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Source: *Oecologia*, Vol. 92, No. 4 (1992), pp. 490-497
Published by: Springer in cooperation with International Association for Ecology
Stable URL: http://www.jstor.org/stable/4220193
Accessed: 17-11-2015 18:19 UTC

Oecologia (1992) 92:490–497

Oecologia

Salt stress limitation of seedling recruitment in a salt marsh plant community

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Received March 26, 1992 / Accepted in revised form June 30, 1992

Summary. Seedling recruitment in salt marsh plant communities is generally precluded in dense vegetation by competition from adults, but is also relatively rare in disturbance-generated bare space. We examined the constraints on seedling recruitment in New England salt marsh bare patches. Under typical bare patch conditions seed germination is severely limited by high substrate salinities. We examined the germination requirements of common high marsh plants and found that except for one notably patch-dependent fugitive species, the germination of high marsh plants is strongly inhibited by the high soil salinities routinely encountered in natural bare patches. Watering high marsh soil in the greenhouse to alleviate salt stress resulted in the emergence of up to 600 seedlings/225 cm^2. The vast majority of this seed bank consisted of *Juncus gerardi*, the only common high marsh plant with high seed set. We tested the hypothesis that salt stress limits seedling contributions to marsh patch secondary succession in the field. Watering bare patches with fresh water partially alleviated patch soil salinities and dramatically increased both the emergence and survival of seedlings. Our results show that seedling recruitment by high marsh perennial turfs is limited by high soil salinities and that consequently their population dynamics are determined primarily by clonal growth processes. In contrast, populations of patch-dependent fugitive marsh plants which cannot colonize vegetatively are likely governed by spatially and temporally unpredictable windows of low salinities in bare patches.

Key words: Halophytes – Salt marsh ecology – Secondary succession – Seed bank – Seedling recruitment

The role of seeds and seedlings in plant population and community dynamics has been the focus of considerable recent attention. Seed production, predation, germination conditions, longevity in the soil, and seedling survival can all influence plant recruitment (for reviews see Fenner 1985; Leck et al. 1989). The factors dictating the success of early life history stages are still poorly understood for most plant species, and even less is known about how seed and seedling biology influence plant community dynamics (but see van der Valk 1981). Seed production may be limited by predation (Louda 1983; Louda 1989), pollen supply (Bierzychudek 1981, Bertness and Shumway 1992a), and resource availability (Stephenson 1981). Germination of seeds may be restricted to "safe sites" where conditions are favorable for seed germination (Harper 1977), but many seeds also have long life spans in the soil which enable them to persist in soil seed banks until conditions favorable for germination occur (Leck et al. 1989). Subsequent seedling survival may be limited by abiotic factors, e.g. nutrient availability, salinity, and soil moisture, or biotic factors, e.g. shading and herbivory (Bazzaz 1979; Fenner 1985; Harper 1977).

Salt marshes are common, well-studied plant communities, yet little is known about seedling recruitment. Previous work on marsh plants has focused on physiological mechanisms for dealing with stressful edaphic conditions (e.g. low oxygen levels, Mendelssohn et al. 1981; salt stress, Hansen et al. 1976) and species interactions between adults (Bertness 1991). The conditions necessary for seed germination and seedling survival are poorly understood for most salt marsh plants (but see Amen et al. 1970; Beadle 1952; Partridge and Wilson 1987; Ungar 1978, 1987), but since marshes are dominated by a small number of species, and we know a great deal about the abiotic and biotic constraints on marsh plants, marsh plant communities are ideal for assessing how seed and seedling biology influence plant population and community dynamics.

Here we examine the seed and seedling dynamics of a New England salt marsh plant community and particularly investigate the role of soil salinities in limiting sexual recruitment. New England salt marshes are dominated by monocultures of perennial turfs that form distinct vegetation zones that parallel changes in tidal elevation (Nixon 1982). Vegetative growth of the dominant perennial turfs is the driving force shaping salt marsh zonation

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patterns (Bertness and Ellison 1987), but New England salt marsh landscapes are interrupted frequently by disturbance-generated bare space (Hartman et al. 1983). Bare patches are formed by the tidal deposition of wrack composed of dead plants from the previous growing season. Wrack carried by tides and storms is deposited onto the high marsh and can remain in place long enough to smother underlying vegetation before being washed away. High marsh bare patches typically become hypersaline as a result of poor drainage and the concentration of salts by solar evaporation of standing tidal water (Bertness et al. 1992).

In this study we examine why sexual recruitment plays such a minor role in the population biology of most New England marsh plants. Specifically, we 1) quantify the role of edaphic factors in dictating seedling emergence from marsh soil seed banks, 2) determine the seed germination requirements of common high marsh plants, and 3) experimentally examine the role of salt stress in limiting seedling success in marsh bare patches. Our results reveal that salt stress in marsh bare patches plays a major role in limiting sexual contributions to bare patch colonization and results in clonal interactions between perennials dominating salt marsh secondary succession.

Study site and species descriptions

Field work was performed at Rumstick Cove in Barrington, Rhode Island (Bertness and Ellison 1987). The seaward border of the high marsh is dominated by the salt marsh hay *Spartina patens*, whereas the terrestrial border of the high marsh is dominated by a monoculture of the rush *Juncus gerardi* (Bertness 1991). These distinct vegetation areas will be referred to below as the *Spartina* and *Juncus* zones. Spike grass, *Distichlis spicata*, is also common in the high marsh and often forms monocultures in chronically disturbed areas (Bertness and Ellison 1987). These monoculture-forming species are rhizomatous perennials which spread throughout their respective zones by vegetative expansion.

In addition to perennial turfs, a number of fugitive dicot species are characteristic of New England high marsh habitats associated with disturbance-generated bare space (Bertness et al. 1992). The annual glasswort *Salicornia europaea* is the most abundant of these and is found exclusively in disturbance patches (Ellison 1987). *Atriplex patula* and *Suaeda linearis* are less common annuals at the study site. The perennials, *Aster tenuifolius* (Salt marsh aster), *Limonium nashii* (Sea lavender), and *Solidago sempervirens* (Seaside goldenrod) are found sporadically throughout the high marsh generally associated with disturbances (Bertness et al. 1992). The woody shrub *Iva frutescens* (Marsh elder) forms a vegetation band that demarcates the terrestrial border of the salt marsh. Below, these plants will be referred to by their generic names.

Methods

Seed availability

Seed production of the dominant turf-forming high marsh perennials, *Spartina*, *Distichlis*, and *Juncus*, was determined by quantifying the seed output of plants collected at the end of the 1990 growing season. Inflorescence density was determined in 20 randomly tossed 100 cm sq quadrats in the *Spartina* and *Juncus* zones and on the *Spartina/Juncus* zone border. Inflorescences ($N = 20$/species/zone) were harvested randomly from each zone and scored for seed set and insect damage (see Bertness et al. 1987 for methods).

We characterized the available soil seed pool and determined the factors influencing seedling emergence from marsh substrate in a greenhouse experiment. In June 1988 blocks (15 × 15 × 3 cm) of marsh peat ($N = 54$/area) were excised from the *Spartina* vegetation zone, *Distichlis* vegetation, and *Juncus* zone vegetation. Nine blocks from each zone were assigned to each of the following treatments: 1) Ideal: full natural sunlight, watered with fresh water, and fertilized weekly with half strength 20-20-20 fertilizer. 2) Shade: similar to Ideal treatment except shaded (80% neutral shade) to mimic light attenuation beneath marsh vegetation in the field. 3) Low nutrient: similar to Ideal treatment, but not fertilized. 4) High nutrient: similar to the Ideal treatment, except fertilized twice each week. 5) Moderate salinity and 6) High salinity: same as Ideal treatment, except bathed in a salt solution of 15 or 30 ppt NaCl respectively. In the greenhouse the blocks were placed in flats flooded with water to just below the surface of the blocks to simulate field conditions. Once a week blocks were randomized between flats, above ground vegetation was removed with scissors, and water was changed. Replicates were censused weekly for seedlings, which were removed with forceps.

To test for the existence of a persistent seed bank (sensu Grime 1989) areas within 8 *Juncus* bare patches were covered with muslin cloth in June 1989 after summer seed germination, but before dispersal of seeds from that year. The following year (May 1990) one substrate block from each of the 8 covered areas was excised (15 × 15 × 3 cm blocks) along with 8 unmanipulated neighboring controls and brought into the greenhouse. After the muslin covers were removed, experimental and control blocks were placed in flats flooded with fresh water and censused for 6 weeks as described above.

Seed germination requirements

Seeds of all common high marsh plants were collected and scored for germination under controlled conditions to test the influence of light and salinity on germination. *Spartina*, *Juncus*, *Distichlis*, *Salicornia*, *Solidago*, *Aster*, *Atriplex*, *Suaeda*, *Limonium*, and *Iva* seeds were collected at the end of the 1988 growing season. Fully developed seeds with no signs of insect damage were stratified between layers of damp filter paper at 4° C for 1 month. After stratification seeds were placed in petri dishes (20 seeds/dish, 10 replicates/treatment) lined with a double layer of filter paper and placed in a growth chamber set for 12 hours of light at 27° C and 12 hours of darkness at 16° C. Seeds were subjected to four treatments: 1) ideal: full light with distilled water, 2) shade: 50% reduction in light (less shading was used than in the previous experiment because of the already reduced light intensity of the growth chamber) with distilled water, 3) full light and moderate salinity (15 ppt NaCl solution), and 4) full light and high salinity (30 ppt NaCl solution). Seed germination was scored weekly for 6 weeks and the positions of replicates within the growth chamber were randomized after every census.

Natural seedling dynamics

Seedling dynamics were studied in the field in artificial bare patches with natural and experimentally-lowered soil salinities. Artificial bare patches (1 m^2) were created by applying a short-lived herbicide (Roundup, Monsanto Co.) to plots and then clipping and removing vegetation. Recolonization of natural patches and patches created in this manner is identical (Bertness 1991). Patches were created in the *Spartina* and *Juncus* zones and on the *Spartina/Juncus* zone border in both 1988 ($N = 18$/zone) and 1989 ($N = 10$/zone) one year before they were used to examine colonization. To examine the role of salinity in bare patch seedling establishment and survival, half of the patches in each group were assigned to an experimental watering treatment. Watered patches were flushed weekly with freshwater from a nearby well following high tides to limit substrate salt accumulation (Bertness et al. 1992).

Patches were censused for newly emerging seedlings in May and August of 1989 and 1990. Since patterns of seedling abundance in first year patches were virtually identical in 1989 and 1990, in this paper first- and second-year patches will be compared using data from our May 1990 census only. Seedlings ($N=8$ individuals/species/patch if possible) of all major species were marked in May 1990 in first and second year patches with color-coded plastic cocktail straws. The following August seedlings were scored as dead or alive. Stunted individuals (<5 cm tall) unlikely to survive to the next growing season or, in the case of annuals, not reaching reproductive maturity were scored as dead. *Limonium*, *Aster*, and *Solidago* were indistinguishable as young seedlings and were treated as a group ($N=8$/group/patch).

Bare patch substrate salinities were monitored monthly (June–August 1990) by squeezing interstitial water from plugs ($5 \times 5 \times 2$ cm) of surface peat through cheesecloth and measuring its salinity with a refractometer. Plugs were excised from the centers of each patch ($N=1$/patch) and control measurements were taken from surrounding vegetation (0.5 m from patches, $N=10$/zone).

Sunlight reaching the surfaces of patches was measured in June and August of 1990 with a LiCor solar monitor (Model 1776). Instantaneous measurements ($\mu E\ m^{-2}\ s^{-1}$) were taken at the surface and .5 m above the surface of patches. Three replicate measurements were made 5–10 cm from the edges of patches and in the centers at least 15 cm from the nearest edge. Light measurements were also made beneath dense vegetation surrounding patches.

Data analysis

Where sample sizes were large enough, results were analyzed using analysis of variance. Post hoc treatment comparisons were made using unplanned multiple comparisons (Scheffé). Light attenuation percentage data were arcsin (square root) transformed and seedling counts were $\log(x+1)$ transformed to meet the assumptions of ANOVA. A sequential Bonferroni correction was applied to the patch seedling ANOVA's (Rice 1989). Seedling survival was tested for independence of watering treatment using G-tests (Sokal and Rohlf 1981).

Results

Seed availability

Seed production varied markedly among the high marsh turf-forming species and between vegetation zones (Table 1). Overall *Juncus* seed production was 30 times higher than *Distichlis*, which in turn was over 10 times higher than *Spartina* seed production ($p<.0001$ 1-way ANOVA, total seed production by species). The ovules of all three species were heavily damaged by insects primarily by grasshoppers (*Conocephalus spartinae*) and case-bearing moth larvae (*Coleophora* sp.; Bertness et al. 1987; Ellison 1991). While ovule and capsule density differed relatively little among zones, differences in herbivory resulted in large differences in the number of seeds produced/m^2 (Table 1).

Examination of the marsh seed bank revealed that *Juncus* dominated the available soil seed pool. Other species comprised only 0.14% of the total numbers of seedlings emerging. A total of 33, 904 *Juncus*, 27 *Salicornia*, 6 *Iva*, 2 *Atriplex*, 1 *Spartina*, and 13 unidentified dicot seedlings emerged across all substrate types during the experiment. The highest seedling emergence occurred in substrate originating in *Juncus* vegetation ($p<.0001$ 2-way ANOVA, substrate type × treatment, Fig. 1). *Juncus* seedling emergence was 50–100 times greater in *Juncus* vegetation than in *Distichlis* or *Spartina* vegetation substrate.

Salinity strongly inhibited *Juncus* seedling emergence in all substrate types (Fig. 1). The responses to germination conditions were similar across all substrate types, but were statistically different only in *Juncus* zone replicates which will be reported here ($p<.0001$ substrate type × treatment interaction, 2-way ANOVA). The ideal, high nutrient, and low nutrient treatments yielded the highest number of seedlings (400–600/replicate) and did not differ from one another ($p>.05$ LSM). Shading reduced seedling emergence by over 50% relative to the other freshwater treatments ($p<.0005$ LSM). Only one *Juncus* seedling emerged from the moderate salinity treatment while none emerged from the high salinity treatment ($p<.0001$ LSM, relative to all fresh water treatments).

Juncus was found to have a persistent seed bank in the *Juncus* zone. Covered substrate yielded 141 ± 29 ($\bar{X} \pm SE$)

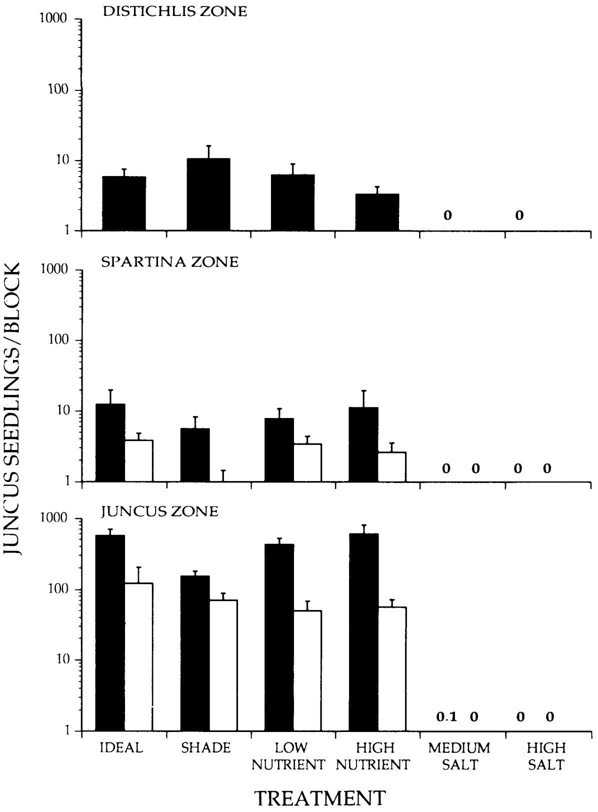

Fig. 1. *Juncus* seedlings ($\bar{X}+SE$) emerging from high marsh substrate ($N=8$ blocks/zone/treatment) collected in *Distichlis* vegetation, *Spartina* zone vegetation, and *Juncus* zone vegetation. Substrate blocks were exposed to ideal (full sun, freshwater, fertilizer), 80% shade, low nutrient (no fertilizer), high nutrient (double fertilizer), medium salt (15 ppt NaCl), and high salt (30 ppt NaCl) treatments. Treatments within zones with the same superscripts are not significantly different ($p>.05$ LSM) (■ = vegetation; □ = patch)

Juncus seedlings/15 × 15 cm^2 replicate. Adjacent controls exhibited dramatically lower seedling emergence with only 28 ± 11 seedlings/replicate ($p < .005$ 1-way ANOVA).

Seed germination requirements

Salinity strongly inhibited seed germination of all the high marsh species tested except for *Salicornia* (Table 2). Seeds of all species germinated best under conditions of fresh water and full light and *Solidago* was the only species whose germination was depressed by shading ($p < .05$ compared to ideal, Scheffé). The response to salinity among the salt sensitive species, however, was not uniform. *Salicornia* was clearly the most salt tolerant species tested and exhibited similar total germination in all treatments ($p > .95$ ANOVA). *Suaeda* was also relatively salt tolerant in contrast to most other species (Table 2). *Atriplex*, *Spartina*, *Limonium*, and *Distichlis* were moderately salt tolerant with no differences between germination in freshwater and moderate salinity treatments, but were inhibited by higher salinities. *Iva*, *Solidago*, *Juncus*, and *Aster* were all very salt intolerant with germination severely depressed by even moderate salinities. Salinity also delayed initial germination times with the germination of all species, except *Salicornia*, under saline conditions lagging behind fresh water treatments by several weeks.

Seedling recruitment to bare patches

Seedlings of *Juncus* were the most common seedling in the first year of bare patch colonization with up to 1500 seedlings emerging in *Spartina/Juncus* and *Juncus* zone patches (Fig. 2). *Salicornia* was the second most common species, averaging 300 seedlings/patch across all zones. These species were the most numerous in second year patches as well, but with reversed relative abundance.

Atriplex, *Iva*, *Limonium*, *Aster*, and *Solidago* occurred at intermediate densities in first and second-year patches and were at least twice as numerous in second-year patches (Fig. 2). Seedlings of the dominant perennial grasses, *Spartina* and *Distichlis*, were rare in all zones in both years (< 1 seedling/patch).

Seedling emergence increased strikingly in response to watering, but the response to fresh water varied between zones. Patches in the *Spartina* zone yielded the smallest number of seedlings overall and watering did not increase seedling emergence. In contrast, watering patches in the *Juncus* zone and on the *Spartina/Juncus* zone border

Table 1. Natural seed production for *Spartina*, *Distichlis*, and *Juncus* across all vegetation zones. Ovules/m^2 and ovules damaged by insects are reported for *Spartina* and *Distichlis* while capsules/m^2 and capsules damaged by insects are reported for Juncus

Species	Zone	Inflorescences/m^2	Ovules (capsules)/m^2	% Damaged by insects	Seeds/m^2
Spartina	*Spartina*	328 ± 97	3154 ± 160	17.0 ± 2.4	164 ± 33
		NS	NS	***	NS
	Spartina/ Juncus	620 ± 140	3293 ± 102	27.6 ± 2.5	95.5 ± 21.8
Distichlis	*Spartina*	176 ± 71	5205 ± 458	0.3 ± 0.2	2295 ± 262
		*	**	***	***
	Juncus	500 ± 119	7335 ± 660	14.3 ± 4.3	1060 ± 316
Juncus	*Spartina/ Juncus*	1710 ± 237	1410 ± 104	50.3 ± 6.4	30100 ± 6281
		NS	***	***	*
	Juncus	1695 ± 183	1940 ± 136	24.2 ± 4.1	61560 ± 13363

Values reported are means ± SE from 20 inflorescences. *$p < .05$, **$p < .005$, 1-way ANOVA for each species with zone as main effect

Table 2. The results of seed germination tests showing the percentage of seeds germinating ($\bar{X} \pm SE$) under each treatment

Species	Ideal: Fresh water, full light	Shade: fresh water, 50% shade	Moderate Salinity: 15 ppt	High Salinity: 30 ppt
Salicornia	56 ± 9^{a}	61 ± 6^{a}	56 ± 6^{a}	59 ± 3^{a}
Suaeda	99 ± 1^{a}	$99 \pm .5^{a}$	34 ± 4^{b}	48 ± 4^{b}
Atriplex	88 ± 2^{a}	90 ± 3^{a}	85 ± 4^{a}	14 ± 4^{b}
Distichlis	90 ± 2^{a}	83 ± 5^{a}	83 ± 5^{a}	$.5 \pm .5^{b}$
Limonium	98 ± 1^{a}	$99 \pm .5^{a}$	94 ± 2^{a}	56 ± 5^{b}
Spartina	42 ± 5^{a}	30 ± 4^{a}	31 ± 4^{a}	10 ± 2^{b}
Iva	46 ± 3^{a}	45 ± 2^{a}	$2 \pm .8^{b}$	0^{c}
Aster	36 ± 3^{a}	34 ± 3^{a}	2 ± 1^{b}	0^{b}
Juncus	90 ± 3^{a}	88 ± 4^{a}	36 ± 5^{b}	0^{c}
Solidago	50 ± 4^{a}	21 ± 4^{b}	6 ± 2^{c}	0^{d}

Treatments with the same superscript are not significantly different from one another ($p > .05$ Scheffé)

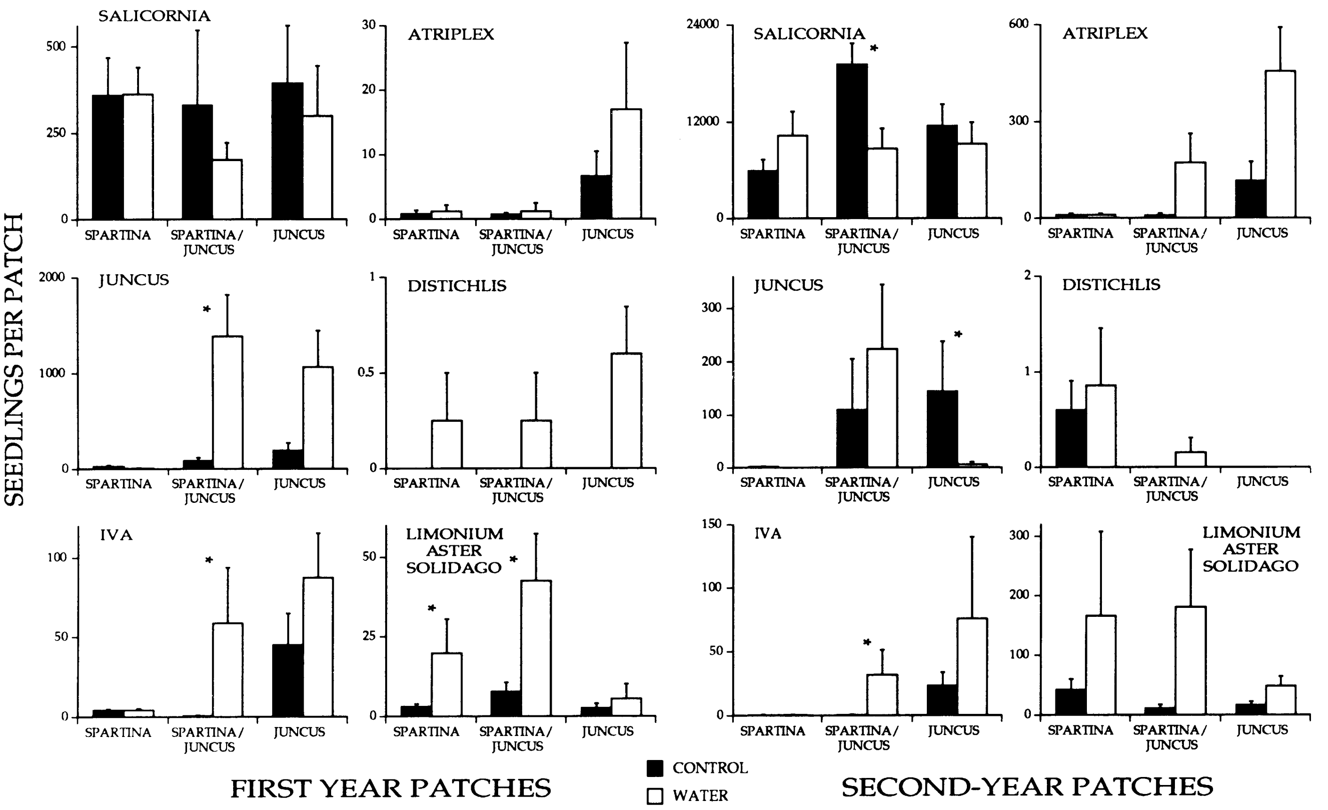

Fig. 2. Seedlings germinating ($\bar{X}+SE$) in 1st and 2nd year bare patches in May 1990. Bare patches (1 m^2) were created in the *Spartina*, *Spartina/Juncus*, and *Juncus* vegetation zones ($N=9$ 2nd year patches/treatment/zone and $N=5$ 1st year patches/treatment/zone) and half were watered with fresh water to ameliorate salt accumulation. *Treatment effects are significantly different at the 5% level after a sequential Bonferroni test on ANOVA results (■ = control; □ = water)

markedly increased seedling emergence. This pattern was more pronounced in first-year than second-year patches. The increase in seedling number was greatest for *Juncus* and the fugitive perennials, *Iva*, *Limonium*, *Aster*, and *Solidago*, but was clearly visible in the other species as well. *Salicornia* was a notable exception to the trend and emerged in slightly larger numbers in unwatered patches.

Seedling survivorship in first-year patches tended to be higher in watered than in unwatered patches for all species in all vegetation zones, suggesting that salt stress limited seedling survival (Fig. 3). Watering more than doubled seedling survivorship in the *Juncus* zone for all species ($p<.05$ *G*-test), except *Salicornia*. Seedlings in patches on the *Spartina/Juncus* border and in the *Spartina* zone showed a similar, but less dramatic response to watering.

Survivorship in second-year patches was much lower than first-year patches and over 50% of all marked seedlings died before the end of the summer (Fig. 3). Watering had fewer significant effects than in first year patches and the trends were usually to lower survivorship in response to watering presumably due to increased competition with vegetative colonizers.

Substrate salinities were markedly higher in bare patches than in surrounding vegetation ($p<.01$ 1-way ANOVA) and varied with patch type (Fig. 4; $p<.0001$ 1-way ANOVA, August census). Salinities were highest in *Spartina* bare patches (25–51 ppt), followed by *Spartina/Juncus* (33–41 ppt) and *Juncus* (37–39 ppt) bare patches (Fig. 4). Salinities of bare patches were generally 10 ppt higher than in adjacent vegetation ($p<.01$ 1-way ANOVA) and watering lowered patch salinities dramatically ($p<.01$ ANOVA). Watering affected patch salinity the most in the *Juncus* and *Spartina/Juncus* zones and least in the more frequently flooded *Spartina* zone. Moreover, salinities were lower in second than first year patches ($p<.01$ ANOVA).

Light availability in the patches dropped as patch canopies closed. Whereas substrate beneath undisturbed vegetation received 0.7–2% of ambient light, first year patches received 20–70% and second year patches received only 8–33% of ambient light (Fig. 5). This two-fold difference in light attenuation reflects substantial canopy closure after two years of patch colonization. Light attenuation was greater on the edges of patches than at centers due to shading by both surrounding vegetation and vegetative colonizers (Fig. 5; $p<.05$ patch type × location × watering treatment ANOVA). Light attenuation also tended to be greater in watered than unwatered patches ($p<.10$ ANOVA).

Discussion

Seedling recruitment is rare in New England salt marshes and is limited by the availability of open space, salt stress, and seed supply. Variation in germination requirements

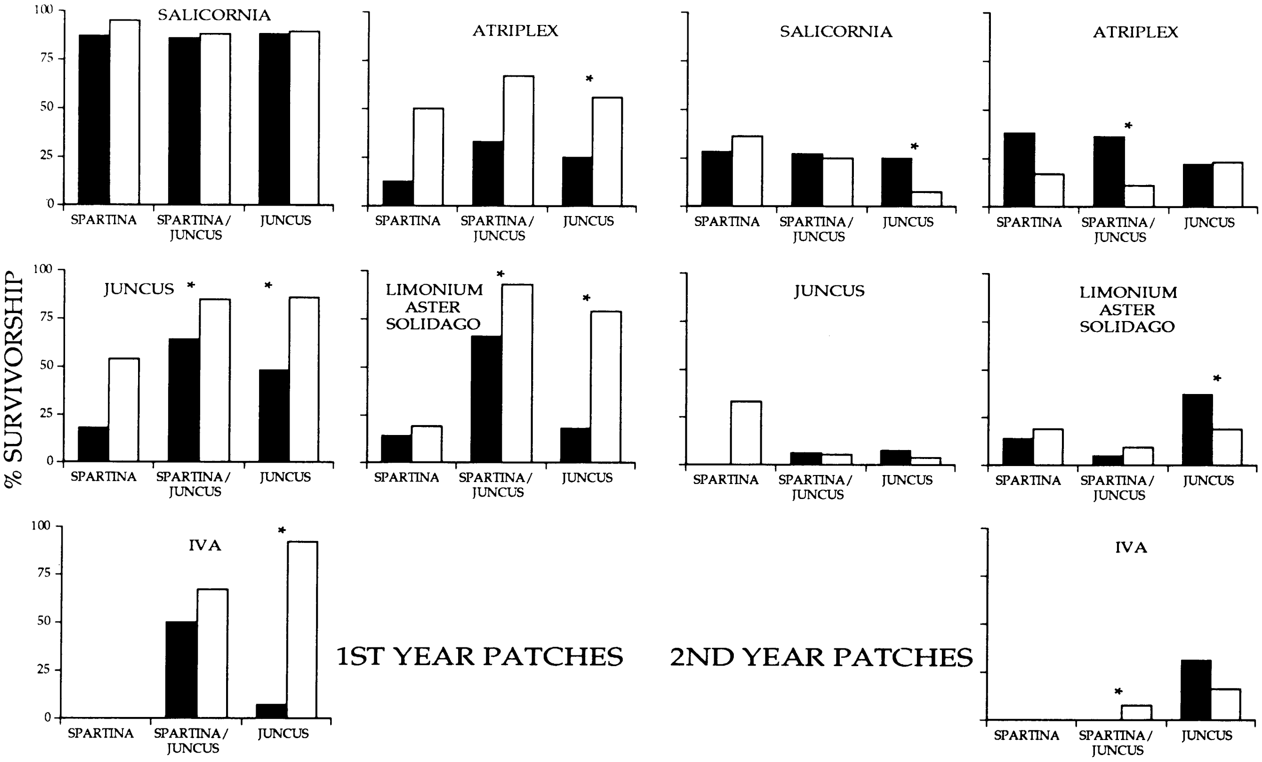

Fig. 3. Survivorship results for seedlings marked in May 1990 and scored for survival in August 1990. Seedlings of each species ($N=8$/ patch if possible) were marked in watered and control patches in the *Spartina*, *Spartina/Juncus*, and *Juncus* vegetation zones. $*p<.05$, G-test (■ = control; □ = water)

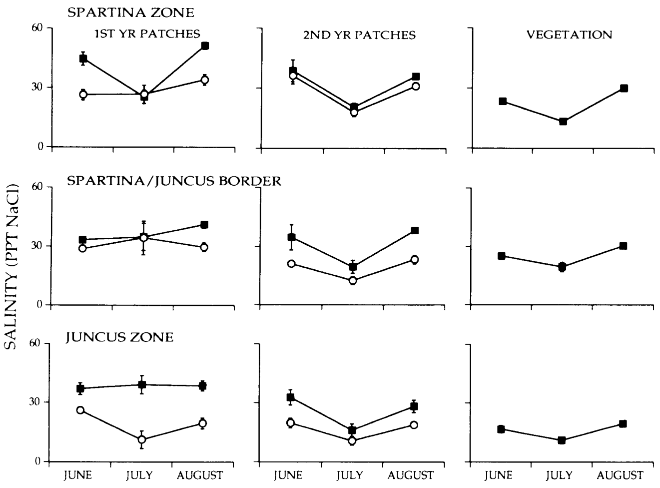

Fig. 4. Substrate salinities in 1st and 2nd year bare patches and surrounding vegetation in the *Spartina* zone, *Spartina/Juncus* zone border, and the *Juncus* zone during the 1990 growing season. Watered patches were flushed with fresh water after high tides to ameliorate salt accumulation. Values plotted represent means ±SE ($N=9$ 1st year patches/zone, $N=5$ 2nd year patches/zone). Due to heavy rainfall, the July measurements hide the 6–49% reduction in salinity present in watered patches on the other sampling dates (—■— = control; —○— = water)

enables some species to germinate under stressful saline conditions while severely restricting most species to low salinity conditions. Our results show that the relative importance of seedling recruitment differs between fugitive species and the turf-forming perennials that dominate the high marsh. New England salt marsh communities are dominated by a small number of perennial species whose spatial distributions are determined by differences in competitive ability and tolerance of the physical environment (Bertness and Ellison 1987). For these dominant species sexual processes play a minor role and their dynamics are maintained primarily by clonal growth. In contrast, fugitive species endemic to salt marsh bare patches depend on sexual recruitment for establishment and survival in the salt marsh community.

Generalizations based on comparisons with other studies of marsh seedling recruitment are difficult to make because of significant differences in species composition, marsh type (low, high, and inland), and geographic locations studied (New England, OH, CA, U.K.). A common theme emerging from studies of salt marsh seedling dynamics is that seed germination and seedling survival are strongly suppressed by hypersalinity (Hansen et al. 1976; Ungar 1978, 1987; Ungar and Riehl 1980) which is a major selective pressure influencing genetic composition (Jeffries 1981) and patterns of succession of marsh flora (Bertness and Shumway 1992b). Moreover, salt marsh seed banks, even at geographically diverse locations, are characterized by single species dominance and low species diversity (Hartman 1988; Hopkins & Parker 1984, Milton 1939).

Safe sites and salt marsh secondary succession

Safe sites are thought to be areas with conditions favorable for seed germination (Harper 1977) and can be species specific and transient in time and space. High marsh plants exhibit marked differences in their ability to germinate under saline conditions. While a few species (e.g. *Salicornia*) are able to germinate under stressful saline conditions, most are restricted to nearly fresh water conditions (Table 2). In addition to precluding germination in some species, saline conditions may retard seed germination in moderately tolerant species up to several weeks relative to more highly tolerant species. Slight differences in relative seed germination times can determine future competitive asymmetries (Ross and Harper 1972; Schmitt and Ehrhardt 1990). In an environment where safe sites are limiting and competition with vegetative colonizers is intense, the consequences of delayed germination are likely to be severe. Under natural conditions low salinity windows are temporally unpredictable and associated with unusually high rainfall. In addition to rainfall, patch size and location in the marsh strongly influence bare patch soil salinities (Bertness et al. 1991) and add to the stochastic nature of safe site availability.

Seed supply and recruitment by dominant high marsh perennials

Differential seed production by the dominant perennials may also have a dramatic impact on future patterns of sexual recruitment in the high marsh. Previous studies, as well as our data, demonstrate that seed set by *Spartina* and *Distichlis* is severely constrained by insect herbivory (Table 1; Bertness et al. 1987; Bertness and Shumway 1992). Despite predation on capsules, *Juncus* produces an order of magnitude more seeds than either *Spartina* or *Distichlis*. In addition to hypersalinity, therefore, seedling recruitment by *Spartina* and *Distichlis* may be further constrained by low propagule supply. Few studies have examined the impact of predispersal seed predation on seedling recruitment patterns in plant communities (Louda 1982, 1983, 1989). The importance of propagule supply in shaping population and community dynamics has recently been recognized in marine intertidal invertebrate communities (Connell 1985; Gaines and Roughgarden 1987; Roughgarden et al. 1987; Underwood and Denley 1984) and deserves further attention in plant communities (see van der Valk 1981).

Sexual recruitment in salt marsh succession

Sexual recruitment in New England marshes is constrained to disturbance-generated bare space that is free of competitors and salt stress. The few seedlings that emerge in vegetated monocultures are unable to compete with the faster growing perennial turfs for sunlight. Hypersaline soil conditions in bare patches severely inhibit seed germination and seedling survival, yet pose little problem for clonally expanding grasses (Bertness 1991; Shumway in review). Together these factors leave a very small window for sexual recruitment in marshes and result in a highly structured community maintained by clonal growth of a few intensely competitive turf-forming species.

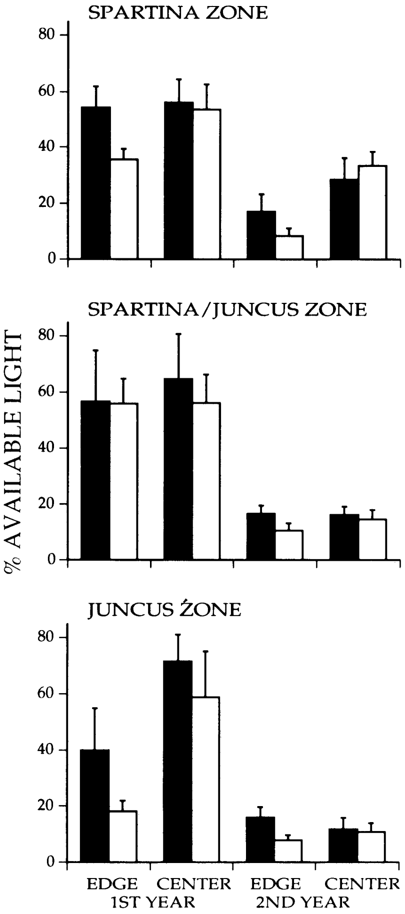

Fig. 5. Percentage of available sunlight reaching the edges and centers of 1st and 2nd year bare patches in the *Spartina*, *Spartina*/*Juncus*, and *Juncus* zones in August 1990. Values plotted are means +SE ($N = 10$–20 patches/zone) (■ = control; □ = water)

Similar patterns are evident in many other clonally dominated communities where sexual recruitment occurs during narrow windows when clonal growth has been interrupted by physical disturbance (Bazzaz 1990). Coral reef communities, for example, are composed primarily of long lived clonal species with a small guild of fugitives. Sexual recruitment is rare on reefs except after disturbance events when larvae of weedy fugitive corals settle readily (Hughes 1985; Hughes and Jackson 1985). Similar patterns have been found in habitats dominated by sea anemones (Ayre 1984), bryozoa (Jackson and Hughes 1985), sponges (Wulff 1991), and other clonal marine invertebrates. The dynamics of salt marsh plant communities appear to be very similar to those of other assemblages dominated by clonal organisms where sexual recruitment plays a minor role relative to clonal growth except during narrow temporal windows following disturbance.

Acknowledgements. We would like to thank the many people who helped with the field work, especially L. Gough, D. Hirata, J. Hoffman, M. Memmott, E. Stephens, and K. Wickler. Comments by J. Antonovics, S. Gaines, D. Morse, and A. Schmitt greatly improved the manuscript. We would like to extend special thanks to the residents of Rumstick Cove, especially E. Lowe and J. Skerry, for access to the field site. This work was supported by grants from the New England Botanical Club to S. Shumway and the National Science Foundation to M. Bertness.

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