Journal of Vegetation Science 12: 61-74, 2001

Spatio-temporal variation of salt marsh seedling establishment in relation to the abiotic and biotic environment

Noe, Gregory B.[1,2*] & **Zedler, Joy B.**[1,3]

[1]*Pacific Estuarine Research Laboratory, San Diego State University, San Diego, CA 92182-1870, USA;*
[2]*Current address: Southeast Environmental Research Center, Florida International University, University Park OE-148, Miami, FL 33199, USA;* [3]*Current address: Botany Department and Arboretum, University of Wisconsin-Madison, 430 Lincoln Drive, Madison, WI 53706, USA;* [*]*Corresponding author; Fax +13053484096; E-mail noeg@fiu.edu*

Abstract. Contrary to our expectations, soil salinity and moisture explained little of the spatial variation in plant establishment in the upper intertidal marsh of three southern California wetlands, but did explain the timing of germination. Seedlings of 27 species were identified in 1996 and 1997. The seedlings were abundant (maximum densities of 2143/m^2 in 1996 and 1819/m^2 in 1997) and predominantly annual species. CCAs quantified the spatial variation in seedling density that could be explained by three groups of predictor variables: (1) perennial plant cover, elevation and soil texture (16% of variation), (2) wetland identity (14% of variation) and (3) surface soil salinity and moisture (2% of variation). Increasing the spatial scale of analysis changed the variables that best predicted patterns of species densities. Timing of germination depended on surface soil salinity and, to a lesser extent, soil moisture. Germination occurred after salinity had dropped below a threshold or, in some cases, after moisture had increased above a critical level. Between 32% and 92% of the seedlings were exotic and most of these occurred at lower soil salinity than native species. However, *Parapholis incurva* and *Mesembryanthemum nodiflorum* were found in the same environments as the native species. In 1997, the year of a strong El Niño/Southern Oscillation event with high rainfall and sea levels, the elevation distribution of species narrowed and densities of *P. incurva* and other exotic species decreased but densities of native and rare species did not change. The 'regeneration niche' of wetland plant communities includes the effects of multiple abiotic and biotic factors on both the spatial and temporal variations in plant establishment.

Keywords: Annual plant; ENSO; Exotic species; Heterogeneity; Soil moisture; Soil salinity; Southern California; Upper intertidal marsh.

Abbreviations: CCA = Canonical Correspondence Analysis; DCA = Detrended Correspondence Analysis; ENSO = El Niño/Southern Oscillation; MSL = Mean Sea Level; NGVD = National Geodetic Vertical Datum.

Nomenclature: Hickman (1993).

Introduction

Many conceptual models have been developed to explain spatial and temporal heterogeneity in the establishment of plants. The 'regeneration niche' concept (Grubb 1977) stresses the importance of plant establishment requirements to the control of community dynamics. The patch dynamics concept (sensu Pickett & White 1985) elaborates this idea by suggesting how a mosaic of different habitats can exist at the same time and allow for species coexistence by providing a heterogeneous spatio-temporal environment (Denslow 1985). Several models concern wetlands. In prairie potholes, seeds are described as passing through 'environmental sieves' during germination and establishment (van der Valk 1981). While the original model included only inundation, additional environmental factors have been added to improve prediction (Galinato & Van der Valk 1986). Weiher & Keddy (1995) also found evidence that multiple environmental 'filters' operate during the germination and establishment of riverine herbaceous plant communities. Salinity and flooding have been considered to be the controlling factors in the establishment and distribution of salt marsh plant communities (reviewed by Ungar 1998). Biotic factors, such as competition and facilitation, have also been found to affect the distribution of halophytes (Snow & Vince 1984; Callaway 1994; Ungar 1998). Both abiotic and biotic factors are often used to explain the zonation of halophytes along intertidal elevation gradients (Gray 1992). While multiple factors are now included in conceptual models of seedling establishment, the relative importance to the prediction of wetland plant establishment has not, to date, been quantified.

Germination and establishment are critical to annual plant assemblages. To persist in a community, annual species must germinate and establish frequently or maintain a long-lived seed bank. In salt marshes, germination is triggered by abiotic factors and seedlings are generally less tolerant of environmental stress than adult plants (Waisel 1972; Bannister 1976; Ungar 1978). The upper intertidal marsh of southern California includes many annual species (Callaway et al. 1990; Noe 1999), including endangered (*Cordylanthus maritimus* ssp. *maritimus*), rare (*Lasthenia glabrata* ssp. *coulteri*) and exotic species that occur in areas with sparse perennial canopies (canopy habitat) and at the edges of salt-accumulating depressions (panne habitat, pers. obs.). In the upper intertidal marsh, tidal inundation is infrequent (15 times in 1997, Noe & Zedler in press). Annual plants germinate after winter rainfall has lowered soil salinity and raised soil moisture, plants typically senesce by summer when soils are hypersaline and soil moisture is low (Callaway et al. 1990; Noe & Zedler in press). Callaway et al. (1990) suggested that soil salinity gradients and germination responses to salinity control the distribution of annual plants in this community. However, moisture requirements may also control halophyte distributions (Ungar 1998), especially in this arid region. In addition to soil salinity and moisture, facilitation and competition with perennial species affect the distribution and abundance of annual plant species in this system (Callaway 1994). The distribution and abundance of annual species may also be influenced by intertidal elevation and soil texture, which are surrogates for other correlated factors. Because soil salinity and moisture are frequently at extremely stressful levels, we hypothesize that soil salinity and moisture will explain more variation in the spatial distribution of species' seedling abundance than perennial cover, elevation, and soil texture.

Spatial and temporal heterogeneity is an inherent characteristic of ecological communities (Wiens 1976; Pickett & White 1985; Kolasa & Pickett 1991). The upper intertidal marsh of southern California has a high level of spatial variation, with obvious patchiness of vegetation, soil salinity and moisture at small scales and high temporal variation due to the mediterranean-type climate (Noe & Zedler in press). This spatial and temporal heterogeneity is likely to lead to high variation in seedling distribution and abundance which are hypothesized to differ between the canopy and panne habitats, among marshes, within the rainy season and between years. High heterogeneity can impede the identification of the effects and importance of multiple factors. Borcard et al. (1992) proposed a technique to quantify the amount of variation in the spatial distribution of species' abundance that can be explained by different sets of environmental variables. This technique uses multiple CCA (ter Braak 1988) to separate the effects of different variables into different components of explained variation. The high level of spatial and temporal variation and presence of multiple environmental variables that could influence species' germination and establishment make the upper intertidal marsh of southern California a model system to quantify the relative importance of multiple factors in the prediction of plant establishment.

The scale at which spatial heterogeneity occurs varies for different abiotic and biotic factors (Allen et al. 1993; Dutilleul & Legendre 1993). In the upper intertidal marsh, the spatial scale of heterogeneity depends on the abiotic or biotic factor. We hypothesize that the relative ability of different environmental variables to predict spatial variation in seedling distributions varies with spatial scales (marsh, habitat, plot).

Our goals are to (1) describe the spatial and temporal variation in the distribution and abundance of seedlings in the southern California upper intertidal marsh, (2) determine the relative importance of soil salinity and moisture, perennial cover, intertidal elevation and soil texture, to the prediction of seedling distribution and abundance, (3) examine the effect of changing spatial scale on the relationship between the abiotic and biotic environment and seedling distribution and abundance and (4) identify the establishment requirements for rare and exotic species.

Methods

Study site

Perennial vegetation in the canopy and panne habitats in the upper intertidal marshes of southern California is sparse compared to other vegetated areas. Panne habitat is defined as a five-meter band at the edge of a salt-accumulating depression (panne) and canopy habitat is defined as an area with relatively sparse vegetation in a matrix of dense perennial vegetation. There are obvious visual differences in annual plant assemblages between the two habitats. The two habitats are found at the same elevation but the panne habitat has more bare ground and less perennial cover than the canopy habitat (Noe & Zedler in press). Dominant perennial plant species in both habitats are *Salicornia subterminalis* and *Monanthochloë littoralis*. Canopy and panne habitats were studied at Sweetwater Marsh National Wildlife Refuge (32° 40' N, 117° 5' W), Tijuana River National Estuarine Research Reserve (32° 35' N, 117° 7' W), and Los Peñasquitos Lagoon (32° 56' N, 117° 5' W) in San Diego County, California (Fig. 1). All three wetlands have upper intertidal salt marsh habitats, but their annual and perennial plant assemblages are different. Sweetwater Marsh has large areas of both habitat types, Tijuana Estuary has large areas of canopy habitat and Los Peñasquitos Lagoon has large areas of panne habitat.

In both the canopy and panne, five $1\,\mathrm{m} \times 1$ m plots (each with 25 0.04-m^2 cells) were randomly located along a line transect. The canopy transects spanned the habitat at random orientations and the panne transects were parallel to the salt panne edge. Two plots were located beyond the habitat type at the ends of each transect, giving a total of five ‘in’ and two ‘out’ plots per transect. ‘Out’ plots were included to sample a broader gradient of environmental conditions than is found within the annual plant habitats and to meet the unimodal abundance-environment relationship assumption of CCA. Two transects in both canopy and panne in Sweetwater Marsh, two transects in canopy habitat at Tijuana Estuary, and two transects in panne habitat at Los Peñasquitos Lagoon were established giving a total of three wetlands, four sites, eight transects and 56 plots.

Seedling density

The number of live seedlings of each species was counted through the 1996-1997 (1996) and 1997-1998 (1997) seasons in four permanent 0.04-m^2 cells in each plot that were chosen randomly without replacement. Individuals were counted when cotyledons were visible. Because of high density, seedlings were counted approximately and classified as follows: 0, 1-10, 11- 20, 21 - 30, 31 - 40, 41 - 50, 51 - 100, 101 - 200 and > 200 individuals per cell. Density class midpoints (201.0 for the 200 + class) were used for analyses. Plot density (#/m^2) is 25× the mean value of the four cells. Species were classified as native or exotic using Hickman (1993).

Weekly sampling occurred from 19 December 1996 to 24 February 1997 and was reduced to approximately monthly from 3 March 1997 until 7 November 1997. At Sweetwater Marsh and Tijuana Estuary, sampling occurred biweekly from 19 November 1997 to 31 December 1997 and then monthly from 9 February 1998 to 5 May 1998. After the first year of study regular sampling at Los Peñasquitos Lagoon was abandoned because high inputs of flood-borne sediment at the beginning of the second year covered the plots. Therefore, data from Los Peñasquitos Lagoon were not used to characterize temporal variation in seedling distribution and abundance. However, analyses of spatial variation included Los Peñasquitos Lagoon in order to maximize the spatial generality of this study.

Abiotic and biotic environment

Surface soil moisture and salinity were sampled in the plots when seedling densities were measured. Soil cores were taken to a depth of 2 cm from 19 December 1996 to 31 March 1997, 10 cm from 5 May 1997 to 2 October 1997 and 2 cm from 7 November 1997 to 5 May 1998. Three cores were taken from random cells (excluding the plant-density sampling cells) and combined for each plot (n = 56 in 1996, n = 42 in 1997).

Soil samples were dried at 60° C for 24 hours and soil moisture was calculated as change in mass divided by dry weight (Gardner 1986). Soils in the upper intertidal marsh are typically too dry to extract interstitial water in the field. Therefore, the salinity of saturated soil pastes was measured on the soil sample after coarse organic matter was removed; the sample was ground with a mortar and pestle and passed through a 1-mm sieve. Reverse osmosis water (salinity = 0‰) was added to the soil sample until the saturation point was reached (Richards 1954). The saturated soil sample was then added to a 10 ml syringe loaded with filter paper and a drop of water was expressed onto a temperature-compensated salinity refractometer (Anon. 1990a). All pastes were mixed by the same person (G.B.N.). Saturated soil paste extracts underestimate field soil salinity concentrations, except when field soils are wet, and control for the different moisture retention capacities of soils with different textures (Richards 1954).

Soil texture, elevation, cumulative perennial cover, perennial canopy height and bare ground were measured in the 1-m^2 plots at the beginning of the study. Soil texture analysis was performed with the Bouyoucos

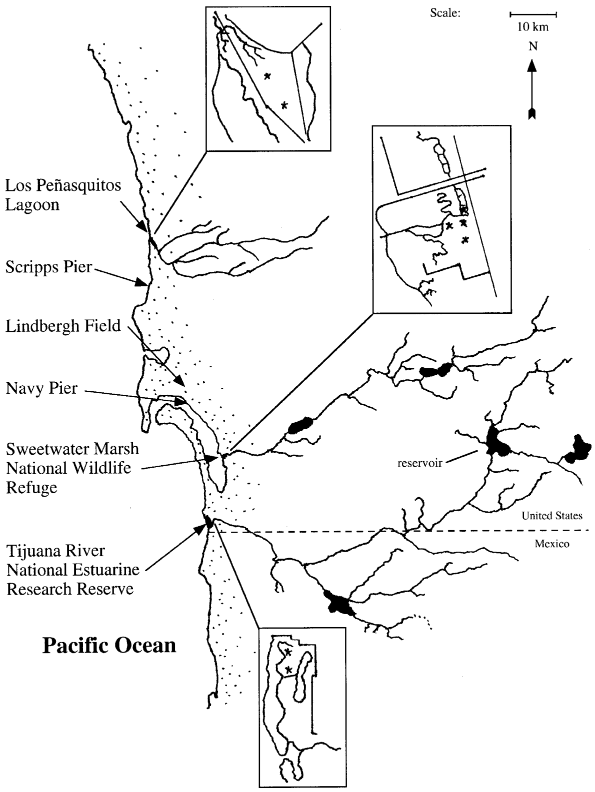

Fig. 1. Map of the southern California coastline, showing coastal wetlands of interest, their associated watersheds, Lindbergh Field and the Scripps and Navy Piers. Inset maps of the three wetlands show the location of transects (*). Note: representation of the Tijuana River watershed in Mexico is not complete; scale is approximate.

(1962) technique on three pooled 2-cm deep soil cores from each plot. Elevation (m NGVD, NGVD = 0.780 m above mean lower low water, 0.628 m below mean high water) was determined in the four permanent seedling count cells in each plot with a Sokkia® kinematic Global Positioning System (vertical accuracy ± 3 cm). Cover of each perennial species and bare ground were estimated by dividing each plot into 100 cells with a grid frame and counting the number of cells occupied by each species or bare ground. Cumulative perennial cover is the sum of the cover of all perennial species and is a measure of canopy layering. Perennial canopy height was estimated by measuring the distance from the soil surface to the horizontal plane of the top of the perennial plants. Cumulative perennial cover, bare ground and perennial canopy height were also estimated within each permanent seedling count cell.

Rainfall and sea surface levels

Soil salinity and moisture are affected by rainfall and tidal inundation (Noe & Zedler in press). Daily rainfall records for 1996-1998 from Lindbergh Field (32° 43' N, 117° 10' W), San Diego County, California (Fig. 1) were obtained from the National Weather Service. Deviations of monthly arithmetic means of hourly sea level elevations from MSL, (19-yr Metonic cycle; National Tidal Datum Epoch) at San Diego Bay (Navy Pier, 32° 44' N, 117° 10' W) and Scripps Pier (32° 52' N, 117° 15' W) (Fig. 1) were obtained from the NOAA Oceanographic Products and Services Division. Salt marshes in the mediterranean-type climate of southern California are subjected to high interannual variability in rainfall, ranging from 9 to 66 cm with a coefficient of variation of 41% over the past 150 yr (Noe & Zedler in press). Although this study occurred over only two years, the rainfall in 1996 and 1997 was typical in that the two years were very different. Therefore, the temporal variation documented in this study can serve as an indication of the variability experienced in southern California salt marshes.

Data analysis

For the analysis of spatial variation in seedling distribution and abundance, we used the maximum seedling density of each species in each 1-m^2 plot during the 1996 season as a measure of germination success. To determine whether the largest source of spatial variation in the maximum density of each species arose from differences between the canopy and panne habitats, among wetlands or in the density of the most abundant species, a DCA of the 1996 season maximum density of each species in each ‘in’ plot (n = 40) was performed with the CANOCO program (ter Braak 1988). A random reordering of the data produced similar site scores, indicating the ordination was stable (Oksanen & Minchin 1997). The relative importance of each of the three sources of spatial variability was tested by determining whether plots separated from each other along the first four axes of the DCA. Non-parametric tests were used to determine if the plots segregated along each axis based on classification by habitat, wetland and whether the density of the most abundant species was greater or less than its median density among all plots. For the dichotomous classifications of habitat type and the relative density of the most abundant species, Mann-Whitney tests (Zar 1996) of plot scores were performed. Kruskal-Wallis tests (Zar 1996) determined if the three wetlands were separated along each axis.

The relative importance of groups of different abiotic and biotic variables to the prediction of plot-scale spatial patterns of each species 1996 season maximum density (n=56) was tested using CCA with the CANOCO program (ter Braak 1988). The technique developed by Borcard et al. (1992) was used to identify the amount of variation in the species matrix that could be explained by different components, or fractions, of the predictor variables. Effects were classified as either (1) surface soil moisture and salinity, (2) ‘other’ predictor variables (i.e., perennial cumulative cover, perennial canopy height, bare ground, surface soil sand and clay content, and elevation), (3) the wetland where the plot was located (wetland identity) and (4 – 6) three components of overlapping prediction among two components (e.g. joint prediction between ‘other’ predictors and salinity and moisture) (Fig. 2). Grouping of variables was used to test the importance of soil salinity and moisture compared to other variables and the effect of wetland

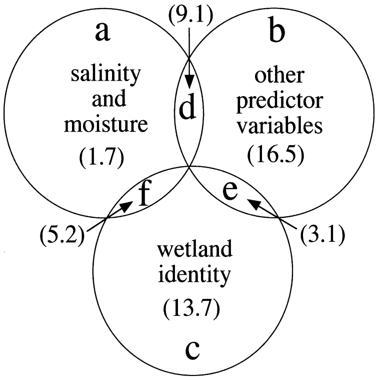

Fig. 2. The components of variation explained by the predictor variables. Values in parentheses are the percent of total variation explained by each component. The letters correspond to components in Table 2.There are three components explained by individual factor groups (a, b and c) and three components that are explained by both of two groups (d, e and f).

identity. Nine CCAs were performed with and without covariates in the analysis (partial CCA) to quantify the amount of variation that could be explained by the six different components. The proportion of species variance explained by each CCA was calculated as the sum of the canonical eigenvalues of the CCA divided by the sum of the species matrix eigenvalues (unconstrained by covariates). Each of the six components of variation was calculated from the proportion of species variance explained by each of the nine CCAs. All CCAs were performed on untransformed species and environment data. Because rare species were of particular interest, they were not downweighted. The significance of the first axis and overall analysis of each CCA was tested with Monte Carlo tests with 999 permutations. Dummy binary variables were created to identify the wetland where plots were located (ter Braak 1988). Because the species matrix of plot maximum density includes data from multiple sampling times, a preliminary analysis of the predictive ability of three different soil moisture and salinity data sets was conducted. Using three separate CCAs, surface soil moisture and salinity at the beginning of the study and after the large initial germination pulse (19 December 1996), during a second period of germination (27 January 1997) and mean values over the period of germination (19 December 1996 to 17 February 1997), were related to the 1996 plot maximum seedling density of each species. The soil moisture and salinity data set that explained the highest proportion of species variation was used in subsequent CCAs to determine the relative importance of groups of factors.

The effect of spatial scale on the relationship between species seedling density and predictive variables was tested by comparing CCAs for cells, plots, transects, and sites. The predictor variables used in this analysis, elevation, perennial cumulative cover, perennial canopy height, bare ground and the cover of the two dominant perennials, *Salicornia subterminalis* and *Monanthochloë littoralis*, were collected independently at the cell and plot scales. Transect and site (e.g. Sweetwater Marsh panne) values were calculated from the next smaller scale (e.g. site density is the mean of two transect mean densities). Seedling densities were collected only at the cell scale and all larger scales are calculated from the next smaller scale. Soil moisture, salinity and texture were not sampled at the cell scale and could not be used in this analysis. Because of the large amount of density data at the cell scale (86016 data points in the 1996 season) maximum density in each cell was not calculated and a single date was used. The predictor variables were related to species densities ('in' and 'out' plots) on 27 January 1997, when a large pulse of germination occurred (Fig. 3). All CCAs were performed on untransformed data, with no downweighting of rare species.

To analyse interannual variation in germination, differences in the maximum density in each plot between the 1996 and 1997 seasons were analysed by paired *t*-tests, stratified by plot (n = 30, Sweetwater Marsh and Tijuana Estuary 'in' plots). Differences in the maximum density of all species combined, and of native, exotic and selected species were tested. Finally, we compared the elevation where the nine most abundant annual species occurred in the two seasons at Sweetwater Marsh and Tijuana Estuary. The less abundant species at these wetlands were found in only a few plots and could not be included in the analysis. The difference between each species' 1996 and 1997 mean elevation, weighted by maximum density, was related to their initial 1996 weighted elevation using Pearson product-moment correlation (n = 9 species). A negative correlation would indicate that species with initially lower elevation increased in elevation and initially higher elevation species decreased in elevation between years. No correlation would indicate that changes in elevation were not related to initial intertidal elevation. A positive correlation would show that the elevation of high elevation species increased and the elevation of low elevation species decreased from the 1996 to 1997 season.

Results

Spatial and temporal variation in seedlings

The seedlings of 27 species were identified in the 1996 and 1997 seasons (Table 1). In the 1996 season, 12 native and five exotic species occurred in Sweetwater Marsh and Tijuana Estuary. The following year, 15 native and five exotic species were found. The seedlings of two native and five exotic species were identified at Los Peñasquitos Lagoon in 1996, with an additional four native and two exotic species that were also observed at the other two wetlands. 18 of the species that established in the two years were annuals. Sweetwater Marsh had the highest species richness with 18 species, Los Peñasquitos Lagoon intermediate with 13 species and Tijuana Estuary, with 10 species, had the lowest species richness (Table 1).

Mean seedling density was variable among wetlands and habitats (Table 1). The mean maximum density of seedlings in each wetland habitat ranged from 419/m^2 in the canopy of Tijuana Estuary in the 1997 season to 4421/m^2 in the panne of Sweetwater Marsh during 1996. Exotic species were a large proportion of seedlings, ranging from 32% in the panne of Sweetwater Marsh in 1997 to 92% in the canopy of Tijuana Estuary in 1996. The seedlings were predominantly annual plants. The annuals *Parapholis incurva* and *Mesembryanthemum nodiflorum*, both exotic, accounted for 48% and 33% of all seedlings

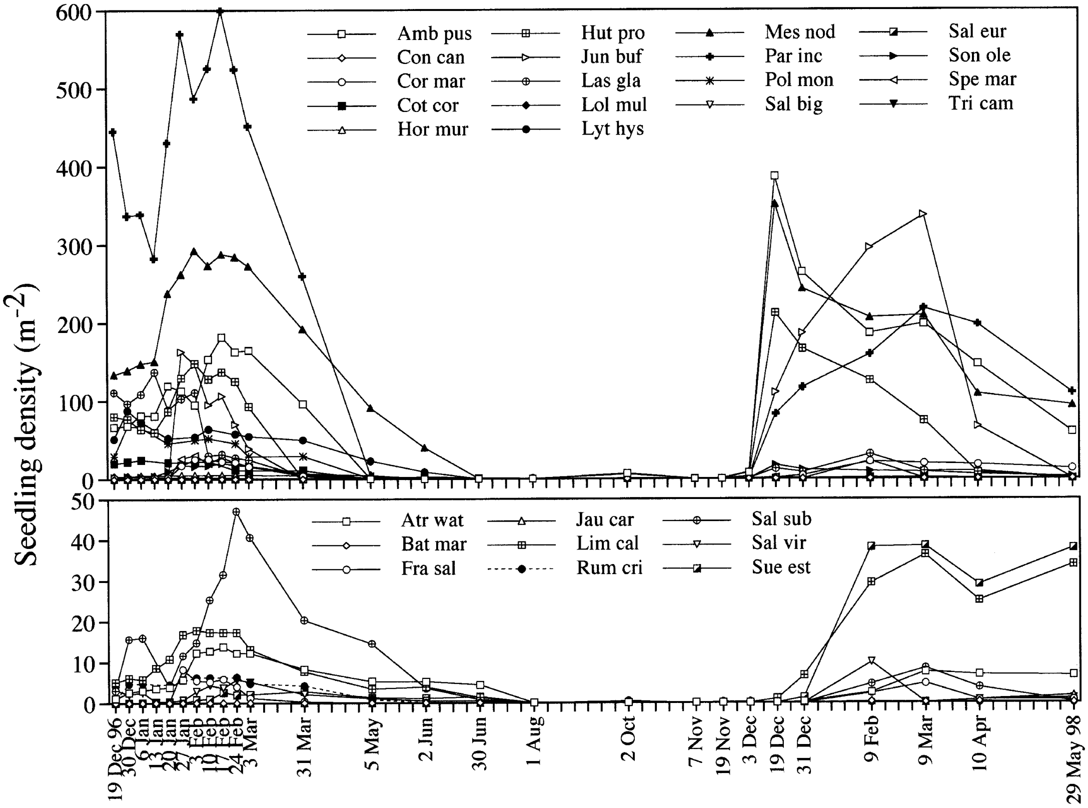

Fig. 3. Mean (n = 40 'in' plots) seedling density of each species through the 1996 and 1997 seasons. Species codes are the first three letters of the genus and specific epithet (Table 1).

in 1996 and 1997, respectively. Some species, such as *Lasthenia glabrata* ssp. *coulteri* and *M. nodiflorum*, were found predominantly in the panne while others, such as *Cordylanthus maritimus* ssp. *maritimus* and most perennials, occurred mostly in the canopy (Table 1). Some species were found only in the plots at Sweetwater Marsh and others only at Los Peñasquitos Lagoon (Table 1). *P. incurva* was the only species found in more than half of the 'in' plots in both seasons; *Limonium californicum* germinated in a majority of the plots in 1997 (Noe 1999).

Similarity in germination among plots in the 1996 season depends on the density of the most abundant species, *P. incurva*. Along the first axis of the DCA of species' maximum density ('in' plots), plots separate from each other based on whether the density of *P. incurva* was above its median ($P < 0.001$). This first axis explains 18% of plot variability in the assemblage. While the wetlands are statistically separated along the first axis ($P = 0.003$), the Tijuana Estuary and Sweetwater Marsh plots intermix (Fig. 4). The second largest source of variation (9%) is attributable to differences among wetlands. Along the second DCA axis, the three wetlands are clearly separated ($P < 0.001$; Fig. 4). The canopy and panne also have different second-axis scores ($P = 0.012$) although there is some overlap (Fig. 4). There is a strong separation of the canopy and panne habitats along the third axis ($P = 0.001$), explaining an additional 6% of the spatial variation in species' maximum densities (Fig. 4). Plots do not separate out by wetland ($P = 0.448$), habitat ($P = 0.518$) or *P. incurva* density ($P = 0.978$) along the fourth DCA axis. The low amount of total variation that could be explained by the first three axes of the DCA could be due to the high heterogeneity of the upper intertidal marsh. Alternatively, unexplained variation could result from a lack of congruence between the data and the unimodal response model of DCA (Økland 1999).

The maximum seedling density of individual plots was lower in 1997 than in 1996, although the difference was not statistically significant (Sweetwater Marsh and Tijuana Estuary 'in' plots, Table 1, $P = 0.283$). *P. incurva* density decreased ($P = 0.032$) substantially in the 1997 season compared to the 1996 season, especially at Tijuana Estuary (Table 1). Largely due to the decline of *P. incurva*, exotic species seedling density also decreased (1053/m^2 in 1996, 654/m^2 in 1997, $P = 0.041$). Native species seedling density did not differ between years (1090/m^2 in 1996, 1164/m^2 in 1997, $P = 0.668$). A similar number of species increased or decreased in density in 1997 compared to 1996 (Table 1). The mean maximum density of two rare

Table 1. Mean maximum density ('in' plots/m^2), species richness and percent of seedlings that were exotic, native, annual, and perennial in 1996 and 1997. Standard errors of the mean are shown in parentheses. Species are classified as native (n) or exotic (e); annual (a) or perennial (p); and forb (f), graminoid (g) or succulent (s). SW-C = canopy habitat of Sweetwater Marsh; SW-P = panne habitat of Sweetwater Marsh; TE-C = canopy habitat of Tijuana Estuary; LPL-P = panne habitat of Los Peñasquitos Lagoon. Blanks indicate absence of the species.

Species	Species classification	1996 SW-C	1997 SW-C	1996 SW-P	1997 SW-P	1996 TE-C	1997 TE-C	1996 LPL-P
Mean seedling density		653 (245)	1519 (627)	4421 (1022)	3518 (767)	1355 (402)	419 (265)	1870 (415)
Amblyopappus pusillus	n,a,f	83 (75)	259 (142)	662 (251)	758 (373)			
Atriplex watsonii	n,p,f	63 (23)	29 (10)				1 (1)	
Batis maritima	n,p,s		1 (1)					
Conyza canadensis	n,a,f							5 (3)
Cordylanthus maritimus ssp. *maritimus*	n,a,f	17 (9)	34 (25)		1 (1)	97 (44)	39 (33)	
Cotula coronopifolia	e,a,f							104 (63)
Frankenia salina	n,p,f	33 (18)	8 (4)	2 (2)	10 (10)	4 (2)	1 (1)	
Hordeum murinum	e,a,g	21 (20)	35 (34)		33 (16)			
Hutchinsia procumbens	n,a,f	4 (3)	142 (101)	755 (165)	593 (120)			
Jaumea carnosa	n,p,s		1 (1)				5 (3)	
Juncus bufonius	n,a,g	79 (79)	277 (276)	689 (281)	919 (422)			
Lasthenia glabrata ssp. *coulteri*	n,a,f	1 (1)	1 (1)	570 (262)	94 (48)			24 (15)
Limonium californicum	n,p,f	81 (42)	107 (49)		3 (1)	2 (1)	11 (3)	
Lolium multiflorum	e,a,g							16 (7)
Lythrum hyssopifolium	e,a,f							361 (172)
Mesembryanthemum nodiflorum	e,a,s	9 (8)	237 (106)	1287 (374)	856 (240)			
Parapholis incurva	e,a,g	169 (103)	267 (134)	356 (85)	228 (89)	1241 (420)	239 (120)	665 (404)
Polypogon monspeliensis	e,a,g							316 (192)
Rumex crispus	e,p,f							29 (9)
Salicornia bigelovii	n,a,s				4 (4)			
Salicornia europaea	n,a,s							11 (10)
Salicornia subterminalis	n,p,s	14 (14)	13 (6)	21 (15)	6 (3)	5 (3)	15 (9)	200 (100)
Salicornia virginica	n,p,s	13 (5)	30 (14)			7 (4)	1 (1)	33 (15)
Sonchus oleraceus	e,a,f	40 (13)	62 (26)	37 (14)	6 (3)			1 (1)
Spergularia marina	n,a,s	16 (16)	1 (1)	41 (19)	6 (3)	1 (1)		105 (94)
Suaeda esteroa	n,p,s	12 (6)	17 (8)				107 (107)	
Trifolium campestre	e,a,f			1 (1)	1 (1)			
# Species		16	18	11	15	7	9	13
Percent exotic		36.5	39.6	38.0	31.9	91.6	56.9	79.8
Percent native		63.5	60.4	62.0	68.1	8.4	43.1	20.2
Percent annual		67.0	86.5	99.5	99.5	98.8	66.3	86.0
Percent perennial		33.0	13.5	0.5	0.5	1.2	33.7	14.0

native species, *Lasthenia glabrata* ssp. *coulteri* ($P = 0.073$) and *Cordylanthus maritimus* ssp. *maritimus* ($P = 0.458$), did not differ between 1996 and 1997.

Mean monthly sea level and annual rainfall differed between the two growing seasons due to a large ENSO event in 1997. Monthly means of hourly sea level observations at Scripps Pier (8 km from Los Peñasquitos Lagoon) and Navy Pier (11 km from Sweetwater Marsh) began to increase relative to MSL in May 1997, peaked at 0.301 m above MSL in December 1997 at Scripps Pier and 0.281 m above MSL in November 1997 at Navy Pier, and returned to near MSL in April 1998 (Fig. 5). Total rainfall at Lindbergh Field was greater in 1997 (45.2 cm) than in 1996 (17.8 cm). Most rainfall occurred in January (1996) and February (1997). Before the onset of large rainfall events in February 1997, surface soil salinity at all sites was greater than in 1996 (Fig. 6), probably because of the increased frequency of tidal inundation and late onset of rainfall.

Changes in the mean elevation of each species between the 1996 and 1997 seasons depended on initial 1996 elevations. For the nine most abundant annual species at Sweetwater Marsh and Tijuana Estuary, the change in seedling elevations between seasons was negatively correlated with 1996 elevations (Pearson product-moment correlation, $r = -0.732$, $P = 0.025$), indicating that species elevation distributions narrowed in the 1997 season. Species present at lower elevations in the 1996 season occurred at higher elevations in the 1997 season. Conversely, higher elevation species in the 1996 season were found at slightly lower elevations in the 1997 season. In the 1997 season, weighted mean elevation changes from the 1996 season ranged from an increase of 0.068 m (*P. incurva*) to a decrease of 0.030 m (*Hutchinsia procumbens*). The lowest and highest weighted-mean-elevation species in 1996 were *Cordylanthus maritimus* ssp. *maritimus* (1.268 m NGVD) and *M. nodiflorum* (1.590 m NGVD), respectively. Mean elevations of higher high tides during the germination period (see below) in 1996 and 1997 were 1.005 m and 1.134 m NGVD, respectively.

In the 1996 season, a large germination pulse occurred in the last week of November 1996 (Fig. 3), immediately before the beginning of this study, follow-

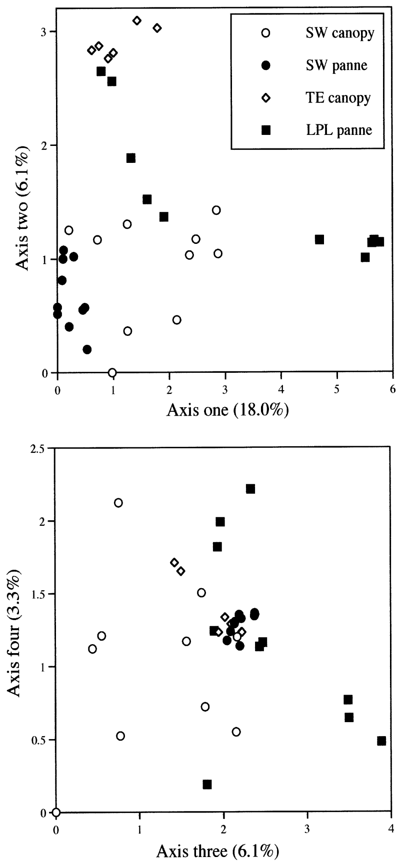

Fig. 4. Detrended Correspondence Analysis of plot-scale species' maximum seedling density in the 1996 season. Plots are labelled by wetland (SW = Sweetwater Marsh, TE = Tijuana Estuary, LPL = Los Peñasquitos Lagoon) and habitat. Each axis lists the amount of species variation explained by that axis.

ing a large rainfall event and an associated decrease in soil salinity and increase in soil moisture (Noe & Zedler in press). Nine annual species germinated at this time. Subsequent to this event, a more prolonged period of germination occurred in January and February 1997. During this period, seven of the nine early-germinating annual species continued to germinate. In addition, four annual species germinated for the first time that season. In this five-week period of germination, species increased in number at differing times. *Salicornia subterminalis* started to germinate on 30 December 1996, while the other perennial seedlings germinated from 27 January 1997 to 24 February 1997.

One large germination pulse occurred in the 1997 season, beginning in the middle of December (Fig. 3). Some species germinated only during this pulse (e.g. *H. procumbens*), while others continued to germinate until March 1998 (e.g. *P. incurva*). *Cordylanthus maritimus* ssp. *maritimus* germinated in late January, after the initial pulse. Perennial seedlings germinated synchronously and were first found on 9 February 1998. Prior to the wet season pulse *Amblyopappus pusillus*, *M. nodiflorum* and *Sonchus oleraceus* germinated in low numbers following an unusually early and heavy rainfall event due to Hurricane Nora on 25 September 1997. These seedlings did not produce seed (G.B.N., pers. obs.).

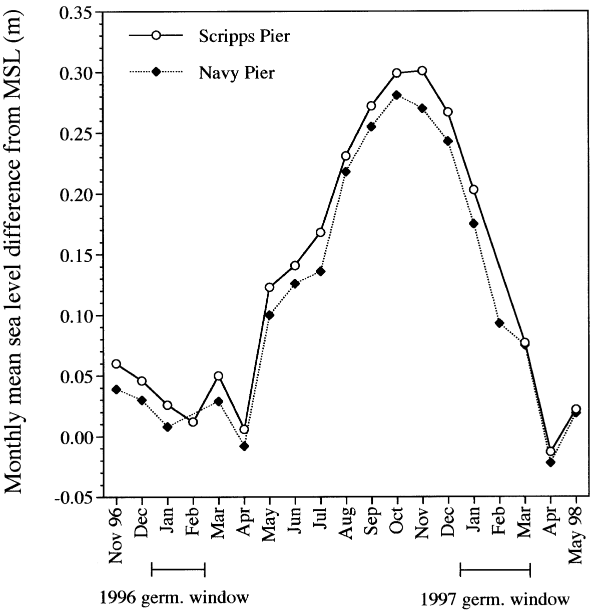

Fig. 5. Deviations of monthly arithmetic means of hourly sea level elevations from Mean Sea Level (MSL) at Scripps Pier and Navy Pier through the duration of the study. The timing of germination in the 1996 and 1997 seasons is indicated.

The timing of germination was coupled to the temporal variability of surface soil salinity at each transect and, to a lesser extent, surface soil moisture. Germination pulses occurred after salinity had dropped below 35‰ in the top two centimeters of soil, with the threshold salinity depending on the salinity level of the transect; the salinity threshold for germination ranged from 10 to 35‰ among transects. The timing of germination depended on surface soil moisture at fewer transects than soil salinity. At most transects, seeds germinated when soil salinity decreased below critical levels, independent of moisture. However, in the panne habitat at Sweetwater Marsh and the canopy habitat at Tijuana Estuary, seed germination was sometimes associated with soil moisture levels increasing above 40% and 45%, respectively.

Relative importance of factors

A preliminary test to identify the most predictive soil moisture and salinity data set was conducted. CCAs

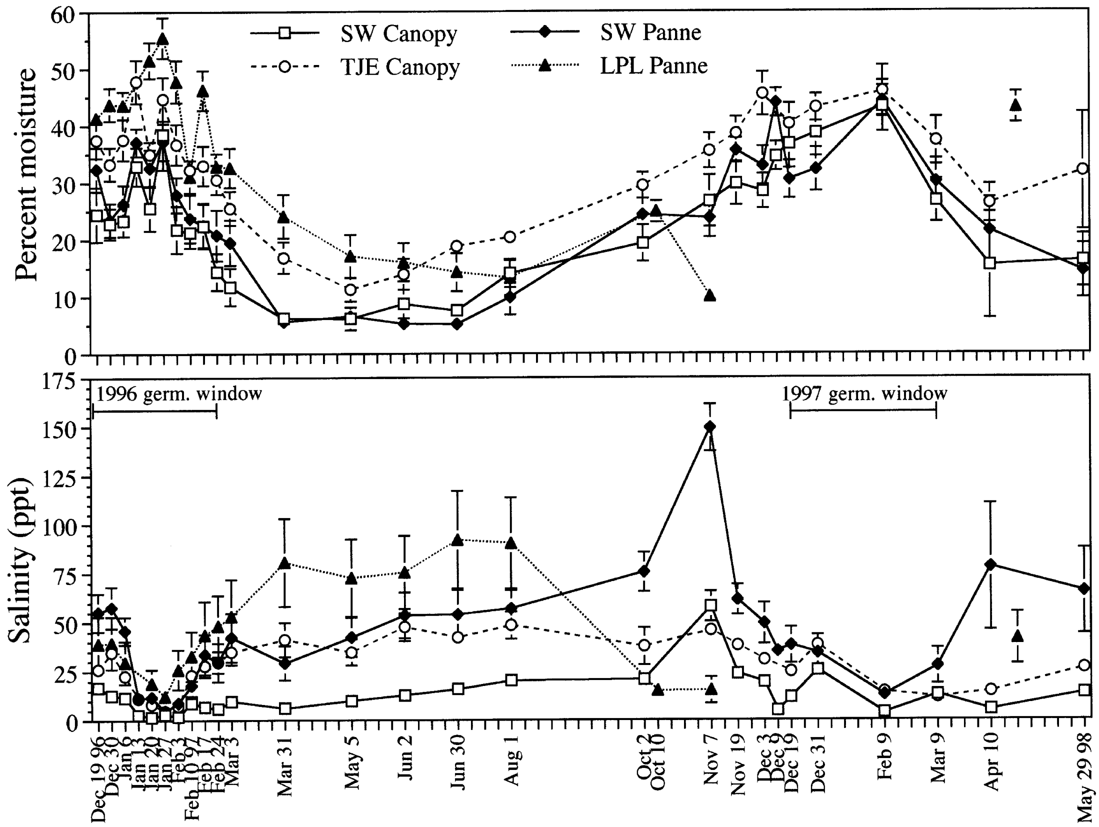

Fig. 6. Mean (± s.e.) surface soil salinity and moisture at the four sites through the duration of the study. The timing of germination in the 1996 and 1997 seasons is indicated.

of surface soil moisture and salinity on 19 December 1996, 27 January 1997 and mean values over the period of germination (19 December 1996 to 17 February 1997) explained 9.0%, 16.0% and 15.3% of the spatial variation in the 1996 plot maximum seedling density of each species, respectively. Thus, we used data obtained on 27 January 1997 for plot surface soil moisture and salinity in subsequent CCAs.

The predictor factors cumulatively explain 49% of the spatial variation in the maximum density of upper intertidal salt marsh seedlings. Partitioning the explainable variation of seedling density into different predictive factors (Table 2) shows that perennial cumulative cover, perennial canopy height, bare ground, surface soil sand and clay content and elevation ('other' predictor variables) statistically explain 16% of the variation (Fig. 2). Surface soil salinity and moisture on 27 January 1997 explains 2% of the variation. 9% of the variation can be explained by both soil salinity and moisture and the 'other' factors. Wetland identity explains 14% of the variation. Salinity and moisture and wetland identity predictive ability overlaps to explain a common 5% and the 'other' predictor variables and marsh identity jointly explain 3% of the variation in seedling density. Site-specific CCAs relating seedling establishment to soil salinity and moisture explain more variation than the CCA that grouped all sites (G.B.N. unpubl. data), suggesting that the high degree of spatial heterogeneity among habitats and wetlands limits the predictive generality of salinity and moisture.

With the effect of wetland identity removed from the analysis, the CCA with both the 'other' predictor variables and surface soil salinity and moisture explains 32% of the variation in maximum seedling density ('All env. - wetland', Table 2). Cumulative perennial cover, bare ground and soil clay content are correlated with the first axis of the ordination, surface soil salinity is strongly correlated with the second axis and perennial canopy height and elevation are highly correlated with both the first and second axes (Fig. 7). The first axis separates the native perennial species seedlings (except for *S. subterminalis*) from the other species, with perennial seedlings found in areas of lower elevation and taller perennial canopies. Native and exotic annual species are found along the breadth of the first axis. The seedlings of three species, *S. subterminalis*, *Salicornia europaea* and *Spergularia marina*, cluster in areas of very high salinity.

Although soil salinity and moisture have less predictive ability than the 'other' predictor variables during germination (Fig. 2, Table 2), plot soil salinity separates the native from the exotic annual species (Fig. 8). The

Table 2. CCA analyses of species maximum seedling density. CCA predictor variables, components of variation (Fig. 2), sum of the canonical eigenvalues, percent of the total species variation explained (Σ Canonical eigenvalues / total inertia) and significance of first axis and CCA (trace) for each analysis are listed. 'All env.' includes soil salinity, soil moisture, perennial cover, perennial canopy height, bare ground, elevation, soil clay content and soil sand content. 'Sal&moist' includes soil salinity and soil moisture. 'Other' includes perennial cover, perennial canopy height, bare ground, elevation, soil clay content, and soil sand content. 'Wetland' denotes marsh identity. a = salinity and moisture alone, b = 'other' variables alone, c = wetland identity alone, d = a +b, e = b + c, f = a + c.

CCA	Components of variation						Σ Canonical eigenvalues	% species variation	*P*-value axis 1	*P*-value CCA
All env. + Wetland	a	b	c	d	e	f	3.223	49.34	0.001	0.001
All env.	a	b		d	e	f	2.329	35.66	0.001	0.001
All env. - Wetland	a	b		d			2.099	32.13	0.001	0.001
Sal&moist	a			d		f	1.048	16.04	0.001	0.001
Sal&moist - Other	a					f	0.452	6.92	0.004	0.003
Sal&moist - Wetland	a			d			0.706	10.81	0.001	0.001
Other		b		d	e		1.877	28.74	0.001	0.001
Other - Sal&moist		b			e		1.281	19.61	0.001	0.003
Other - Wetland		b		d			1.672	25.60	0.001	0.001

native annual species are found in areas with mid to high salinity while the exotic species are found in areas with low salinity. Exceptions include *Conyza canadensis*, a native annual found in low salinity areas and the exotic annuals *Hordeum murinum*, *P. incurva*, and *M. nodiflorum* are found in areas of medium soil salinity. Both native and exotic annual species are found across the spatial range of moisture levels.

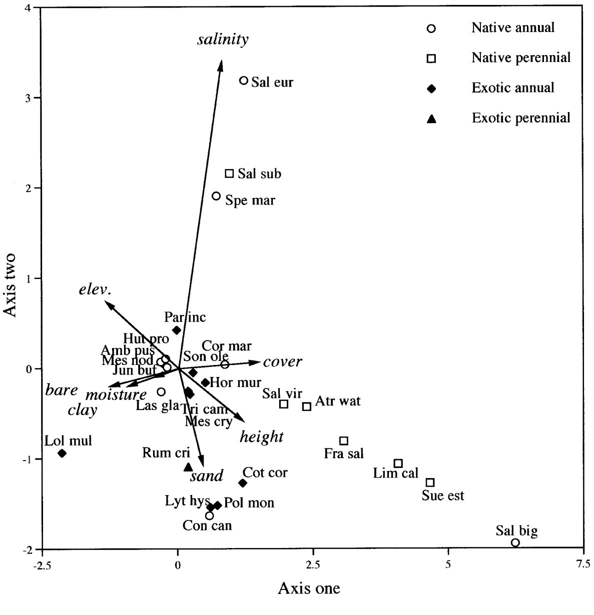

Fig. 7. CCA of plot-scale species maximum seedling density in the 1996 season in relation to surface soil salinity and moisture on 27 January 1997, clay content, sand content, elevation, bare ground, cumulative perennial cover and perennial canopy height. Environmental vector biplot scores are scaled (×4). The effect of wetland identity has been removed as a covariate. Axis 1 explains 12.5% of the species variance and 32.3% of the species-environment relationship. Axis 2 explains a cumulative 23.0% of the species variance and 59.2% of the species-environment relationship. For full species names, see Table 1.

Effect of spatial scale

The relationship between the spatial variation in the maximum density of seedlings and the predictor variables shifts at different spatial scales, with the variables

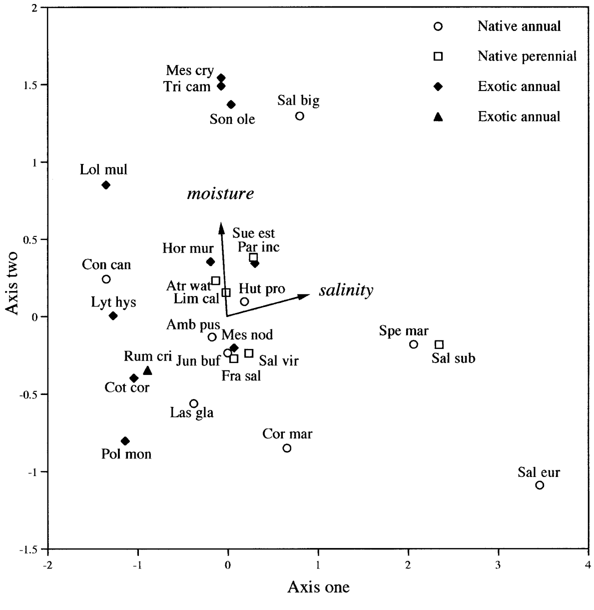

Fig. 8. CCA of plot-scale species maximum seedling density in the 1996 season in relation to 27 January 1997 surface soil salinity and moisture. The effect of wetland identity has been removed as a covariate. The first axis explains 10.0% of the species variance and 76.4% of the species-environment relationship. The second axis explains a cumulative 13.1% of the species variance and 100.0% of the species-environment relationship. For full species names, see Table 1.

Table 3. Correlation among predictor variables and species axis one and two from CCAs of 27 January 1996 seedling density of each species at the cell (n = 224, 0.04-m^2), plot (n = 56, 1-m^2), transect (n = 8, 7 plots) and site (n = 4, 2 transects) scale. Predictor variables include intertidal elevation, cumulative perennial cover, bare ground, *Salicornia subterminalis* cover, *Monanthochloë littoralis* cover, and perennial canopy height. Monte Carlo permutation tests (axis one, overall) and percent of species variation explained by predictor variables: Cell P = 0.001, P = 0.001, 14.9%; Plot P = 0.001, P = 0.001, 25.6%; Transect P = 0.129, P = 0.571, 86.0%; Site not applicable, predictor variables outnumber sites.

	Cell		Plot		Transect		Site	
Predictor	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Elevation	–0.57	0.48	–0.06	–0.69	0.13	–0.02	0.42	–0.86
Perennial cover	0.54	–0.21	0.26	0.71	–0.11	0.51	0.08	–0.98
Bare ground	–0.49	0.29	–0.18	–0.73	0.16	–0.45	0.01	–0.98
S. subterminalis	0.07	–0.22	–0.11	0.37	–0.48	0.20	–0.87	0.36
M. littoralis	0.32	–0.28	0.00	0.58	–0.26	0.39	0.10	0.95
Canopy height	0.40	–0.24	0.21	0.45	–0.11	0.34	0.04	0.98

having the most predictive ability in CCAs changing as scale increases. At the smallest scale measured (cell; 0.04 m^2) elevation and cumulative perennial cover best explain the greatest source of spatial variation in species density while elevation is most highly correlated with the second most important source of variation (Table 3). At the next scale, (plot; 1-m^2), cumulative perennial cover and canopy height are the most important gradients structuring the assemblage. The second largest source of variation at the plot scale is correlated with bare ground, cumulative perennial cover and elevation. At the transect scale, *S. subterminalis* cover explains the most variation, while cumulative perennial cover is associated with the secondary variation in densities. *S. subterminalis* cover is also most highly associated with variation at the site scale (two transects, e.g. Sweetwater Marsh panne), with the other predictor variables explaining the second largest source of variation. Spatial variation in soil moisture and salinity is not related to intertidal elevation within the elevation band of upper intertidal marsh in southern California, although it is often correlated with cumulative perennial cover (Noe & Zedler in press).

Discussion

Assemblage structure and heterogeneity

A diverse and dense assemblage of seedlings, primarily annuals, was identified in the upper intertidal marsh of the three wetlands (Table 1). Despite the high spatial heterogeneity, nearly half of the variation in seedling density could be explained by the combination of abiotic and biotic variables and differences among wetlands (Fig. 2, Table 2). Similarity of germination among the plots was affected most by the density of the most abundant species, *P. incurva*, indicating that the spatial pattern of abundance of this species dominates spatial patterns of the seedling assemblage (Fig. 4). Finally, differences between the canopy and panne habitats accounted for the least amount of plot variation. These results are contrary to our expectation that differences between the two habitat types would be large. Differences among the three wetlands accounted for a relatively large amount of seedling assemblage spatial variation. Therefore, extrapolating details from a study conducted in one salt marsh to other salt marshes is not recommended.

Interannual variability in the density of seedlings was high. The 1997 season was characterized by the strong ENSO event and a 250% increase in rainfall compared to the 1996 season although this did not result in increased maximum seedling density (Table 1). Exotic species generally had a lower maximum seedling density in 1997 than in 1996; the mean maximum density of the most prevalent exotic, *P. incurva*, decreased almost 60% in 1997 (Table 1) although it was found in the same number of plots (Noe 1999). Callaway & Sabraw (1994) also found that different amounts of rainfall, implemented experimentally, affected the structure and diversity of a southern California annual plant community by changing the abundance and elevation distribution of individual species. The complex responses observed probably depended on both the timing and quantity of rainfall (Callaway & Sabraw 1994). High temporal variation is typical of the mediterranean-type climate of southern California (Noe 1999) and the two years documented in this study serve as an indication of the variability typically experienced in southern California salt marshes.

The lack of an increase in germination and upward shift in elevation of the lower elevation species is probably due to another impact of ENSO on intertidal communities: higher sea level. In San Diego, monthly mean values of hourly sea levels were as much as 0.3 m higher than normal

(MSL) during the 1997 season (Fig. 5). Higher elevation plots that had not previously been observed inundated were under as much as 0.2 m of sea water during the higher high tides in the winter of 1997-1998 (G.B.N. pers. obs. at Tijuana Estuary). Increased sea level could negate the impact of increased rainfall on soil salinity levels, replacing salts in the soil surface before they could be leached into lower layers (Noe & Zedler in press). Finally, water is probably the primary dispersal mechanism for seeds in the upper intertidal marsh of southern California and increased frequency and duration of tidal inundation during the ENSO may have resulted in altered seed distributions.

The mean elevation, weighted by density, of each of the most abundant annual species narrowed in the 1997 season; lower elevation species were found at higher elevations and higher elevations species were found at lower elevations. The degree of change in mean higher high tide elevations and species' mean elevations between years were similar, although the mean elevation of higher high tides was below that of the most abundant species. The restriction of higher elevation species to lower elevations could be a response to displacement by competition with upland and transition zone species (Callaway & Sabraw 1994; Ungar 1998) that thrived with increased rainfall but were above the elevations affected by increased sea level. Annual plants were generally more robust in 1997 regardless of elevation (G.B.N. pers. obs.). The ENSO event provides insight into the potential effects of increased sea level on the upper intertidal salt marsh. In southern California, the transitional zone between upper intertidal marsh and uplands has been heavily developed and disturbed. There may be inadequate suitable habitat for upper intertidal marsh species to move upwards in response to higher sea levels.

Upper salt marsh annual plant species had asynchronous changes in density due to differences in germination, survival and mortality during the 1996 and 1997 seasons (Fig. 3). In 1996, some species germinated late in the season (e.g. *Juncus bufonius*), some set seed and died early (e.g. *H. procumbens*), while others set seed and died late in the summer (e.g. *M. nodiflorum*). While germination appeared more synchronous in the 1997 season, this may be an artefact due to less frequent sampling in 1996. Weekly sampling of soil salinity and moisture may be necessary to predict the temporal variation in the germination of individual species (Noe & Zedler in press). Finally, the asynchronous changes in species' densities indicates that seedling density on a particular day is not the best description of density during the whole season. A quantity, such as maximum density, may better describe seedling density by integrating information over the entire season.

Relative importance of salinity and moisture

Contrary to previous studies which stress the importance of soil salinity and moisture on salt marsh plant distributions (Purer 1942; Snow & Vince 1984; Beare & Zedler 1987; Callaway et al. 1990; Latham et al. 1991; Burchill & Kenkel 1991; Shumway & Bertness 1992; García et al. 1993; Kuhn & Zedler 1997; Callaway & Zedler 1998; Pan et al. 1998) surface soil salinity and moisture predicted a very small proportion of the spatial variation in the maximum seedling density of upper intertidal marsh species during the 1996 season (Fig. 2, Table 2). The primary source of spatial variation in seedling distributions is associated with elevation and cumulative perennial canopy cover and height (Fig. 7). Other studies have also found that plant canopy affects the distribution of annual plants in southern California intertidal marsh (Callaway 1994; Fellows 1999) and seedlings in a Netherlands salt marsh (Bakker & de Vries 1992), and that interspecific interactions are important forces structuring salt marsh communities (Bertness & Leonard 1997; Ungar 1998). In addition, soil salinity and moisture and perennial cover could interact to influence species distributions (Callaway & Walker 1997). For example, Callaway (1994) found that soil salinity was lowest under the canopy of perennial plants in a southern California upper intertidal marsh. Soil salinity and moisture, as used in this study, and the 'other' predictive variables, which included perennial cover, explained a common 9% of the species spatial variation in maximum abundance and ca. five times the amount of variation that soil salinity and moisture explained independently (Fig. 2, Table 2). The remaining 51% of unexplained spatial variation in germination could be due to random variation or other factors, such as landscape proximity of seed sources, granivory, nutrient levels, competition among seedlings or herbivory.

Despite the low predictive ability of soil salinity and moisture in explaining the spatial variation in the maximum germination of species (Fig. 2, Table 2), the timing of germination depended on soil salinity decreasing below critical levels and to a lesser extent on soil moisture increases. Similarly, Ehrenfeld et al. (1997) found that temporal variation in environmental gradients was as important as spatial variation. In addition, soil salinity correlated strongly with the second most important axis of variation in the seedling assemblage (Fig. 7) and separated native and exotic annual species (Fig. 8).

Scaling effects

Increasing the spatial scale changes the variables that best predict patterns of species densities (Table 3). The relative ability of elevation, cumulative perennial cover, and *S. subterminalis* cover to explain variation in seedling abundance changes with increasing spatial scale. This suggests that different processes could control seedling establishment at the micro-habitat (cell) and marsh-wide scale. The predictive variables used in this analysis were limited to those that were quantified at all four scales and precluded the inclusion of soil moisture, salinity and texture. At the plot scale, which included all of these soil variables, perennial cumulative cover and canopy height, bare ground and elevation were important predictors of species distributions (Fig. 7), suggesting robustness of the scaling analysis. In addition, spatial variation in soil moisture and salinity is not related to elevation, although it is often correlated with perennial cover within the upper intertidal marsh (Noe & Zedler in press).

Exotic species

Exotic species appear to be 'swamping' the seed banks of the upper intertidal marsh in southern California. California has only 10% of its historical coastal wetland acreage remaining (Anon. 1990b) and many endangered species are dependent on this habitat. Potential impacts of exotic species in the upper intertidal marsh of southern California include negative effects on an endangered plant (*Cordylanthus maritimus* ssp. *maritimus*, Fellows 1999) and an endangered bird species (Callaway & Zedler 1998). The exotic species *Parapholis incurva* and *Mesembryanthemum nodiflorum* were among the most abundant species for both the 1996 and 1997 seasons (Table 1). Although *P. incurva* and *M. nodiflorum* were very abundant and produced seed (G.B.N. pers. obs.) at similar abiotic factor levels as the native species, other exotic species were confined to areas of low salinity (Fig. 7 and 8). This provides partial support for the suggestion that limiting freshwater inputs or adding salts in the intertidal marsh of southern California could control certain exotic species (Beare & Zedler 1987; Kuhn & Zedler 1997; Callaway & Zedler 1998). It will not be able to eliminate all exotic species in this way because *P. incurva* and *M. nodiflorum* occupy the same sites as the native species, including an endangered plant species (Noe 1999), and are more tolerant of salinity during germination than native annual species (Noe & Zedler 2000).

Conclusion

Spatial and temporal variation of germination and establishment in response to the abiotic and biotic environment together constitute the ‘regeneration niche’ in this system. Temporal and spatial variation in seedling density were best explained by different factors. Soil salinity and moisture predicted less of the spatial variation in species’ density than perennial plant cover, soil texture, and elevation or wetland identity, although only half of the spatial variation in seedling density could be explained by all of the factors. However, soil salinity and moisture did explain the timing of germination; germination occurred after soil salinity decreased below or soil moisture increased above thresholds. In addition, increasing the spatial scale of the study changed the abiotic variable that was most predictive of seedling density. These results support the need for conceptual models to include multiple abiotic and biotic factors in order to explain the spatial and temporal variation of wetland plant establishment.

Acknowledgements. This work was funded in part by an award from the Earth Island Institute to the Pacific Estuarine Research Laboratory. G.B.N. received awards from the San Diego State University Joint Doctoral Program, scholarships from the Achievement Rewards for College Scientists (ARCS) Foundation for four years, and a two-year National Estuarine Research Reserve fellowship from the Sanctuaries and Reserves Division, Office of Ocean and Coastal Resource Management, National Ocean Service, National Oceanographic and Atmospheric Administration. Vicki Tripolitis, Meghan Fellows and Bruce Nyden assisted with the field work. Comments by Jan Bakker, Laurie Boorman, Boyd Collier, Michael Johnson and an anonymous reviewer improved the manuscript.

References

Anon. 1990a. *A manual for assessing restored and natural coastal wetlands with examples from southern California*. Pacific Estuarine Research Laboratory. California Sea Grant Report No. T-CSGCP-021, La Jolla, CA.

Anon. 1990b. *Estuaries of the United States: vital statistics of a national resource base*. Special National Oceanic and Atmospheric Administration 20th Anniversary Report, Strategic Assessment Branch, Office of Oceanography and Marine Assessment, Washington, D.C.

Allen, T.F.H., King, A.W., Milne, B.T., Johnson, A. & Turner, S. 1993. The problem of scaling in ecology. *Evol. Trends Plants* 7: 3-8.

Bakker, J.P. & de Vries, Y. 1992. Germination and early establishment of lower salt-marsh species in grazed and mown salt marsh. *J. Veg. Sci.* 3: 247-252.

Bannister, P. 1976. *Introduction to physiological plant ecology*. John Wiley and Sons, New York, NY.

Beare, P.A. & Zedler, J.B. 1987. Cattail invasion and persistence in a coastal salt marsh: the role of salinity reduction. *Estuaries* 10: 165-170.

Bertness, M.D. & Leonard, G.H. 1997. The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* 78: 1976-1989.

Borcard, D., Legendre, P. & Drapeau, P. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73: 1045-1055.

Bouyoucos, G.J. 1962. Hydrometer method improved for making particle size analysis of soils. *Agron. J.* 54: 464-465.

Burchill, C.A. & Kenkel, N.C. 1991. Vegetation-environment relationships of an inland boreal salt pan. *Can. J. Bot.* 69: 722-732.

Callaway, J.C. & Zedler, J.B. 1998. Interactions between a salt marsh native perennial (*Salicornia virginica*) and an exotic annual (*Polypogon monspeliensis*) under varied salinity and hydroperiod. *Wetlands Ecol. Manage.* 5: 179-194.

Callaway, R.M. 1994. Facilitative and interfering effects of *Arthrocnemum subterminale* on winter annuals. *Ecology* 75: 681-686.

Callaway, R.M. & Sabraw, C.S. 1994. Effects of variable precipitation on the structure and diversity of a California salt marsh community. *J. Veg. Sci.* 5: 433-438.

Callaway, R.M. & Walker, L.R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78: 1958-1965.

Callaway, R.M., Jones, S., Ferren, W.R. Jr., & Parikh, A. 1990. Ecology of a mediterranean-climate estuarine wetland at Carpinteria, California: plant distributions and soil salinity in the upper marsh. *Can. J. Bot.* 68: 1139-1146.

Denslow, J.S. 1985. Disturbance-mediated coexistence of species. In: Pickett, S.T.A. & White, P.S. (eds.) *The ecology of natural disturbance and patch dynamics,* pp. 307-323. Academic Press, San Diego, CA.

Dutilleul, P. & Legendre, P. 1993. Spatial heterogeneity against heteroscedasticity: an ecological paradigm versus a scientific concept. *Oikos* 66: 152-171.

Ehrenfeld, J.G., Han, X., Parsons, W.F.J. & Zhu, W. 1997. On the nature of environmental gradients: temporal and spatial variability of soils and vegetation in the New Jersey Pinelands. *J. Ecol.* 85: 785-798.

Fellows, M.Q. 1999. *Recovery of a rare and endangered hemiparasite: Interactions and effects of native and exotic hosts.* M.Sc. Thesis, San Diego State University, San Diego, CA.

Galinato, M.I. & Van der Valk, A.G. 1986. Seed germination traits of annuals and emergents recruited during drawdowns in the Delta Marsh, Manitoba, Canada. *Aquat. Bot.* 26: 89-102.

García, L.V., Marañón, T., Moreno, A. & Clemente, L. 1993. Above-ground biomass and species richness in a Mediterranean salt marsh. *J. Veg. Sci.* 4: 417-424.

Gardner, W.H. 1986. Water content. In: Klute, A. (ed.) *Methods of soil analysis, part I. Physical and mineralogical methods - Agronomy Monograph 9,* pp. 493-544. ASA-SSSA, Madison, WI.

Gray, A.J. 1992. Salt marsh plant ecology: Zonation and succession revisited. In: Allen, J.R.L. & Pye, K. (eds.) *Salt marshes: Morphodynamics, conservation, and engineering significance,* pp. 63-79. Cambridge University Press, Cambridge.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Biol. Rev.* 52: 107-145.

Hickman, J.C. (ed.) 1993. *The Jepson manual: higher plants of California*. University of California Press, Berkeley and Los Angeles, CA.

Kolasa, J. & Pickett, S.T.A. 1991. *Ecological heterogeneity.* Springer-Verlag, New York, NY.

Kuhn, N.L. & Zedler, J.B. 1997. Differential effects of salinity and soil saturation on native and exotic plants of a coastal salt marsh. *Estuaries* 20: 391-403.

Latham, P.J., Pearlstine, L.G. & Kitchens, W.M. 1991. Spatial distributions of the softstem bulrush, *Scirpus validus,* across a salinity gradient. *Estuaries* 14: 192-198.

Noe, G.B. 1999. *Abiotic effects on the annual plant assemblage of southern California upper intertidal marsh: does experimental complexity matter?* Ph.D. Dissertation. San Diego State University, San Diego, CA.

Noe, G.B. & Zedler, J.B. 2000. Differential effects of four abiotic factors on the germination of salt marsh annuals. *Am. J. Bot.* 87: 1679-1692.

Noe, G.B. & Zedler, J.B. In press. Variable rainfall limits the germination of upper intertidal marsh plants in Southern California. *Estuaries.*

Økland, R.H. 1999. On the variation explained by ordination and constrained ordination axes. *J. Veg. Sci.* 10: 131-136.

Oksanen, J. & Minchin, P.R. 1997. Instability of ordination results under changes in input data order: explanations and remedies. *J. Veg. Sci.* 8: 447-454.

Pan, D., Bouchard, A., Legendre, P. & Domon, G. 1998. Influence of edaphic factors on the spatial structure of inland halophytic communities: a case study in China. *J. Veg. Sci.* 9: 797-804.

Pickett, S.T.A. & White, P.S. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, San Diego, CA.

Purer, E.A. 1942. Plant ecology of the coastal salt marshlands of San Diego County, California. *Ecol. Monogr.* 12: 82-111.

Richards, L.A. (ed.) 1954. *Diagnosis and improvement of saline and alkali soils.* Agricultural Handbook No. 60. United States Department of Agriculture, Washington, DC.

Shumway, S.W. & Bertness, M.D. 1992. Salt stress limitation of seedling recruitment in a salt marsh plant community. *Oecologia (Berl.)* 92: 490-497.

Snow, A.A. & Vince, S.W. 1984. Plant zonation in an Alaskan salt marsh II. An experimental study of the role of edaphic conditions. *J. Ecol.* 72: 669-684.

ter Braak, C.J.F. 1988. *CANOCO – a FORTRAN program for canonical community ordination*. Microcomputer Power, Ithaca, NY.

Ungar, I.A. 1978. Halophyte seed germination. *Bot. Rev.* 44: 233-264.

Ungar, I.A. 1998. Are biotic factors significant in influencing the distribution of halophytes in saline habitats? *Bot. Rev.* 64: 176-199.

Van der Valk, A.G. 1981. Succession in wetlands: A Gleasonian approach. *Ecology* 62: 688-696.

Waisel, Y. 1972. *Biology of halophytes*. Academic Press, San Diego, CA.

Weiher, E. & Keddy, P.A. 1995. The assembly of experimental wetland plant communities. *Oikos* 73: 323-335.

Wiens, J.A. 1976. Population responses to patchy environments. *Annu. Rev. Ecol. Syst.* 7: 81-120.

Zar, J.H. 1996. *Biostatistical analysis*. Prentice Hall, Upper Saddle River, NJ.

Received 8 September 1999;
Revision received 6 June 2000;
Accepted 17 July 2000.
Coordinating Editor: J.P. Bakker.