

RESTORING ASSEMBLAGES OF SALT MARSH HALOPHYTES IN THE PRESENCE OF A RAPIDLY COLONIZING DOMINANT SPECIES

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Abstract: Establishing species-rich plant communities is a common goal of habitat restoration efforts, but not all species within a target assemblage have the same capacity for recruitment and survival in created habitats. We investigated the development of a tidal salt marsh plant community in the presence of a rapidly colonizing dominant species, *Salicornia virginica*, in a newly created habitat in Mugu Lagoon, California, USA. We planted rooted cuttings of *S. virginica*, *Distichlis spicata*, *Jaumea carnosa*, and *Frankenia salina* in single- and mixed-species stands, where each species was planted alone or in combination with *S. virginica* in 4 m² plots. We measured species percent cover, recruit density, canopy structure, and aboveground biomass after three growing seasons. When planted alone, *S. virginica* achieved the greatest cover, up to 70%, followed by *J. carnosa* (55%), *F. salina* (35%), and *D. spicata* (12%). Total percent cover was about 30% lower than in a reference site. For each species, average percent cover and aboveground biomass per plant were generally similar between single-species and mixed planting treatments, suggesting that on the time scale of this study, competition between species was weak. Canopy structure (height, number of layers) and total aboveground biomass of all species were largely unaffected by planting treatments, although *S. virginica* was shorter when planted with *J. carnosa*. *Salicornia virginica* recruits constituted approximately 98% of the cover of seedling recruits into the created site. Despite intense *S. virginica* recruitment, our intervention in the successional process by planting species with poorer colonization abilities, particularly *J. carnosa* and *F. salina*, prevented *S. virginica* from completely dominating the canopy, thus increasing vascular plant richness in the created site. Artificially increased richness may enhance some ecosystem functions and create a seed source to facilitate the persistence of a diverse plant assemblage in restored sites.

Key Words: biomass, competition, diversity, pickleweed, recruitment, restoration, richness, succession

INTRODUCTION

Increased focus on the preservation of biodiversity has shifted conservation programs from emphases on single target species to community- and ecosystem-level restoration efforts (Dobson et al. 1997, Ehrenfeld and Toth 1997, Palmer et al. 1997, Zedler et al. 2001, Peterson and Lipcius 2003). Ecological responses to biodiversity can include increased biomass (Tilman et al. 2001, Callaway et al. 2003) and productivity (Naeem et al. 1994), enhanced nutrient accumulation (Ewel et al. 1991, Callaway et al. 2003), increased stability of ecosystem processes (Tilman 1996), higher resilience following disturbance or stress (Tilman and Downing 1994), stronger resistance to invasion (Hector et al. 2001), and for plant assemblages, increased structural and trophic support for associated fauna (Knops et al. 1999). Thus, restoration strategies that incorporate species assemblages may alter the types or rates of development of multiple ecosystem processes occurring in restored habitats (Zedler et al. 2001, Boyer and Fong 2005), presumably toward those of natural systems.

Restoration of diverse communities presents a challenge when not all species within a target assemblage have the same capacity for recruitment and establishment in restored areas. In particular, species with high recruitment rates (Seabloom and van der Valk 2003) or high levels of stress tolerance (Emery et al. 2001) can dominate restored sites and create monospecific or low diversity assemblages. Competitive dominants with high productivity rates (Callaway et al. 2003) and tolerance of harsh physical conditions, particularly in frequently flooded low salt marsh zones (Pennings and Callaway 1992), can suppress recruitment of additional species. Competition for resources such as nutrients (Warren 2000, Emery et al. 2001) can subsequently maintain low species diversity. Restoration of natural species richness levels under these circumstances is particularly challenging. Inoculation or transplantation of poor faunal (Brady et al. 2002) and plant (Cione et al. 2002) colonizers can increase species richness and create communities that more closely resemble natural conditions.

Salt marsh systems are experiencing a loss of species diversity through a variety of mechanisms, including habitat degradation, alterations of hydrology and nutrient input, and invasions of non-native species (Silliman and Bertness 2004). Restoration efforts often seek to stem this loss and maintain relatively natural plant and animal assemblages. Salt marshes on the west coast of the United States are the focus of extensive restoration efforts, as nearly

70% of the coastal and inland wetlands in that region have been lost or degraded in the last century (Dahl 1990). However, restoring plant communities with natural diversity levels remains a challenge (Zedler et al. 2001). In salt marshes in southern California, the native halophyte *Salicornia virginica* L. (pickleweed) has rapid recruitment rates (Lindig-Cisneros and Zedler 2002, Callaway et al. 2003, Zedler et al. 2003), high tolerance of elevated sediment salinities characteristic of created areas (Barbour and Davis 1970), high productivity (Callaway et al. 2003), and efficient nitrogen utilization (Covin and Zedler 1988, Boyer et al. 2001). These weedy characteristics may lead to rapid *S. virginica* establishment in created habitats and the formation of monospecific stands (Callaway et al. 2003). Our goal was to investigate the competitive dynamics between *S. virginica* and other salt marsh halophytes in order to assess whether *S. virginica* inhibited the development of a diverse marsh vascular plant canopy. We hypothesized that *S. virginica* would competitively dominate the created site in terms of percent cover and aboveground biomass through rapid growth of transplanted cuttings, precluding the establishment of other halophyte species during the initial development of the restored marsh. Later in marsh development, we expected that high natural recruitment rates would further increase *S. virginica* cover in the restored area. We also predicted that planting other halophyte species in single- and mixed-species assemblages would limit *S. virginica* dominance and facilitate the development of a more diverse marsh canopy.

METHODS

We established study plots in a created marsh and an adjacent reference site at Mugu Lagoon, Navy Base Ventura County, southern California, USA (34°11' N, 119°12' W). The created wetland site had been filled to upland elevation with sandy dredge spoils from the main lagoon in about 1950. Dredging the site to tidal elevation in fall 1997 formed an area of mudflat and tidal creeks with graded banks around the perimeter, on which fifty-five 2 × 2 m plots were installed in 1998 (Figure 1). Using a surveying level, we placed the upper edge of each of the plots 0.6 m above mean sea level (MSL) and the lower edge 0.4 m above MSL, approximately encompassing the elevation of the marsh plain in this region of Mugu Lagoon. Qualitative observations suggested that plant establishment and growth patterns were similar at the high and low elevations of the plots; therefore, we report data for the lower portions of the plots only. Based on position relative

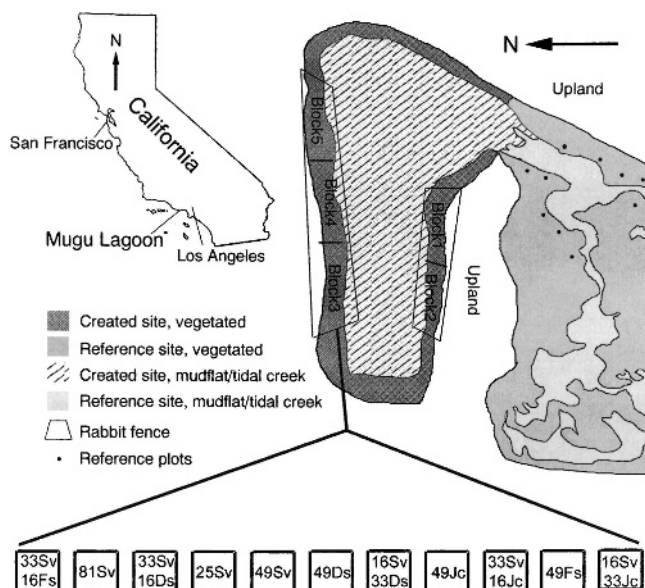


Figure 1. Schematic of study site based on an aerial photo. An example of plot layout within a block is displayed, where Sv = *Salicornia virginica*, Ds = *Distichlis spicata*, Jc = *Jaumea carnosa*, and Fs = *Frankenia salina*.

to the tidal creek entry, the site was split into five blocks of 9–13 plots each. The number of plots per block was determined by the amount of area available at the target elevation. Ten 0.25 m² plots at the same upper elevation (0.6 m above MSL) were concurrently established in the reference site as part of a separate monitoring study.

In March 1998, we planted rooted cuttings (cultivated from local Mugu Lagoon stock by the Tree of Life Nursery, San Juan Capistrano, CA) of four species commonly found in the upper marsh and marsh plain at Mugu Lagoon (Onuf 1987): *Salicornia virginica* (pickleweed), *Distichlis spicata* (L.) Greene (saltgrass), *Jaumea carnosa* (Less.) Gray (salt marsh daisy), and *Frankenia salina* (Molina) IM Johnston (alkali heath). In 45 of the plots, cuttings were planted in 7 × 7 arrays with 25 cm between plant centers. The nine planting mixtures in the 7 × 7 arrays were each of the four species alone (49 plants/plot), 33 *S. virginica* with 16 *D. spicata*, *J. carnosa*, or *F. salina*, and 16 *S. virginica* with 33 *D. spicata* or *J. carnosa* (insufficient *F. salina* were available from the nursery for this treatment) (Figure 1). To monitor the development of the *S. virginica* canopy, *S. virginica* was also planted in 5 × 5 (33 cm between plant centers) and 9 × 9 (20 cm between plant centers) arrays. One replicate of each treatment was randomly assigned to one plot within each block (n = 5 for all treatments). Blocks 1 and 2 did not have sufficient space for the complete

treatment array, and so the five replicates of both treatments with *F. salina* were randomly distributed among blocks 3, 4, and 5.

We maintained the created site plots on a biweekly basis by removing macroalgal mats that rafted onto the plots and removing vascular plant recruits (mostly *S. virginica*). In fall 1998, we installed a chicken wire fence surrounding the study plots to exclude rafting macroalgal mats and reduce herbivory by rabbits. We ceased recruit removal in fall 1999 when it became impossible to distinguish recruits from the original study plants.

At the end of the first growing season (October 1998), we assessed survival of the planted individuals. Mortality was low, and the few dead plants were not replaced. Survival was not quantified in following years when we were unable to distinguish individual plants from each other.

We non-destructively monitored the development of the canopy in all created site plots by measuring percent cover of each species in April 1998 (two weeks after planting) and at the end of the growing season in October 1998, October 1999, and October 2000. Percent cover was determined with the point-intercept method (Robson and Sheehy 1981) by placing in each plot a 0.25 m² plexiglass sheet containing 49 holes that accommodated a vertically oriented laser pointer. We calculated per capita percent cover by dividing the total percent cover of each species by the number of individuals originally planted in the plot. We estimated recruit density in October 2000 (one year after weeding had ceased) by calculating percent cover of species that had not been originally planted in the plots. We also determined percent cover of each species in the reference plots in July 1999.

In October 2000, we made more detailed measurements of canopy characteristics in all created site plots. Canopy structure was measured using the point quadrat method of Wilson (1959) as modified by Keer and Zedler (2002). Ten evenly spaced pins (one mm diameter) were lowered vertically through the canopy and held upright by a PVC frame. The height of each branch-pin contact point was recorded. We calculated average canopy height (sum of the heights of all hits/number of hits) for each species in the plot. To estimate canopy complexity, we calculated for each species in the plot the number of layers in the canopy as the total number of hits divided by the number of pins that were hit. In addition, we measured aboveground biomass within each plot in October 2000 by collecting all biomass within a 0.1 m² circular area, separating the tissue by species, and drying plant material to obtain dry weights. We calculated per capita aboveground

biomass by dividing the biomass of each species by the number of individuals originally planted in the plot.

F_{\max} tests confirmed that all variances were homogeneous, and transformation of the data was unnecessary. Final total and per capita percent cover (in October 2000), number of canopy layers, average canopy height, total aboveground biomass, and per capita aboveground biomass of each species in the created site plots were analyzed with blocked one-factor ANOVA, where the factor was the original planting density of each species. For *S. virginica* response variables, there were eight levels within the planting density factor: 16 *S. virginica* with 33 *D. spicata*, 16 *S. virginica* with 33 *J. carnosa*, 33 *S. virginica* with 16 *D. spicata*, 33 *S. virginica* with 16 *J. carnosa*, 33 *S. virginica* with 16 *F. salina*, and 25, 49, and 81 *S. virginica* alone (Figure 1). For *D. spicata* and *J. carnosa* response variables, there were three levels within the planting density factor: 16 with 33 *S. virginica*, 33 with 16 *S. virginica*, and 49 (alone). For *F. salina* response variables, there were two levels within the planting density factor: 16 *F. salina* with 33 *S. virginica* and 49 *F. salina*. Significant planting density effects were further examined with Tukey-Kramer post-hoc tests.

Recruit abundance was too patchy to use statistical analyses, and so means and standard errors of recruit percent cover (percent cover of species occurring in plots where they were not originally planted) as well as reference conditions are reported without any statistical analysis.

RESULTS

Survival of the planted individuals at the end of the first growing season (October 1998) was generally high for all species. Over 91% of *S. virginica* cuttings survived, as did over 88% of *D. spicata*, 98% of *J. carnosa*, and 92% of *F. salina*.

Total *S. virginica* percent cover in all treatments, whether planted alone or in mixture with other species, increased by a factor of 10 to 20 from April 1998 to October 2000 (Figure 2a). Total percent cover was significantly greater in the high (81 plants) and low (25 plants) density treatments (~70% cover) than in mixtures with *J. carnosa* or *F. salina*, where *S. virginica* cover was only 40% (Table 1, Figure 2a). Mixtures with *D. spicata* and 49 *S. virginica* alone formed an intermediate group with about 55% cover. Block effects were significant for most response variables.

Per capita *S. virginica* percent cover in all treatments, whether planted alone or in mixture with other species, increased by over an order of

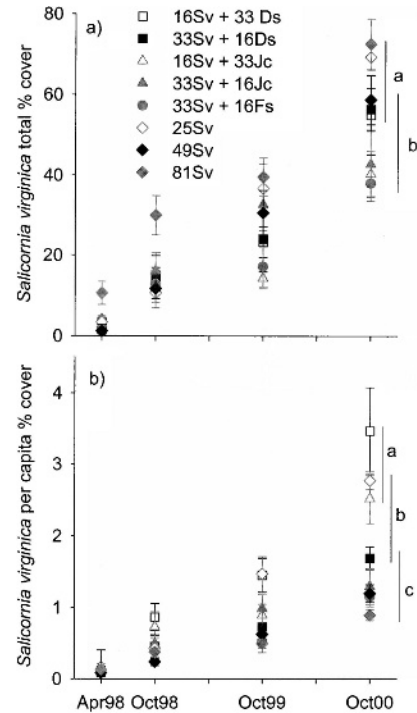


Figure 2. Changes in *Salicornia virginica* (Sv) a) total and b) per capita percent cover when planted alone or in mixtures with *Distichlis spicata* (Ds), *Jaumea carnosa* (Jc), or *Frankenia salina* (Fs). Significant post-hoc Tukey-Kramer tests in October 2000 denoted ($p \leq 0.05$). In all figures, bars represent SE.

magnitude in most treatments over the study period (Figure 2b). Per capita percent cover was significantly greater in treatments where only 16 or 25 *S. virginica* individuals had been planted than in most plots where 33, 49, or 81 individuals had been planted (Table 1).

Total and per capita percent cover of each of the other three species also increased over time, but each responded differently to planting density treatments (Table 1). *Distichlis spicata* total cover increased by a factor of 3 to 10 relative to initial cover but was not significantly affected by planting density (Figure 3a). *Distichlis spicata* did not achieve more than 15% total cover during the study period. Per capita *D. spicata* cover was significantly greater in the lowest density mixed treatment (33 *S. virginica* + 16 *D. spicata*) than in the *D. spicata* alone treatment (Tables 1, 2).

Jaumea carnosa total cover increased by a factor of 3 to 20 over the course of the study (Figure 3b). Total cover was significantly greater when planted alone than when mixed with *S. virginica* at low densities (33 *S. virginica* + 16 *J. carnosa*) (Table 1). Per capita *J. carnosa* cover was not significantly affected by planting density (Tables 1, 2).

Table 1. Results of a blocked one-factor ANOVA of original planting density on total and per capita percent cover of four plant species.

	Total % cover				Per capita % cover			
	df	MS	F	p	df	MS	F	p
<i>Salicornia virginica</i>								
Block	4	763.54	6.12	0.0011	4	1.18	4.08	0.0099
Density	7	707.99	5.67	0.0004	7	4.10	14.19	<0.0001
Residual	28	124.87			28	0.29		
<i>Distichlis spicata</i>								
Block	4	165.67	5.24	0.0227	4	0.17	3.90	0.0481
Density	2	43.38	1.37	0.3076	2	0.20	4.60	0.0469
Residual	8	31.64			8	0.04		
<i>Jaumea carnosa</i>								
Block	4	962.46	6.33	0.0134	4	1.72	3.54	0.0605
Density	2	929.90	6.12	0.0245	2	0.78	1.60	0.2595
Residual	8	152.08			8	0.49		
<i>Frankenia salina</i>								
Block	2	787.00	5.13	0.0502	2	2.03	2.727	0.1437
Density	1	547.23	3.57	0.1078	1	1.25	1.68	0.2430
Residual	6	153.35			6	0.74		

Frankenia salina total cover increased by a factor of 4 to 20 during the study period but was not significantly affected by planting density (Table 1, Figure 3c). Per capita *F. salina* cover also increased

over time but was not significantly affected by planting density (Tables 1, 2).

Salicornia virginica height was the only additional canopy characteristic significantly affected by planting density treatment (df = 7, MS = 30.79, F = 4.38, p = 0.0022). Tukey-Kramer tests indicated that *S. virginica* was often shorter when planted in mixture with *J. carnosa* than when planted alone (49 plant density) or in mixture with *D. spicata* (Figure 4a). None of the heights of the other three species were affected by planting density (all p > 0.05; Table 2). The number of canopy layers, total aboveground biomass, and per capita aboveground biomass of all four species were statistically similar among planting treatments (all p > 0.05; Table 2, Figure 4b–4c), although *S. virginica* biomass tended to be lower in mixtures with other species. Likewise, *S. virginica* per capita aboveground biomass was not affected by planting treatments (data not shown).

Salicornia virginica constituted approximately 98% of the percent cover attributable to seedling recruits. *Salicornia virginica* appeared to recruit into the plots independently of the other species planted there, reaching about 25% cover in all plots where it had not been originally planted (Table 3). Recruits of *J. carnosa*, *F. salina*, and *Limonium californicum* Boissier (sea lavender) were detected at very low densities in one or two plots each. In addition, one *Atriplex* sp. and several *Cordylanthus maritimus* Nutt. ex Benth. ssp. *maritimus* (salt-marsh bird's beak) recruits were noted near the study plots.

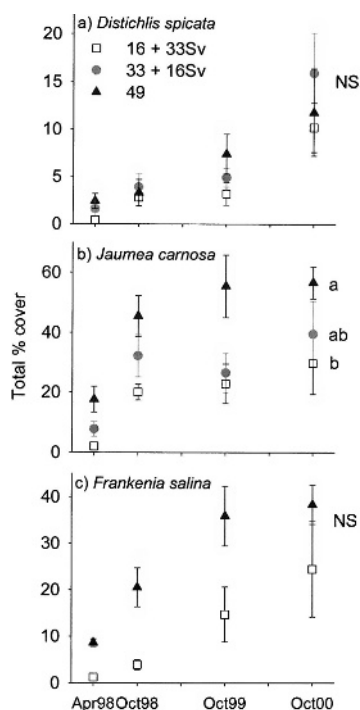


Figure 3. Changes in a) *Distichlis spicata*, b) *Jaumea carnosa*, and c) *Frankenia salina* total percent cover when planted alone or in mixtures with *Salicornia virginica* (Sv). Significant post-hoc Tukey-Kramer tests in October 2000 denoted (p ≤ 0.05). NS indicates no significant density effects. Note different y-axes.

Table 2. Characteristics of *Distichlis spicata* (Ds), *Jaumea carnosa* (Jc), and *Frankenia salina* (Fs) in October 2000 in response to planting density treatments. Sv = *Salicornia virginica*. Values given are means \pm SE. Letters (a, b) denote significant results from Tukey-Kramer post-hoc tests.

TREATMENT	Per capita % cover	Mean plant height (cm)	# Layers	Total aboveground biomass (g dry weight/0.1 m ²)	Per capita aboveground biomass (g dry weight/individual)
<i>Distichlis spicata</i>					
33 Sv + 16 Ds	0.6 \pm 0.2 (a)	4.1 \pm 2.1	0.8 \pm 0.3	1.9 \pm 0.4	0.11 \pm 0.03
16 Sv + 33 Ds	0.5 \pm 0.1 (ab)	3.9 \pm 2.0	1.0 \pm 0.4	4.2 \pm 1.6	0.13 \pm 0.05
49 Ds	0.2 \pm 0.1 (b)	1.8 \pm 0.5	0.8 \pm 0.2	4.9 \pm 2.1	0.10 \pm 0.04
<i>Jaumea carnosa</i>					
33 Sv \pm 16 Jc	1.9 \pm 0.6	4.6 \pm 1.7	1.7 \pm 0.3	21.9 \pm 6.6	1.37 \pm 0.41
16 Sv + 33 Jc	1.2 \pm 0.3	5.0 \pm 2.0	1.9 \pm 0.2	24.8 \pm 9.6	0.74 \pm 0.29
49 Jc	1.1 \pm 0.1	3.5 \pm 0.7	1.9 \pm 0.4	31.3 \pm 5.2	0.64 \pm 0.11
<i>Frankenia salina</i>					
33 Sv \pm 16 Fs	1.5 \pm 0.6	5.0 \pm 0.6	1.7 \pm 0.5	10.8 \pm 6.2	0.67 \pm 0.38
49 Fs	0.8 \pm 0.1	5.8 \pm 0.8	1.7 \pm 0.2	17.6 \pm 2.2	0.36 \pm 0.04

The reference site was dominated by *S. virginica* (average 62.3 \pm 9.7 SE % cover) (Figure 5). *Frankenia salina* (15.6 \pm 7.7), *Suaeda* spp. (5.4 \pm

3.3), and *J. carnosa* (3.9 \pm 4.1) also occurred in the reference site. In addition, *D. spicata*, *L. californicum*, and *C. maritimus* ssp. *maritimus* were observed in the reference site but not in study plots. Comparison of cumulative percent cover (averaged over all plots) between the reference and created sites suggests that although total created site cover approached reference conditions over the study period, plant cover in the created site in October 2000 was still approximately 30% lower than in the reference site, primarily due to lower *S. virginica* cover. *Frankenia salina* and *Suaeda* spp. were more common in the reference site and *D. spicata* and *J. carnosa* were more common in the created site.

DISCUSSION

Salicornia virginica Dominance

Planting multiple species in the created marsh facilitated rapid establishment of a mixed species assemblage with similar richness as in the reference area, although relative species composition, particularly of rarer species, varied between created and reference sites. Some traditional approaches to restoration assume that natural successional processes will return the restored habitat to a natural state once appropriate hydrology has been restored (Suding et al. 2004). However, the vigorous development of the *Salicornia virginica* canopy in the created site and the very low occurrence of recruits of other species suggest that, without our planting efforts, other species would not have become established in the created site or at least would have taken much longer than the three years of our study to colonize the area. By planting other species in mixture with *S. virginica*, even at low densities, we in

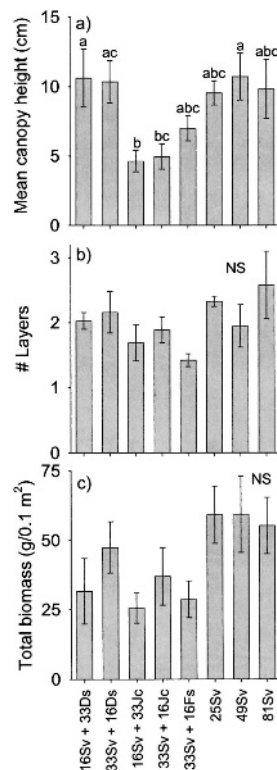


Figure 4. *Salicornia virginica* canopy characteristics in October 2000 when planted alone or in mixtures with *Distichlis spicata* (Ds), *Jaumea carnosa* (Jc), or *Frankenia salina* (Fs): a) average height of the *S. virginica* canopy, b) number of *S. virginica* layers in the canopy, and c) total aboveground biomass. Significant post-hoc Tukey-Kramer tests denoted ($p \leq 0.05$). NS indicates no significant density effects.

Table 3. Average percent cover \pm SE of recruited species that were not originally planted in the plots in October 2000. “-” indicates a plot where the target species was planted and recruits were undetectable; “0” indicates no recruits detected.

TREATMENT	SPECIES				
	<i>Salicornia virginica</i> (Sv)	<i>Distichlis spicata</i> (Ds)	<i>Jaumea carnosa</i> (Jc)	<i>Frankenia salina</i> (Fs)	<i>Limonium californicum</i> (Lc)
Ds only	26.9 \pm 5.8	-	0.2 \pm 0.2	0	0
Jc only	24.5 \pm 2.8	0	-	0.2 \pm 0.2	0
Fs only	23.3 \pm 3.7	0	0	-	0
Sv only	-	0	0.4 \pm 0.4	0.2 \pm 0.2	0.2 \pm 0.2
16 Sv + 33 Ds	-	-	0	0	0
16 Sv + 33 Jc	-	0	-	0.2 \pm 0.2	0
33 Sv + 16 Ds	-	-	0.2 \pm 0.2	0	0
33 Sv + 16 Jc	-	0	-	0	0
33 Sv + 16 Fs	-	0	0	-	0

effect facilitated rapid colonization of plants with poor dispersal abilities, enabling additional species, particularly *Jaumea carnosa* and *Frankenia salina*, to establish among *S. virginica* in the created site. This technique of inoculating restored sites with more slowly-colonizing species in order to increase plant diversity has been used successfully in a variety of habitats, including coastal sage scrub (Cione *et al.* 2002), freshwater wetlands (Fraser and Kindscher 2001), and salt marshes (Lindig-Cisneros and Zedler 2002).

Salicornia virginica readily established in the created site due in part to its weedy characteristics, including its capacity for rapid colonization. Tidal dispersal of *S. virginica* seeds from the adjacent reference area facilitated its colonization of the created site, a pattern seen at other tidal marsh

restoration sites in southern California (Lindig-Cisneros and Zedler 2002, Zedler *et al.* 2003). Generally, salt marsh plants have relatively limited dispersal capacity, with seed distributions reflecting adult plant distribution (Jefferies *et al.* 1981, Rand 2000). In our study, this pattern was evidenced by the lack of recruits in the created site of other taxa like *Suaeda* spp. that commonly occurred in the reference site. Longer-distance dispersal relies heavily on tidal transport (Huiskes *et al.* 1995). Thus, connectivity between the natural and created marshes favors species like *S. virginica* that have the capacity for prolific seed production (Huiskes *et al.* 1995, Rand 2000), tide-mediated dispersal, and high germination rates (Hopkins and Parker 1984, Sullivan 2001). At our study site, the reference and created areas were directly connected by a wide tidal creek, which may have given *S. virginica* an advantage over other halophyte species such as *Distichlis spicata* that often use vegetative growth to colonize new habitat (Bertness and Ellison 1987). Planting additional species in the created area can reduce these *S. virginica* advantages by augmenting adult species richness, which in turn influences future seed bank composition, particularly for those species that tend to recruit in close vicinity to parent plants (Rand 2000).

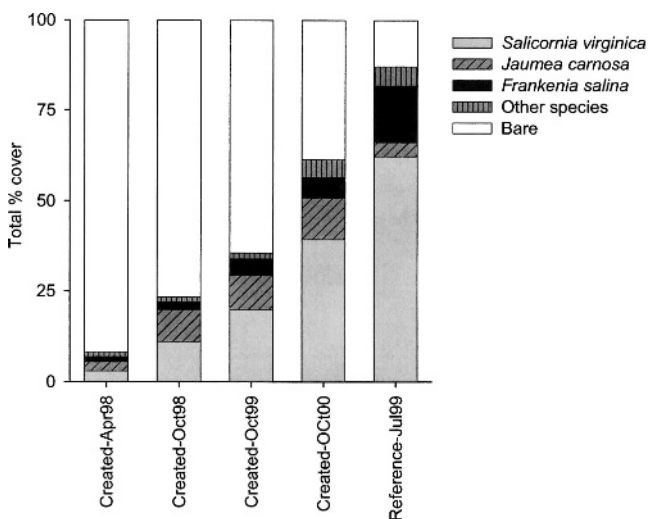


Figure 5. Changes over time in the cumulative percent cover of all species observed in the created site, compared to reference site conditions in July 1999.

The Role of Competition

Interspecific competition probably played a smaller role than recruitment in the dominance of *S. virginica* in our created site. Competition would have been suggested by lower per capita aboveground biomass or cover when planted in mixed assemblages than when planted alone (Engelhardt and Ritchie 2001), but per capita biomass and cover of all species were generally similar between single-

species and mixed planting treatments. Furthermore, planting either *J. carnosa* or *F. salina* prevented *S. virginica* from entirely dominating the canopy. Even *D. spicata* did not appear to be competitively impacted by *S. virginica*, as *D. spicata* generally grew poorly over the course of the study, even when planted alone. *Distichlis spicata* thrived at a higher elevation in a separate restoration project at Mugu Lagoon (K.E. Boyer, unpub. data), suggesting that we planted it at an elevation too low for successful establishment. Thus, despite strong colonization pressure from *S. virginica*, interspecific competition did not appear to be strongly influencing community composition on the time scale of this study. This pattern contrasts to previous studies in which interspecific competition is an important factor regulating the establishment of native species in restored freshwater wetlands (Budelsky and Galatowitsch 2000), grasslands (Dyer and Rice 1997), and salt marshes (Esselink et al. 2000). Competition can also regulate *S. virginica* zonation patterns in other southern California salt marshes (Pennings and Callaway 1992). However, initial plant density can strongly impact the magnitude of competitive interactions, and even our densest planting treatment spaced plants 20 cm apart, which may have been sufficient to alleviate interspecific competitive pressure during the early development of the created site (Huddleston and Young 2004). Intraspecific competition, however, particularly between individuals of *S. virginica*, may have limited recruitment of new *S. virginica* seedlings into the study plots, although we did not specifically measure recruit density in treatments where *S. virginica* was planted alone. Lindig-Cisneros and Zedler (2002) observed lower *S. virginica* recruitment into plots planted with conspecifics, suggesting strong intraspecific competition in this species.

Comparison to Reference Conditions

Despite the intense recruitment of *S. virginica* into the created site, we were able to establish a plant assemblage with a level of richness comparable to reference site conditions, as a total of seven species were noted in both reference and created areas. The resemblance of our created site to reference conditions was partly artificial, as we planted more *S. virginica* than any other species, and we may have somewhat underestimated reference site diversity by using smaller study plots than in the created area. Nevertheless, vigorous *S. virginica* recruitment and establishment in our created site occurred in a similar manner as in a well-documented restoration project in Tijuana River Estuary (TJE), California (Call-

away et al. 2003, Zedler et al. 2003). In the years following marsh creation at TJE, high levels of recruitment (Lindig-Cisneros and Zedler 2002) and survival (Zedler et al. 2003) paralleled our observations at Mugu Lagoon and provide strong support for the assertion that *S. virginica* is likely to colonize created sites unaided, particularly sites close to prodigious seed banks (Hopkins and Parker 1984). We concur with other investigators in the region that planting *S. virginica* is probably not required when restoring halophyte assemblages in southern California tidal marshes (Lindig-Cisneros and Zedler 2002, Callaway et al. 2003). If this restoration strategy is pursued and focus is placed on other species, then the created marsh assemblage would likely consist of clusters of species mixed with *S. virginica*, separated by areas dominated by *S. virginica*. This spatial pattern resembles the natural marsh areas at Mugu Lagoon (R.F. Ambrose, pers. obs.).

The ultimate goal of most revegetation efforts is to reinstate a suite of ecosystem functions, and establishing communities with natural levels of species richness can facilitate achievement of that objective. The species we planted in conjunction with *S. virginica* are known to augment ecosystem functions through contributions to primary productivity (Sullivan and Moncreiff 1988) and nutrient retention (Callaway et al. 2003). In addition, species-rich assemblages can increase canopy complexity (Keer and Zedler 2002), which can in turn augment the value of the stand as foraging habitat for fish during high tide (Rozas and Reed 1993) and nesting grounds for marsh birds (Marshall and Reinert 1990). These functions may not be achieved for a long time if a monospecific stand develops in the new habitat, emphasizing the importance of focusing restoration efforts on those species least likely to colonize the created area.

CONCLUSIONS

Intervention in the successional process by planting species with poorer dispersal and colonization abilities increased the vascular plant richness in the created site, which in turn may enhance some ecosystem functions and create a seed source to facilitate future development of a diverse plant assemblage. Competition between plant species was generally weak during these early developmental stages of the created site, suggesting that planting efforts are likely to be successful in establishing species other than *S. virginica*. Enabling multiple species to establish early in the development of the marsh will promote the persistence of mixed-species

stands with spatial structures resembling natural areas.

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