclusively in disturbance-generated bare areas, and colonizes by seeds that are often dispersed by the wrack, which provides suitable habitat. Ellison (1987) has shown experimentally that *Sa. europaea* is competitively subordinate to each of the marsh perennials and that patch populations are rapidly displaced by the vegetative invasion of perennials.

We hypothesize that interspecific competition is a major determinant of the typical zonation pattern of New England salt marsh plant communities and that competitive dominance among these marsh plants is dictated by differences in plant morphology. Among the marsh perennials, species that invade and occupy space as dense mats of rhizomes and tillers, or species with a phalanx morphology (Lovett Doust 1981) appear competitively superior to species that invade and occupy space with adventitious rhizomes and fewer tillers, or species with a guerilla morphology (Lovett Doust 1981). Species with guerilla morphologies, however, more rapidly colonize suitable habitats vegetatively. The importance of growth form in mediating patterns of space utilization and competitive interactions in plant communities is just beginning to be appreciated (e.g., Lovett Doust 1981, Turkington and Harper 1981, Armstrong 1982, Bell 1984, Schmid and Harper 1985), even though it was suggested early in this century as a driving force in the organization of prairie communities (Clements et al. 1926). In sessile marine invertebrates, clonal morphology has been shown to be important in understanding patterns of space utilization and competitive interactions as well as the structure of marine communities (Buss 1979, Jackson 1979, Hughes and Jackson 1985). Our results also support the notion that, among plants of similar size, clonal plants are competitively superior to solitary plants, as has been shown for marine invertebrates (Jackson 1977). We suggest that the competitive dominance of phalanx morphology plants over guerilla

morphology plants, and clonal plants over solitary plants, may be a general organizing feature of many plant communities.

Competitive dominance among the marsh plants we have examined appears to result in competitively superior plants dominating favorable habitats, displacing subordinates to less desirable habitats that may serve as spatial or temporal refuges. Wilson and Keddy (1986) and Snow and Vince (1984) have made similar suggestions for lake shore and Alaskan salt marsh plant communities, respectively. While verification of this scenario of the spatial patterning of marsh communities will require experimental testing, our results suggest that it is as realistic a working hypothesis as the prevailing opinion that edaphic rather than biotic factors are the principal determinants of the zonation of salt marsh plant communities (Cooper 1982).

Spatial pattern generation in salt marsh plant communities

Our results suggest that the stereotyped patterning of New England salt marsh plant communities represents an interactive product of physical constraints on plant success, predation pressure, physical disturbance, and interspecific competition. A steep gradient in physical factors across the habitat (Table 2) generates a parallel gradient in potential plant success (Fig. 4). Consumers dramatically reduce the seed set of some plants in the community, minimizing the importance of seedlings in overall community dynamics (Bertness et al. 1986). Temporally and spatially predictable disturbances provide refuges for disturbance-resistant and rapidly colonizing species, while competitive interactions appear to result in species replacements based on morphological differences among the component species. Evaluation of the relative importance and interaction of all those factors is needed for a complete understanding of the spatial patterning of marsh plant communities.

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