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Seed dispersal, habitat suitability and the distribution of halophytes across a salt marsh tidal gradient

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Summary

1 The relative importance of seed availability and the post-dispersal environment in causing the distribution and abundance patterns of five halophytic forbs and a shrub was investigated across a New England salt marsh tidal gradient. Seed traps and soil samples were used to assess the spatial pattern of seed availability across the marsh, and experimental seed additions were performed to examine the effects of tidal elevation and interspecific competition with dominant grasses and rushes on seedling emergence and survivorship.

2 Seed distributions strongly paralleled adult plant abundance patterns across the marsh, suggesting localized dispersal with limited movement out of parental environments.

3 Adding seeds typically increased seedling densities by at least an order of magnitude, thus lack of seed availability may be important in limiting plant abundance within marsh zones.

4 Post-dispersal factors were primarily responsible for determining species distribution patterns across zones. Lower limits to the distribution of species typically found at high-marsh elevations were determined by intolerance to abiotic conditions in the lower marsh zones. In contrast, species typically found at low-marsh elevations were precluded from the high marsh due to competitive suppression by dominant plants. Patterns of post-dispersal success were strongly reinforced by limited dispersal.

5 Seed dispersal patterns and post-dispersal factors may therefore interact to generate distribution and abundance patterns in salt marsh plant communities.

Key-words: competition, fugitive species, seed-seedling dynamics, recruitment, zonation

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Introduction

There is a growing recognition that patterns of dispersal and recruitment can exert influences on local population and community dynamics that equal or surpass those of post-dispersal factors, such as abiotic stress and species interactions, which have been the traditional focus of much of the work in community ecology (Connell 1985; Gaines & Roughgarden 1985; Roughgarden *et al.* 1987; Underwood & Fairweather 1989; Tilman 1997). As investigating the importance of any one factor or demographic stage in isolation can lead to erroneous conclusions about the determinants of pattern in natural communities (Underwood & Denley 1984), studies that consider the effects of both dispersal/recruitment dynamics and post-dispersal processes are critical (Menge & Sutherland 1987; Jones 1991; Eriksson & Ehrlén 1992; Schupp & Fuentes 1995; Tilman 1997). Here, I examine the influence of both factors on the distribution and abundance patterns of a group of salt marsh plants across a tidal gradient.

Initial patterns of seed dispersal (i.e. 'seed rain' *sensu* Harper 1977) determine the habitats that could potentially be occupied by a given species, establishing a template for further population dynamics (Bazzaz 1991; Schupp 1995). Nevertheless, it is often assumed that seed dispersal plays a minimal role in limiting either the quantity or pattern of plant recruitment (Schupp & Fuentes 1995). Dispersal has, however, been demonstrated to limit the extent of populations, often quite strikingly

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(Primack & Miao 1992; Scherff *et al.* 1994). The supply of propagules can influence plant distribution patterns (Pemadasa & Lovell 1974; Platt & Weiss 1977; Rabinowitz 1979; Aguiar & Sala 1997), and also explain spatial variation in plant density across microhabitats (Mott & McComb 1974; Reader & Buck 1986). Furthermore, dispersal can be an important proximate determinant of species composition, abundance and richness in grassland plant communities (Tilman 1993, 1997). Cumulatively, these studies underscore the need to examine the extent to which patterns in plant communities reflect variation in the arrival or availability of seeds.

Components of the plant's environment, acting at subsequent life-history stages, will modify the initial pattern of seed supply to give the final distribution of adult organisms. Processes operating at early stages, where mortality is often most intense, are generally acknowledged to be particularly important in determining such patterns (Harper 1977; Grime 1979; Keddy & Ellis 1984). The combination of environmental attributes required for the successful emergence of seedlings – the regeneration 'safe-site' or 'niche' (Grubb 1977; Harper 1977) – may include abiotic factors, such as water availability or soil characteristics, as well as biotic factors, such as the absence of competition or predation. While successful seedling recruitment depends upon both the availability of seeds and the suitability of the post-dispersal environment (or microsite) for seedling emergence and growth (Harper 1977), their relative contribution has rarely been investigated within the same system (but see Reader & Buck 1986; Salonen & Setala 1992; Scherff *et al.* 1994; Aguiar & Sala 1997).

New England salt marshes are dense plant assemblages subject to strong tidal influences. It has been hypothesized (Reed 1947; Pielou & Routledge 1976) and, more recently, demonstrated (Bertness 1991a,b) that physiological stress limits the lower borders of plant distribution in salt marsh systems, while competition sets the upper borders (see Bockelmann & Neuhaus 1999 for a notable exception). The dominant grasses and rushes, which are the focus of these studies, spread clonally, but sexual reproduction via seeds is likely to be important for many salt marsh forbs. Both physiological parameters, such as salinity and soil oxygen availability (Ungar 1987; Shumway & Bertness 1992), and competition with dominant perennials (Ellison 1987; Bertness *et al.* 1992a; Brewer *et al.* 1998) have been shown to influence seedling emergence and/or survival of some forbs, but their importance for seedling recruitment across salt marsh zones has not previously been investigated.

Plants in other systems often display leptokurtic seed shadows with the vast majority of seeds landing close to the parent plant (Okubo & Levin 1989; Willson 1992), thus patterns of seed distribution across the landscape are often tightly coupled to patterns of adult plant distribution. However, salt marshes are characterized by regular tidal flushing, and the seeds of most salt marsh species are buoyant in sea water for days or even months (Koutstaal *et al.* 1987), so one might expect a decoupling between initial patterns of seed input, determined by the location of adult plants, and final patterns of seed availability across marsh zones. Tidally driven flow dynamics do affect seed dispersal and deposition in some tidal marshes (Hopkins & Parker 1984; Koutstaal *et al.* 1987; Huiskes *et al.* 1995), and seed bank studies have demonstrated considerable overlap in species composition and diversity across areas of the marsh that differ in their dominant vegetation type (Baldwin *et al.* 1996), suggesting that seeds can be widely dispersed in these systems.

The primary objectives of the present study were: first, to determine the spatial pattern of seed availability across the marsh for five halophytic forbs and a shrub; and second, to examine the effects of tidal elevation and competition with dominant plants on seedling emergence and seedling survivorship over 2 years, in order to assess their influence on patterns of plant distribution and abundance.

Methods

STUDY SITES AND ORGANISMS

The study was conducted between August 1995 and September 1997 at Rumstick Cove in Barrington, Narragansett Bay, Rhode Island, USA. Narragansett Bay is characterized by semi-diurnal tides and a tidal amplitude of 0.8–2.0 m. Rumstick Cove is typical of Southern New England salt marshes which are characterized by dense monospecific stands of perennial plants that form bands, or zones, across an elevation gradient (Niering & Warren 1980; Nixon 1982; Bertness & Ellison 1987). The seaward edge is dominated by the grass *Spartina alterniflora* Loisel., which is replaced by *Spartina patens* (Aiton) Muhl. and then the rush, *Juncus gerardi* Loisel., at higher elevations. The ecology of these clonal species has been extensively studied (Bertness 1991a,b). Near the terrestrial border, the marsh is dominated by the shrub *Iva frutescens* L. *Iva* is more sparsely distributed (< 1 individual $0.25\,\mathrm{m}^{-2}$) and stunted in morphology at the lower limits of its range, forming a stunted *Iva* zone that is distinct from the tall *Iva* zone in which shrubs are generally greater than 1 m in height and form a closed canopy (Bertness *et al.* 1992b). Each zone in the salt marsh spans approximately 10–15 cm of the elevational range, leading to differences in flooding frequencies from an average of 18 days a month in the *S. patens* zone to less than 1 day a month in the high marsh (Hacker & Bertness 1999). A group of less abundant halophytic forbs (herbaceous dicots), which represents more than half the total species richness in the salt marsh, is interspersed within the matrix of dominant plants. Five of these forbs, *Salicornia europaea* L., *Atriplex patula* var. *hastata* L., *Aster tenuifolius* L., *Solidago sempervirens* L. and *Limonium nashii* (Walter) Britton., and the shrub *Iva frutescens*, were chosen for study.

Atriplex and *Salicornia* (Chenopodiaceae) are annuals which produce seeds that are variable in size (*Atriplex*: 1.5–3.5 mm in length; *Salicornia*: 1.5–2.0 mm in length), and which lack any obvious dispersal structures. *Aster* and *Solidago* (Asteraceae) are perennials which produce small (1.5–2 mm in length) pappus-bearing, wind-dispersed seeds. *Limonium* (Plumbaginaceae) is a perennial which produces relatively large seeds compared to the other salt marsh forbs, and like the large-seeded shrub *Iva* (Asteraceae) lacks any obvious dispersal mechanisms. It is common to find entire inflorescences of *Limonium* and *Salicornia* in the strandline in marshes, and entire *Salicornia* plants have floatation times considerably longer than individual seeds (Koutstaal *et al.* 1987), thus seeds may be dispersed long distances while still attached to parent plants. All the plants studied flower and disperse seeds between early September and November.

DISTRIBUTION OF ADULT PLANTS

The distributions of adult forbs and *Iva* at Rumstick Cove were quantified using random stratified sampling in August 1995. The number of individuals of all species were counted in 0.5 × 0.5 m quadrats that spanned approximately 200 m of shoreline in each zone ($n = 150$ quadrats zone^{-1}). Four dominant vegetation zones, *Spartina patens*, *Juncus gerardi*, stunted *Iva frutescens* and tall *Iva frutescens*, were surveyed. The *Spartina alterniflora* zone was excluded because it forms only a narrow band of vegetation at Rumstick Cove and occurs at a tidal elevation below the tolerance range of all the marsh forbs, except *Salicornia*.

SEED RAIN AND SOIL SEED AVAILABILITY

Patterns of seed rain across the salt marsh were quantified by haphazardly placing 100 seed traps in each of the four zones. Traps were made of Styrofoam plates, 22 cm in diameter (*c.* 380 cm^2), covered with a thin layer of Tanglefoot$^{\text{TM}}$ insect trap. This resinous material remains sticky even after repeated submergence in salt water and is able to effectively trap seeds of salt marsh species (Ellison 1987). Traps were secured to the marsh soil surface with wire stakes in the first week of September 1995 (to correspond with the onset of dispersal) and were collected at the end of November (after most seeds had dispersed). Tidal fluxes dislodged some traps and it was difficult to relocate some traps in dense vegetation in the high marsh, consequently only 79 traps were recovered in the *S. patens* zone, 77 in the *Juncus* zone, 82 in the stunted *Iva* zone and 59 in the tall *Iva* zone. Recovered traps were returned to the laboratory and the seeds were identified to species and counted.

I estimated soil seed bank composition using methods similar to those in previous marsh studies (Hopkins & Parker 1984; Shumway & Bertness 1992). Thirty 20 × 20 × 5 cm (400 cm^2) blocks of marsh peat were excised from each zone in the middle of May 1997 as seedlings were beginning to emerge. Blocks were transported to the glasshouse, randomly placed into plastic trays and watered daily with fresh water from the tap. Freshwater has been reported to stimulate germination in most salt marsh species (Chapman 1974; Ungar 1978). Every other week, above-ground vegetation was clipped to the base to ensure maximum light penetration to the substrate surface, and blocks were re-randomized to minimize potential effects of tray or bench position on seedling emergence. Following collection of samples, all seedlings that had already emerged were identified to species, counted and then removed with forceps, and this process was repeated once every 2 weeks until the end of September 1997. The total number of seedlings of each of the six study species removed in each block was then calculated. Seedling numbers are likely to reflect both the transient and persistent seed bank. *Juncus gerardi* was the only other species commonly to emerge from blocks, and numbers for this species were not quantified.

EXPERIMENTAL ADDITION OF SEEDS

To determine the effects of marsh zone and presence of vegetation on seedling emergence and establishment success, seeds of the six experimental species were added to 30-cm diameter plots in a factorial design with two vegetation treatments (with or without vegetation) across the four dominant marsh zones. Ten randomly located replicate plots per vegetation × zone combination were established for each species (480 plots in total), spanning approximately 300 m parallel to the shoreline. All above-ground vegetation within 30-cm diameter plots was clipped at the substrate surface with scissors before the seeds were added to vegetation removal plots. Regrowth was clipped to ground level at 2-week intervals throughout the growing season (May–September).

Mature seeds were collected by hand from natural populations at Rumstick Cove in October and November 1995. Collected seeds were bulked and groups of approximately 500 seeds (estimated by weight) of the relevant species were added to each plot in November so that they experienced natural temperature, salinity and tidal conditions throughout the winter. To prevent loss of seeds due to tidal flushing, plots were covered with 30 × 30 cm squares of white nylon mesh cloth (organza), whose edges were pinned to the substrate surface with wire. A total of 9 out of 480 plots were lost over the winter, possibly due to ice or wrack. Covers were removed as soon as seeds began germinating in late-April. It is unlikely that seeds were lost from plots after removal of covers as propagules had become saturated due to repeated tidal submergence over the winter; seeds of salt marsh plants generally lose buoyancy within days to weeks (Koutstaal *et al.* 1987).

An additional 36 plots with and without vegetation, to which no seeds were added, were established in each marsh zone to provide an estimate of natural background seedling emergence across the marsh. Covers were placed in half of these plots: a three-way ANOVA revealed that neither the main effect of cover, nor its interactions with zone or vegetation removal, significantly affected background seedling emergence for the two most abundant species (*Salicornia* main effect of cover: $F_{1,270} = 3.49$, $P = 0.06$); *Iva* main effect of cover: $F_{1,270} = 0.23$, $P = 0.63$). Seedling abundances of the other four species were so low that statistical analysis was precluded. Data for covered and uncovered controls were therefore pooled.

The number of seedlings in control plots, to which no seeds had been added, was counted on 25 May 1996 when the majority had emerged. The mean number of seedlings from control plots, in each treatment × zone combination, was used to correct for the effects of natural emergence in addition plots. Addition plots were thinned to densities of approximately 30 individuals per plot (424 seedlings m^{-2}), and the remaining seedlings were counted on May 27. Thinned seedlings were carefully removed from plots with forceps, so as not to disturb neighbouring seedlings, placed into envelopes, taken back to the laboratory and counted. Total per cent emergence for each plot was calculated, correcting for seedling removal and in the case of *Iva* and *Salicornia* for control emergence.

Survival of the remaining first-year seedlings was monitored monthly from 5 June to 18 September 1996. The percentage of seedlings surviving this interval was calculated for each experimental plot. The number of surviving individuals was again counted on 15 September 1997 and survival percentages through the second year (Sept 1996–Sept 1997) were calculated. Very few *Solidago* or *Iva* seedlings survived to the end of the first growing season in the *S. patens* and *Juncus* zones, thus second-year survival percentages were not calculated in these zones.

Salinity, redox potential and light levels were quantified in each plot in June, July and August 1996. Salinity measurements were taken two weeks after the maximum high tide. Cores of peat, 3-cm diameter × 3-cm deep, were excised in each plot, squeezed through cotton gauze cloth, and the salinity of the extracted pore water was quantified using a hand-held NaCl refractometer (precision of ± 1 g kg^{-1}). Soil redox potential was measured in a random sample of 30 plots per treatment per zone by removing a 1-cm diameter × 5-cm deep plug from the substrate and inserting a redox electrode into the soil (Orion Research Incorporated, portable pH/ISE meter, model 230 A, fitted with platinum redox electrode, model 96–78–00, filled with 4 mol/L KCL saturated with Ag/AgCl reference solution; Orion Research Inc., Beverly, MA, USA). Measurements were taken 1 week after the monthly peak tide. Light levels were measured on cloudless days between 10:00 and 14:00 with a LI-COR solar monitor (Model 1776; Lincoln, NE, USA). Instantaneous measurements (μE m^{-2} s^{-1}) were taken both 5 cm above the soil surface (the height of the sensor) and above the grass/shrub canopy in each experimental plot.

STATISTICAL ANALYSES

All analyses were run using JMP version 3.1 (SAS 1995). Adult, seedling and seed counts within a sampling unit were converted to presence/absence data due to the high numbers of zero counts. Chi-square analysis was used to test the null hypothesis that plant distribution (frequency of occurrence) was constant across zones. Where this analysis was significant, frequency of occurrence was compared in all zones (six comparisons per species) and these values were bonferroni adjusted to control for multiple tests. Seed addition data (emergence, survival and environmental traits) were analysed using two-way ANOVAs, with two fixed factors, vegetation treatment (2 levels) and marsh zone (4 levels). Following a significant zone effect, Tukey-Kramer (HSD) tests were performed to compare means in all zones. Following a significant vegetation effect, contrast statements were used to compare least squares means in each vegetation treatment within each zone, and these tests were also bonferroni adjusted. Cochran's tests were used to test for homogeneity of variances. All data were transformed when necessary to meet the assumptions of ANOVA.

Results

DISTRIBUTION OF ADULT PLANTS

The frequency of occurrence of all species studied varied across zones significantly (Table 1), except for *Limonium* for which too few plants were present to allow analysis. *Atriplex*, *Iva* and *Solidago* occurred primarily in the stunted *Iva and* tall *Iva* zones of the upper marsh and were rare or absent in the *Juncus* and *S. patens* zones at lower elevations (Fig. 1,

Table 1 Effect of marsh zone on the frequency of occurrence of adult plants, seeds in seed traps, and seedlings emerging from soil samples (Pearson's Chi-square). Analyses were not carried out for *Limonium* due to low overall densities of both seeds and adults

	Adult Plants			Seed Traps			Soil Seed Pool		
Species	d.f.	χ^2	P	d.f.	χ^2	P	d.f.	χ^2	P
Aster	3	50.1	0.0001	–	–	–	3	17.3	0.0006
Atriplex	3	66.5	0.0001	3	25.2	0.0001	3	21.7	0.0001
Iva	3	408.9	0.0001	3	130.7	0.0001	3	68.6	0.0001
Salicornia	3	61.0	0.0001	3	103.3	0.0001	3	14.3	0.0025
Solidago	3	188.9	0.0001	3	22.0	0.0001	3	29.0	0.0001

Table 1). For the other three species no individuals were encountered in the tall *Iva* zone, and *Aster* and *Salicornia* were more frequently encountered in the lower marsh zones (Fig. 1, Table 1).

SEED RAIN AND SOIL SEED AVAILABILITY

Similar patterns of seed distribution across marsh zones were obtained from both seed trap and soil seed pool estimates (Fig. 2). Seeds of *Limonium* and *Aster* were rarely found in seed traps (seven *Limonium* seeds and five *Aster* seeds were found across all zones) and only two *Limonium* seedlings emerged from soil samples. For each of the remaining species, the frequency of occurrence of seeds varied significantly across marsh zones (Table 1) and generally paralleled the patterns for adult plants (Figs 1 & 2). Seeds of the high-marsh species, *Atriplex*, *Iva* and *Solidago*, generally occurred with greater frequency in high-marsh zones (Fig. 2). *Solidago* and *Atriplex* seeds were never found in the lowest marsh zone. Seeds of the two low-marsh species, *Salicornia* and *Aster* (soil samples only), occurred with greater frequency in the lower two marsh zones (*S. patens* and *Juncus*) than in the stunted and tall *Iva* zones (Fig. 2).

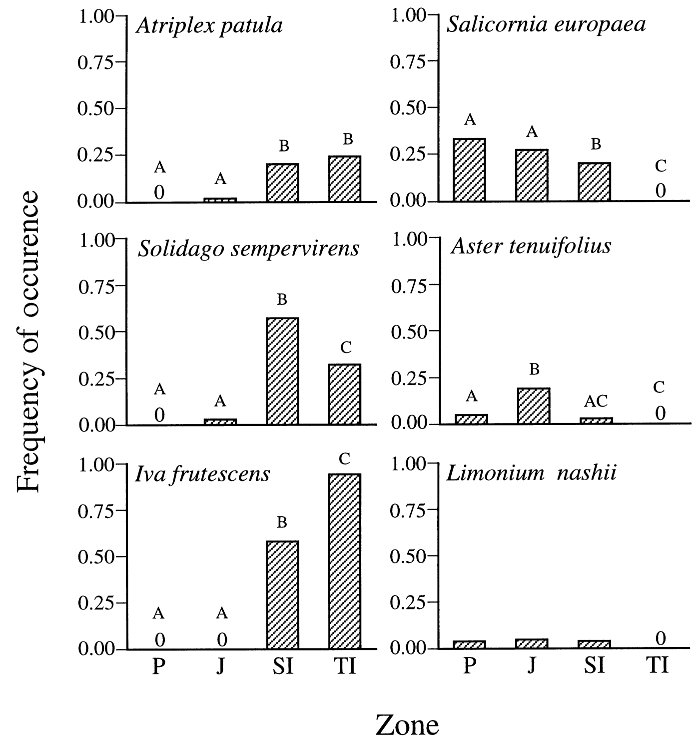

Fig. 1 Distribution of adult salt marsh forbs and one shrub across four vegetation zones: *Spartina patens* (P), *Juncus gerardi* (J), stunted *Iva frutescens* (SI) and tall *Iva frutescens* (TI). Bars represent frequency of occurrence in 0.25 m^2 quadrats ($n =$ 150 quadrats $zone^{-1}$); those with different letters differ significantly (Chi-square test).

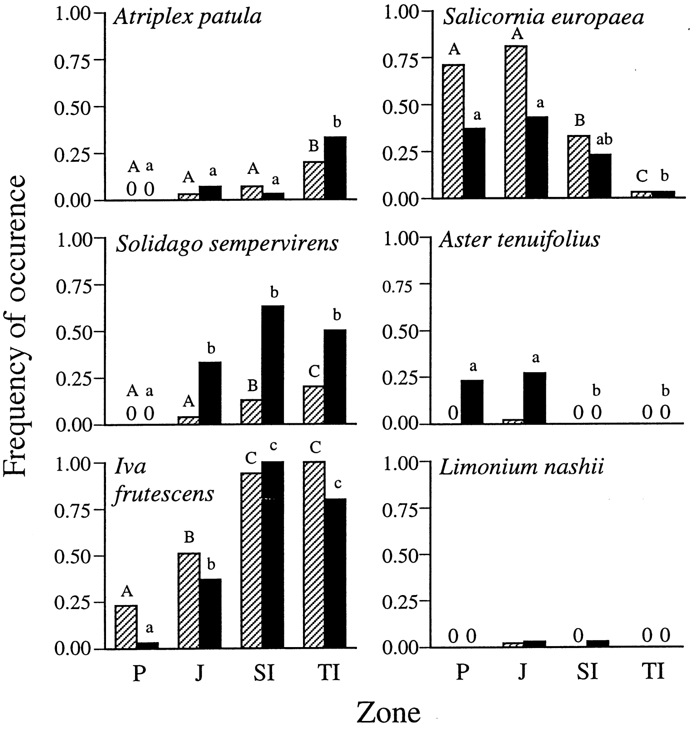

Fig. 2 Patterns of seed supply and seedling composition of soil samples across marsh zones. Bars represent frequency of occurrence of seeds on 22-cm diameter seed traps (hatched bars) and seedlings emerging from 20 × 20 × 5 cm blocks of substrate (black bars) in each marsh zone. *Post hoc* comparisons were made within each sampling type, and are summarized using capital letters for seed bank samples and lower case letters for soil samples; means with different letters differ significantly (Chi-square test).

EXPERIMENTAL ADDITION OF SEEDS

Patterns of salinity, redox potential and light availability in seed addition plots were similar across months, and only July data are presented. Salinity generally decreased with increasing tidal elevation, with the exception that the *Juncus* zone had slightly higher salinities than the *S. patens* zone (Fig. 3, Table 2). Salinity was very slightly, but significantly, reduced in vegetated compared with cleared plots except in the tall *Iva* zone, leading to a significant zone × treatment interaction (Fig. 3, Table 2). Redox potential (a measure of soil oxygen availability) was lowest in the *S. patens* zone and generally increased with increasing tidal elevation, although the *Juncus* and stunted *Iva* zones did not significantly differ from each other (Fig. 3). Redox potential was not affected by vegetation removal (Fig. 3, Table 2). Light availability varied very slightly but significantly across zones. Vegetation removal significantly increased light availability, which was five to tenfold greater in cleared plots than in controls. The magnitude of light reduction by the canopy depended on zone, as demonstrated by a significant zone × vegetation interaction (Table 2). Results of one-way ANOVAs run on cleared and control plots separately indicated that light in cleared plots did not vary significantly across zones ($F_{3,235} = 0.829$, $P = 0.479$); however, it did vary significantly across zones in vegetated plots ($F_{3,233} = 25.846$, $P = 0.0001$), where light availability was significantly greater in the stunted *Iva* zone compared with all other zones (Fig. 3).

Natural seedling density in control plots was low. The number of *Aster*, *Atriplex*, *Limonium* and *Solidago* seedlings was very rarely more than one individual per plot in any zone, except for *Solidago* in the stunted *Iva* zone, but *Iva* and *Salicornia* seedlings were relatively more abundant (Table 3). In plots where seeds were added, seedlings of all species emerged across all zones and both vegetation treatments. Adding seeds increased seedling numbers by at least an order of magnitude over those in control plots under most conditions (Table 3).

Emergence in seed addition plots differed significantly across zones for the three high-marsh species (*Iva*, *Atriplex* and *Solidago*), with fewer seedlings emerging in the lower marsh zones, nearly half as many in the *S. patens* zone than in the stunted *Iva* zone, but there was no suppression by the plant canopy (Fig. 4, Table 4). In contrast, emergence was independent of zone for two of the low-marsh species, *Salicornia* and *Aster*, both of which showed reduced emergence under vegetation in the tall and stunted *Iva* zones, and significantly so for *Salicornia*

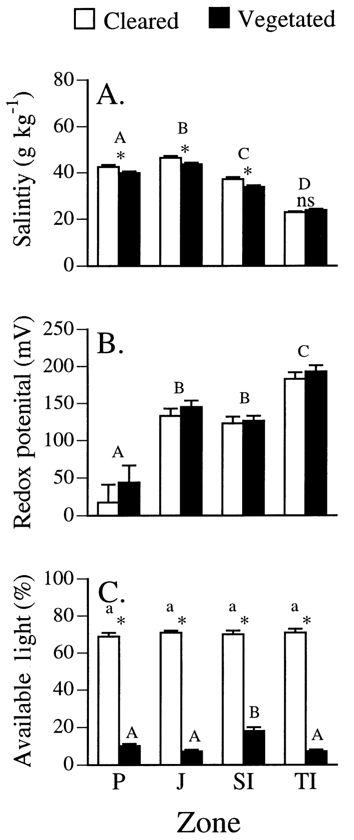

Fig. 3 Edaphic parameters measured in experimental plots in July 1996: (a) pore water salinity (g kg^{-1}), (b) soil redox potential (mV), and (c) light availability (% of ambient). Bars represent means ± 1 SE of 60 plots for salinity and light, and a random subsample of 30 plots for soil redox for each zone × treatment combination. Zones with different letters differ significantly (Tukey-Kramer HSD tests), as do vegetation treatments marked with a * (contrast statements).

(Table 4). Emergence of *Limonium* seedlings was significantly affected by both zone and vegetation presence, with a significant interaction between these two factors (Table 4). Suppression by the canopy for this species was significant in the *S. patens* and tall *Iva* zones only (Fig. 4).

First-year seedling survival of the species that are naturally common in the upper marsh (*Atriplex*, *Iva* and *Solidago*) was highest in the tall *Iva* zone and decreased with tidal elevation (Fig. 5, Table 4). The presence of vegetation significantly reduced survival of *Iva* seedlings particularly in the tall *Iva* zone, where seedling survival under the canopy was less than a quarter of that in cleared plots (Fig. 5). In contrast, survival of *Atriplex* and *Solidago* was not significantly affected by vegetation (Table 4). First-year survival for the species common in the lower marsh was more variable. Survival of *Salicornia* seedlings was significantly higher in the tall *Iva* zone than in the lower three zones (Fig. 5), whereas *Limonium* and *Aster* survived equally well in all zones (Table 4). The presence of vegetation generally reduced survival of all low-marsh species (Fig. 5, Table 4). *Post hoc* contrasts between treatments within each zone revealed that *Aster* survival was significantly reduced in the presence of vegetation except in the stunted *Iva* zone, and *Limonium* survival was significantly lower in all but the tall *Iva* zone. However, *Salicornia* survival was only reduced by vegetation in the tall *Iva* zone (Fig. 5).

Second-year survival for the high-marsh perennials, *Solidago* and *Iva*, was only analysed for the upper two zones due to low survival elsewhere (Figs 5 & 6). Survival of both species was greater in the tall *Iva* zone than in the stunted *Iva* zone, a pattern consistent with the first-year data (Figs 5 & 6), but the difference was only significant for *Iva* (Table 4). Vegetation had no effect on either species. Second-year survival for the two low-marsh perennials, *Aster* and *Limonium*, did not differ significantly across zones (Table 4), again reflecting the first-year data. Survival of both species was generally lower in vegetation plots than in vegetation removal plots, leading to a significant overall effect of vegetation treatment for both species (Table 4). However, this effect was not significant in either the stunted or tall *Iva* zone for *Aster*, leading to a significant zone × treatment interaction (Fig. 6, Table 4), or for *Limonium* in stunted *Iva* (Fig. 6).

Table 2 Effects of marsh zone and vegetation treatment on soil edaphic conditions and light availability (two-way ANOVAs). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = not significant

	Salinity			Redox Potential			Available Light		
Source	d.f.	MS	*F*	d.f.	MS	*F*	d.f.	MS	*F*
Zone (Z)	3	10491.57	363.19***	3	259781.55	45.56***	3	0.18	8.97***
Vegetation (V)	1	464.82	16.09***	1	10101.04	1.77 NS	1	57.57	2859.06***
Z × V	3	109.21	3.78*	3	1413.82	0.25 NS	3	0.30	14.71***
Error	465	28.89		239	5702.03		465	0.02	

Table 3 Seedling emergence in seed addition and control plots across marsh zones. Values represent the mean ± 1 SE number of seedlings per plot (707 cm^2) emerging in each zone in control plots (n = 72 plots/zone) and seed addition plots (n = 20 plots/species/zone) pooled across vegetation treatments

Species	*Patens*	*Juncus*	Stunted *Iva*	Tall *Iva*
Aster				
Control	0.06 ± 0.03	0.13 ± 0.07	0.05 ± 0.04	0.00
Addition	150.10 ± 16.99	119.10 ± 20.97	142.00 ± 18.90	117.50 ± 17.21
Atriplex				
Control	0.00	0.14 ± 0.07	0.21 ± 0.09	0.21 ± 0.07
Addition	100.30 ± 13.95	98.72 ± 20.14	221.05 ± 10.44	217.10 ± 14.07
Iva				
Control	0.00	0.56 ± 0.14	6.65 ± 0.86	20.68 ± 1.85
Addition	21.35 ± 5.11	57.45 ± 8.21	140.85 ± 15.18	93.00 ± 12.30
Limonium				
Control	0.01 ± 0.01	0.01 ± 0.01	0.00	0.00
Addition	228.70 ± 24.24	287.30 ± 15.33	307.91 ± 11.35	255.10 ± 17.56
Salicornia				
Control	11.56 ± 1.31	5.06 ± 0.56	2.42 ± 0.44	0.15 ± 0.05
Addition	74.20 ± 10.57	61.30 ± 6.61	96.10 ± 16.53	67.60 ± 13.04
Solidago				
Control	0.00	0.00	2.06 ± 0.59	0.57 ± 0.14
Addition	9.47 ± 3.12	39.39 ± 11.15	74.00 ± 14.50	52.21 ± 15.56

Discussion

Both seed availability and post-dispersal environment appear to be important determinants of recruitment patterns as previously suggested by Eriksson & Ehrlén (1992) and Tilman (1997). Seed availability limits seedling recruitment within zones that are naturally occupied by a species, and thus may play a role in limiting plant abundance. However, post-dispersal factors predominate in

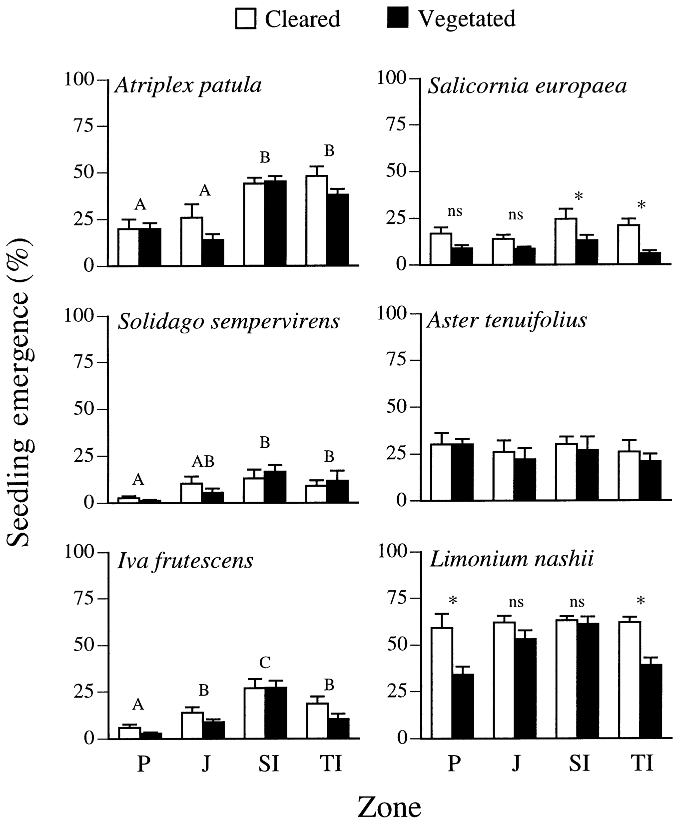

Fig. 4 Percentage of seeds emerging as seedlings in seed addition plots across marsh zones. Bars represent untransformed means ± 1 SE (n = 10 plots per species per zone per treatment). Codes as in Fig. 3.

Table 4 Effects of marsh zone and vegetation treatment on the proportion of seedlings emerging and surviving through the first and second growing seasons for each species (two-way ANOVAs on arcsin square root transformed data). AP, annual plants; $P < 0.05$, ** $P < 0.01$, ***$P < 0.001$, NS = not significant

		Emergence			Survival year 1			Survival year 2		
Species	Source	d.f.	MS	*F*	d.f.	MS	*F*	d.f.	MS	*F*
Aster	Zone (Z)	3	0.049	1.13 NS	3	0.215	1.84 NS	3	0.115	1.40 NS
	Vegetation (V)	1	0.027	0.62 NS	1	2.787	23.87***	1	0.528	6.40**
	Z × V	3	0.007	0.17 NS	3	0.080	0.69 NS	3	0.391	4.73**
	Error	70	0.043		70	0.117		55	0.083	
Atriplex	Zone (Z)	3	0.558	20.58***	3	1.941	22.72†***	AP	AP	AP
	Vegetation (V)	1	0.046	1.69 NS	1	0.224	2.63 NS	AP	AP	AP
	Z × V	3	0.021	0.77 NS	3	0.190	2.23 NS	AP	AP	AP
	Error	70	0.027		72	0.085		AP	AP	
Limonium	Zone (Z)	3	0.095	3.78**	3	0.024	0.27 NS	3	0.217	1.64 NS
	Vegetation (V)	1	0.495	19.72***	1	1.651	18.42***	1	4.658	35.30***
	Z × V	3	0.072	2.85*	3	0.068	0.76 NS	3	0.317	2.40 NS
	Error	72	0.025		72	0.089		61	0.131	
Iva	Zone (Z)	3	0.414	20.43***	3	2.450	28.17***	1	0.469	18.62**
	Vegetation (V)	1	0.047	2.32 NS	1	3.444	39.60***	1	0.059	2.34 NS
	Z × V	3	0.009	0.46 NS	3	0.752	8.65***	1	0.053	2.09 NS
	Error	70	0.020		72	0.086		28	0.025	
Salicornia	Zone (Z)	3	0.033	1.84 NS	3	0.433	8.33†***	AP	AP	AP
	Vegetation (V)	1	0.346	19.17***	1	0.205	3.94*	AP	AP	AP
	Z × V	3	0.026	1.42 NS	3	0.123	2.38 NS	AP	AP	AP
	Error	70	0.018		72	0.052		AP	AP	
Solidago	Zone (Z)	3	0.188	6.23***	3	4.792	37.53***	1	0.229	1.15 NS
	Vegetation (V)	1	0.006	0.20 NS	1	0.231	1.81 NS	1	0.001	0.004 NS
	Z × V	3	0.024	0.78 NS	3	0.065	0.51 NS	1	0.025	0.13 NS
	Error	66	0.030		60	0.127		25	0.200	

† test should be considered with caution due to heterogeneity of variances.

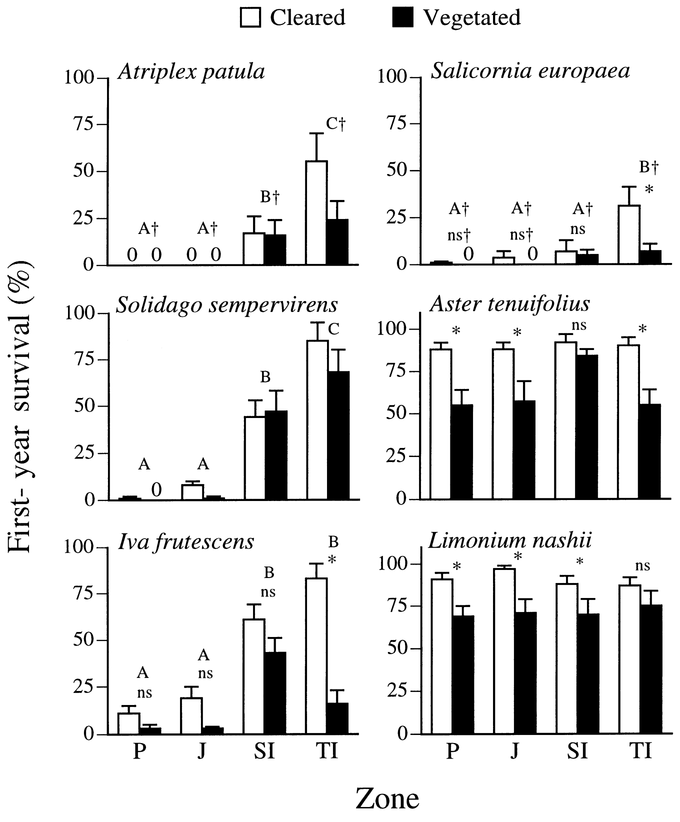

Fig. 5 Percentage of emerged seedlings surviving to the end the first growing season. Bars represent untransformed means ± 1 SE ($n = 10$ plots per species per zone per treatment). Codes as in Fig. 3. Tests marked with a † should be considered with caution due to heterogeneity of variances (Cochran's test).

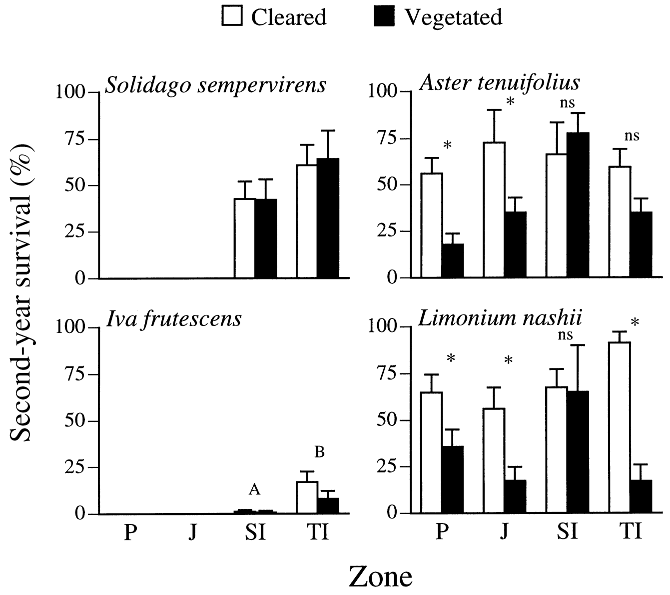

Fig. 6 Percentage of seedlings alive at the end of the first growing season (September 1996) that survived to the end of the second growing season (September 1997). Bars represent untransformed means ± 1 SE ($n = 10$ plots per species per zone per treatment). Codes as in Fig. 3.

determining patterns of plant recruitment (and ultimately plant distribution) across marsh zones.

SEED DISPERSAL

The spatial distribution of seeds was highly heterogeneous across the salt marsh. For five of the six experimental species, patterns of seed abundance and distribution (measured as seed rain and/or soil seed composition) paralleled patterns for adult plants. A similar positive association between extant vegetation and seed bank composition has also been observed in freshwater tidal wetlands (Hopkins & Parker 1984; Parker & Leck 1985). This pattern seems to be the result of greater seed input where adults are more abundant, with little subsequent dispersal out of the parental environment (i.e. dispersal limitation), although *Salicornia* and *Iva* seeds were present in zones unoccupied by adults suggesting that cross zone dispersal does occur.

Secondary dispersal of seeds commonly occurs after initial movement from the parent plant to the substrate surface (Chambers & MacMahon 1994; Aguiar & Sala 1997), however, the similarity of distribution patterns in seed traps, which measure primary and early secondary dispersal, and in soil samples, which integrate dispersal processes that potentially take place over longer time periods, suggests that there is minimal rearrangement of propagules after initial dispersal. Thus, the general rule of localized dispersal in plant populations seems to hold in this system, despite the potential for broad-scale seed dispersal and secondary rearrangement of propagules by tidal action. Similar results have been reported in other coastal habitats, such as sand dunes (Ehrenfeld 1990) and cobble-beach plant communities (Bruno 2000).

An alternative explanation for the association between distributions of seeds and adult plants is that tidal sorting of propagules determines the patterns of initial seed distribution and this in turn could determine adult plant distribution, as has been suggested in mangrove communities (Rabinowitz 1979). This hypothesis, however, requires the differential deposition of propagules of different species to different zones. Propagules with similar morphologies, sizes or modes of dispersal might be expected to become trapped on similar substrate types, as demonstrated by Peart & Clifford (1987) and Chambers (1991), or to disperse to the same zones. In the present study, the two similarly sized ‘wind-dispersed’, pappus-bearing species of Asteraceae (*Aster* and *Solidago*) show opposite patterns of seed abundance across marsh zones. Similarly, *Salicornia* and *Atriplex*, which lack any obvious dispersal structures and have similar floatation times (Koutstaal *et al.* 1987), also show opposing patterns of seed distribution. Differences in seed supply across zones do not therefore appear to be related to dispersal mode or propagule characteristics, and the heterogeneity of seed availability across the marsh is more likely to be a function of localized dispersal than the result of tidal sorting.

The overall abundance of seeds (346 ± 32 seeds m^{-2} estimated from seed traps) was quite low compared to those found in many salt marsh systems (see Ungar 1987 for review), but was similar to those in another New England salt marsh (Hartman 1984). Seed limitation of seedling recruitment in this system is consequently strong. Consistently higher numbers of seedlings of all species emerged in seed-addition plots compared to the 0–20 individuals per plot in the controls. Seed limitation may be due to low production, or to loss of seeds from the system before they become successfully trapped on the substrate surface. Previous investigations have demonstrated that tidal export of seed from marshes can be substantial (Huiskes *et al.* 1995), suggesting that propagule loss to unsuitable habitats could be important. However, the limited evidence for extensive propagule movement in this system, together with the considerable seed retention observed in similar forb communities in cobble beach systems (Bruno 2000), suggests that limited seed availability is more likely to be due to the sparse distribution of adults of most species across the landscape, which results in low overall yearly seed production.

Overall, seed dispersal in these species is restricted to at least some degree. For four of the six species in which seed availability was restricted to zones in which adult plants occurred, dispersal limitation may be responsible for restricting plant distributions. If this is the case, however, overcoming this limitation by adding seeds should extend distributions into previously unoccupied areas.

POST-DISPERSAL ENVIRONMENT

Effects of marsh zone on patterns of plant recruitment across the marsh are likely mediated by differences in soil edaphic conditions that vary predictably with tidal elevation. Salinity was generally higher, and soil oxygen availability lower, in the low-marsh zones, and conditions became relatively more benign with increasing tidal height in the stunted and tall *Iva* zones. This pattern seems to be characteristic of Southern New England marshes and has been observed consistently at Rumstick Cove (Bertness & Ellison 1987; Hacker & Bertness 1999). Removal of vegetation (and thus competition) substantially increased light availability. The importance of post-dispersal factors in limiting seedling emergence and survival differed predictably between high- and low-marsh species.

The high-marsh species in this study (*Atriplex*, *Iva* and *Solidago*) appear to be intolerant of the harsh environmental conditions in the low marsh, but relatively insensitive to shading by vegetation. Emergence was reduced in lower marsh zones suggesting that seed germination is inhibited by the high salinities or low redox potentials there. Salinity is known to inhibit germination and/or seedling survival in some shoreline habitats (Ungar 1987; Shumway & Bertness 1992), and low oxygen availability can negatively affect germination in freshwater wetlands (van der Valk 1981). Nevertheless, seedlings of all species were able to emerge in all four experimental marsh zones suggesting that plant distributions are unlikely to be limited at this stage. Marsh zone had a much more pronounced effect on seedling survival. None of the high-marsh species survived to reproductive maturity in the *S. patens* or *Juncus* zones, and adult plants of some of the same species are known to be sensitive to abiotic stress (Hacker & Bertness 1999). Survival was not generally affected by competition with dominant marsh plants for these species, with the exception of *Iva*, which was inhibited in the high marsh where adults of this species are dense.

In contrast, the low-marsh species (*Aster*, *Limonium* and *Salicornia*) resemble classic fugitive species (*sensu* Hutchinson 1951), as previously suggested by Bertness *et al.* (1992a). They are generally stress tolerators and, for the most part, emerged and survived equally well across all marsh zones. However, they were susceptible to vegetative suppression by competitively superior zonal dominants. Only *Salicornia* survival varied across zones, perhaps due to an outbreak of the herbivorous beetle, *Erynephala maritima*, in early summer, which can cause high seedling mortality especially in the low marsh where densities of *Salicornia* are normally highest (T. A. Rand, personal observation; Ellison 1987). Removal of vegetation tended to increase emergence rates and dramatically increased survival for all three low-marsh species. Higher rates of seedling establishment in vegetation gaps are likely to link the distribution and abundance of low-marsh species to patterns of disturbance across the marsh, as suggested previously (Ellison 1987; Brewer *et al.* 1998). Gap dependence is also a common feature of many other grassland plants (Platt 1975; Gross & Werner 1982; Goldberg & Werner 1983) and may be especially important in dense plant assemblages, such as these New England salt marshes, where light availability is severely attenuated by the canopy.

Although competition with the zonal dominants had important effects on emergence and survival of the low-marsh species, neither the attenuation of light nor the suppression of lower marsh species by vegetation varied consistently across zones. Thus, limits to the upper distributions of low-marsh forbs do not result from an increase in the competitive effect of vegetation, as has been found for the matrix-forming grasses (Bertness 1991a,b) and some freshwater tidal wetland species (Parker & Leck 1985), but are more likely to be due to the scarcity of vegetation-free safe sites in the upper marsh. The most common disturbance agent, floating plant debris or wrack, is often caught on *Iva* stems at the lower edge of dense *Iva* stands, and even if wrack penetrates into the tall *Iva* zone, this shrub is less susceptible to smothering by wrack than are the grasses and rushes. Vegetation-free microsites are therefore likely to be infrequent in the high marsh. Although competitive exclusion by the canopy in the tall *Iva* zone was not complete, less than 20% of *Aster* and 15% of *Limonium* individuals survived through the second growing season, and none produced seed. In contrast, a high percentage of individuals reproduced in the second year in vegetation removal plots (T. A. Rand, unpublished data). Thus, lower rates of gap formation in the tall *Iva* zone coupled with strong competitive suppression are likely to limit the successful recruitment of low-marsh plants in this zone. A quantification of gap frequency across zones will be needed to fully understand how this limits the distribution dynamics of such species.

These results generally support the theory that physiological stress limits the lower borders of vascular plant distribution in salt marsh systems, while competition sets the upper limits (Reed 1947; Pielou & Routledge 1976; Bertness 1991a,b). Upper limits to distribution of the low-marsh forbs appear to be determined by the lack of safe-sites, free from competition from dominant plants, while lower limits of the high-marsh species are set by strong abiotically driven inhibition of seedling emergence and survival in the lower marsh zones.

In summary, post-dispersal factors predominate in determining the pattern of plant recruitment across zones. Although dispersal into unoccupied zones was limited, overcoming this limitation by experimentally adding seeds did not extend plant recruitment into previously unoccupied zones due to subsequent post-dispersal factors affecting seedling mortality. However, recruitment of seedlings within those zones naturally occupied by adult plants was seed limited and this may influence the abundance of certain species. Thus, both seed dispersal and post-dispersal factors can influence recruitment dynamics in important ways, and should be studied together to successfully advance our understanding of plant population and community dynamics.

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