EFFECTS OF COMPETITION, DISTURBANCE, AND HERBIVORY ON *SALICORNIA EUROPAEA*[1]

Aaron M. Ellison[2]
*Graduate Program in Ecology and Evolutionary Biology, Brown University, Box G,
Providence, Rhode Island 02192 USA*

Abstract. The effects of interspecific competition, physical disturbance, and insect herbivory on the distribution and abundance of *Salicornia europaea* in a New England salt marsh were studied using manipulative field experiments.

In New England salt marsh plant communities, *S. europaea* is restricted to disturbance-generated patches. *S. europaea* was unable to colonize successfully low-marsh habitats that were flooded daily by tides, because seedlings germinating in these areas could not anchor in soft substrate and were easily uprooted. In high-marsh habitats, *S. europaea* seeds reliably colonized recently created patches because the seed's hairy coat bound to the plant debris that created the patches. *S. europaea* was successful in naturally occurring and artificially maintained patches. However, it was rapidly outcompeted for light by perennials in undisturbed areas and eventually was overgrown by perennials growing into the patches. When the perennial canopy was removed, *S. europaea* increased in biomass and fecundity relative to conspecifics that were beneath the perennial canopy. *S. europaea*, however, was attacked by insect herbivores more frequently in patches than beneath the perennial canopy and this herbivore pressure reduced survivorship in patches to approximately the same level as beneath the perennial canopy.

Interactions among physical disturbance, seed dispersal patterns, interspecific competition, and herbivory appear to be major factors controlling patterns of distribution and abundance of *Salicornia* in New England salt marsh plant communities.

Key words: competition; disturbance; germination; glasswort; halophytes; herbivory; Salicornia europaea; *salt marsh; seed dispersal.*

INTRODUCTION

Studies in rocky intertidal (e.g., Paine and Levin 1981) and subtidal (Sebens 1985) marine communities have demonstrated that disturbance, competition, and predation are tightly coupled processes responsible for maintaining community pattern in these habitats, but similar investigations into the interactions among physical disturbance, competition, and herbivory have not been done in native terrestrial plant communities. Salt marsh plant communities are ideal for such a study because only a few species grow in each well-defined area of marsh habitats. In striking contrast to the extensive investigations into the effects of environmental and edaphic factors on marsh plant success (e.g., Jefferies and Rudmik 1984), surprisingly little is known about how the plant species within salt marshes interact with each other. Experimental studies of the mechanisms of marshland colonization and the population dynamics of marsh plant species are needed to develop a clear understanding of the forces responsible for structuring and maintaining marsh plant communities.

In this report, I document the effects of competition, physical disturbance, and herbivory on the distribution and abundance of the annual glasswort *Salicornia eu-*

ropaea L. (Chenopodiaceae) in a Rhode Island salt marsh. I document the extent of morphological variation among *S. europaea* individuals, present the results of experimental studies quantifying long- and short-range seed dispersal, the effects of interspecific competition with each of the other common plant species in the marsh, and investigate the impact of herbivory on *S. europaea* growth and reproduction.

STUDY SPECIES

Salicornia europaea is a succulent, annual, halophytic plant that grows as a series of cylindrical internodes with regular branching (de Fraine 1912, Anderson 1974). The plant lacks leaves; the internodes consist of a photosynthetic outer cortex surrounding a central pith. Basal internodes often shed their fleshy cortex and/or undergo secondary thickening and lignification (G. Berlyn, *personal communication*). At the end of the growing season, each green internode produces six flowers in two cymules of three each and each flower sets one seed. Within a cymule, the median flower produces a large ovoid seed (mean seed length 1.8 mm: Ungar 1979) and the two lateral flowers each set one small seed (mean seed length 1.1 mm: Ungar 1979). Large seeds show little dormancy and germinate more rapidly than small seeds, which exhibit prolonged dormancy (Ungar 1982, Philipupillai and Ungar 1984).

Few animals eat *S. europaea* in southern New En-

gland. The beetle *Erynephala maritima* Lac. (Chrysomelidae; taxonomy follows Blake [1936]) occasionally is found grazing on young internodes of *S. europaea* (Valiela et al. 1985), and larvae of the case-bearing moths *Coleophora caespititiella* Zeller and *C. cratipennela* Clemens (Coleophoridae; taxonomy follows Forbes [1923]) consume some of the seeds prior to dispersal.

Annual species of *Salicornia* are common in salt marshes and salt pans throughout the world. In Europe, where this genus has been studied most extensively, it is the first colonizer of open tidal flats and often forms extensive monocultures (Wiehe 1935, Brereton 1971, Joenje 1978). In the United States, annual *Salicornia* species often dominate the lower, highly saline regions of inland salt pans (Ungar et al. 1979, McGraw and Ungar 1981, Riehl and Ungar 1982), but on North American coastal marshes the two annual species of *Salicornia*, *S. europaea* and *S. bigelovii*, primarily are confined to and are the first colonizers of disturbance-generated patches high in the marsh (Steiner 1935, Chapman 1940, Neuenschwander et al. 1979, Hartman et al. 1983; taxonomy of all plants discussed follows Gleason and Cronquist [1963]). These patches are created when spring tides wash wrack, consisting of dead stems of *Spartina alterniflora* (Gramineae) and/or *Zostera marina* L. (Najadaceae), up onto the marsh, and the wrack kills the vegetation below it. When the wrack decomposes, a patch of bare ground remains (Neuenschwander et al. 1979, Reidenbaugh and Banta 1980, Hartman et al. 1983).

STUDY SITE

These studies were conducted from May 1983 through October 1985 at Rumstick Cove, a protected embayment of Smith Cove, in Barrington, Bristol County, Rhode Island, USA (Bertness 1984). Like other New England intertidal salt marshes, Rumstick Cove is dominated by four perennial species, each of which occurs in distinct zones of the marsh delineated by tidal height. The low marsh, from +0.1 to +1.2 m mean tidal height, is flooded twice daily by high tides and is a virtual monoculture of *Spartina alterniflora*. Tall-form *Sp. alterniflora* (Valiela et al. 1978) forms an ≈5 m wide band from +0.1 to +1.0 m mean tidal height (the tall *Sp. alterniflora* zone), and short-form *Sp. alterniflora* (Valiela et al. 1978) forms an ≈3 m wide band from +1.0 to +1.2 m mean tidal height (the short *Sp. alterniflora* zone) (Bertness 1984). The high marsh, flooded only by spring tides and during storms, is dominated by the grass *Spartina patens* Muhl. from +1.2 to +1.4 m mean tidal height (the *Sp. patens* zone), and by the rush *Juncus gerardi* Loisel. above +1.4 m mean tidal height (the *Juncus* zone). The grass *Distichlis spicata* (L.) Greene is found at low density scattered throughout the high marsh, often in small monocultures. The high marsh ends abruptly at the higher high water line, where woody vegetation begins to dominate. Throughout the paper, all species will be referred to generically with the exception of the two *Spartina* species, which will be referred to specifically.

METHODS

Distribution

To determine the distribution of *Salicornia* at Rumstick Cove, in May 1983 I surveyed 50-m transects, parallel to the water at 5-m intervals, from the marsh edge to the highest reaches of the marsh (a total of nine transects). Every 5 m along each transect, I counted the total number of *Salicornia* individuals in a 50 × 50 cm quadrat. The quadrat was subdivided with string into 100 subquadrats, 5 × 5 cm, and the percent cover of the grasses, rushes, and bare space in each quadrat was determined by counting the number of subquadrats in which each occurred. Since only three large disturbance-generated patches were encountered in the transects, I located three additional large patches in the high marsh (two ≈1 m² and one 15 m²) dominated by *Salicornia*. In size and location, these patches were representative of disturbance-generated patches found throughout Rumstick Cove (Bertness and Ellison 1987). In each of these large patches, I censused all the vegetation. To assess the change in vegetation pattern over time within these patches, I laid out 25 × 25 cm square quadrats edge to edge so that each patch was entirely covered by quadrats, and marked them with small plastic flags. I counted all the *Salicornia* and estimated the percent cover of perennial plants in each quadrat (as described above) within each large patch in May 1983, when the quadrats were first laid out, and every September thereafter through 1985.

Morphological variation

To examine morphological variation of *Salicornia* throughout the marsh, monthly during the 1984 growing season (May–August), I randomly sampled 15 *Salicornia* individuals from each of eight types of areas: beneath the canopies of tall- and short-form *Sp. alterniflora,* in patches in both the tall and short *Sp. alterniflora* zones, beneath the canopies of the three dominant high-marsh perennials, and in patches in the high marsh. I excavated each *Salicornia* that was sampled with roots intact, and measured the shoot height (ground level to top of crown), shoot basal diameter (above the hypocotyl), and tap root depth of each plant, and estimated the maximal lateral spread of its fine rootlets. I also counted the total number of branches (including secondary and tertiary branches, and so on), and counted the total number of fertile, sterile, and insect-damaged internodes on each plant. After measurement, plants were individually dried (95°C for 48 h) and weighed (±0.001 g).

Seed dispersal and germination

To determine the extent of seed dispersal within patches, I located five large patches (>4 × 4 m) in the

TABLE 1. Natural variation of morphological characters ($\bar{X} \pm 1$ SE) of *Salicornia* plants found beneath the canopies of the perennial marsh species and in bare patches in the marsh. Fifteen *Salicornia* plants were harvested from each type of area on 15 August 1984.*

Character†	Beneath canopy of:‡			
	short *Spartina alterniflora*	*Spartina patens*	*Distichlis*	*Juncus*
Biomass (mg)	1110 ± 138[a]	100 ± 19[a]	110 ± 2[a]	250 ± 54[a]
Height (mm)	170 ± 18[a]	260 ± 13[b, c]	230 ± 17[b]	290 ± 19[b, c]
Stem diam. (mm)	2.4 ± 0.16[a]	0.7 ± 0.08[a]	0.6 ± 0.08[a]	0.9 ± 0.13[a]
No. branches	34 ± 4.4[a]	3 ± 1.1[a]	5 ± 1.0[a]	19 ± 5.1[a]
Root depth (mm)	25 ± 2.9[a]	13 ± 1.5[a]	12 ± 1.7[a]	12 ± 1.5[a]
Root spread (mm)	38 ± 8.7[a]	6 ± 1.2[b]	9 ± 1.4[b]	19 ± 4.5[b]
No. seeds produced	1740 ± 181.8[a]	197 ± 40.2[a]	222 ± 30.8[a]	740 ± 137.8[a]

* Biomass data were log-transformed prior to analysis to normalize variances. Data are presented untransformed.
† For a given character, values with different superscripted letters are significantly different (Scheffé test for multiple comparisons among means).
‡ No *Salicornia* plants could be located beneath the tall-form *Spartina alterniflora* canopy in August.

high marsh, and in each, removed all *Salicornia* plants but the most centrally located individual. In September, prior to seed dehiscence, black plastic plates (10 × 10 × 1 cm) coated with Tangle-Trap adhesive (Forestry Supply Company) were fastened to the ground with thin wire in four concentric rings of six plates each. The plates were spaced equally around the circumference of each ring, and the four rings were 10, 20, 100, and 200 cm (radial distance) from the solitary plant. Tangle-Trap is not water soluble and remains sticky after the plates are covered by the tide. After dehiscence, I counted in situ all the seeds that stuck to each plate.

Although the seed-plate technique assessed local seed dispersal, the seed plates provided no information on long-range dispersal and patch colonization. In the spring of 1984, I noticed that *Salicornia* seedlings were abundant beneath piles of freshly deposited wrack. To determine if wrack transport was involved in the long-range dispersal of *Salicornia* seeds, in late summer 1984, prior to dehiscence, I created 60 artificial bare patches (50 × 50 cm) in the high marsh by clipping all the vegetation in each quadrat to ground level. I fenced half of these patches with 1 m high plastic mesh (1.5 cm mesh-size Vexar) to exclude the wrack, and left half of the patches unfenced as controls. The following spring, I removed the wrack deposited over the winter from the unfenced quadrats, and throughout the spring and summer censused the control and fenced quadrats for *Salicornia* seedlings. To control for seeds already present in the soil, I fenced off another 16 artificial patches (created as described above, 50 × 50 cm) in late summer 1984. In January 1985, I haphazardly collected several bales of wrack from Rumstick Cove and separated it randomly into two halves. One-half was sterilized in an autoclave (25 min, 170 kPa) and the other half was left untreated. The following day, I covered eight randomly chosen clipped quadrats with 2 cm of sterilized wrack and eight quadrats with 2 cm of unsterilized control wrack, tying it in place

with monofilament fishing line. In May 1985, I removed the wrack from these quadrats, and censused for *Salicornia* seedlings throughout the spring and summer.

Because time of emergence may affect seedling size and subsequent performance (e.g., Ross and Harper 1972), I examined emergent *Salicornia* seedlings throughout the marsh once a month in April, May, and June of 1984. On each sampling date, I measured the maximum cotyledon length and width of 250 newly emerged seedlings with fully open and fused cotyledons, and without internodes. To control for variation among sampling sites, no more than 10 seedlings were measured within any given 250 cm². No seedling was measured on more than one sampling date.

Interspecific competition

To determine the effects of the marsh perennials on the survivorship, morphology, and fecundity of *Salicornia*, in April 1984 I established five quadrats in monocultures of each of the perennials. In monocultures of tall- and short-form *Sp. alterniflora*, the quadrats were 1.0 × 1.5 m, while in the high marsh, the quadrats were 1.0 × 1.0 m. Because *Salicornia* is rare under the canopy (see Results: Interspecific Competition), I put the quadrats in areas in each zone where I could find emergent *Salicornia* seedlings. Each quadrat was divided into two equal subquadrats, and I randomly designated one subquadrat as a removal subquadrat and the other as a control. In removal subquadrats, I clipped the aboveground perennial vegetation to ground level every 2 wk until production ceased (6 wk in the low marsh and 12–16 wk in the high marsh). All *Salicornia* individuals were marked with small straws every other week in control and removal subquadrats, and different straw colors were used to distinguish biweekly cohorts. In September 1984, after 24 wk, all surviving *Salicornia* individuals were harvested, morphological parameters were mea-

TABLE 1. Continued.

	In patches in the:	
tall *Spartina alterniflora* zone	short *Spartina alterniflora* zone	upper marsh
1110 ± 259[a]	3900 ± 371[b]	3560 ± 231[c]
270 ± 14[b, c]	450 ± 20[a]	460 ± 17[a]
3.3 ± 0.35[a]	5.7 ± 0.27[b]	4.4 ± 0.20[c]
42 ± 10.5[a]	202 ± 28.8[b]	160 ± 12.6[b]
29 ± 4.3[a]	45 ± 3.2[b]	31 ± 1.5[a]
54 ± 3.9[a]	85 ± 5.3[c]	66 ± 5.1[c]
1177 ± 223.6[a]	8340 ± 969.2[b]	6589 ± 455.5[c]

sured for each individual as described above, and all individual plants were dried and weighed (±0.001 g).

Since only the aboveground vegetation was clipped in the removal experiments, perennial roots were left intact and often resprouted. *Salicornia* success in clipped areas may have been affected by live roots in the soil. To control for the effect of root interference on growth, and to examine shading effects in the absence of root competition, *Salicornia* plants in a large natural patch in the high marsh were artificially shaded. *Salicornia* in this patch were thinned so that 45 solitary plants were each centrally located in 25 × 25 cm quadrats. Fifteen plants were shaded to 50% of ambient light levels with black plastic mesh (Vexar), 15 were shaded to 90%, and 15 were unshaded controls. At the end of the growing season, all plants were monitored as in the perennial removal experiments. Ground-level solar radiation was determined in the above experiments with a LI-COR-1776 light meter. Light readings were taken on cloudless days between 1100 and 1400, on 15 May and 15 July.

Herbivory

To quantify the amount of herbivory inflicted on *Salicornia* by *Erynephala maritima*, the number of internodes on each plant with visible chewing marks was counted. Coleophorid moths leave easily seen round holes in an internode after they have fed on a given internode's seeds. The number of internodes on each plant with round holes was used as the measure of moth seed predation. Herbivory was measured for all *Salicornia* plants used in the interspecific competition experiments.

Statistical analyses

Comparisons among treatments were made using Analysis of Variance (GLM procedure of the Statistical Analysis System [SAS version 82.3, Cary, North Carolina]), and data were transformed when appropriate to normalize distributions (Sokal and Rohlf 1981). Data are presented untransformed. Scheffé tests were used throughout to compare among treatment means. One standard error (SE) was used throughout as the measure of variation.

RESULTS

Distribution and natural variation

Salicornia was exceedingly rare beneath the canopy of the perennial marsh species. Over all the transects sampled in 1983, *Salicornia* was present in only 6 of 90 quadrats sampled and occurred at densities of 40–2700 plants/m². These occurrences in the transects were confined to patches (see also Bertness and Ellison 1987). In the patches followed for 3 yr, the density of *Salicornia* ranged from ≈1600 to ≈9600 plants/m² in May 1983, but as perennials vegetatively invaded these patches, the *Salicornia* populations in the two smaller patches were eliminated in one summer, while the third and largest patch was overgrown completely by the perennials in three summers (Fig. 1).

When *Salicornia* did germinate under the perennial canopy, it did not grow as well as it did in patches. *Salicornia* plants growing in patches were larger in all measured parameters than were individuals growing beneath the pure canopies of *Sp. alterniflora, Sp. patens, Distichlis,* and *Juncus* at all sampling dates ($P <$ .05, ANOVA), so only the August sample results are presented (Table 1). *Salicornia* growing in patches produced far more seeds than plants growing beneath the perennial canopies throughout the marsh ($P <$ .05, ANOVA; Table 1). The morphology and fecundity of *Salicornia* growing beneath the perennial canopy were
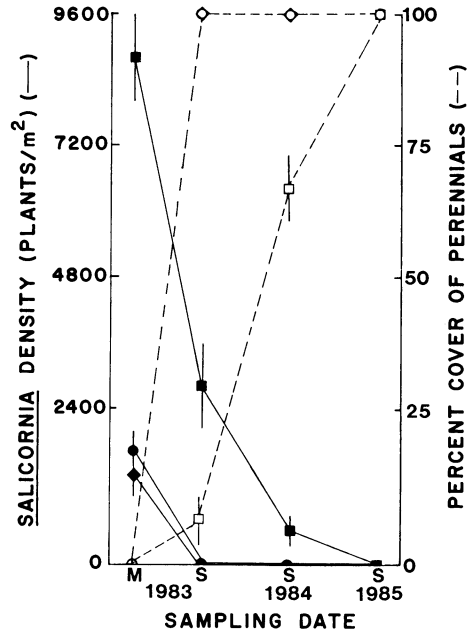

FIG. 1. Population dynamics of *Salicornia europaea* in three bare patches over the 3-yr study period. Each symbol (square, circle, and diamond) represents the population of a single patch. Solid symbols connected by solid lines represent the mean number (±1 SE) of *Salicornia* plants/m² in each patch and open symbols connected by dotted lines represent the mean percent cover/m² (±1 SE) of the invading perennial plants in each patch.
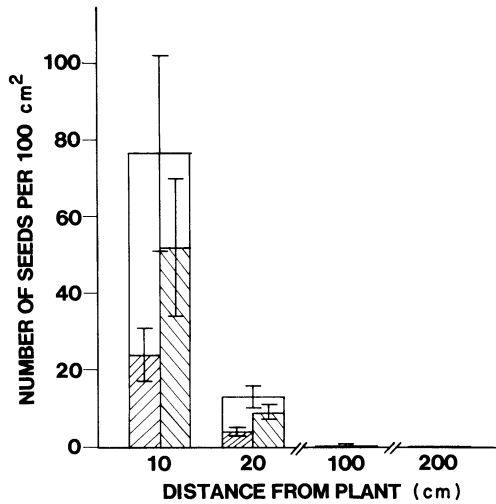
FIG. 2. The mean number of *Salicornia* seeds (±1 SE) recovered on the 100 cm² sticky plates. The open bar is the total number of seeds per plate. Because each set of plates covered successively less of the total area of the ring (see Methods: Seed Dispersal and Germination), number of seeds per 100 cm² is corrected for the total area of the ring by dividing the area covered by the plates by the total area of the ring. The inset hatched bars are the number of large seeds (▨) and the number of small seeds (▧) recovered on each plate.

not dependent on the canopy species, however. For example, *Salicornia* was no smaller under the canopy of *Sp. alterniflora* than under the canopy of any of the other perennial species ($P > .05$, Scheffé test; Table 1). *Salicornia* was not equally successful among bare patches in the different marsh zones, however. Among patches, the largest plants were found in the short *Sp. alterniflora* zone, and the smallest in the tall *Sp. alterniflora* zone ($P < .05$, Scheffé test). *Salicornia* growing in high-marsh patches were much larger than those found in patches in the tall *Sp. alterniflora* zone ($P < .05$, Scheffé test), and were somewhat smaller than those in short *Sp. alterniflora* zone patches ($P < .05$, Scheffé test).

Seed dispersal and germination

Nearly half the seeds of *Salicornia* fell within 10 cm of the parent plant, and almost no seeds were recovered >1 m away from the parent plant (Fig. 2). Nearly twice as many small seeds as large seeds were recovered at each distance sampled (Fig. 2), reflecting the differential production of large and small seeds and suggesting that the two seed morphs do not differ appreciably in dispersal distance. Although only ≈50% of the total seeds produced by the plant (as determined by counting the number of vacant bracteoles on the plant) were recovered on the sticky plates, very few seeds were observed >20 cm from the parent plant, suggesting that a substantial number of seeds were dispersed long distances.

In my examination of artificial patches created to monitor long-distance seed dispersal, mean *Salicornia* seedling density was 59.6 ± 14.64 individuals/m² in the quadrats exposed to wrack, and 3.6 ± 1.04 seedlings/m² in the fenced quadrats ($P < .001$, ANOVA). The preponderance of seedlings in exposed quadrats strongly supports the hypothesis that wrack transport is important for long-distance seed dispersal. Passive transport by water appears to be insufficient for long-distance dispersal, because few seedlings occurred in the fenced quadrats even though water could freely flow through the mesh and the mesh size was >100 times as large as a *Salicornia* seed. A mean of 33.6 ± 5.80 *Salicornia* seedlings/m² were found in quadrats covered with control wrack, while in quadrats covered with sterile wrack, only 9.2 ± 2.80 seedlings/m² were found ($P < .001$, ANOVA).

Salicornia seedlings that germinated early in the growing season were larger than those that germinated later in the summer. Seedlings that germinated in early April (mean cotyledon area = 1.85 mm²) were significantly larger than those that germinated in early May (mean cotyledon area = 1.23 mm²) ($P < .0001$, ANOVA). However, seedlings that germinated in early June were the same size (mean cotyledon area = 1.18 mm²) as those that germinated in May ($P > .10$, ANOVA) but smaller than those that germinated in April ($P < .0001$, ANOVA), suggesting that large seeds germinate early in the spring and small seeds germinate later in the summer (see also Philipupillai and Ungar 1984).

Interspecific competition

Salicornia germinated throughout the summer in all the control and perennial removal plots. The total number of seedlings marked for the first time at each census in all the zones is given in Table 2, and these data show that the majority of seedlings in all zones were found in mid- to late spring. Beneath the perennial canopy in May, 441.5 ± 133.76 $\mu E \cdot m^{-2} \cdot s^{-1}$ of photosynthetically active radiation (PAR) reached the marsh surface, while in the removal areas 1935.2 ± 28.05 $\mu E \cdot m^{-2} \cdot s^{-1}$ PAR was available to *Salicornia*. By July, the perennial canopy blocked up to 90% of the ambient light (198.1 ± 79.0 $\mu E \cdot m^{-2} \cdot s^{-1}$ in the control areas vs. 1880.1 ± 26.99 $\mu E \cdot m^{-2} \cdot s^{-1}$ in the removal areas). Light available beneath the canopies did not decline further after July.

In the tall *Sp. alterniflora* zone, emergent *Salicornia* seedlings were found at each of the first five censuses both in removal areas and under the canopy. None of the marked *Salicornia* plants survived to maturity in either of these control or removal areas, however. In contrast, many marked individuals survived in the short *Sp. alterniflora* zone and in the high marsh. There were dramatic differences in plant morphology and fecundity between plants in the control and removal areas. The observed patterns were qualitatively identical in

TABLE 2. Total number of seedlings of each cohort that emerged and were marked in each of the five types of monocultures. Each value given is the number of seedlings of each cohort summed by treatment over the five replicates in each zone. Cohort 1 was marked on 11 April 1984, and successive cohorts were marked at 2-wk intervals thereafter.

Zone	Treatment	Cohort							
		1	2	3	4	5	6	7	8
Tall *Spartina alterniflora*	Removal	95	39	5	13	3	0	0	0
	Control	104	44	7	8	2	0	0	0
Short *Spartina alterniflora*	Removal	197	116	58	47	4	5	0	0
	Control	155	71	34	44	5	5	0	0
Spartina patens	Removal	216	45	41	61	46	7	4	3
	Control	235	90	51	46	19	14	5	0
Distichlis	Removal	96	43	27	59	5	9	5	2
	Control	88	57	19	35	4	5	0	0
Juncus	Removal	506	64	109	87	36	7	0	1
	Control	461	93	41	22	6	13	0	0

the short *Sp. alterniflora* zone and in the high-marsh quadrats, and to avoid redundancy, only the results from the *Sp. patens* zone are presented (Fig. 3).

In *Sp. patens* monocultures, *Salicornia* from the first, third, and fourth cohorts in the removal areas were heavier, had more branches, and produced far more seeds than did corresponding individuals beneath the canopy ($P < .01$, ANOVA, all cases; Fig. 3). Third and fourth cohort individuals in the removal areas were taller than their counterparts growing in the shade ($P < .05$, ANOVA; Fig. 3), and first and fourth cohort individuals in the *Sp. patens* removal areas had larger root systems than same-aged individuals beneath the canopy ($P < .01$, ANOVA; Fig. 3). Insufficient sample size precluded statistical analyses of the second, and fifth through eighth cohorts, but individuals of those cohorts in removal areas tended to be larger in all measured parameters than those beneath the *Sp. patens* canopy. An increase in all measured morphological parameters and fecundity of *Salicornia* individuals was observed in all marsh zones following perennial canopy removal ($P < .01$, MANOVA). There were no differences in *Salicornia* morphology and fecundity among cohorts within removal or control areas in the low marsh and in *Sp. patens* and *Distichlis* monocultures ($P > .10$, MANOVA). However, in the *Juncus* zone, time of emergence (cohort) did significantly affect plant morphology and fecundity ($P < .01$, MANOVA). That is, although early-germinating plants could have been larger because they had more time to grow and preempt space (Ross and Harper 1972), emergence time did *not* affect final plant size and fecundity anywhere in the marsh except in the *Juncus* zone.

Survival of *Salicornia* was not significantly affected by perennial canopy removal in the short *Sp. alterniflora* zone or in the high marsh ($P > .05$, ANOVA, all zones, all cohorts). Because the quadrats were placed deliberately in areas where *Salicornia* was found in early spring, the finding that these particular plants survived beneath the canopy does not imply that *Salicornia* was growing everywhere beneath the perennial

canopy. Rather, *Salicornia* rarely occurs beneath the canopy and although it may survive occasionally, it rarely grows large enough to reproduce.

When plants in a disturbance-generated patch in the high marsh were artificially shaded, they were many times smaller and far less likely to survive than the unshaded controls (Table 3). Unshaded plants were as large as plants growing in other patches at equivalent tidal heights (cf. Tables 1, 3), but were larger than *Salicornia* plants growing in the experimental removal areas in the high marsh (cf. Table 3, Fig. 3), suggesting that live perennial roots indeed interfered with *Salicornia* growth in the perennial removal areas. Artificially shaded *Salicornia* plants were morphologically identical to and as small as plants growing under the high-marsh perennial canopy (cf. Table 3, Fig. 3), suggesting that light reduction by the perennials was responsible for the observed changes in *Salicornia* morphology, size, and seed production beneath the perennial canopies.

Herbivory

In the short *Sp. alterniflora* zone, no insect damage was observed (Fig. 4). In the *Sp. patens* and *Juncus* zones, however, insect damage was severe in the re-

TABLE 3. Results of the high-marsh patch experiment controlling for root competition (plants surrounding target *Salicornia* were uprooted). Values are means ± 1 SE.

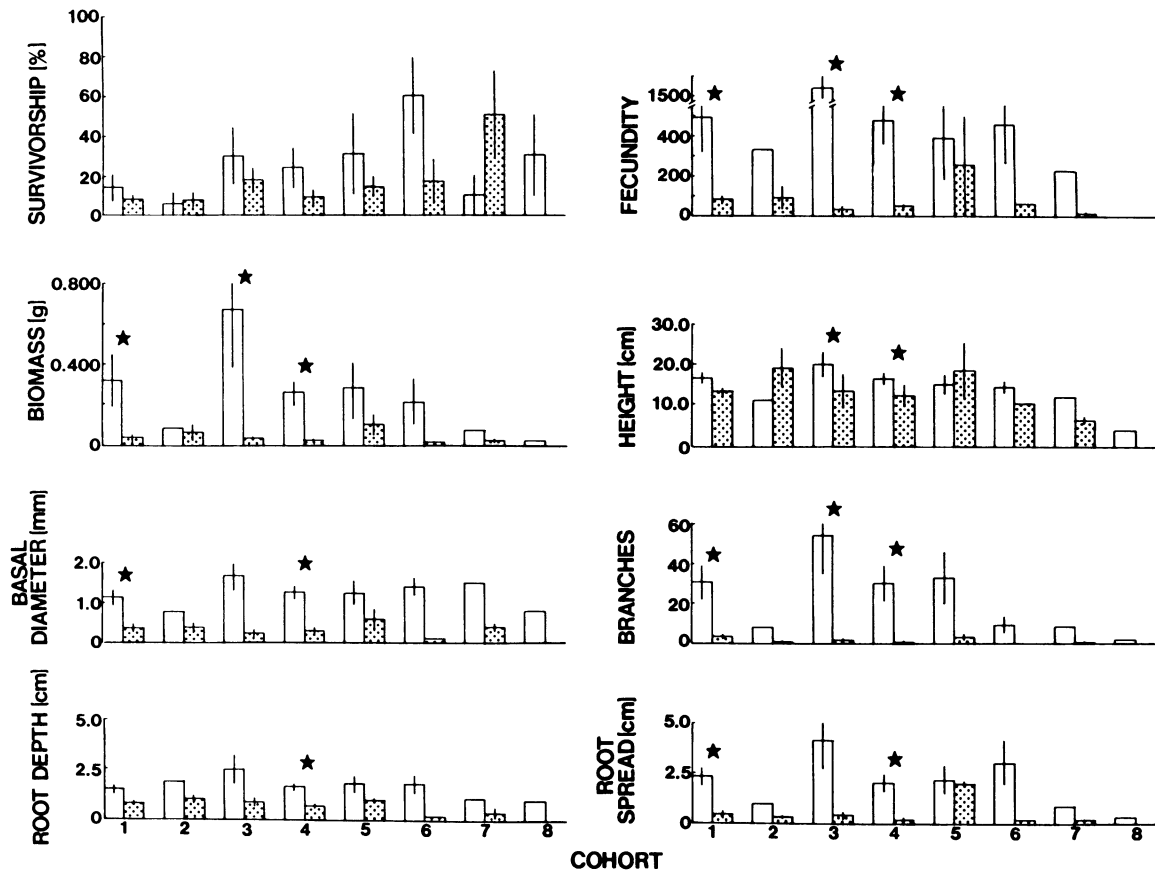| Character	*Salicornia* treatment		
	Control	50% shade	90% shade
Biomass (mg)	682 ± 135.5	36	11 ± 2.1
Height (mm)	256 ± 25.5	122	95 ± 11
Basal diameter (mm)	1.8 ± 0.14	0.6	0.2 ± 0.02
No. branches	150.3 ± 15.44	2	0.6 ± 0.40
Root depth (mm)	25 ± 3.3	12	11 ± 0.2
Root spread (mm)	67 ± 4.4	2	2 ± 0.5
No. seeds produced	1522 ± 250.3	0	0
No. survivors	(15)	(1)	(5)

FIG. 3. Mean values (± 1 SE) of the survivorship and various morphological characters of *Salicornia europaea* in *Spartina patens* monocultures. Open bars: areas where *S. patens* was removed; shaded bars: areas where the canopy was left intact. Values for each surviving cohort are shown. A star over a pair of bars indicates significant differences at $P < .05$ (ANOVA) between individuals in the two treatments within a given cohort. Bars without a standard error line represent single plants, and statistical comparisons were not possible when only one plant in a given cohort survived.

moval areas, yet virtually absent beneath the perennial canopies (Fig. 4). Although moths were absent from the *Sp. patens* zone, beetles were present throughout the summer (A. M. Ellison, *personal observation*), and in this zone, as many as 20% of the internodes of each *Salicornia* plant were damaged by beetles (Fig. 4). Little beetle damage was evident in the *Juncus* zone (Fig. 4), and moth larvae did not appear until late summer (August–October: A. M. Ellison, *personal observation*). Moths ate significantly more *Salicornia* seeds in the *Juncus* removal areas than beneath the canopy ($P < .01$, ANOVA; Fig. 4).

DISCUSSION

Patch dependence

Salicornia was found predominantly in disturbance-generated patches lacking other vegetation throughout the marsh (Fig. 1; Bertness and Ellison 1987). When growing in patches, *Salicornia* was 3–10 times larger and produced >100 times as many seeds as when it grew beneath the perennial canopy (Table 1). Within

patches, among zones, the largest plants were found in the short *Sp. alterniflora* zone, and the smallest in the tall *Sp. alterniflora* zone (Table 1). It has been shown that *Salicornia* is nutrient-limited in marshes (Jefferies 1977, Jefferies and Perkins 1977, Loveland and Ungar 1983) and soil nutrients are known to decrease with increasing tidal height (Valiela and Teal 1974). If soil nutrients were the only factor limiting *Salicornia* success, the largest plants, not the smallest, should have been found in the tall *Sp. alterniflora* zone. Other factors that appear to affect *Salicornia* success in the tall *Sp. alterniflora* zone are tidal inundation, sedimentation, and substrate hardness. Wiehe (1935) found that in a British marsh, *Salicornia* seedlings could only become established in areas where daily tidal inundation did not occur. At Rumstick Cove, the tall *Sp. alterniflora* zone is covered by high tides twice daily, while the short *Sp. alterniflora* zone is flooded only by 80% and the high marsh by <50% of the high tides (Bertness and Ellison 1987). The tides also deposit sediment on the marsh surface. Bertness and Grosholz (1985) found that at Rumstick Cove, sedimentation decreased over
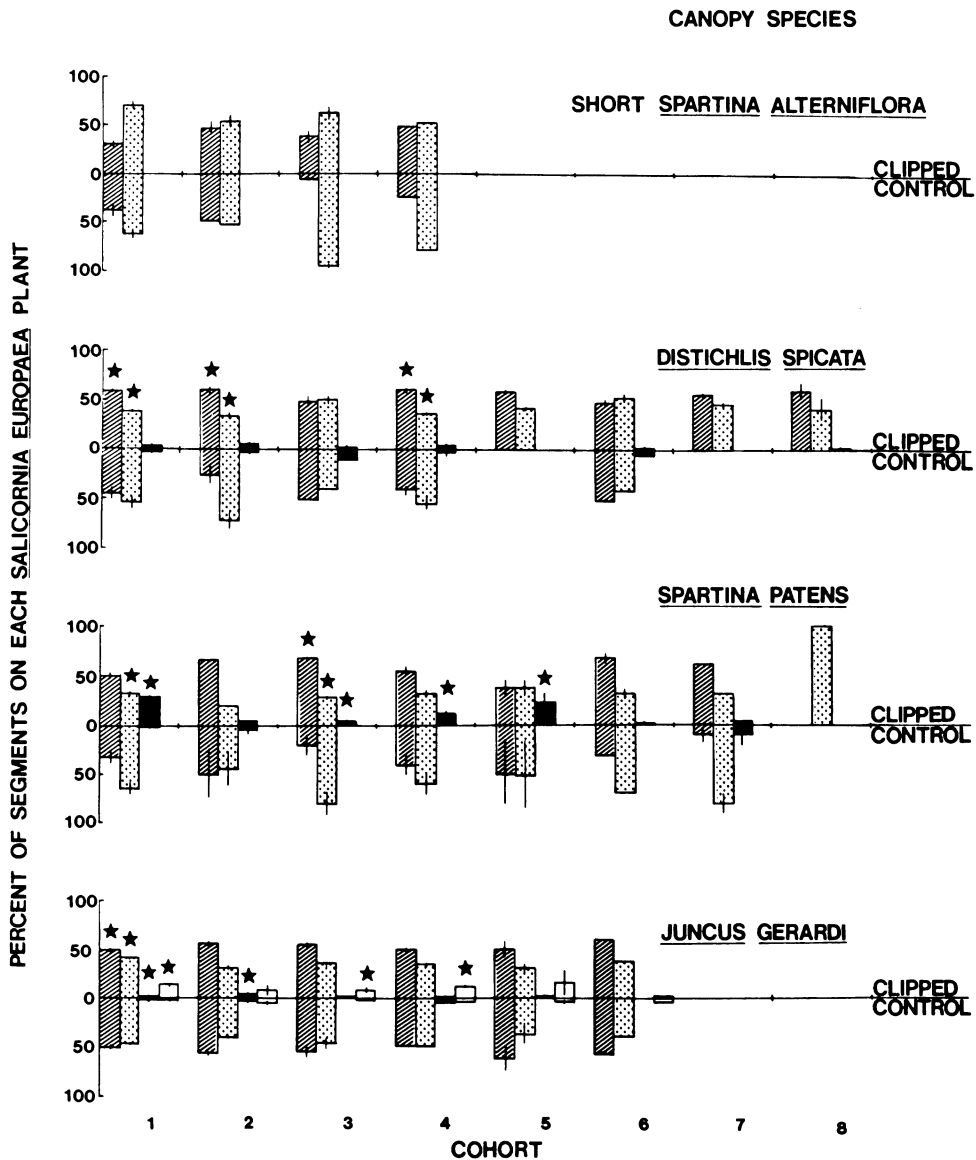
CANOPY SPECIES

FIG. 4. Percent of internodes of each *Salicornia europaea* plant (mean ± 1 SE) that were fertile (▨), sterile (☐), eaten by the beetle *Erynephala maritima* (■), and attacked by case-bearing moth larvae (☐). Results are given for plants growing in monocultures of the four perennial species where the canopy species was removed (above the 0 line) and where the canopy species was left intact (below the 0 line). A bar with a star over it indicates that the percentage differed significantly (*P* < .05, ANOVA) for individuals of a given cohort between treatments.

five orders of magnitude from the leading edge of the marsh to the high marsh. *Salicornia* seedlings in the low marsh are often buried under sediment (A. M. Ellison, *personal observation*), and sedimentation undoubtedly prevents successful establishment of *Salicornia* in the tall *Sp. alterniflora* zone. Substrate hardness also decreases with decreasing tidal height (Bertness and Miller 1984), and *Salicornia* roots may not be able to anchor successfully in the fine mud of the lower marsh.

Above +1.0 m mean tidal height, the decrease in

Salicornia size within patches with increasing tidal height probably reflects nutrient availability. The absence of size and fecundity differences among plants beneath the different perennial canopies of the different marsh zones (Table 1), however, probably indicates that *Salicornia* success is more sensitive to light availability than to nutrient levels. Experimental removal of the perennial canopy supports this hypothesis. *Salicornia* size, biomass, and fecundity increased significantly when the perennial canopy was removed experimentally (Fig. 3), and artificially shaded plants were

similar in morphology, size, and fecundity to plants growing beneath the perennial canopy (cf. Tables 1, 3, Fig. 3). *Salicornia* growing beneath the perennial canopy did not differ in size or morphology among zones (cf. Table 1, Fig. 3), indicating that the perennials have competitively equivalent effects (sensu Goldberg and Werner 1983) on *Salicornia* throughout the marsh. However, plants growing in the perennial removal areas were smaller than plants in natural patches, but *larger* than those growing in the shade (cf. Tables 1, 3, Fig. 3). This suggests that live roots in the removal areas affected *Salicornia* growth but that interspecific root competition effects were not as strong as the effects of competition for light.

Although *Salicornia* flourishes in natural patches and where the perennial canopy is removed, density-dependent mortality is not evident among *Salicornia* populations in patches (Joenje 1978, Jefferies et al. 1981, Hartman and Engler 1982, Ellison 1987). However, *Salicornia* in patches was damaged by insects more severely than was *Salicornia* beneath the canopy (Fig. 4). It may be easier for insects to find *Salicornia* in patches than beneath the canopy, as suggested by the resource concentration hypothesis (Root 1973). Beetles grazing on young internodes could affect plant growth rate and survivorship. There were no differences in *Salicornia* survivorship between plants growing beneath perennial canopy and in the perennial removal areas (Fig. 3), and beetle damage may have been responsible for reducing plant survivorship in the removal areas to equal that of the controls. The absence of among-cohort differences in plant biomass and fecundity within treatments in *Sp. patens* and *Distichlis* monocultures appears to result from beetles feeding indiscriminately among different-aged individuals. This hypothesis is supported by the observation that early-germinating plants were larger than late-germinating plants in the *Juncus* zone, where beetles were rare. Case-bearing moth larvae reduced *Salicornia* fecundity in the *Juncus* zone, but moth infestation did not begin until late summer when plant growth had ceased, and could not have affected final plant size.

The patches where *Salicornia* refuged were "short-lived" resources (Fig. 1) that were soon overgrown by the perennial vegetation. The two smaller patches followed were overgrown in a single summer, and the larger patch followed was overgrown in three summers. Bertness and Ellison (1987) followed over 100 similar patches for 3 yr, and found that the perennials grew vegetatively into patches at a constant rate and that the perennials rarely recruited by seed. Because the perennials colonize patches at a constant rate, large patches are overgrown more slowly than small ones, and *Salicornia* populations in large patches persist longer than populations in small ones (Fig. 1). To persist in the salt marsh community, however, *Salicornia* must produce seeds and disperse them to new patches before they are overgrown by the perennial vegetation.

Recruitment

Many *Salicornia* seedlings were found in areas exposed to wrack, while very few seedlings germinated in artificial patches protected from wrack by mesh fences. The absence of seedlings in the fenced patches indicates that passive dispersal by water is insufficient to account for recruitment into new patches because seeds in the water could pass through the mesh fence. A plausible mechanism that explains how *Salicornia* seeds are transplanted long distances by wrack is based on the morphology of the seeds. *Salicornia* seeds have many fine hairs on their surfaces (Dalby 1963). Dalby (1963) suggested that these hairs trap air bubbles and enable the seeds to float in the water. The hairs can also latch onto the passing wrack in the water much as Velcro hooks bind to fabric; when the wrack lands, the seeds are deposited onto the ground. Conveniently, the wrack is responsible for patch creation (Neuenschwander et al. 1979, Reidenbaugh and Banta 1980, Hartman et al. 1983), and *Salicornia* seeds, by "hitchhiking" on the prime agent of disturbance in the marsh, are passively transported to new patches. Seeds of the marsh perennials lack hairs and cannot bind onto passing wrack in the same way as *Salicornia* seeds do. Although the other species' seeds float in the water (A. M. Ellison, *personal observation*), the ability of *Salicornia* seeds to hitchhike on the agent of patch creation enables *Salicornia* to colonize new patches more reliably than the other species in the marsh.

More than 50% of the seeds produced by a single *Salicornia* plant, however, landed within 20 cm of the parent plant (Fig. 2). In the absence of the sticky plates to which seeds adhered, it is possible that more of the seeds that landed near the parent plant would have floated away in the water. Although *Salicornia* produce seeds of two sizes, the results of this study showed that seed size does not affect dispersal distance. Each plant produced twice as many small seeds as large ones and twice as many small seeds were recovered on each of the sticky plates (Fig. 2). Although differential dispersal ability has been suggested as an adaptive explanation for seed polymorphism (e.g., Harper et al. 1970, Cavers 1983), the results of this study do not support that hypothesis for *Salicornia*. It has also been suggested that seeds of different morphs may have different germination requirements, and that somatic seed polymorphism is an adaptation to varying environments (Harper et al. 1970, Ungar 1979). Philipupillai and Ungar (1984) have shown that large seeds germinate all at once early in the summer, and that only small *Salicornia* seeds persist in the seed bank. The results presented here show that newly emergent seedlings are larger earlier in the summer, and this observed difference is best explained by differences in the timing of germination of the two seed morphs. *Salicornia* seeds are merely folded-over embryos (Maheswari Devi and Rama Rao 1982), and large seeds have larger embryos

and hence initially larger seedlings than small ones do. Alternatively, early seedlings could be preempting available space and interfering with late seedlings' growth (Ross and Harper 1972). However, the observation that May and June seedlings are *identical* in size argues strongly against this latter hypothesis.

Reliable long-distance colonization of new patches by *Salicornia* seeds ensures its persistence in the marsh community. Local seed dispersal, on the other hand, creates dense monocultures within patches that persist until the *Salicornia* populations are overgrown and outcompeted by the perennial marsh plants. *Salicornia* growing in patches also are more likely to be attacked by insect herbivores. The interactions among disturbance, seed dispersal patterns, interspecific competition, and herbivory are major factors determining patterns of distribution and abundance of *Salicornia* in this New England salt marsh.

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