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SECONDARY SUCCESSION DYNAMICS IN ESTUARINE MARSHES ACROSS LANDSCAPE-SCALE SALINITY GRADIENTS

CAITLIN MULLAN CRAIN,[1] LINDSEY K. ALBERTSON,[2] AND MARK D. BERTNESS

Department of Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island 02912 USA

Abstract. Secondary succession plays a critical role in driving community structure in natural communities, yet how succession dynamics vary with environmental context is generally unknown. We examined the importance of seedling and vegetative recruitment in the secondary succession of coastal marsh vegetation across a landscape-scale environmental stress gradient. Replicate bare patches were initiated in salt, brackish, and oligohaline marshes in Narragansett Bay, Rhode Island, USA, and allowed to recover unmanipulated or with colonizing seedlings or vegetative runners removed for three years. Seed dispersal and seed bank studies were conducted at the same sites. We found that rates of recovery were 3–10 times faster in brackish and oligohaline marshes than in salt marshes. The fast pace of recovery in oligohaline marshes was driven by seedling colonization, while recovery was dominated by vegetative runners in brackish marshes and by both seedlings and runners in salt marshes. Seed and seedling availability was much greater in oligohaline marshes with up to 24 times the seed bank density compared with salt marshes. In contrast to the facilitated succession generally found in salt marshes, oligohaline marshes follow the tolerance model of succession where numerous species colonize from seed and are slowly displaced by clonal grasses whose recovery is slowed by preemptive competition from seedlings, contributing to the higher species diversity of oligohaline marshes. These findings reveal fundamental differences in the dynamics and assembly of marsh plant communities along estuarine salinity gradients that are important for conceptually understanding wetlands and for guiding the management and restoration of various types of coastal marshes.

Key words: brackish marsh; coastal marsh restoration; community assembly; estuarine salinity gradient; functional groups; life history strategy; oligohaline marsh; salt marsh; secondary succession; seed banks; seedling dynamics.

INTRODUCTION

Disturbance and community recovery are known to play major roles in the community dynamics and species diversity of natural systems (Connell and Slatyer 1977, Sousa 1979). Community response to disturbance depends on three critical stages: (1) dispersal and supply of colonists (Bazzaz 1991, Levine and Murrell 2003), (2) colonist establishment or recruitment (Keddy and Ellis 1985, Rand 2000), and (3) species interactions during secondary succession (Connell and Slatyer 1977, Bertness and Shumway 1993). Environmental context can influence each of these stages, since recruitment can be dependent on abiotic conditions (Noe and Zedler 2000), species interactions can shift across environmental gradients (Bertness and Callaway 1994, Crain 2008), and adult occupancy has direct feedbacks on the supply of new colonists (Rand 2000). While the importance of abiotic factors in driving plant colonization and community assembly has been well studied, here we examine how variation in environmental stress across landscape spatial scales drives shifts in the supply of colonists and subsequent species interactions and dictates the trajectory of secondary succession and assembly of estuarine plant communities.

Coastal wetland plants experience strong gradients in physical stress across landscape scales in estuaries as salinity and other marine influences (e.g., sulfides) decline from salt marshes to brackish and low-salinity oligohaline marshes upriver. Wetland vegetation mirrors this shift, varying from low-diversity systems generally dominated by perennial grasses in salt marshes, to higher diversity systems of grasses and forbs in oligohaline marshes (Odum 1988, Crain et al. 2004). Marshes at all salinities are subject to tidal influence and physical disturbance from wrack deposits (Brewer et al. 1998*a*), ice scouring (Ewanchuk and Bertness 2003), small-mammal herbivory (Crain 2008), or human activities that can open up bare space on the marsh surface.

Disturbance-generated bare space is known to be important for competitively subordinate species in both salt and fresh marshes (Wilson and Keddy 1988, Bertness et al. 1992, Baldwin and Mendelssohn 1998).

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[1] Present address: Center for Ocean Health, 100 Shaffer Road, Santa Cruz, California 95060 USA.
E-mail: crainc@biology.ucsc.edu

[2] Present address: Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California 93106 USA.

However, differences in environmental conditions across estuarine salinity gradients likely drive differences in the supply of colonists and species interactions during secondary succession. Bare areas in salt marshes become hypersaline due to lack of plant shading, and high-salt-tolerant seedlings use this space opportunistically as competitive refuges from dominant plants (Bertness et al. 1992, Allison 1995, Pennings and Richards 1998). Vegetative runners, clonally integrated to plants in less harsh environments, also penetrate bare areas of the salt marsh (Allison 1995, Brewer et al. 1998*b*). These early colonists shade and engineer the environment, lowering salinities, and enabling climax species to recolonize in a classic example of facilitated succession (Bertness and Shumway 1993). Bare areas in less saline marshes do not become hypersaline, and competitive interactions between plants are relatively more important in these marshes (Crain et al. 2004, Crain and Bertness 2005). Studies in low-salinity wetlands have also emphasized the importance of seed banks (Leck and Simpson 1995, Baldwin et al. 1996), while the importance of sexual reproduction in salt marshes is thought to be low due to salt stress and herbivory (Bertness et al. 1987, Shumway and Bertness 1992, Noe and Zedler 2000). No studies, however, have investigated how succession dynamics vary across landscape-scale estuarine salinity gradients where both species pools and environmental conditions change.

To examine how environmental stress influences propagule availability and plant succession, we conducted experiments in coastal wetlands of southern New England with varying salinities. We addressed the following questions: (1) How does the rate and trajectory of community recovery vary across estuarine salinity gradients? (2) How does the supply and pool of sexual recruits vary across estuarine salinity gradients? and (3) Does the role of different functional groups (annual seedlings vs. perennial runners) in secondary succession shift across estuarine salinity gradients? To address these questions, we conducted a field experiment to quantify the rate and mechanisms of secondary succession and quantified seed dispersal and seed bank dynamics in marshes across estuarine salinity gradients of southern New England. Together, these experiments reveal how wetland secondary succession and community assembly vary with shifting environmental context, which is an important ecological understanding for restoring and managing wetlands in changing environments.

METHODS

Study sites

Secondary succession and seed bank experiments were conducted in representative salt (>28 ppt), brackish (10–20 ppt), and oligohaline (0–5 ppt) marshes in Narragansett Bay, Rhode Island, USA. Experiments were located within the *Spartina patens* (Ait.) Muhl zone common to marshes of all salinities at mid-tidal elevations. Salt marsh sites for the secondary succession experiment were located in two marshes (Nag East and West) on Prudence Island and a brackish and oligohaline marsh site were located along two rivers entering Narragansett Bay, the Barrington and Palmer Rivers (see Crain et al. 2004 for further site descriptions). Seed bank study sites were distributed 50–100 m apart in Nag West salt marsh and in brackish and oligohaline regions of the Barrington River. Co-occurring species in the *S. patens* zone varied in marshes with different salinities. In salt and brackish marshes, *S. patens* dominates >95% of the zone, with *Salicornia maritima* Wolff and Jefferies and *Distichlis spicata* L. occurring in the salt marsh, and *D. spicata*, *Pluchea odorata* (L.) Cass. var. odorata, and *Schoenoplectus robustus* (Pursh) M. T. Strong occurring in the brackish marsh. In oligohaline marshes, the *S. patens* zone had much greater plant species diversity, including *Agrostis stolonifera* L., *Solidago sempervirens* L., *Festuca rubra* L., *Eleocharis* spp., and *Argentina anserina* (L.) Rydb. In addition to changes in plant composition, the aerial coverage of the *S. patens* zone itself changes across the estuarine salinity gradient. In salt marshes, *S. patens* is the sole dominant zone of mid-tidal elevations, whereas in brackish marshes, stands of *Schoenoplectus robustus and Phragmites australis* (Cav.) Trin. ex Steud. are also common, and in oligohaline sites *S. robustus*, *P. australis*, *Typha angustifolia* L., and *Juncus gerardii* Loisel. occur in mid-tidal elevations (see Crain et al. 2004).

Secondary succession experiment

A secondary succession experiment was conducted to examine how variation in environmental stress shifts the importance of different functional groups (seedlings vs. vegetative runners) and drives secondary succession dynamics in estuarine marsh vegetation. Experimental bare areas (0.25 m^2) were created to mimic natural bare areas created by wrack deposition or ice scour (Bertness and Shumway 1993). Eighteen bare areas were established in each of six marsh sites (two marsh sites of each salinity: salt, brackish, and oligohaline). Plots were marked in August 2002 and treated with RoundUp systemic herbicide (Scotts Miracle-Gro Company, Marysville, Ohio, USA) during peak growing season so that plants fully incorporated the herbicide, killing both above- and belowground tissues. The following April, plots were cleared of aboveground biomass with a weed-whacker (see Crain et al. 2004).

The artificial bare patches were then randomly assigned to three weeding treatments: control, runners (vegetative growth) removed, or seedlings (sexual colonists) removed ($n = 6$ per treatment/salinity/marsh site) in May 2003. Weeding treatments were maintained every two weeks in spring and less frequently later in the growing season when less regrowth was observed. Seedlings were removed by manual weeding and vegetative runners were removed by cutting the vegetative growth with a knife as far below the surface or outside the plot as possible and removing the runner. After two growing seasons, the plots at oligohaline and most brackish sites had recovered enough from seedlings so that maintaining treatments became unfeasible without destroying seedling-derived vegetation, and the runner removal treatment was terminated. The percentage of species and bare space cover in experimental plots was assessed by counting the number of cells of a 100-square grid occupied by each species (>1 species could occupy the same square). Percentage cover was then standardized to total cover in the plot and corrected to 100. Cover estimates were taken at the end of the growing season in 2003, 2004, and 2005.

For analysis, percentage cover data was arcsine square-root transformed and salinity treatments were pooled across river sites, since the main effect of river was never significant, enabling us to better interpret interactions of interest. Reduction in bare space cover was used as a measure of plot recovery and analyzed at the end of each growing season with a two-way ANOVA testing the effects of salinity, weeding treatment, and their interaction. To investigate species interactions between functional groups, percentage cover of seedlings and runners was analyzed annually with the same two-way ANOVA (salinity [S], weeding treatment [W], S × W), but with only two levels of weeding treatment (control vs. opposite group removed), since removal of the target group was excluded from the analysis. Post hoc comparisons were performed using Tukey's hsd.

To compare succession trajectories, the effect of weeding treatment on plant species composition was analyzed at each salinity using analysis of similarity. Plant percent cover data after three years of recovery (fall 2005) were square-root transformed and a similarity matrix constructed using the Bray-Curtis similarity index. Similarities were projected in two-dimensional space using nonmetric multidimensional scaling (nMDS). Analysis of similarity (ANOSIM) on a scale of 0 (indistinguishable) to 1 (all similarities within groups are less than any similarity between groups) tested for the effect of weeding treatment on plant community composition. MDS and ANOSIM were performed using PRIMER software (Clarke and Gorley 2001).

Seed bank dynamics

To examine how the pool of sexual recruits varies across estuarine salinity gradients, we conducted seed bank and seed dispersal studies. Sampling was done in April, July, and November 2004 and in April 2005 to compare the seed bank over a growing season and between years. At each sampling period, five soil cores (diameter 10 cm to a depth of 5 cm) were removed from four salt, brackish, and oligohaline marsh sites (total of 20 cores per salinity). Soils were air dried for three days and then spread evenly across 3 cm depth potting soil (Metro 360, Scotts Horticultural Products Company, Marysville, Ohio, USA) in trays (40 × 20 cm) in the greenhouse. Trays were distributed randomly and regularly repositioned, received ambient sunlight with fluctuating greenhouse temperatures from 20° to 28°C, and watered with fresh water as needed to stay moist. Most coastal marsh species prefer growing in freshwater and have maximum seed germination there (Shumway and Bertness 1992, Crain et al. 2004), so germination under freshwater conditions is a good measure of seed bank potential.

Germinating seedlings were identified to species when possible and weeded from the trays. When seedlings were unidentifiable, they were transplanted into larger pots and grown until identification was possible. Trays were monitored until germination ceased, which occurred approximately 9–12 weeks after initial coring. The total number of species (richness) and of individuals of each species (abundance) was recorded for each core.

To examine seed bank persistence, we conducted a seed-barrier experiment. Prior to seed dispersal in late summer 2004, five plots in four marshes of each salinity were flagged. Aboveground vegetation in a 20 cm radius of each plot was removed with a weed-whacker to limit local seed rain. At each site, half of the plot was covered with weed-block cloth pinned to the surface with gardening stakes to prevent dispersing seeds from contacting the soil, and the other half of the plot was left open. In April 2005, soil cores were removed as previously described from underneath the barrier and from paired open areas. Cores were taken to the greenhouse and germinating seeds were quantified as just described to determine the effect of removing one year of fall-dispersing seeds on the composition and abundance of seeds in the seed bank.

To examine the delivery of seeds to marshes of different salinity through seed dispersal, seed traps were placed at each of the seed block plots described above ($n = 20$ traps per salinity) in late summer 2004. Seed traps were styrofoam plates (22 cm diameter) coated with Tanglefoot sticky trap (The Tanglefoot Company, Grand Rapids, Michigan, USA), which effectively captures dispersing seeds and remains sticky despite submersion in water for several months (Rand 2000). Plates were set flush with the marsh sediment on 26 July 2004, collected and replaced on 13 September, and collected again on 14 November. The identity and number of seeds on each plate were scored using a magnifying lens.

For data analysis, seed bank density and seed trap data were square-root ($x + 0.5$) transformed. The total number of seedlings germinating in seed bank studies (seed density) in each of three seasons of 2004 was analyzed in a two-way partly nested ANOVA testing the effects of salinity, season, salinity × season, site(salinity) and site(salinity) × season interaction. Seed bank density in April 2005 was analyzed with a two-way partly nested ANOVA testing the effects of salinity, site(salinity), barrier treatment, and all interactions. Seeds collected on seed traps in 2004 were analyzed using a nested ANOVA testing the effect of salinity and site(salinity).

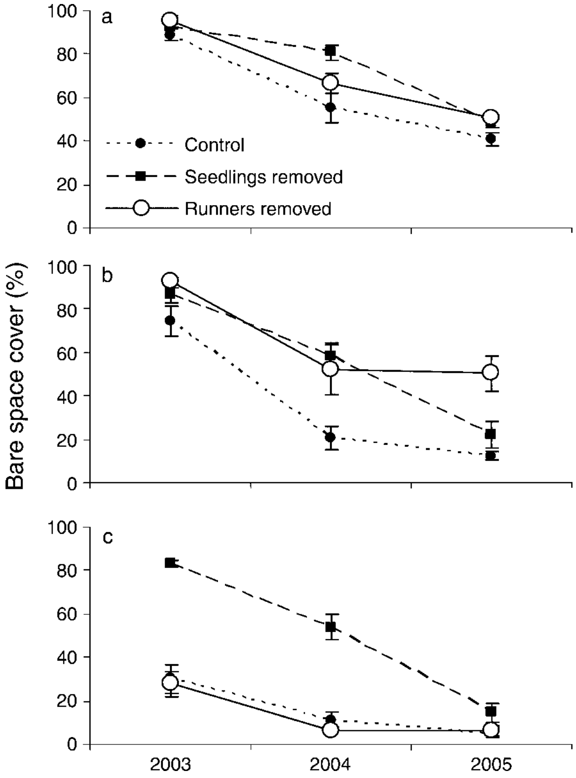

FIG. 1. Percent cover (mean ± SE) of bare space in plots that varied in removal treatment in (a) salt, (b) brackish, and (c) oligohaline marshes in September of three years of the succession study in marshes on Narragansett Bay, Rhode Island, USA. Bare plots were initially established in early spring 2003.

RESULTS

Secondary succession experiment

The rate of succession, measured by the percentage of bare space in plots, varied significantly across salinity in all years of the study (Fig. 1). In control plots, bare space after one season of recovery was 90%, 75%, and 25% in salt, brackish, and oligohaline marshes, respectively, and still differed across salinity after three years (40%, 12%, 4%). Weeding treatment significantly affected bare space in plots, but this effect varied with salinity (Table 1, Fig. 1), indicating that the roles of functional groups in succession shift across salinity.

To identify how functional groups influenced bare space, post hoc comparisons of weeding treatments were conducted for each salinity and year of the study. In salt marshes, weeding treatment effects on bare space cover changed over time. In the first year, neither weeding treatment significantly influenced bare space. In year two, only seedling removals had significantly more bare space than controls, and in year three only runner removals had more bare area than controls (Tukey's hsd). This reversal over time indicates that seedlings drove initial recovery, while runners were responsible for vegetative cover in the longer term. In brackish marshes, bare space was significantly greater in both removal treatments than controls in 2004, but in 2005, runners were able to take advantage of available space, converging on control treatments, and only runner removal plots had more bare space than controls (Tukey's hsd). In oligohaline marshes, bare space colonization by seedlings dominated secondary succession dynamics, and runner removal had no significant effect on bare space cover in any year. As in the other marshes, runner cover increased slowly over the study in seedling removal plots, so that while bare space in these plots was significantly greater than controls in years one and two, it was not significantly different by year 3 (Tukey's hsd).

The importance of seedling and runner recruitment differed by salinity and over the course of succession. Seedling cover in year one was only significantly influenced by salinity (Fig. 2, Table 1), as the cover of seedling recruits was significantly higher in oligohaline than brackish or salt marshes. The effect of runner removal (weeding) on seedling recruits was not significant until years two and three, and the salinity × weeding interaction was only significant in year three (Table 1). In post hoc comparisons within salinity, the

TABLE 1. Results of a two-way ANOVA on percent bare space and cover of seedlings and vegetative runners in secondary succession plots that vary by salinity and weeding treatment, in marshes on Narragansett Bay, Rhode Island, USA.

		2003			2004			2005		
Cover	Treatment	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*
Bare space	Salinity	55.54	2, 104	**<0.0001**	33.54	2, 104	**<0.0001**	74.50	2, 103	**<0.0001**
	Weeding	9.80	2, 104	**0.0001**	26.51	2, 104	**<0.0001**	9.61	2, 103	**0.0002**
	S × W	11.33	4, 104	**<0.0001**	4.02	4, 104	**0.0047**	6.70	4, 103	**<0.0001**
Seedling cover	Salinity	95.73	2, 68	**<0.0001**	16.03	2, 67	**<0.0001**	61.26	2, 67	**<0.0001**
	Weeding	0.14	1, 68	0.71	4.63	1, 67	**0.04**	21.36	1, 67	**<0.0001**
	S × W	0.76	2, 68	0.47	2.63	2, 67	0.08	3.94	2, 67	**0.02**
Runner cover	Salinity	5.10	2, 69	**0.01**	17.20	2, 70	**<0.0001**	28.69	2, 68	**<0.0001**
	Weeding	0.51	1, 69	0.48	2.70	1, 70	0.11	7.67	1, 68	**0.01**
	S × W	1.97	2, 69	0.15	3.80	2, 70	**0.03**	3.07	2, 68	**0.05**

Notes: Marsh salinity variables were: salt, brackish, and oligohaline marshes. Weeding treatments were: control, runners removed, seedlings removed. For analysis of seedling and runner cover, plots where that functional group was weeded were excluded from the analysis, so the weeding effect had only two levels (i.e., control vs. runner removal for seedling cover). Boldface type indicates significance at the $P \leq 0.05$ level.

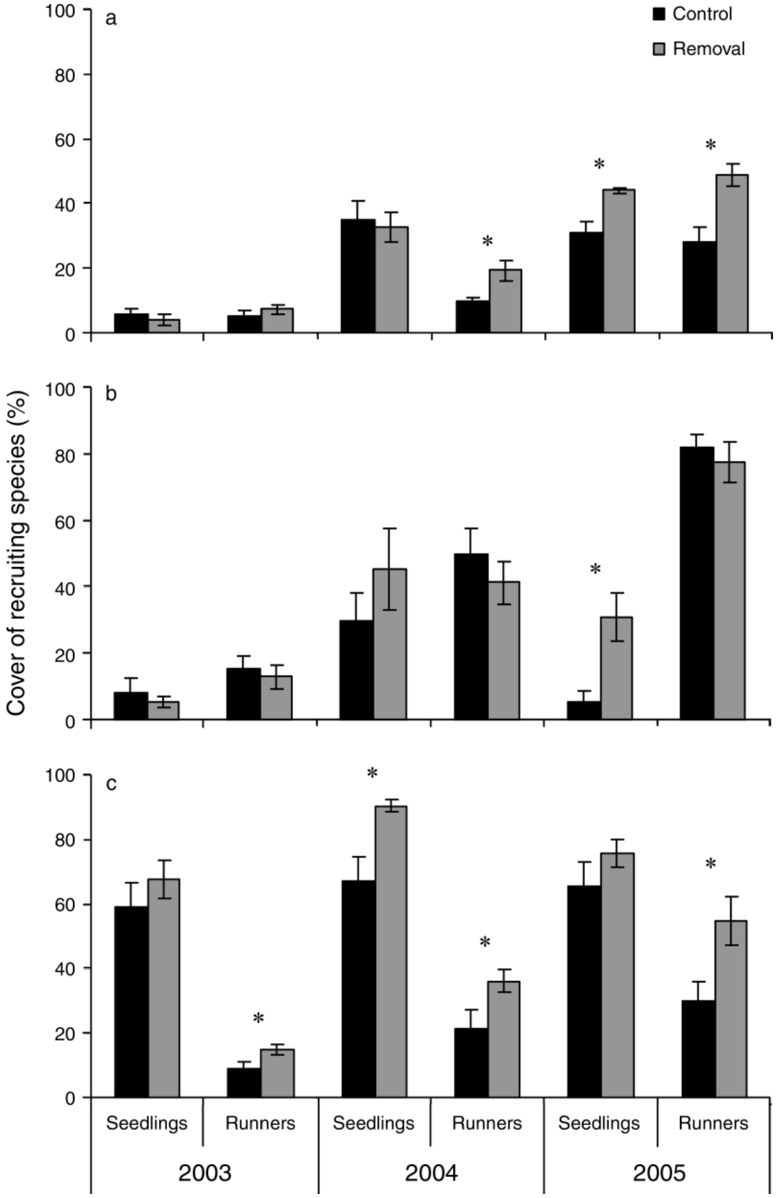

FIG. 2. Percent cover (mean ± SE) of species that recruited from seedlings or runners in control plots or plots where the other functional group was removed over three years of succession in (a) salt, (b) brackish, and (c) oligohaline marshes. Single asterisks signify statistically different cover in control vs. removal plots at the $P < 0.05$ level.

effect of runner removal on seedling cover was only significant in year three in salt and brackish marshes and year two in oligohaline marshes, indicating a time lag until runner cover is substantial enough to competitively suppress seedlings.

Runner cover in succession plots also varied due to salinity and seedling removal over time. Runner cover was only significantly influenced by salinity in year one, and the salinity × weeding interaction was significant in years two and three (Table 1), again showing that biotic interactions gain in importance over time. Within salinity, post hoc comparisons showed that the effect of seedling removal in salt marshes was significant for runner cover in years two and three and in oligohaline marshes in every year. In brackish marshes, seedling removal never significantly influenced runner cover (Fig. 2).

After three years of succession, the effect of weeding treatments on plant community composition varied depending on marsh salinity. In the salt marsh, both runner and seedling removal significantly altered community composition compared with controls (ANOSIM, $P = 0.001$ for both seedling and runner removal vs. control). In the brackish marsh, runner removal significantly altered community composition compared with controls, but seedling removal did not (ANOSIM, $P = 0.4$ for seedling removal vs. control and $P = 0.001$

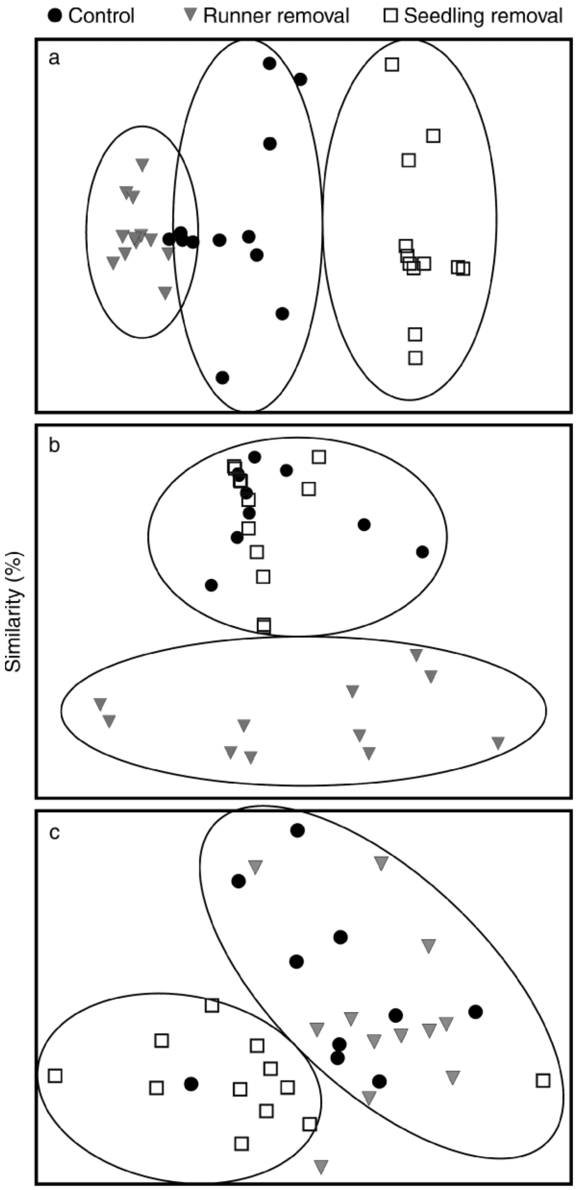

FIG. 3. Nonmetric multidimensional scaling on vegetation percent cover in fall 2005, after three years of recovery, within the (a) salt, (b) brackish, and (c) oligohaline marshes in plots that varied by removal treatment. Plots at greater distances were more dissimilar in composition. Significantly different groups ($P = 0.001$), as determined by ANOSIM, are circled.

for runner removal vs. control) while in oligohaline marshes, the opposite pattern was found where only seedling removal significantly altered composition compared with control (ANOSIM, $P = 0.001$ for seedling removal vs. control and $P = 0.46$ for runner removal vs. control; Fig. 3).

Seed bank dynamics

The density of seeds in marsh seed banks varied significantly across salinity and with time (Fig. 4, Table 2). In spring 2004, seed bank density in the oligohaline marsh was 8 and 24 times greater than brackish and salt marshes, respectively. The effect of salinity on seed bank density varied seasonally (salinity × season interaction, $F_{4,18} = 12.15$; $P < 0.0001$), since total germination declined from spring to fall. Seed bank density varied significantly across sites nested within salinity, and this effect also varied with season (site[salinity] × season interaction, $F_{6,179} = 4.13$; $P = 0.0007$). The number of seeds trapped during passive dispersal also declined significantly as marsh salinity increased ($F_{2,9} = 47.15$; $P < 0.001$; Table 2) and across sites within salinity ($F_{2,59} = 9.08$; $P < 0.001$).

When plots were prevented from receiving seed rain in fall 2004, the number of germinating seeds the following spring was lower in plots with seed barriers compared with open plots ($F_{1,111} = 11.19$; $P = 0.0011$), varied across salinity ($F_{2,12} = 102.48$; $P < 0.0001$) and site nested within salinity ($F_{3,111} = 10.88$; $P < 0.0001$) with no significant interactions. Examination of germinating seedlings indicated that the species largely responsible for differences in seedling density between barrier and open plots was *Typha angustifolia* in the oligohaline marsh and *Salicornia maritima* and *Spartina patens* in the salt marsh.

DISCUSSION

Our results reveal that the dynamics of secondary succession and assembly of marsh plant communities shift across landscape-scale estuarine salinity gradients of southern New England. Salt marshes are edaphically harsh habitats where seedling recruitment was limited and bare patch colonization was slow and dependent on vegetative runners integrated with nonstressed neighbors. Previous studies in larger bare patches have shown that succession in New England salt marshes is dependent on facilitation (Bertness and Shumway 1993). In contrast, bare patch colonization and secondary succession in oligohaline marshes was much more rapid, driven largely by seedling recruitment, and secondary succession followed a tolerance model of succession where competitive interactions slowed rates, but did not prevent succession. Thus marshes along estuarine salinity gradients, while superficially similar due to similar dominant species, have dramatically different assembly rules, respond differently to natural and human disturbances, and must be managed and restored accordingly.

Pace of succession across environmental gradients

The pace of marsh vegetation recovery from disturbance varied significantly across the estuarine salinity gradient. Bare space in control plots was more than two times greater in brackish and three times greater in salt than in oligohaline marshes after one season. Moreover, while bare space decreased over time at all marsh salinities, initial differences in colonization set recovery trajectories, and after three years, bare space in salt and

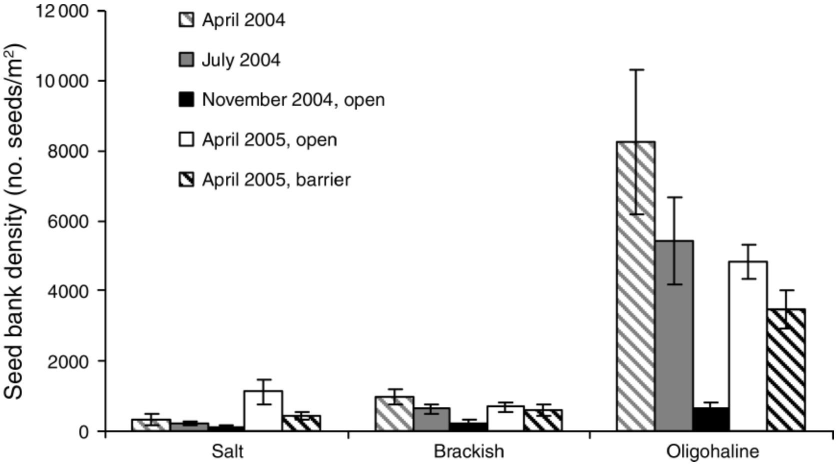

FIG. 4. Seed bank density (mean ± SE) in marshes of different salinity over seasons and in plots where fall seed rain was experimentally removed (barrier vs. open).

brackish marshes was still more than four and three times greater, respectively, than in oligohaline marshes.

Longer recovery time from disturbance under harsher environmental conditions has been found previously in salt marshes due to variation in physical stress across intertidal elevations (Bertness and Ellison 1987), with freshwater input (Bertness and Shumway 1993), and with varying bare patch size (Shumway and Bertness 1994). We found that the pace of secondary succession also varies across landscape-scale stress gradients in estuaries, with succession being significantly faster in the more benign oligohaline and brackish marshes.

Bare patches in salt marshes become hypersaline due to increased evaporation rates in the absence of vegetation that ameliorates environmental conditions (Bertness et al. 1992). Hypersaline soils limit seedling germination and performance (Shumway and Bertness 1992, Baldwin et al. 1996, Noe and Zedler 2000). In brackish and oligohaline marshes, the potential for the development of hypersaline soils is reduced, making the background physical environment less limiting to seed germination and seedling survival (Crain and Bertness 2005) and thus recovery is much more rapid. Consequently, environmental stress is an important factor driving the pace of postdisturbance recovery and the effects of disturbance are more persistent over time in salt marshes.

Shifting role of functional groups across environmental gradients

The roles of seedlings and vegetative runners in secondary succession shift across estuarine salinity gradients. In the salt marsh, both functional groups have important roles during secondary succession. Removal of either group slowed the rate of succession substantially (Fig. 1), and after three years of recovery, community composition in control treatments (as assessed by MDS) was an equal mix of the species present in the two removal treatments. Salt marshes are relatively species poor and few species dominated each functional group, with *Salicornia maritima* the only seedling germinating in the field in any abundance, and *Distichlis spicata* and *Spartina patens* the only runners. While previous studies have documented facilitative succession in salt marshes, we found competitive interactions between functional groups, since both seedlings and runners benefit from removal of the other. This may be due in part to the small size of our experimental plots, where severe hypersalinity does not develop because of shading by neighboring plants (Shumway and Bertness 1994). In addition, both functional groups contain an early-successional species, *Salicornia* recruits from seed and *Distichlis* from runners, and both of these species have been previously shown to facilitate the climax community (Bertness 1999). Potentially, these two early colonists have redundant roles as facilitators, and so removal of either functional group results in competitive release for the other group, while facilitation is still important for establishment of the *S. patens* climax community.

In the brackish marsh, vegetative runners were almost exclusively responsible for driving the pace of recovery (Fig. 1) and composition (Fig. 3) of succession plots. This pattern was not apparent until the third year of recovery where control and seedling removal plots in the brackish marshes had recovered substantially and runner removal plots still had significant bare space. In the first two years, the importance of runners was masked by the ability of seedlings to respond opportunistically to bare space. The availability of seedling colonists, however, was quite patchy, with one brackish site having substantial recruitment of a single species, *Pluchea odorata*, while the other did not. The brackish marsh is intermediate between the two others in that the environmental conditions are less severe, enabling succession to proceed quickly in the absence of any

TABLE 2. Species list (with growth strategy) and densities of seeds caught in seed traps (T), seedlings germinating from the seed bank (B), and seedlings colonizing bare patches in the field (F).

	Salt			Brackish		
Species	T (no./m^2)	B (no./m^2)	F (% cover/0.25 m^2)	T (no./m^2)	B (no./m^2)	F (% cover/0.25 m^2)
Salicornia maritima (A)	0	12.74 (2.74)	3.8 (1.7)	0	70.06 (32.64)	0.17 (0.16)
Distichlis spicata (P)	5.26 (0.14)	0	0	294.78 (5.26)	0	0
Iva frutescens (P)	0	0	0.43 (0.43)	0	0	1.01 (0.69)
Spartina patens (P)	6.58 (0.12)	25.48 (14.9)	0	198.72 (3.48)	414.01 (109.3)	1.34 (0.66)
Phragmites australis (P)	79.0 (0.76)	0	0	84.22 (0.65)	6.37 (6.37)	0
Juncus gerardii (P)	0	356.69 (157.27)	0	0	369.43 (154.62)	0.32 (0.21)
Carex spp. (P)	1.32 (0.05)	0	0	26.32 (0.23)	6.37 (6.37)	0
Triticum aestivum (A)	0	76.43 (43.74)	0	0	0	0
Eleusine indica (A)	0	6.37 (6.37)	0	0	0	0
Pluchea odorata (A)	0	0	0	0	0	3.97 (1.42)
Festuca rubra (P)	0	0	0	0	0	0
Triglochin maritima (P)	0	0	0	0	0	0
Typha angustifolia (P)	0	0	0	56.59 (0.82)	0	0
Agrostis stolonifera (P)	0	0	0	0	6.37 (6.37)	0
Solidago sempervirens (P)	0	0	0	0	38.22 (26.3)	0
Aster spp. (A)	0	0	0	0	0	0
Atriplex patula (A)	0	0	0	0	6.37 (6.37)	0
Cyperus strigosus (P)	0	0	0	0	0	0
Rorippa islandica (A)	0	0	0	0	0	0
Paspalum laeve (P)	0	0	0	0	6.37 (6.37)	0
Schoenoplectus robustus (P)	0	0	0	0	0	0
Amaranthus cannabinus (A)	0	0	0	0	6.37 (6.37)	0
Clethra alnifolia (P)	0	0	0	0	0	0
Unidentified species	0	12.74 (8.77)	0	117.12 (2.19)	44.59 (19.11)	0
Average total density	92.12 (21.98)	331.21 (152.53)	N/A	777.75 (193.23)	974.52 (218.95)	N/A
Species richness	4	7	2	6	13	4

Notes: Growth strategy is annual (A) or perennial (P). The table reports densities of seeds caught in traps (T, no./m^2) and seedlings germinating from the seed bank (B, no./m^2) in April 2004, and percent cover of seedlings colonizing bare patches in the field in runner removal plots (F, % cover/0.25 m^2) in the first year of the secondary succession study. N/A = not applicable. Numbers are means with standard errors in parentheses. $N = 20$ sticky traps (22 cm diameter), 20 soil cores (diameter 10 cm to a depth of 5 cm), and 12 bare plots (0.25 m^2) for seed traps, seed bank, and field colonists, respectively. Total number of unidentified species was 1, 7, 0 for seed traps, seed bank, and field colonists, respectively. Species richness includes unidentified species, which in some cases were >1. Scientific authorities for species not previously listed in the manuscript text are as follows: *Eleusine indica* (L.) Gaertn., *Iva frutescens* L., *Triticum aestivum* L., *Triglochin maritima* L., *Atriplex patula* L., *Cyperus strigosus* L., *Rorippa islandica* (Oeder) Borbas, *Paspalum leave* Michx., *Amaranthus cannabinus* (L.) Sauer, and *Clethra alnifolia* L.

facilitation. However, the supply of seedling recruits in the brackish marsh is much less diverse or abundant compared with the oligohaline marsh, giving runners the advantage in driving succession dynamics.

As opposed to patterns in salt and brackish marshes, recovery and secondary succession in oligohaline marshes was dominated by seedlings that were responsible both for the pace of recovery (Fig. 1) and community composition (Fig. 3) of succession plots. Previous research in oligohaline marshes has documented the opportunistic use of disturbance patches for seedlings that are rare in undisturbed marsh (Baldwin and Mendelssohn 1998). Seedling removal significantly benefited runner cover in all years of the study (Fig. 2), indicating that seedlings slowed the invasion of dominant graminoids. However, because these graminoids successfully invaded into control plots with high initial seedling cover over time, succession in these marshes is not inhibited by early colonists. Instead, succession follows a tolerance model (sensu Connell and Slatyer 1977) where all species can occupy the physical conditions present, but are distributed over time due to growth strategy and competitive hierarchies. Seedlings opportunistically occupy early-successional niches, but eventually are displaced by dominant grasses.

In marshes of all salinities, interactions between functional groups tended to shift from neutral to negative over the course of secondary succession (Fig. 2). Initially, biomass is so low that biotic interactions play a minimal role, but as biomass accumulates over time, competition between functional groups increases. This trend follows general trends of species interactions across productivity gradients (Wilson and Keddy 1986, Gaudet and Keddy 1995).

Dynamics of estuarine salinity gradients may vary in other regions such that local climatic conditions drive hypersalinity in brackish areas or freshwater flooding pulses in salt marshes. These local climatic conditions may alter succession dynamics from the unidirectional salinity gradient found in estuarine marshes of New

Table 2. Extended.

Oligohaline		
T (no./m^2)	B (no./m^2)	F (% cover/0.25 m^2)
0	0	0
110.54 (1.87)	0	0
0	0	0
288.2 (1.57)	267.52 (84.15)	4.58 (1.12)
356.64 (3.52)	89.17 (29.37)	0
0	2834.4 (630.13)	18.84 (8.8)
39.48 (0.76)	70.06 (45.72)	4.8 (2.21)
0	0	0
0	0	0
0	70.06 (26.9)	8.87 (4.19)
0	0	1.13 (1.13)
0	0	0.90 (0.53)
1418.65 (14.64)	318.47 (139.09)	2.32 (0.7)
0	3949.05 (1805.97)	18.14 (6.45)
0	528.66 (103.44)	15.5 (3.55)
0	6.37 (6.37)	0
0	0	0
0	6.37 (6.37)	0
0	6.37 (6.37)	0
0	0	0
0	0	0.94 (0.52)
0	0	0
0	6.37 (6.37)	0
123.7 (2.36)	121.02 (75.91)	0
2337.21 (428.56)	8267.52 (2064.51)	N/A
6	14	10

England; however these deviations are likely predictable based on background soil salinities. Just as climatic shifts across latitude influence the importance of positive and negative plant interactions within salt marshes (Pennings and Richards 1998, Bertness and Ewanchuk 2002), background salinity levels likely drive the degree of seedling recruitment and subsequent species interactions during succession in estuarine marshes. For instance, facilitation during secondary succession is extremely important for disturbance recovery in salt marshes of the southeastern United States where soils are regularly hypersaline, more so than in New England (Pennings and Richards 1998). In salt marshes of California dominated by high-seed-producing plants, disturbance recovery is nonetheless driven by vegetative runners (Allison 1995), since seedling germination is limited by high salinities (Noe and Zedler 2000). However, in years of high freshwater input to salt marshes, seedling recruitment increases (Zedler 1983, Allison 1992) and is likely more important in succession dynamics. While soil salinities and species composition vary in estuarine marshes of the world, we suspect that the overall trends in succession dynamics across estuarine salinity gradients described here apply generally across other systems experiencing gradients in limiting physical stressors.

Seed bank dynamics across estuarine gradients

The importance of seed dispersal, seed bank density, and bare patch colonization by seedlings is dramatically greater in oligohaline than brackish or salt marshes, likely due to the larger species pool, greater seed production, and less limiting environmental conditions in less saline marshes. Salt and sulfides restrict and limit the number of halophytes capable of living in salt marshes. Because more species can persist in oligohaline marshes, there is a greater number of seed-producing plants with local seed dispersal (Parker and Leck 1985, Rand 2000). In addition, because bare spaces do not become hypersaline in oligohaline marshes, seed banks are a more important strategy than in salt marshes, which rely on vegetative regrowth (Brewer and Bertness 1996). Together these factors lead to a large local species pool and seed bank in oligohaline marshes that can successfully germinate in the field (Table 2). This landscape scale variation in species pool sets the stage for variation in secondary succession dynamics.

Previous studies have shown that while seed banks will vary with zones of aboveground vegetation (Parker and Leck 1985), in perennial-dominated systems there tends to be low similarity between seed bank composition and aboveground vegetation, since high seed dispersal leads to well-mixed seed banks (Ungar and Woodell 1993, Baldwin et al. 1996, Egan and Ungar 2000). One study that examined seed banks across a landscape spatial scale in tidal freshwater wetlands found high species overlap, but greater variation across sites than studies within marsh zones (Peterson and Baldwin 2004). We found a similar pattern where higher species richness is found in seed banks than in dominant vegetation (Crain et al. 2004), but seed bank density and diversity also varied significantly across a landscape-scale estuarine salinity gradient, mirroring the diversity gradient in aboveground vegetation. Soil salinity has been shown to limit seedling germination (Shumway and Bertness 1992, Baldwin et al. 1996, Noe and Zedler 2000) and likely is a dominant driver of the seed bank patterns found in the current study.

Annual variation in seed bank densities leads to temporal shifts in the role and importance of marsh seed banks at all salinities (Fig. 4). In a 10-year study of seed bank dynamics in a tidal freshwater wetland, Leck and Simpson (1995) found substantial annual variation in seed bank and field emergence of seedlings. Interannual variation in climate (Maranon 1998) and freshwater input (Shumway and Bertness 1992) are several factors responsible for this yearly variation in seed bank emergence. Because interannual variation in climate has also been shown to influence species interactions such as the importance of facilitation (Bertness and Ewanchuk 2002), yearly variation in both colonist supply and subsequent species interactions likely drive secondary succession trajectories.

While seed banks can be viable for long periods of time, they are also dependent on periodic replenishment through seed dispersal. In our study we found that when the current year's seed input was experimentally removed, much of the seed bank remained viable, indicating effective seed dormancy for over a year. However, seed bank density was significantly lower in barrier compared with open plots (Fig. 4), indicating that yearly seed dispersal is important for seed bank replenishment. Variation in seed replenishment across a salt marsh successional sequence in Holland led to declining seed banks in older marshes, since few seed-producing plants occur locally in these older marshes (Wolters and Bakker 2002). A similar mechanism drives variation in seed bank density across the estuarine salinity gradient, where local seed inputs decline in saltier marshes leading to lower seed bank densities.

Implications for coastal marsh management and restoration

Coastal marshes are ecologically and economically important habitats that provide critical ecological services such as storm buffering, biochemical filtering, and the provision of nursery ground. These habitats have been heavily degraded historically (Bromberg and Bertness 2005, Lotze et al. 2006) and continue to be threatened by human impacts such as invasive species, eutrophication, and habitat loss (Silliman and Bertness 2004). Consequently, coastal marsh restoration has become a major effort internationally, and restoration efforts are proceeding at an unprecedented rate (Zedler 2000). Understanding community assembly rules across estuarine salinity gradients is an essential component to making restoration efforts of coastal marshes successful (Weiher and Keddy 1995) and for managing marshes whose physical conditions are changing due to human impacts such as freshwater diversion and climate change.

Marsh restoration efforts attempt to utilize community assembly rules in natural systems to improve restoration success. However, during restoration, communities are often assembled on soils that are devoid of biotic feedbacks, both from seed banks, whose density and composition depend on local seed input, and adult plants, whose ecosystem engineering can aerate the soil and shade the substrate, reducing salinities and evaporative water loss. Researchers have identified that plantings of adult conspecifics that provide environmental feedbacks (Callaway et al. 2003, Halpern et al. 2007) or augmentation of seed banks (Leck 2003, Morzaria-Luna and Zedler 2007) can aid vegetation colonization success and thereby improve restoration goals. This study indicates that the value of such approaches will vary depending on the physical context of the restoration effort, with seed banks being more viable in less saline marshes and clonal ramets and biotic feedbacks important in more saline marshes. These fundamental differences in community assembly rules in varying environmental contexts have important implications for wetland restoration success.

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