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Variable Rainfall Limits the Germination of Upper Intertidal Marsh Plants in Southern California

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ABSTRACT: Temporal variation in rainfall created a germination window for seedling establishment in the upper intertidal marshes of southern California. In this highly variable climate, total annual rainfall was highly variable, as was the timing and size of rainfall during the wet season. Daily rainfalls > 3.0 cm were rare in the long-term record but created germination opportunities that had two components: low salinity and high moisture. During the 1996–1997 wet season, only one-day rainfalls > 3.0 cm resulted in large increases in soil moisture and decreases in soil salinity. Germination in the upper intertidal marsh of three wetlands followed two large (> 3.0 cm) rainfall events in the relatively dry 1996–1997 season and multiple medium and small rainfall events in the wetter 1997–1998 season. In addition to rainfall, plant cover and soil texture influenced spatial and temporal variation in soil salinity and moisture. Daily and weekly sampling adequately described soil moisture and salinity so that germination could be predicted; monthly sampling would have missed the low-salinity and high-moisture events that trigger germination.

Introduction

Southern California intertidal salt marshes occur in a Mediterranean-type climate characterized by long, dry summers and winters with variable precipitation. The region's small watersheds and low streamflows result in salt marshes that are dominated by marine hydrology punctuated with brief rainfall events that lower salinity (Zedler et al. 1992). It has been hypothesized that salt marsh plant community dynamics are greatly influenced by this annual period of low salinity, termed the low-salinity gap (Zedler and Beare 1986; Zedler et al. 1992), especially in the upper intertidal marsh (elevation approximately 1.2 to 1.6 m, National Geodetic Vertical Datum [NGVD]) where tidal inundation is infrequent during most of the winter (Zedler 1982). Low-salinity gaps also occur in high intertidal marsh of other regions with Mediterranean-type climates (Álvarez Rogel et al. 2000).

Several annual plant species in the upper intertidal marsh germinate in winter after rainfall lowers soil salinity and raises soil moisture, and senesce by late summer when soils are hypersaline and dry (Callaway et al. 1990; Noe and Zedler In press). The germination of salt marsh plants responds to salinity (Kingsbury et al. 1976; Ungar 1978; Woodell 1985; Zedler and Beare 1986; Callaway et al. 1990; Shumway and Bertness 1992; Kuhn and Zedler 1997; Noe and Zedler 2000) and moisture (Fink and Zedler 1990; Kuhn and Zedler 1997; Noe and Zedler 2000), suggesting that halophytes follow the environmental sieve concept developed for prairie potholes (van der Valk 1981) and herbaceous riverine wetlands (Weiher and Keddy 1995). No studies have documented temporal changes in soil salinity or moisture and plant establishment in upper intertidal marshes.

Variability in the annual low-salinity gap, resulting from variation in both total annual rainfall and the timing of rainfall within the wet season, affects the structure and diversity of the annual plant community in the upper intertidal marsh (Callaway and Sabraw 1994; Noe and Zedler In press) and southern California salt marshes in general (Zedler and Beare 1986; Zedler et al. 1992). Two studies that characterized the low-salinity gap in upper intertidal marshes were based on infrequent sampling (biweekly in Callaway et al. 1990; monthly in Kuhn and Zedler 1997). Studies relating rainfall and soil salinity in the upper intertidal marsh have been based on one-month (de Leeuw et al. 1991) or two-month (Álvarez Rogel et al. 1997) sampling intervals, making short-term salinity responses to rainfall difficult to characterize. The optimal sampling frequency would predict the conditions that stimulate germination. It is likely that the daily variability in rainfall affects the daily and weekly variability of soil salinity and moisture, which in turn stimulates germination. Historical patterns of variation in annual, within wet season,

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and daily rainfall should indicate the degree of possible variation in soil salinity and moisture and seed germination. We hypothesize that rare, large rainfalls create a low-stress temporal window of low salinity and high moisture that stimulates germination.

Southern California upper intertidal marshes support several sensitive annual plant species, among them a federal and state-listed endangered plant species. Exotic species are abundant (Noe and Zedler In press) and most extensive during prolonged periods of low salinity following urban and irrigation runoff or sewage spills (Kuhn and Zedler 1997; Callaway and Zedler 1998). Annual plants are prevalent in areas with sparse perennial canopy, both in vegetated areas (canopy habitat) and along the edges of salt pannes (panne habitat; Noe and Zedler In press). These two habitats have different annual plant assemblages and are thought to have differing soil moisture and salinity dynamics. Understanding the factors that influence native and exotic species, control community dynamics, and differentiate habitats, is needed to improve the management and restoration of upper intertidal marshes.

The objectives of this study are to characterize precipitation variability in the long-term rainfall record, to characterize and determine the abiotic and biotic factors that affect soil moisture and salinity content and variation in the upper intertidal marsh, to test the effect of temporal sampling frequency on the description of variation in soil salinity and moisture, to compare soil salinity and moisture in the canopy habitat to the panne habitat, and to link precipitation variability, soil moisture and salinity, and plant establishment.

Methods

Study Location

Sparse perennial canopy (canopy) and salt panne edge (panne) habitats of the high salt marsh were studied at Sweetwater Marsh National Wildlife Refuge (Sweetwater Marsh 32°40′N, 117°5′W), Tijuana River National Estuarine Research Reserve (Tijuana Estuary 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 extensive upper intertidal marshes that differ in annual and perennial species. Dominant perennial plant species in both habitats are *Salicornia subterminalis* and *Monanthochloë littoralis.*

Rainfall

The daily (1927–1997) and monthly (1850–1997) rainfall records of Lindbergh Field (32°44′N, 117°10′W), San Diego County, California (Fig. 1) were obtained from the National Weather Service. In addition, daily rainfall was measured with a rain gauge at Sweetwater Marsh from November 13, 1996 to January 28, 1997. The gauge was checked between 1000 and 1400 the day following a rainfall event. The 1996 rainyear (July 1996 to June 1997) daily rainfall record for Sweetwater Marsh (12 km from Lindbergh Field) was completed by adding Lindbergh Field data from July 1996 to November 1996 and February 1997 to June 1997 to the November 1996 to February 1997 Sweetwater Marsh rain gauge data.

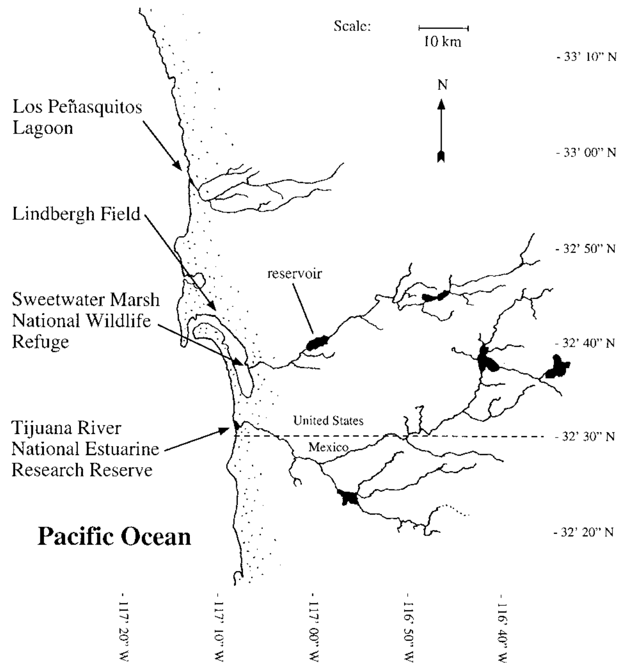

Fig. 1. Map of southern California coastline showing coastal wetlands that were studied, their associated watersheds, and Lindbergh Field. Note: representation of Tijuana River watershed in Mexico is not complete, scale is approximate.

Soil Salinity and Moisture

Intensive sampling of the soil environment took place at Sweetwater Marsh, where both canopy and panne habitats are present. The soil environment was sampled less frequently, but for a longer time, in both habitats at Tijuana Estuary and Los Peñasquitos Lagoon. In both the canopy and panne habitats at Sweetwater Marsh, five 1 × 1 m soil monitoring plots each with twenty-five 0.04-m² cells were randomly placed within a grid encompassing a representative area of each habitat. Five similar vegetation monitoring plots were randomly located along a line transect spanning the soil monitoring grid in both habitat types. One additional transect in the same configuration was placed in both habitat types at Sweetwater Marsh, for a total of two transects per habitat. Two vegetation monitoring transects were established in both the canopy habitat at Tijuana Estuary and the panne habitat at Los Peñasquitos Lagoon.

Surface soil moisture and salinity were measured in both the soil and vegetation monitoring plots. In the soil monitoring plots, soil sampling occurred weekly from November 13, 1996 to January 28, 1997. After each rainfall event, additional sampling occurred daily for 5 d. Soil cores (3.1 $cm^2 \times$ 2 cm deep) were taken from 3 random cells and pooled into one sample for each soil monitoring plot. In the vegetation monitoring plots, sampling occurred weekly from December 19, 1996 to February 24, 1997 and then monthly from March 3, 1997 until August 1, 1997. Sampling continued at irregular intervals during the 1997–1998 germination season. Soil cores were taken to a depth of 2 cm from December 19, 1996 until March 31, 1997, to a depth of 10 cm from March 31, 1997 to August 1, 1997, and to a depth of 2 cm thereafter. One core was taken from each of three random cells (excluding four plant-density sampling cells) and pooled into one sample for each vegetation monitoring plot. Soil was collected to a depth of 2 cm during the period of germination so that conditions at the surface of the soil where germination occurs were characterized while still collecting sufficient soil to measure salinity and moisture. Between periods of germination, soil was collected to 10 cm in order to characterize a larger portion of the rooting zone of the annual plants. Measurements of salinity or moisture in the 0–2 cm and 0–10 cm cores were highly correlated when the two core depths were simultaneously collected on March 31, 1997 (Noe unpublished data).

Soil moisture was determined gravimetrically. Each soil sample was dried at 60°C for 24 h. Soil moisture was calculated as change in mass divided by dry weight (Gardner 1986). After coarse organic matter was removed, the same soil 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 hand-held Reichart Scientific temperature-compensated salinity refractometer (Pacific Estuarine Research Laboratory 1990). One person mixed all saturated soil pastes. Extracts of saturated soil pastes underestimate field soil salinity concentrations, except when field soils are wet, but they control for the different moisture retention capacities of soils with different textures (Richards 1954). Instead of estimating the salt concentrations of field soils, the salinity of saturated soil paste extracts is a measure of the salt mass of field soils. Soils in the upper intertidal marsh are typically too dry to extract interstitial water in the field.

Biotic and Abiotic Environment

Soil texture, plot elevation, cumulative plant cover, and bare ground were assessed in both the soil and vegetation monitoring plots. Soil texture analysis was performed by the Bouyoucos (1962) technique on three pooled, 2-cm deep soil cores from each plot. Plot elevation was determined at three random points in each plot with a kinematic Global Positioning System (GPS; vertical accuracy ± 3 cm). Precision and accuracy of the GPS measurements were verified with readings of fixed benchmarks of known elevation. Plant cover 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 plant cover was calculated by summing the cover of all species. Verified daily higher high tide sea levels in San Diego Bay were obtained from the National Ocean Service. Using plot elevations and the tidal attenuation factor for Sweetwater Marsh (Williams personal communication), we determined when individual plots were inundated by the higher hide tide of each day of the study.

Germination

Seedling density was quantified in the vegetation monitoring plots of Sweetwater Marsh, Tijuana Estuary, and Los Peñasquitos Lagoon during the 1996–1997 (1996) wet season and Sweetwater Marsh and Tijuana Estuary during the 1997 season. The number of live seedlings was counted through the 1996 and 1997 seasons in four permanent 0.04-m^2 cells in each plot that were chosen randomly without replacement. Individuals were counted when their cotyledons were visible. Because of high density, seedlings were counted approximately and classified into density classes of 0, 1–10, 11–20, 21–30, 31–40, 41–50, 51–100, 101–200, and more than 200 individuals 0.04 m^{-2}. Density class midpoints, and 201.0 for the 200+ density class, were used for analyses. Plot (1-m^2) density is an average of the total number of seedlings (all species combined) in the four 0.04-m^2 cells. Seedling density was then averaged across all the plots for each sampling time.

Data Analysis

The 1850–1997 monthly rainfall record was analyzed for trends and variability in rainfall. Patterns in the 1927 to 1996 daily rainfall record were also described. The 1996 rainyear total rainfall, monthly rainfall, and seasonal distribution of monthly rainfall were compared to the 1850–1996 record with *z*-tests and the Kolmogorov-Smirnov goodness-of-fit test. Differences between Sweetwater Marsh and Lindbergh Field daily rainfall were examined with a paired *t*-test to test the assumption that the two sites received similar rainfall.

Multiple regressions were performed to determine the effect of abiotic and biotic factors on soil salinity and moisture content and temporal variation in the soil monitoring plots. Soil salinity and moisture content on days before and after large rainfall events were related to soil texture (percent clay and sand), plot intertidal elevation, cumulative plant cover, and bare ground. The coefficients of variation of soil salinity and moisture, calculated from the data collected between November 13, 1996 to January 28, 1997, were related to the same predictor variables. The assumptions of normality and homogeneity of variance were met for the moisture data and for the log-transformed salinity data. Because cumulative plant cover and bare ground were highly correlated, separate multiple regressions were performed with either cumulative plant cover or bare ground included in the model. The models with cumulative plant cover had higher explanatory power and statistical significance than models including bare ground, except for the coefficient of variation of soil moisture.

Differences between canopy and panne habitat soil monitoring plots were tested by *t*-tests for each of the above variables. The spatial correlation between soil moisture and salinity at all three marshes was assessed by calculating the Pearson product-moment correlation of salinity and moisture on multiple days, December 19, 1996, December 30, 1996, January 6, 1997, January 20, 1997, and January 27, 1997 (n = 40 vegetation monitoring plots). The temporal correlation between soil salinity and moisture in both habitat types was determined with a Pearson product-moment correlation of mean salinity and mean moisture from November 13, 1996 to January 28, 1997 (n = 10 soil monitoring plots).

The effect of sampling frequency on the characterization of soil salinity and moisture trends in the soil monitoring plots was analyzed by comparing the full data set, the weekly sampling data, and a monthly sampling data set for differences in prediction of low-salinity and high-moisture events.

Results

Rainfall

Total rainfall in a rainyear (July to June) is low ($\bar{x}$ = 25.4 cm) and highly variable (coefficient of variation [CV] = 41.0%) in the long-term record

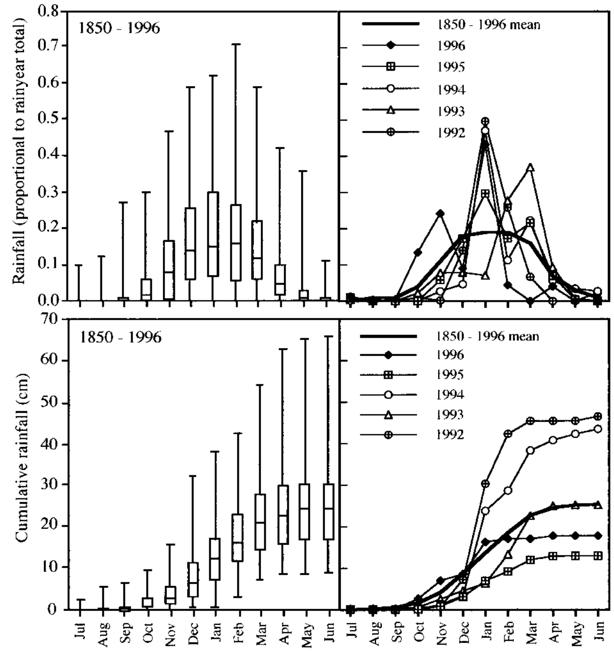

Fig. 2. Proportion of rainyear rainfall occurring each month (upper graphs) and cumulative monthly rainfall (lower graphs) over the long-term record (1850–1996; left graphs) and the past five rainyears (right graphs). Box plots include mean, quartiles, and range.

(1850–1996). Minimum and maximum values are 8.8 cm (in 1960) and 66.0 cm (in 1883). In southern California, 94% of the rain falls between October and April (Fig. 2). Individual rainyears have unique timing of rainfall, e.g., early rainfall in 1996, mid-season rainfall in 1994, a late season rainfall in 1993, and more typical rainfall timing in 1995.

The 1996 rainyear had large rainfall in October to November (6.7 cm) and January (7.7 cm), low rainfall from February to June (1.5 cm), and low rainyear total rainfall (17.8 cm) (Fig. 2). There was no statistical difference between the 1996 rainyear and the long-term record for rainyear total rainfall (p = 0.465, *z*-test), October and November total rainfall (p = 0.312, *z*-test), January rainfall (p = 0.555, *z*-test), February through June total rainfall (p = 0.153, *z*-test), or the cumulative monthly distribution of rainfall (p = 0.186, Kolmogorov-Smirnov test).

There was an average of 43 d (SD = 10.8) of rainfall per rainyear in the 1927 to 1996 daily rainfall record. Seventy-eight percent of daily rainfall totals were < 1.0 cm and only 3% were > 3.0 cm. Rainfalls > 3.0 cm occurred on August 16 at the earliest and April 28 at the latest and 21 years had no daily rainfalls > 3.0 cm. The 1996 rainyear had two daily rainfalls > 3.0 cm (Fig. 3). In the 71 years of the long-term daily rainfall record, only 22 years

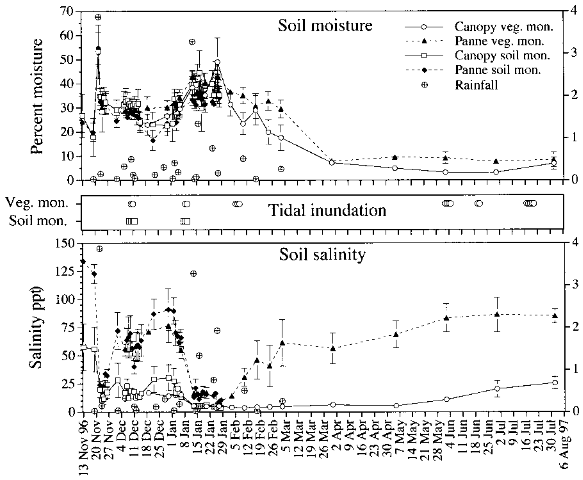

Fig. 3. Mean soil moisture and salinity (SE) in canopy and panne habitats in the soil monitoring plots (soil mon.) and nearby vegetation monitoring plots (veg. mon.), daily rainfall, and the timing of tidal inundation (a majority of plots inundated). Soil cores were taken in the top 2 cm of soil from November 13, 1996 to March 3, 1997, and subsequently in the top 10 cm of soil.

(30.1%) had two or more rainfalls > 3.0 cm. Sweetwater Marsh and Lindbergh Field did not differ in daily rainfall from November 1996 to February 1997 (p = 0.992, paired *t*-test), indicating the feasibility of combining rainfall data from the two locations.

Soil Salinity and Moisture

Both the canopy and panne habitats at Sweetwater Marsh exhibited high temporal variation in surface soil salinity and moisture. Saturated soil paste extracts were hypersaline in the perennial habitat (58‰) and extremely hypersaline in the panne habitat (> 130‰) on November 13, 1996 when soil monitoring began and decreased to lowest salinity of 4‰ in the canopy habitat and 7‰ in the panne habitat on January 26, 1997 (Fig. 3). Temporal variation of salinity in both habitats was high (CV: canopy = 78.1%, panne = 69.8%) through the course of the study. Spatial variation in the soil monitoring plots at any given time was also high, with large variability about the mean. The panne habitat had higher salinity than the canopy habitat except immediately following large rainfall events. Soil moisture in both habitats was also variable (CV: canopy = 21.1%, panne = 20.7%) through time, but less than for salinity. Soil moisture in the two habitats was similar through the duration of the wet season. A majority of the soil monitoring plots was tidally inundated by higher high tides in early December 1996 and early January 1997. In the nearby vegetation monitoring transects, a majority of the plots were inundated by the higher high tides for only a few consecutive days of each tidal cycle in early December 1996, early January 1997, early February 1997, early June 1997, late June 1997, and middle July 1997.

Temporal and spatial variation of soil salinity and moisture were explained using multiple regressions with soil texture (percent clay and sand), plot elevation, cumulative plant cover, and bare ground included as the predictor variables (Table 1). In the soil monitoring plots at Sweetwater Marsh, plots with high temporal variability of soil moisture had less bare ground, while temporal variation in soil salinity could not be predicted. On days before large rainfalls, plots with more clay had higher soil moisture (November 19, 1996) or the spatial variation of soil moisture could not be predicted (January 6, 1997). On days after rainfalls > 3.0 cm (November 22, 1996 and January 13, 1997), plots with more clay and more cumulative plant cover had higher soil moisture. Plots with low soil salinity had high cumulative plant cover (November 19, 1996) or both high cumulative plant cover and high soil sand content (January 6, 1997) on days before large rainfalls. Following these large rainfalls, plots with more cumulative plant cover

TABLE 1. Multiple regressions explaining temporal and spatial variation of soil salinity and moisture. The temporal coefficient of variation (CV) of soil moisture and salinity and soil moisture and salinity content on November 19, 1996, November 22, 1996, January 6, 1997, and January 13, 1997 in the soil monitoring plots at Sweetwater Marsh were related to elevation, clay content, sand content, and either cumulative perennial plant cover or bare ground (n = 10; canopy and panne plots pooled for analysis).

Parameter	Significant Variable(s) in Model	Standardized Coefficient	Model p-value	adj. r^2
Moisture CV	Bare ground	−0.79	0.076	0.583
Salinity CV	Sand content	0.97	0.164	0.411
Nov. 19 moisture	Clay content	0.89	0.010	0.823
Nov. 22 moisture	Cumulative cover, Clay content	0.84, 0.63	0.002	0.902
Jan. 6 moisture	None		0.355	0.150
Jan. 13 moisture	Cumulative cover, Clay content	0.75, 0.54	0.003	0.893
Nov. 19 salinity	Cumulative cover	−0.73	0.064	0.611
Nov. 22 salinity	None		0.607	0.000
Jan. 6 salinity	Sand content, Cumulative cover	−0.56, −0.49	0.010	0.823
Jan. 13 salinity	Cumulative cover	−0.74	0.004	0.876

TABLE 2. A comparison of the canopy (n = 5) and panne (n = 5) soil monitoring plots at Sweetwater Marsh. The temporal coefficient of variation (CV) of soil moisture and salinity, soil moisture and salinity levels on November 19, 1996, November 22, 1996, January 6, 1997, and January 13, 1997, and their possible covariates in the two habitats were compared with *t*-tests.

Variable	Canopy Mean (SE) (Range)	Panne Mean (SE) (Range)	*t* test p-value
Moisture CV	29.4 (2.9) (21.8–36.6)	25.0 (2.8) (15.8–31.9)	0.296
Salinity CV	74.8 (9.3) (53.0–107.5)	76.1 (2.4) (67.2–81.1)	0.900
Nov. 19 percent moisture	17.9 (7.8) (6.5–48.4)	19.9 (3.9) (9.9–32.2)	0.834
Nov. 22 percent moisture	53.3 (11.1) (18.3–87.2)	54.8 (6.6) (35.2–68.8)	0.908
Jan. 6 percent moisture	31.2 (3.9) (21.4–41.6)	29.4 (3.7) (19.6–41.2)	0.750
Jan. 13 percent moisture	39.6 (5.8) (24.3–59.8)	33.2 (2.4) (27.6–41.9)	0.347
Nov. 19 salinity (‰)	55.8 (19.7) (20–127)	122.8 (11.3) (91–137)	0.023
Nov. 22 salinity (‰)	20.0 (7.1) (7–46)	24.2 (4.6) (12–39)	0.635
Jan. 6 salinity (‰)	13.2 (2.6) (8–22)	66.0 (7.9) (50–96)	0.002
Jan. 13 salinity (‰)	5.4 (0.6) (4–9)	13.4 (2.5) (9–20)	0.031
Elevation (m NGVD)	1.487 (0.02) (1.409–1.534)	1.482 (0.03) (1.418–1.585)	0.887
% clay	11.8 (3.78) (4.4–28.3)	21.5 (0.89) (20.0–25.0)	0.082
% silt	21.4 (6.18) (0.0–32.0)	32.7 (2.35) (25.0–38.7)	0.146
% sand	66.8 (3.22) (58.6–77.5)	45.8 (2.46) (36.3–52.5)	0.002
% bare ground	4.4 (3.94) (0–22)	44.0 (11.77) (15–80)	0.037
% cumulative perennial plant cover	132.4 (16.31) (61–159)	64.0 (16.28) (20–120)	0.029

had lower soil salinity (January 13, 1997) or the spatial variation in soil salinity could not be explained by the predictor variables (November 22, 1996). A comparison of the canopy and panne habitat soil monitoring plots indicated that the canopy habitat had higher soil sand content and cumulative plant cover and lower bare ground and soil salinity than the panne habitat (*t*-tests; Table 2).

The amount of daily change in soil moisture and salinity depended on the size of rainfall events (Fig. 3). In the 1996 rainyear, no rainfall or small daily rainfalls (< 0.25 cm) were associated with a decrease in soil moisture and increase in soil salinity, although there was variability in the response. Medium rainfalls (between 0.25 and 3.0 cm) were associated with small increases or decreases in soil moisture and moderate decreases in soil salinity. Large rainfalls (> 3.0 cm) were associated with large increases in soil moisture and large decreases in soil salinity. The canopy and panne habitats had similar responses of soil moisture and salinity to rainfall amount.

Spatial variations in surface (0–2 cm) soil salinity and moisture were uncorrelated in the vegetation monitoring plots of Sweetwater Marsh, Tijuana Estuary, and Los Peñasquitos Lagoon. Pearson product-moment correlations were not significant for either the canopy or panne habitats on December 19, 1996 (canopy: $p = 0.464$; panne: $p = 0.436$), December 30, 1996 (canopy: $p = 0.087$; panne: $p = 0.410$), January 6, 1997 (canopy: $p = 0.197$; panne: $p = 0.283$), January 20, 1997 (canopy: $p = 0.359$; panne: $p = 0.864$), or January 27, 1997 (canopy: $p = 0.328$; panne: $p = 0.558$). Mean surface soil salinity and moisture in the soil monitoring plots at Sweetwater Marsh were negatively related over time (November 13, 1996 to January 28, 1997) in the canopy habitat ($r = -0.726$, $p = 0.001$) and the panne habitat ($r = -0.768$, $p = 0.001$).

The temporal frequency of sampling influenced the characterization of soil moisture and salinity (Fig. 4). For soil moisture, weekly sampling beginning on November 13, 1996 would have missed a large increase in moisture above 50% and quick decline between November 19 and November 25, 1996 in both the canopy and panne habitats fol-

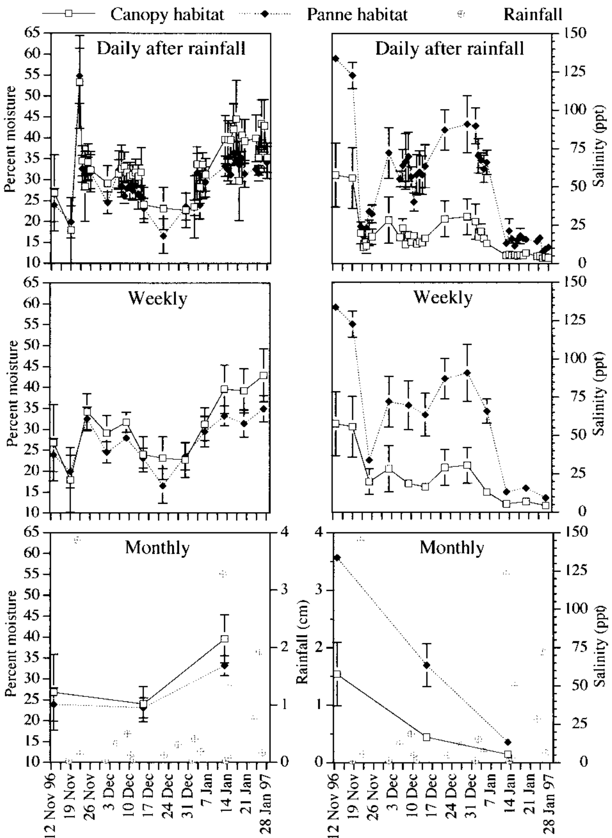

Fig. 4. The effect of sampling frequency on surface (2 cm) soil moisture and salinity (mean ± SE) in the soil monitoring plots at Sweetwater Marsh during the 1996 rain year.

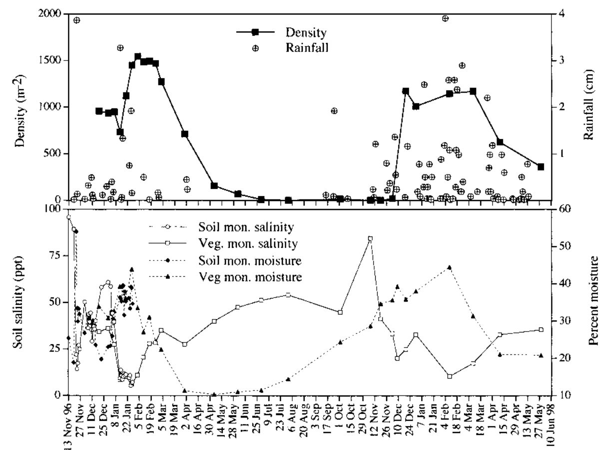

Fig. 5. Mean seedling density (all species combined, all three wetlands), mean soil moisture, and mean soil salinity in the soil monitoring plots (soil mon.) of Sweetwater Marsh and vegetation monitoring plots (veg. mon.) of Sweetwater Marsh, Tijuana Estuary, and Los Peñasquitos Lagoon. Los Peñasquitos Lagoon data is not included after August 1997.

lowing the largest rainfall of the year. Weekly sampling in the panne habitat would have shown salinity decreasing to 34‰ following this large rainfall compared to 18‰ documented by daily sampling. Similarly, weekly sampling in the canopy habitat would have indicated a decrease in salinity to 20‰ compared to 11‰ documented by daily sampling.

Monthly sampling beginning on November 13, 1996 would have missed the lowest and highest moisture levels recorded and the moisture fluctuations in both habitats (Fig. 4). For soil salinity, monthly sampling would not have recorded the large decrease in salinity following the largest rain of the year and subsequent increase in salinity. Moderate salinity fluctuations in the panne habitat and a large increase in salinity from December 15, 1996 to January 13, 1997 in both habitats would not have been evident with a monthly sampling regime.

Germination Pulses

Large pulses of seed germination (increases in seedling density) occurred twice during the 1996 season and once during the 1997 season (Fig. 5). The first large increase in the total density of seedlings (all species combined) occurred following the 3.9 cm rainfall on November 22, 1996. Quantification of seedling density began immediately after this unexpected, early-season event. No seedlings were observed prior to the rainfall and many new seedlings were observed in the week after the rainfall (Noe personal observation). A second germination pulse lasting two weeks followed the 3.3 cm rainfall on January 13, 1997. In the 1997 season, germination did not follow a specific rainfall event. Instead, seeds germinated in large numbers in December 1997 after multiple small and medium rainfall events over the previous month. Only a few seedlings appeared following the dry season rainfall (2.0 cm on September 25, 1997) and the 3.9 cm rainfall on February 4, 1998. Soils had high salinity (40‰) and low moisture (24%) following the dry season rainfall.

Discussion

Reduced salinity is a prerequisite for the germination of seeds of even the most salt-tolerant halophytes (Chapman 1974; Ungar 1978). In intertidal marshes of southern California, soil salinity declines with rainfall in winter (termed the low-salinity gap by Zedler et al. 1992) and seedlings appear in areas of sparse vegetation. Seedling establishment in the upper intertidal marsh occurred following decreases in soil salinity below 10–35‰ (Noe and Zedler In press). In addition, soil moisture increases following rainfall. Soil moisture must exceed 40% for germination to occur in this system (Noe and Zedler In press). Here we argue that the low-salinity gap concept should be revised to include soil moisture conditions.

Soil Moisture and Salinity Dynamics

Surface soil salinity in the canopy habitat was consistently lower and less temporally variable than in the panne habitat, although soil salinity was highly variable through time in both habitats (Fig. 3). The duration of low salinity during the 1996 rainyear also differed between habitats. The degree of salinity decrease in the canopy habitat during the rainy season was similar to that found by Callaway et al. (1990) and Kuhn and Zedler (1997). However, salinity in the panne habitat decreased far below what Callaway et al. (1990) measured at Carpinteria Marsh in 1986–1987, a wetter rainyear than 1996. There were few differences in surface soil moisture between the canopy and panne habitats and soil moisture was highly variable through time (Fig. 3).

There was a negative temporal correlation between surface soil salinity and moisture. In any plot, soil salinity decreased when soil moisture increased. During the 1996 wet season, substantial increases in soil moisture or decreases in soil salinity occurred only after two rainfalls larger than 3.0 cm (Fig. 3). This relationship of soil salinity change in response to rainfall amount is corroborated in soil microcosms. Leeds (1996) found that experimental rainfalls of 5.4 cm were necessary to decrease soil salinity in small greenhouse pots for the length of the study, 12 d. Rainfalls of < 2.7 cm decreased soil salinity for only a few days before salinity returned to pre-rainfall levels (Leeds 1996).

Soil salinity and moisture were not spatially correlated in the vegetation monitoring plots of either the canopy or panne habitats at Sweetwater Marsh, Tijuana Estuary, and Los Peñasquitos Lagoon. In other words, the soil moisture in a plot could not be predicted by the soil salinity in that plot. The lack of a spatial relationship between surface salinity and moisture indicates that there is not a strong spatial gradient from low moisture and high salinity to high moisture and low salinity in the upper intertidal marsh.

Soil moisture was higher in areas with more plant cover on days following large rainfall events, but not on days immediately before the large rainfalls (Table 1). This is most likely a result of lower evaporation rates in areas with high perennial plant cover; perennial plants in the upper intertidal marsh of southern California grow very slowly during winter months (Noe personal observation) and likely transpire slowly. The lack of a relationship between soil moisture and plant cover in the weeks following the large rainfalls indicates that the effect of high cover on soil moisture is temporary. Soil moisture varied less in areas with more bare ground. The rate of water loss in these areas may be faster than the sampling frequency, whereas areas with less bare ground, and more cover, held soil moisture long enough to be measured before infiltrating or evaporating.

Soil salinity was lower in areas with high perennial cover before large rainfalls and after the second large rainfall. This may be a result of lower evaporation rates and less vertical advection bringing high salinity water to the surface underneath perennial plant cover. Callaway (1994) also found that soil moisture was higher and soil salinity was lower under upper intertidal marsh canopies of southern California in April. The relationship between plant cover and soil moisture and salinity may change at other times of the year when annual species are larger and more productive and perennial species are more photosynthetically active.

Soils with more clay content had higher soil moisture before the first large rainfall and after both large rainfalls, suggesting higher water holding capacity (Table 1). Soils with more sand had lower soil salinity before one of the large rainfalls and higher temporal variability of salinity. Soils with high clay and low sand content had higher moisture and salinity and less salinity variability. While Zedler (1982) found that temporal variability in soil salinity increased with intertidal elevation and Callaway and Sabraw (1994) concluded that salinity decreased with elevation, there was no relationship between elevation and salinity or salinity temporal variability within the narrower intertidal elevation range of this study.

The mechanisms responsible for the dynamics of soil moisture and salinity were likely evaporation, infiltration, leaching, and advection. These mechanisms have been identified by research on the salinification process in arid-region agriculture (Kovda 1946; Shainberg and Shalhevet 1984; Frenkel and Meiri 1985). In the salt marsh, infiltration of the top centimeters of soil by large rainfall events increased soil moisture content and decreased salt levels by dilution and leaching of salts into lower soil. Smaller rainfall events did not leach salts into lower (below 2 cm) soil depths. Evaporation decreased soil moisture content, increased salt concentration, and created a hydrostatic gradient, advection, that brought salt water from the subsurface to the soil surface (Greenblatt 1997). Further evaporation led to the deposition of salts in the surface soil layers (Greenblatt 1997). Decreasing soil water content lowered evaporative flux and advection rates and eventually the advective current stopped (Hillel 1971). Tidal inundation added salts to the soil surface, although tidal inundation was infrequent in the upper salt marsh (Fig. 3).

This model of soil moisture and salinity dynamics is supported by the analysis of the effect of rainfall amount on soil moisture and salinity change, the negative temporal correlation between moisture and salinity in the soil monitoring plots during the rain season, and the higher soil moisture and lower soil salinity associated with higher cumulative plant cover. Álvarez Rogel et al. (2000) also hypothesized that rainfall quantity, plant cover, and soil texture influenced seasonal salinity patterns in Mediterranean salt marshes. Finally, these evaporation and advection dynamics were also observed in soil microcosms (Noe 1999). Surface soil salinity rapidly increased in open-top pots with high evaporation rates until the tops of the pots were closed. There was little evaporation in closed-top pots and surface soil salinity did not change.

Seedling Germination

Germination events seemed to depend on the history of rainfall, occurring after single large-size rainfalls in dry years or multiple small or medium-sized rainfalls in wet years. The two germination pulses in the dry 1996 season occurred after large (> 3.0 cm) rainfalls changed soil moisture and salinity enough to stimulate germination (Fig. 5). The germination pulse in the wet 1997 season did not occur following a large rainfall but instead occurred after multiple small and medium rainfalls. The early season medium-sized rainfall in the 1997 rainyear did not germinate many seeds because soil salinity was high, soil moisture was low, and the rainfall was not large enough to change soil salinity and moisture sufficiently to stimulate germination. Surprisingly, few seeds germinated following the large (3.9 cm) rainfall on February 4, 1997 and associated low salinity and high moisture. It is possible that the large germination pulse earlier in the 1997 season depleted the seedbank. While there was spatial variability in seedling density and variability in the timing of germination of individual species, the three large germination pulses were a general trend among the two habitats, three wetlands, and multiple species (Noe and Zedler In press). Although temperature and photoperiod differs during different periods of the wet season, the germination of southern California upper intertidal marsh species is affected more by soil salinity than temperature or photoperiod (Noe and Zedler 2000).

Precipitation Variability

Rainfall in southern California is highly variable. From 1850 to 1997, total rainyear rainfall had a CV of 41.0% and a large range (9 to 66 cm). Annual rainfall in southern California and Baja California is correlated with the El Niño-Southern Oscillation Index (Pavía and Badan 1998), with either positive or negative extremes in California rainfall occurring during El Niño years (Peterson et al. 1995; Harrison and Larkin 1998). For example, the 1996 rainyear was characterized by slightly below average rainfall, 18 cm, while the 1997 rainyear had a strong El Niño-Southern Oscillation event with total rainfall (45 cm) far above average. The timing of rainfall during the October to April wet season is also highly variable (Fig. 2). Zedler et al. (1992) concluded that not one year in the long-term record could be described as having a normal monthly distribution (within 10% of the mean) of average monthly rainfall for all months. Large rainfalls are rare in the historic record and the number of large rainfalls in a rain season is variable. An average of one rainfall larger than 3.0 cm occurred per rainyear and 30% of the years did not have a rainfall larger than 3.0 cm.

In the upper intertidal marsh, tidal immersion is infrequent (Fig. 3) and soil salinity is influenced more by rainfall events than estuarine water salinity (de Leeuw et al. 1991). The regeneration niche (Grubb 1977) in the upper intertidal marsh is a brief time when germination and establishment is stimulated by large rainfalls that increase soil moisture and decrease soil salinity. The variable rainfall patterns typical of southern California lead to variability in the frequency, duration, timing, and amplitude of changes in soil salinity and moisture. Because germinating and establishing plants respond to their immediate surrounding environment (Harper 1977), variation in soil salinity and moisture could have large effects on the germination window and community dynamics.

Effect of Temporal Sampling Scale

In a system with high variability and fast return to pre-rainfall conditions (Fig. 4), infrequent sample collection mutes variability and ignores important system dynamics. Neither the weekly nor monthly sampling frequencies accurately predicted soil moisture and salinity dynamics characterized by the regime of daily sampling after rainfall. While a weekly sampling regime may suffice for most analyses, a monthly sampling regime missed the high-moisture and low-salinity events that stimulate germination: salinity below 35‰ and moisture above 40% (Noe and Zedler In press). The low-salinity gap in salt pannes at Carpinteria Marsh (Callaway et al. 1990) exhibited less salinity reduction than in the salt panne in this study. The 12 to 17 d sampling frequency used by Callaway et al. (1990) may have missed short, but large, decreases in soil salinity following rainfall during the wet 1986 rainyear.

An accurate description of the abiotic environment is important for understanding the gap dynamics of plant communities (Pickett and White 1986). The complexity of how details of physical factors affect germination and establishment are important (Bazzaz 1996). In California desert, Beatley (1974) determined that no two years have the same rainfall regime and that the timing and quantity of individual rains were critical for determining the dynamics of the plant community. Vivian-Smith and Handel (1996) concluded that small changes in environmental conditions present in the field during the colonization phase can alter community composition. Bliss and Zedler (1998) found that vernal pool seedbanks respond to soil moisture differently depending on the timing of rainfall, duration of inundation, and the duration of increased soil moisture before the onset of inundation. It has also been shown that the duration, frequency, extent, and seasonality of inundation and soil saturation controls vegetative composition in freshwater wetlands (Carter et al. 1994). Finally, Noe (1999) found that the germination and establishment of an 11-species assemblage of salt marsh annual plants in experimental microcosms responded to differing amplitudes, durations, frequencies, and seasonal timing of low-salinity and high-moisture events.

The high variability of rainfall in southern California leads to variation in the conditions critical for germination in the upper intertidal marsh. This regeneration niche of high moisture and low salinity occurs at different times and for different durations depending on plant cover, soil texture, and recent rainfall history. Because the establishment of salt marsh and exotic invading species responds to the complexities of this germination window (Fig. 5; Callaway and Sabraw 1994; Noe 1999), temporal variability in rainfall exerts considerable control on community dynamics.

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