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SALT MARSH VEGETATION RESPONSE TO EDAPHIC AND TOPOGRAPHIC CHANGES FROM UPLAND SEDIMENTATION IN A PACIFIC ESTUARY

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Abstract: This study investigated how changes in salt marsh soil properties and topography on sediment fans related to shifts in salt marsh plant community composition in the Elkhorn Slough Watershed, California, USA. Several sediment fans have formed in this watershed as soil eroding from farms moved downslope, filling marshes, mudflats, and channels. Sandy sediment deposition increased marsh plain elevation and altered edaphic properties by increasing bulk density and decreasing soil moisture, salinity, and soil nitrogen compared to reference sites. These changes created a strong wetland-upland gradient and influenced the development of well-defined vegetation zones from wetland to upland: pickleweed (*Salicornia virginica*), cattail (*Typha* spp.) and bulrush (*Scirpus* spp.), and arroyo willow (*Salix lasiolepis*). Based on statistical analysis, arroyo willow grew in a distinct edaphic environment, and its expansion into the salt marsh was restricted by elevation in tidal areas greater than 1.80 m NAVD 88, spring soil moisture levels lower than 20%, and year-round salinity levels lower than 2.67 dS/m. Cattail and bulrush were present in transitional environmental conditions with fluctuating salinity and at an elevation similar to that of the pickleweed community. The hydrogeologic setting played a part in this change, as the contribution of upland sandy soils likely facilitated the emergence of new edaphic properties including lower salinity, lower soil moisture, and reduced soil nutrients. The findings in this study underline the importance of on-going erosion-control efforts to estuarine conservation in Central California.

Key Words: salt marsh, *Salix lasiolepis*, sedimentation, classification and regression trees (CART), watershed land use

INTRODUCTION

Watershed inputs to wetlands are greatly controlled by the wetland's landscape position or its hydrogeologic setting (HGS) (Bedford 1999). The HGS is defined by climate and physiographic characteristics that control the development and maintenance of a wetland and determine the spatial distribution of different wetland types (Winter 1988, Winter 1992, Bedford 1999, Godwin et al. 2002). When disturbance occurs in the HGS, such as through land-use change, upland inputs to wetlands also change, causing potential wetland degradation or loss.

Relationships between land-use change, upland inputs, and their effects on wetland productivity and plant community dynamics have been established in other studies. For example, an increase in agriculture and urban land use increased watershed sediment yield and produced high organic carbon levels in estuaries and subsequent changes in estuarine primary productivity (Howarth et al. 1991, Hopkinson and Vallino 1995). Anthropogenic changes in water-level fluctuations have led to *Phalaris arundinacea* L. invasion in grass- and sedge-dominated wetlands (Owen 1999). Urbanization increased freshwater runoff and establishment of brackish and riparian species in salt marshes (Greer and Stow 2003). Further, in many cases, high nutrient inputs have driven *Typha* spp. invasion in wetlands (Wetzel and van der Valk 1998, Gustafson and Wang 2002, Woo and Zedler 2002).

In addition to changes in salinity and nutrient loading, sediment delivery from upland watersheds is an additional important driver of wetland change. While sediment accretion from river silt, organic matter, or marine deposits is fundamental to the development and maintenance of salt marshes (Chmura et al. 1992, Callaway et al. 1997, Weis et al. 2001, Watson 2004), elevated levels of upland sediment can drive large-scale changes in wetlands in different, sometimes contrasting ways. For example, in some cases, increased sediment has caused poor seed germination (Jurik et al. 1994, Wang et al. 1994, Wardrop and Brooks 1998, Gleason et al. 2003), while in other cases, it increased soil bulk density, lowered soil organic matter, and elevated nitrate and phosphorus concentrations, leading to higher species richness, greater biomass, and more shrub species (Johnston 2003, Koning 2004, Nakamura et al. 2004). Bulk density and organic matter changes, along with reduced wetland microtopography, have also facilitated species invasion and loss of plant diversity (Vivian-Smith 1997, Werner and Zedler 2002). Further, sedimentation has caused increased biomass and forest expansion by lowering groundwater levels and increasing nutrients (Nakamura et al. 2004). In contrast, sedimentation has also reduced biomass of wetland tree and herbaceous species (Ewing 1996).

In California, USA, specifically, sediment from upland sources may speed development of a marsh and create conditions for plant establishment on mudflats. For example, sediment from extreme storm events in Southern California raised elevations enough on a mudflat to allow *Spartina foliosa* Trin. to establish (Ward et al. 2003). Salt marsh can also recover from sediment disturbance, although at times with a change in species distribution, as demonstrated in Bolinas Lagoon in Northern California (Allison 1995, 1996). Upland sediment may drive shifts in salt marsh habitat, but there is not a strong record of how sedimentation can lead to salt marsh loss. Further, there is a need to document how sediment alters the physical properties of wetland soils and their effect on species distribution and abundance (Werner and Zedler 2002).

This paper addresses the influence of upland sediment inputs on a coastal salt marsh in Central California. Because of upland soil erosion several sediment fans have formed in pickleweed (*Salicornia virginica* L.) salt marsh in Elkhorn Slough, California located on the coast of Monterey Bay (Dickert and Tuttle 1980). Automated classification and change-detection of historical aerial photos revealed that, where sediment fans formed, arroyo willow (*Salix lasiolepis* Benth.) and several brackish and freshwater taxa, including cattail (*Typha* spp.) and bulrush (*Scirpus* spp.), replaced salt marsh present in the 1970s and 1980s (Byrd et al. 2004). Arroyo willow groves now cover a majority of the old salt marsh area. The objectives of this study were 1) to analyze how sediment changed salt marsh soil physical and chemical properties and topography and 2) to determine how these changes related to the distribution of new plant species.

We addressed these objectives by 1) documenting sediment deposition into wetlands in the study area for two years, 2) investigating changes to marsh soil and topography, and 3) examining possible vegetation responses to these changes. We hypothesized that upland sediment altered soil properties and marsh topography and that the sediment texture affected other soil properties on the fans. These changes produced new environmental gradients, as compared to undisturbed salt marsh. We also hypothesized that these new conditions led to new plant species establishment and that their distribution was related to environmental gradients on the fans. Given that arroyo willow is currently the dominant species on the fans, we hypothesized that arroyo willow establishment occurred once an environmental threshold was reached, and pickleweed cover is not currently increasing.

The Study Area

This study took place in Elkhorn Slough, located on the coast of Monterey Bay, California (Figure 1). The Elkhorn Slough watershed is small (182 km^2), and the slough extends 11.4 km inland from Moss Landing. Elkhorn Slough is a seasonal estuary surrounded by more than 1,420 ha of tidal marsh and flats (Caffrey et al. 2002), making it one of the largest salt marsh systems in California (Dickert and Tuttle 1985). Steep hills rise 30 to 100 m from the marsh; while many hills are cultivated, the uplands are also characterized by oak woodland, grassland, and maritime chaparral communities.

The Elkhorn Slough region has a Mediterranean climate, with a monthly mean temperature range of 11.1° to 15.4°C and an average annual rainfall of 55.3 cm that occurs generally between October and May (Caffrey et al. 2002). A majority of the soils in the watershed uplands are derived from the Aromas sands formation, an aeolian sandy parent material producing soils with high sand content that are highly erodible when disturbed. The major soil series present in the hills adjacent to the slough are Arnold loamy sand, Santa Ynez sandy loam, and Elkhorn sandy loam. The marsh soil type is Alviso sandy clay loam (USDA-NRCS 2004).

While Elkhorn Slough contains a National Estuarine Research Reserve and other protected lands, intense farming since 1970, especially strawberry farming, has produced high soil erosion rates in the watershed (Dickert and Tuttle 1980, USDA-SCS 1984). Rates have been estimated at 74 metric tons/hectare/year (USDA-SCS 1994). Most soil erosion

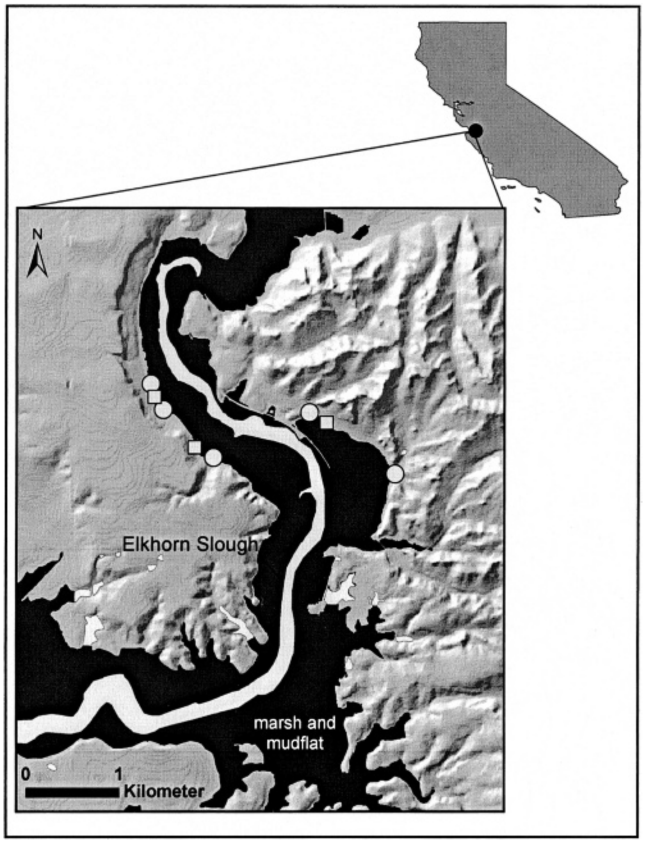

Figure 1. Project Area in the Elkhorn Slough Watershed, California, USA. Circles represent sediment fans and squares represent reference sites. Site with tidal influence are on the west side of the slough and sites removed from tidal influence are on the east side of the slough.

occurs as large volumes of water erode vegetated slopes located below agricultural fields, forming large gullies, which are the predominant sediment source. Streambank erosion is a minor problem in comparison (USDA-SCS 1984). Water carries sediment down steep drainages located between the farms and the marsh, where it is deposited at the base of slopes, forming alluvial fans that fill marshes, mudflats, and channels.

Sediment transport in these drainages normally occurs during episodic, extreme winter storm events, with little transport during intervening periods. Stream flow deposits are formed on the fans when surges of sediment-laden water spread out from the end of a stream channel, resulting in sheet-like deposits of sand. As the stream spreads out on areas of lower relief, sediment loads are quickly dumped, causing the stream channel to choke and the stream to shift sideways across the fan (Boggs 1987). The shifting of the stream channel from year to year results in the formation of multiple lobes of stream flow deposits. As the lobes are deposited, the alluvial fan builds with a cross-section that is generally wedge- or lens-shaped. By 1980, at least 30 sediment fans had formed in salt marsh, ponds, and freshwater marsh of Elkhorn Slough (Dickert and Tuttle 1980).

METHODS

Site Selection

As in many coastal salt marshes, the vegetation in the study sites existed in distinct, often monotypic, zones. On the sediment fans, dominant plant communities present along a wetland – upland gradient were pickleweed, cattail and bulrush, and arroyo willow, with virtually no transition zone between each community. The cattail and bulrush community was dominated by *Typha latifolia* L., *T. angustifolia* L., their hybrid *T.* × *glauca* Godr., and *Scirpus californicus* (C. A. Mey.) Steud., according to field observations. To determine the effects of sedimentation on marsh physical and chemical properties and species distribution, we studied five sediment fans that were down-slope from active farming. The fans were chosen because of their similarity in upland land use, size (the cross-sections were approximately 200 meters), vegetation patterns, and soil type characterized by high sand content. The fans were also well-distributed around the Elkhorn Slough watershed. Three were on the west side of the slough, which was tidally influenced, and two were on the east side of the slough, which were blocked from tidal influence by levees.

Three reference sites adjacent to the fans, characterized as relatively undisturbed pickleweed salt marsh, were also selected. Their upper boundary was defined by the ecotone separating salt marsh from upland grasses or shrubs. Based on interpretation of 1980 aerial photos, the current vegetation cover and composition on the reference sites was representative of what was historically present on the sediment fan sites prior to disturbance from sediment. The reference sites received less freshwater inputs than the sediment fans since they were adjacent but not connected to the steep drainages contributing upland inputs to the fans. However, they were contained within the same catchments as the adjoining fans. Reference sites with freshwater inputs but no sediment were not available since sediment fans have formed at the base of most drainages in Elkhorn Slough.

Field Sampling Design

Permanent transects running from upland to wetland were established at each site to sample

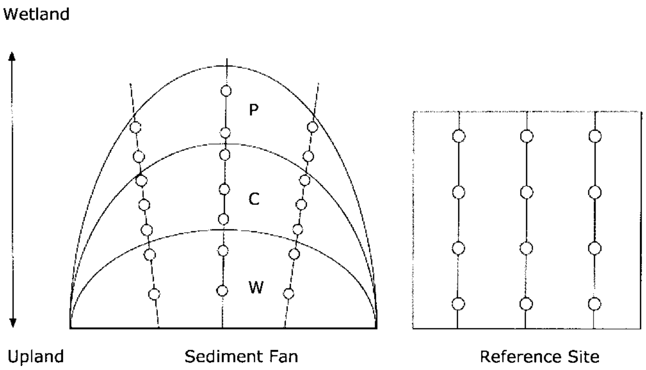

Figure 2. Sampling design on sediment fans and reference sites. P, C, W symbols represent vegetation communities pickleweed, cattail and bulrush, and arroyo willow on the sediment fans.

elevation, soil physical and chemical properties, and plant species cover (Figure 2). On the sediment fans, transects were systematically placed 50 meters apart, with the first transect location chosen randomly. The number of transects per site ranged from four to five, depending on the size of the fan. Sample points were placed in the center and edge of each plant community, or zone, resulting in a stratified systematic sampling design. This design was chosen to capture the entire range of environmental conditions in which each plant community was found and to discriminate differences at the transition between plant communities. There were three transects in the reference sites running 25 meters from upland to wetland. Four sample points were established systematically along each transect. Overall, 170 permanent sampling points were established among the eight sites.

Sampling of Sediment Deposition

Sedimentation rates on alluvial fans and reference sites were monitored over two winters: 2002–2003 and 2003–2004. Stakes were placed along the established transects before November 1 of each year, and their height above ground was recorded. In April, the height of the stakes above the sediment surface was measured again to quantify the depth of sediment accumulation over the winter.

Sampling of Soil Properties

The following variables were sampled over a two-year period beginning in August 2002: soil texture, soil salinity, soil moisture, soil nitrate (NO_3-N), and soil ammonium (NH_4-N). Nitrogen mineralization and nitrification rates were calculated from soil incubations (Hart et al. 1994). A sub-set of soil samples was also analyzed for bulk density. These variables were chosen because of their potential to influence plant distribution and the likelihood that upland sediment had altered them. The soil texture of the sediment had a visibly high sand content compared to the silty-clay of the marsh soil. Nitrogen was sampled because nitrate and ammonium runoff from farms in the Elkhorn Slough watershed have been recorded at high levels over several years, and Elkhorn Slough is generally nitrogen-limited (Caffrey et al. 1997). Other California salt marshes have been found to be nitrogen-limited (Boyer and Zedler 1998, Boyer et al. 2001), and nutrient inputs can contribute to cattail invasion in freshwater systems (Wetzel and van der Valk 1998, Woo and Zedler 2002). Salinity gradients also influence salt marsh species distribution (Barbour and Davis 1970, Pennings and Callaway 1992, Kuhn and Zedler 1997), while willows require freshwater for establishment (Sacchi and Price 1992, Orians et al. 1999, Karrenberg et al. 2002).

Soil was sampled to a depth of 30 centimeters to capture the bulk of the root zone for all dominant species. Sampling occurred in August 2002, April and August 2003, and April 2004. These dates were chosen to account for the difference in some variables between spring (the end of the rainy season when freshwater flows and agricultural runoff is higher) and late summer (the height of the dry season when biomass is at its peak and salinity especially is at its highest point). Soil texture and bulk density were sampled once. Soils were tested for salinity on all four dates, and soil moisture and soil nitrogen were sampled in April and August 2003 and April 2004.

Soil Physical Properties. Soil moisture was measured gravimetrically (Gardner 1986). Soil bulk density was determined by volumetric sampling (Blake and Hartge 1986). Soil texture, or soil particle size, was analyzed using the hydrometer method described by Sheldrick and Wang (1993). Soil salinity, or electrical conductivity, was determined by the saturation paste extraction method (Rhoades 1982), chosen because samples at the upper end of the transects were too dry to extract interstitial water. Saturation paste extracts with electrical conductivity over 30 dS/m are slightly overestimated due to a non-linear relationship between electrical conductivity and soil dilution (University of California Division of Agriculture and Natural Resources Analytical Laboratory [DANR lab], Richards 1954).

Soil Chemical Properties. Soils were sampled, hand-homogenized, and placed into plastic bags.

They were then immediately placed into coolers for transport back to U.C. Berkeley, where they were stored at 4°C for a maximum of 48 hours before being processed for nitrogen content. Soil samples were then extracted with 2 M KCl solution to remove nitrate and ammonium. Extractions were analyzed by the flow injection analyzer method (Switala 1999, Wendt 1999) at the DANR Analytical Lab at U.C. Davis. Mineralization and nitrification rates were estimated through 7-day lab incubations of soil samples as described by Hart et al. (1994). Lab incubations were stored in sealed polyethylene bags containing head-space to preserve soil moisture.

Sampling of Marsh Topography

Topographic surveys were conducted because salt marsh species distribution is strongly influenced by elevation (Zedler et al. 1999, Noe and Zedler 2001). Elevation surveys occurred in November 2003 when plants had senesced. Benchmarks were permanently established within line-of-site of all study sites, and their elevation was measured with a Trimble® 5800 GPS system using real-time kinematic (RTK) GPS. The readings were in NAVD 88 with a precision of +/− 2 centimeters. NAVD 88 is approximate to mean lower low water (MLLW) in Elkhorn Slough (NOAA-NGS 2005). Conversions to the tidal datum were not conducted because they would be based on out-of-date tidal benchmarks (pre-1989 7.1 Loma Prieta earthquake).

Elevation surveys on the sediment fans were conducted using a level and stadia rod and were referenced to benchmark readings. Survey readings were taken every 2 meters along the wetland – upland gradient of each transect. The dominant plant species at each survey point was recorded. Overall survey error was on average 0.5 cm over 25 meters (the average transect length).

Sampling of Plant Community Distribution

Plant surveys were conducted in late August for three consecutive years: 2002 through 2004. At each of the 170 permanent sampling points, the plant community was recorded and a quarter-meter quadrat was used to estimate the cover of each species according to the Braun-Blanquet cover class system (Mueller-Dombois and Ellenberg 1974). Cover class values were then converted into the means of each class. Relative cover for each species was calculated as the cover of one species as a percent of total plant cover (Barbour et al. 1999).

Statistical Analyses

Sediment Deposition. The stake height reading in November was subtracted from the reading in April to determine sediment accumulation over the winter. Mean and median sediment accumulation rates were then calculated.

Soil Properties and Marsh Topography. Multiple analyses of variance (MANOVA) were conducted for all combined April and August data to test for differences in mean vectors among four groups: reference sites, pickleweed (located on the sediment fans), cattail and bulrush (cattail), and arroyo willow. Following that, each variable was tested for significant differences among groups using one-way ANOVAs.

Relationships to Sediment Texture. Since the sediment was high in sand content, the percent sand variable was tested for correlations with other soil variables using Pearson correlation coefficients.

Environmental Gradients. Moisture and salinity changes along elevation gradients were compared between reference and fan sites according to season and tidal influence using multiple regression. Salinity and moisture data were log-transformed to normalize the data in the regression analysis. The multiplicative change in salinity or moisture between reference and fan sites for any given elevation was calculated from the regression equations. These analyses were conducted in Intercooled Stata 8.2 (StatacorpLP 1985–2004).

Plant Community Distribution. Data matrices for each season were generated that attributed soils data, elevation data, and the plant community, or zone, to each data point. Our analytical objective was to classify the plant data based on environmental variables in order to determine the range of edaphic and topographic conditions in which each plant community was found. A common multivariate technique for classification is linear discriminant analysis, but it requires assumptions of multivariate normal distribution and homogeneity of variance-covariance matrices (Tabachnick and Fidell 1996) that often do not reflect the data structure of ecological datasets (Austin and Smith 1989). To avoid violating these assumptions, we chose the classification and regression tree (CART) analytical method, executed in the software package R 1.9.1. (The R Foundation 2004).

Classification trees are a non-parametric alternative to linear discriminant analysis with several advantages. Data do not require transformations, and any combination of categorical and continuous predictor variables may be used. Classification trees can handle missing data, and they have the ability to capture hierarchical and non-linear relationships and expose interactions among predictor variables (Feldesman 2002). Because of these advantages, they have been successfully used to analyze complex ecological datasets (De'ath and Fabricus 2000, Vayssieres et al. 2000).

Rpart (in R 1.9.1) creates classification trees using the BFOS algorithm (binary recursive partitioning algorithm) that splits the response variable into increasingly homogeneous binary subsets based on thresholds in predictor variables (Breiman et al. 1984). The final result is a binary decision tree that permits the classification of new cases. Each successive split in the tree corresponds to a threshold value of one explanatory variable. At each split, data are divided between two branches according to the threshold value into two mutually exclusive groups. The terminal nodes, or leaves, represent the final classification result (De'ath and Fabricus 2000, Vayssieres et al. 2000). Interactions are identified when two or more predictor variables occur more than once on a single branch. Cross-validation is used to determine the length of tree (number of leaves), which is a balance between misclassification error and tree size (smaller trees are preferred to prevent overfitting). Not all predictor variables may determine splits in the tree – those not influencing classification of response variables will not appear on the tree. All data were analyzed for each season, with data from year one used to predict classification of data from year two. For each tree, resubstitition accuracy and cross-validation accuracy values were calculated.

Arroyo Willow Establishment. To determine if there is an environmental threshold that limits willow presence on a sediment fan, additional CART analyses were conducted using data points within 5 meters of the cattail/willow transition zone.

Plant Community Changes. The average percent cover of pickleweed, cattail, and arroyo willow on the sediment fans was calculated for 2002, 2003, and 2004. For each species, one-way ANOVAs were used to test for significant differences in percent cover among years. Analyses were conducted in Intercooled Stata 8.2 (StatacorpLP 1985–2004).

RESULTS

Sediment Deposition

During winter 2002–2003, average deposition was 1.15 cm, with a range of 0 to 13 cm and a median value of 0.5 cm. Higher deposition rates were observed in some areas during the 2003–2004 winter. Average sedimentation was 4.18 cm, with a range of 0 to 22.9 cm and a median value of 1.5 cm.

Soil Properties and Marsh Topography

Reference sites differed significantly from at least one plant community on the sediment fans for most soil variables and elevation (Table 1). Bulk density (0.48 g/cc) was lowest on reference sites, while salinity (April: 87 dS/m, August: 146 dS/m), moisture (April: 142%, August: 117%), and spring NO_3-N (3.23 ug/g) and NH_4-N (13.46 ug/g) values were highest on reference sites. Reference site average elevation was significantly lower compared to the willow zone (1.34 m vs. 1.92 m) and percent sand (39%) was lower than the cattail and willow zones.

On the sediment fans, some variables changed gradually from wetland to upland, while others changed abruptly from one plant community to the next. Bulk density increased along the wetland-upland gradient from 0.93 to 1.26 g/cc, with a significant gain from pickleweed to cattail (Table 1). In comparison, percent sand jumped from one zone to the next (ranging from 36% to 81%). Elevation increased gradually from 1.34 to 1.45 meters moving from pickleweed to cattails. It then increased significantly from cattails, at 1.45 meters, to willows, at 1.92 meters.

In the spring, electrical conductivity, or salinity, dropped significantly from the pickleweed to cattail zone (from 38.2 to 6.6 dS/m) (Table 1) but showed similarities between cattails and willows. Soil moisture decreased with increasing proximity to the uplands (from 66.3% to 16.7%), with significant differences between the pickleweed and cattail zones and similarities among the cattails and willows. April soil NH_4-N decreased from pickleweed to cattail to willow (from 7.51 to 1.29 ug/g), with significant differences between pickleweed and cattail. There was no difference in nitrogen mineralization and nitrification among all zones. However, mineralization rates were slightly negative in the reference and pickleweed sites, compared to a slightly positive rate in the cattail and willow sites, indicating nitrogen immobilization taking place where pickleweed grew.

In August, the salinity gradient along the sediment fan became greater than in April. In contrast to the spring, salinity differences between the cattails and willows were significant (31.2 vs. 5.5 dS/m) (Table 1) as the cattails became more saline, while in the willows, conditions remained somewhat fresh to brackish. There was little change in soil moisture

Table 1. One-Way ANOVAs of all variables. Significant F values ($p < 0.05$) are in bold. Degrees of freedom are in parentheses. Means and standard deviations provided. Means sharing a superscript letter are not significantly different based on the Tukey-Kramer HSD test.

	F value	Reference	Pickleweed	Cattail	Willow
Bulk density (g/cc)	**88.78** (3, 145)	$0.48^{A} \pm 0.18$	$0.93^{B} \pm 0.26$	$1.14^{C} \pm 0.21$	$1.26^{C} \pm 0.13$
Elevation (m)	**11.42** (3, 133)	$1.34^{A} \pm 0.43$	$1.34^{A} \pm 0.40$	$1.45^{A} \pm 0.37$	$1.92^{B} \pm 0.51$
Percent sand	**25.87** (3, 135)	$39.37^{A} \pm 21.70$	$35.55^{A} \pm 22.58$	$59.79^{B} \pm 27.24$	$81.26^{C} \pm 20.08$
April					
Electrical conductivity (dS/m)	**113.16** (3, 286)	$86.62^{A} \pm 50.13$	$38.19^{B} \pm 35.15$	$6.64^{C} \pm 10.04$	$0.99^{C} \pm 0.77$
Gravimetric soil moisture	**73.21** (3, 244)	$141.92^{A} \pm 87.03$	$66.26^{B} \pm 41.43$	$36.74^{C} \pm 12.29$	$16.70^{C} \pm 9.23$
NO_3-N (µg/g soil)	**20.63** (3, 241)	$3.23^{A} \pm 1.64$	$1.85^{B} \pm 0.77$	$1.87^{B} \pm 0.82$	$1.88^{B} \pm 1.39$
NH_4-N (µg/g soil)	**25.27** (3, 241)	$13.46^{A} \pm 13.95$	$7.51^{B} \pm 7.71$	$3.23^{C} \pm 3.06$	$1.29^{C} \pm 1.09$
N mineralization (µg/g/day)	1.093 (3, 241)	-0.16 ± 1.12	-0.38 ± 1.51	0.10 ± 2.47	0.02 ± 0.16
Nitrification (µg/g/day)	0.74 (3, 241)	0.06 ± 0.28	0.06 ± 0.13	0.18 ± 1.03	0.07 ± 0.17
August					
Electrical conductivity (dS/m)	**120.44** (3, 209)	$146.38^{A} \pm 59.19$	$74.13^{B} \pm 37.43$	$31.22^{C} \pm 26.81$	$5.52^{D} \pm 9.20$
Gravimetric soil moisture	**29.09** (3, 141)	$117.42^{A} \pm 79.18$	$65.69^{B} \pm 62.66$	$31.39^{C} \pm 21.14$	$8.33^{C} \pm 9.66$
NO_3-N (µg/g soil)	1.31 (3, 139)	1.70 ± 0.92	1.34 ± 0.64	1.94 ± 2.53	1.35 ± 0.83
NH_4-N (µg/g soil)	**10.81** (3, 142)	$6.38^{A} \pm 4.36$	$8.83^{A} \pm 11.05$	$2.71^{B} \pm 3.21$	$1.25^{B} \pm 0.75$
N mineralization (µg/g/day)	**8.17** (3, 141)	$-0.02^{A} \pm 0.64$	$-0.95^{B} \pm 1.69$	$-0.10^{A} \pm 0.59$	$0.01^{A} \pm 0.12$
Nitrification (µg/g/day)	0.86 (3, 141)	0.04 ± 0.14	-0.01 ± 0.08	0.03 ± 0.22	0.05 ± 0.12

from April to August, although soil dried out in the willows to an average of 8.3%. Again, soil NH_4-N dropped along the wetland-upland gradient (from 8.83 to 1.25 ug/g). Pickleweed sites had significantly higher NH_4-N levels than the cattail and willow zones. Nitrogen mineralization rates were significantly lower in the pickleweed than in all other groups, again indicating nitrogen immobilization.

Relationships to Sediment Texture. Sedimentation into the salt marsh led to change in soil texture from silty-clay to sand. Percent sand was significantly correlated with other tested soil variables ($p < 0.05$) based on Pearson correlation coefficients (Table 2). Percent sand was positively correlated with bulk density and negatively correlated with April and August soil moisture, April and August salinity, April and August NH_4-N and April and August NO_3-N (Table 2).

Table 2. Correlations between percent sand and other soil variables. All correlations are significant ($p < 0.05$).

	Percent Sand
Bulk density (n = 148)	0.67
April	
Electrical conductivity (n = 269)	−0.45
Gravimetric soil moisture (n = 255)	−0.57
NO_3-N (n = 255)	−0.25
NH_4-N (n = 255)	−0.41
August	
Electrical conductivity (n = 203)	−0.46
Gravimetric soil moisture (n = 135)	−0.49
NO_3-N (n = 135)	−0.27
NH_4-N (n = 135)	−0.28

Environmental Gradients. Gradients on tidal and non-tidal sites were compared separately because elevation in non-tidal, subsided areas was on average lower than tidal areas, and gradients would not be comparable. The change in salinity with respect to elevation, or the salinity gradient, was not significantly different between sediment fans and reference sites for any given season or tidal condition (Table 3). In each situation, however, there was a multiplicative change in salinity between reference and sediment fans for any given elevation value. The greatest difference was found in the April non-tidal sites, where fitted salinity on the reference site was 9.15 times the value on the sediment fan sites for any elevation.

The change in moisture with respect to elevation, or the moisture gradient, was not significantly different between sediment fans and reference sites for any given season or tidal condition except the April tidal sites (Table 3). As with salinity, there was a multiplicative change in soil moisture between reference and sediment fans for any given elevation.

Plant Community Distribution

For all four sampling dates, salinity (electrical conductivity) was the most important variable

Table 3. Multiple regression results showing differences in salinity and moisture along elevation gradients between reference and sediment fan sites. Data were analyzed separately for tidal and non-tidal sites according to season. Salinity and moisture data were log-transformed. Percent values represent the gradient, or percent decrease in salinity or moisture with 0.1-meter increase in elevation. Sr/Sf ratios represent the multiplicative change in salinity from fan sites to reference sites for any given elevation. Sr = salinity in reference sites, Sf = salinity in fan sites. Mr/Mf ratios represent the multiplicative change in soil moisture from fan sites to reference sites for any given elevation. Mr = soil moisture in reference sites, Mf = soil moisture in fan sites. The only gradient difference was found in moisture levels between tidal fan and reference sites in April. The 95% confidence intervals are provided in parentheses.

	April		August	
Comparison	Regression	Salinity Gradient, = $\text{Salinity}_{\text{ref}}/\text{Salinity}_{\text{fan}}$ (95% confidence intervals)	Regression	Salinity Gradient, = $\text{Salinity}_{\text{ref}}/\text{Salinity}_{\text{fan}}$ (95% confidence intervals)
Non-tidal reference vs. fan	$R^2 = 0.74$ $F_{(2, 91)} = 131$ $p < 0.001$	27% (21%, 32%) Sr = Sf*9.15 (5.67, 14.76)	$R^2 = 0.67$ $F_{(2, 61)} = 63$ $p < 0.001$	40% (33%, 47%) Sr = Sf*4.52 (5.67, 10.53)
Tidal reference vs. fan	$R^2 = 0.75$ $F_{(2, 160)} = 233$ $p < 0.001$	35% (32%, 38%) Sr = Sf*4.62 (3.25, 6.49)	$R^2 = 0.62$ $F_{(2, 130)} = 104$ $p < 0.001$	28% (24%, 32%) Sr = Sf*2.96 (1.99, 4.38)
Comparison	Regression	Moisture Gradient, $\text{Moisture}_{\text{ref}}/\text{Moisture}_{\text{fan}}$ (95% confidence intervals)	Regression	Moisture Gradient, $\text{Moisture}_{\text{ref}}/\text{Moisture}_{\text{fan}}$ (95% confidence intervals)
Non-tidal reference vs. fan	$R^2 = 0.73$ $F_{(2, 77)} = 102$ $p < 0.001$	15% (11%, 18%) Mr = Mf*2.69 (2.08, 3.46)	$R^2 = 0.60$ $F_{(2, 47)} = 35$ $p < 0.001$	Mr = Mf*3.60 (1.65, 7.85)
Tidal reference vs. fan	$R^2 = 0.69$ $F_{(3, 134)} = 99$ $p < 0.001$	reference: 32% (26%, 38%) fan: 14% (11%, 17%) Mr = Mf*91.84*$e^{(-2.32\text{elevation})}$	$R^2 = 0.60$ $F_{(2, 79)} = 60$ $p < 0.001$	Mr = Mf*2.01 (1.43, 2.83)

separating the four vegetation communities – reference sites, pickleweed, cattails, and willows – as it produced the first bivariate split in each classification tree (Figure 3). The threshold level for these splits varied among all dates from 76.5 dS/m in August 2003 to 11.5 dS/m in April 2004.

In August, elevation was another important variable that separated willows from other groups at a threshold level of about 1.8 meters. Also, levels of percent sand divided cattail and pickleweed. Generally, based on August data, willows appeared at salinity levels lower than 2.8 dS/m and at elevations greater than 1.85 meters. Cattails grew where salinity was less than 44.3 dS/m and percent sand content was greater than 30%. Pickleweed existed where salinity was greater than 77.5 dS/m but less than 133.6 dS/m, and percent sand was less than 30%. Reference sites were characterized by very high salinity levels (>133.6 dS/m). August 2002 resubstitution accuracy was 80.9%, and cross-validation accuracy was 66.2%. August 2003 resubstitution accuracy was 77.9%, and cross-validation accuracy was 68.3% (Table 4).

The April 2003 data produced the most complex tree (Figure 3). After salinity, soil moisture, percent sand, and elevation variables contributed to data classification. The repeated appearance of soil moisture and elevation along one branch of the tree indicates an interaction between the two variables. In contrast, the April 2004 data classification was much more driven by a salinity gradient; pickleweed and reference sites were separated from cattail and willow sites at a threshold level in electrical conductivity of 11.54 dS/m. Cattails were separated from willows at a salinity threshold level of 1.18 dS/m. Generally, based on April data, spring environmental conditions for willow included salinity levels less than 1.18 dS/m, soil moisture less than 20%, and if greater than 20%, then elevation greater than 1.85 m. Cattails existed in areas with elevation less than 1.08 m, or if greater, than with soil moisture less than 45.8%. Pickleweed was present in areas with lower percent sand. April 2003 resubstitution accuracy was 77.2% and cross-validation accuracy was 55.0%. April 2004 resubstitution accuracy was 74.7% and cross-validation accuracy was 63.4% (Table 4).

A high percentage of willow data points fell within the willow class in both April and August and maintained relatively high classification levels in the cross-validation test. Reference sites were poorly classified and most often confused with pickleweed present on sediment fan. Pickleweed classification was less accurate in the spring than in August; this species was confused for reference sites and cattail.

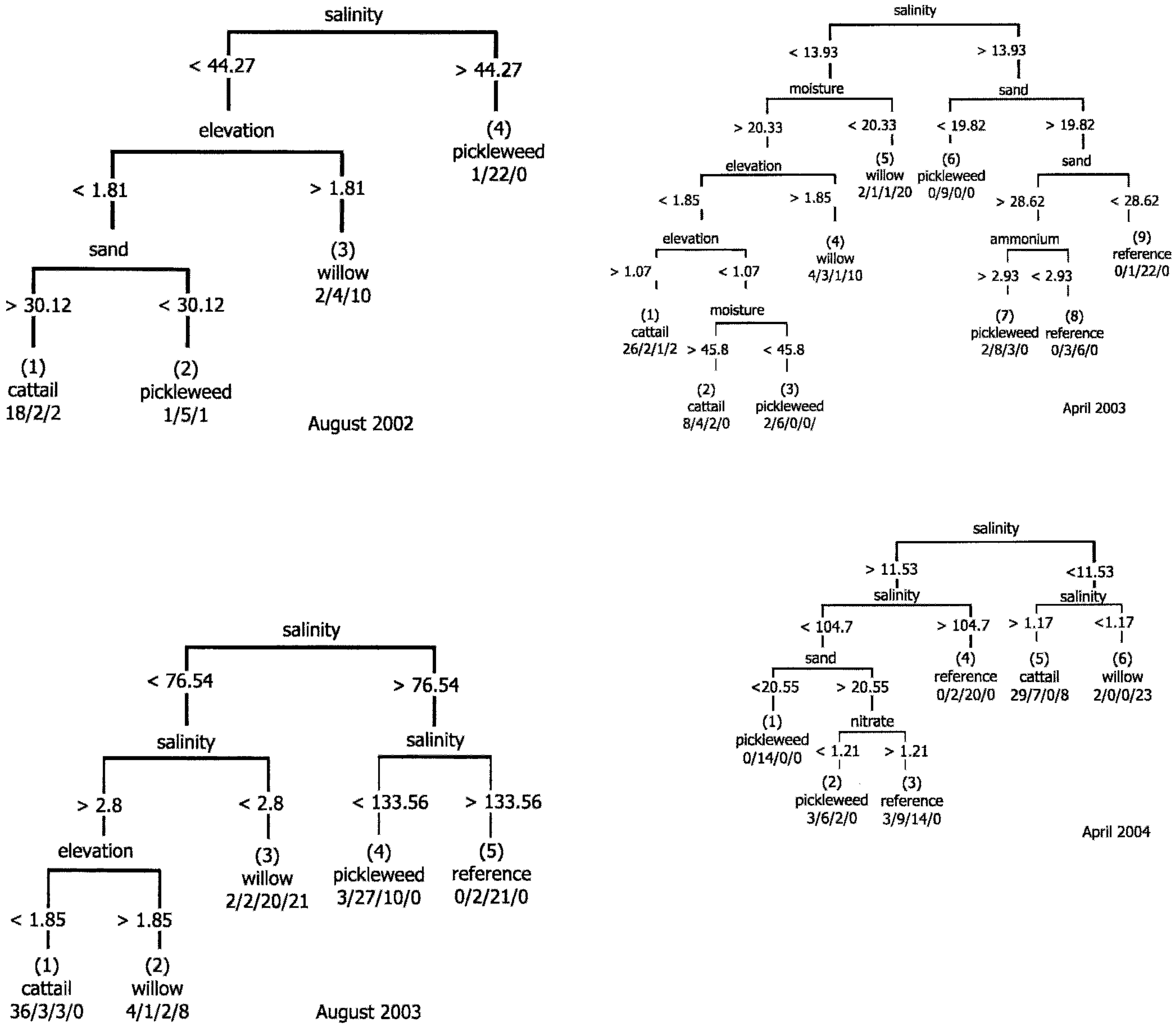

Figure 3. Classification trees for August 2002, 2003, and April 2003, 2004. Labels of nodes represent datatypes assigned to that node, in order: cattail/pickleweed/reference/willow.

Cattails were equally confused for pickleweed and willow (Table 4).

The August 2002 model was used to predict classification of August 2003 data (Table 5). Overall prediction accuracy was 64%. This low value was mostly due to inaccurate classification of cattails (33% accuracy, similar to that of chance alone). Prediction of April 2004 data classification, using the April 2003 data, was somewhat more accurate (73%).

Arroyo Willow Establishment. The willow data points were classified relatively accurately in the classification tree analysis, which suggests that willows grew in edaphic conditions and at elevations that are distinctly different from other species found on the sediment fan. For both April and August, the elevation threshold separating cattail and willow was 1.85 meters and was the first bivariate split in both trees. In the spring, the second split was defined by a moisture-level threshold of 20.3%. In August, the second split was defined by salinity threshold of 2.67 dS/m (Figure 4). The willow data points were classified consistently for both April (100%) and August (96%) (resubstitution accuracy) (Table 6).

Plant Community Changes. Twenty four species with relative cover of at least 0.5% were identified,

Table 4. Cross-validation accuracy matrices for August 2002, 2003, and April 2003, 2004. Each row represents the distribution of data from one plant community into four classes: reference (R), pickleweed (P), cattail (C), and willow (W). The Class Accuracy column shows how accurately data from each plant community were classified.

August 2002

Cross-Validation Matrix
Accuracy: 66.2%

Actual	P	C	W	Class Accuracy
pickleweed	23	6	4	69.7%
cattail	8	12	2	54.5%
willow	1	2	10	76.9%

August 2003

Cross-validation Matrix
Accuracy: 68.3%

Actual	R	P	C	W	Class Accuracy
reference	21	10	3	2	58.3%
pickleweed	6	21	5	3	60.0%
cattail	1	5	33	6	73.3%
willow	0	0	5	24	82.8%

April 2003

Cross-validation Matrix
Accuracy: 55.0%

Actual	R	P	C	W	Class Accuracy
reference	21	11	2	2	58.3%
pickleweed	12	11	10	4	29.7%
cattail	1	8	25	10	56.8%
willow	0	2	5	25	78.1%

April 2004

Cross-validation Matrix

Accuracy: 63.4%

Actual	R	P	C	W	Class Accuracy
reference	25	9	2	0	69.4%
pickleweed	12	19	6	1	50.0%
cattail	3	3	24	7	64.9%
willow	0	0	9	22	71.0%

Table 5. Classification predictions of August 2003 and April 2004 data based on previous years' data. *August 2003 reference sites were not predicted because there were no reference sites in the August 2002 model. Each row represents the distribution of data from one plant community into four classes: reference (R), pickleweed (P), cattail (C), and willow (W). The Class Accuracy column shows how accurately data from each plant community were classified.

August 2003 Predictions*

Accuracy: 64.2%

Actual	P	C	W	Class Accuracy
pickleweed	33	2	0	94.3%
cattail	25	15	5	33.3%
willow	1	6	22	75.9%

April 2004 Predictions

Accuracy: 73.2%

Actual	R	P	C	W	Class Accuracy
reference	29	6	0	1	80.1%
pickleweed	6	29	2	1	76.3%
cattail	2	6	22	7	59.5%
willow	0	1	6	24	77.4%

with pickleweed being the most dominant (Table 7). Based on plant surveys, the average percent cover of pickleweed and arroyo willow did not significantly change from 2002 to 2004 (Table 8). Average cover of cattails decreased between 2002 and 2003, although there is a large variance in samples for each sample year. There is no statistically significant data on pickleweed recovery, but in the field over the three summers, we observed an extensive die-off of cattail on several transects. By August 2004, pickleweed had begun to establish in these areas where cattails were dominant two years prior.

DISCUSSION

Sediment Deposition

Capturing rates of sedimentation on an alluvial surface such as a sediment fan is a challenge since rates may vary widely along different transects and even at different points on the same site. Patterns of deposition change annually as water flows divert their course. Sedimentation may only occur in an isolated area or along one transect in a particular site, and a sampling scheme may miss a specific location where deposition occurred. However, high deposition rates were recorded during the 2003–2004 winter. This winter experienced below-average rainfall; 2004 rainfall was 49.91 cm. In contrast, rainfall levels have been more than double that amount in past El Niño years; 1983 rainfall was 122.81 cm and 1998 rainfall was 104.47 cm (WRCC

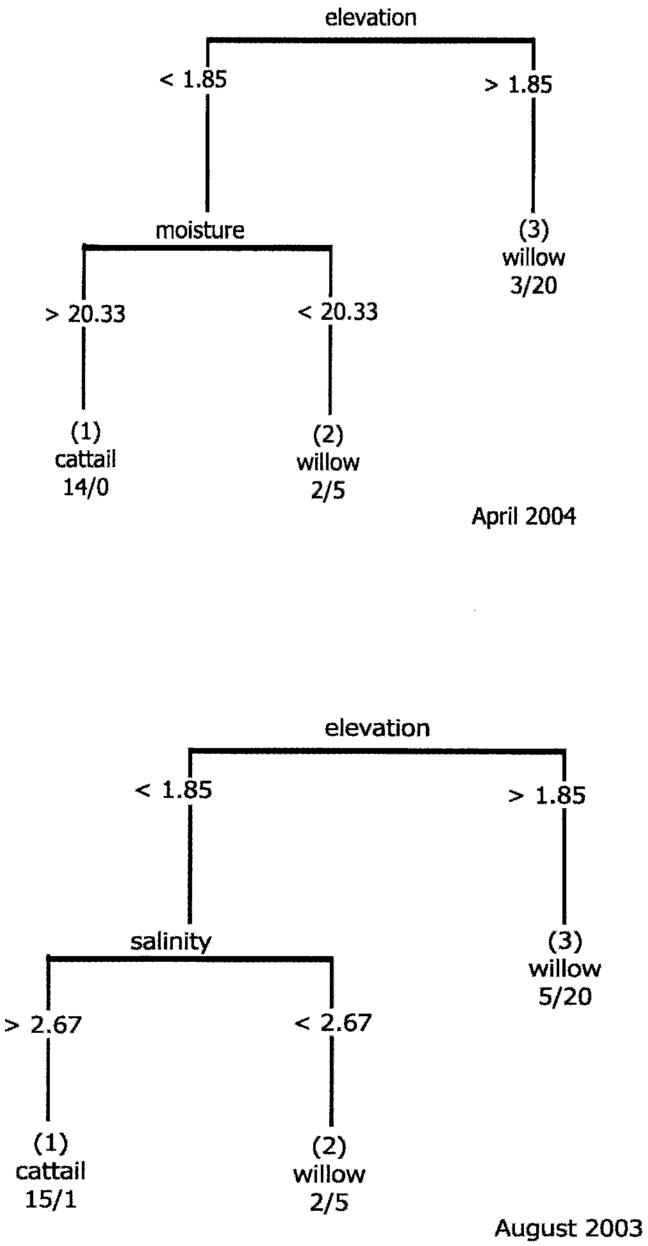

Figure 4. Classification trees for April and August cattail/willow transition zone data Labels of nodes represent datatypes assigned to that node, in order: cattail/willow.

2005). These results show that, in some areas, significant sedimentation is possible even in relatively dry years. In contrast, tidal erosion is also occurring in Elkhorn Slough; pickleweed salt marsh is being eroded and replaced by mudflat (van Dyke and Wasson 2005). There are little data on estuarine sediment budgets for this area, but it is possible that upland sediment sources may counterbalance the effects of tidal erosion on a limited scale by maintaining an elevation suitable to pickleweed in some areas.

Table 6. Cross-validation accuracy matrices for cattail/willow transition zone data. Each row represents the distribution of data from one plant community into two classes: cattail (C) and willow (W). The Class Accuracy column shows how accurately data from each plant community were classified.

April			
Cross-Validation Matrix Accuracy: 79.5%			
	Class		
Actual	C	W	Class Accuracy
cattail	11	11	50.0%
willow	7	19	73.1%
August			
Cross-Validation Matrix Accuracy: 62.5%			
	Class		
Actual	C	W	Class Accuracy
cattail	11	11	50.0%
willow	7	19	73.1%

Soil Properties and Marsh Topography

The primary effect of sediment accumulation over several years was the increase in salt marsh elevation to at least 0.6 meter above the marsh plain. The series of sediment fans changed the physical structure of the marsh by adding topographic variability in the form of sloping ground to what was previously a relatively flat marsh plain. The elevation of the sediment fans reached 2 to 2.5 meters NAVD 88, depending whether the site had subsided, while the undisturbed marsh plain ranged from 0.5 to 1.8 meters NAVD 88, depending again on subsidence. This dramatic increase in elevation created opportunities for new species to establish and new plant communities to dominate, as salt marsh species are highly sensitive to slight changes in elevation. A difference in just a few centimeters may separate marsh plain and high marsh species (Zedler et al. 1999).

Relationships to Sediment Texture. The sandy composition of the sediment was related to several other changes in salt marsh physical and chemical properties. Deposition of sandy sediment and the formation of sediment fans corresponded with higher bulk density, lower salinity, lower soil moisture, and lower soil nitrogen. Bulk density more than doubled on the sediment fans as compared to reference salt marsh sites and was highly correlated with increases in percent sand on the fans. This can be attributed to the higher bulk

Table 7. Relative cover of species in 2002, 2003, and 2004. Only those species with cover greater than 0.5% are listed.

Species	2002 Fan	2003 Fan	2004 Fan	2003 Ref.	2004 Ref.
Salicornia virginica L.	39.1%	38.0%	40.7%	81.1%	91.5%
Typha latifolia L.	18.3%	9.9%	6.6%	*	*
Salix lasiolepis Benth.	14.5%	23.5%	21.8%	*	*
Jaumea carnosa (Less.) Gray	3.9%	3.6%	7.6%	*	*
Typha angustifolia L.	3.0%	*	*	*	*
Rubus ursinus Cham. & Schlecht.	2.7%	1.4%	1.3%	*	*
Polypogon monspeliensis (L.) Desf.	2.6%	*	0.8%	*	*
Juncus effusus L.	1.7%	0.6%	1.2%	*	*
Scirpus robustus Pursh	1.6%	1.1%	1.0%	*	*
Conyza canadensis (L.) Cronq.	1.6%	0.7%	0.6%	*	*
Urtica dioica L.	1.5%	2.3%	0.6%	*	*
Polygonum puntatum Ell.	1.4%	0.6%	3.3%	*	*
Conium maculatum L.	1.2%	2.0%	1.6%	*	*
Baccharis douglasii DC.	1.2%	5.8%	3.7%	*	*
Distichlis spicata L. Greene	1.2%	1.3%	2.1%	6.2%	3.5%
Equisetum hyemale L. ssp. *affine* (Engelm.) Calder & R. H. Taylor	0.9%	1.6%	1.2%	*	*
Scirpus californicus (C. A. Mey) Steud.	0.9%	*	0.5%	*	*
Atriplex trianglularis Willd.	0.7%	0.8%	3.1%	*	*
Epilobium sp.	0.6%	0.5%	*	*	*
Anthemis cotula L.	0.6%	*	*	*	*
Brassica sp.	*	0.5%	*	*	*
Picris echiodes L.	*	0.9%	*	*	*
Polygonum persicaria L.	*	*	1.3%	*	*
Salix laevigata Bebb	*	*	0.5%	*	*
Frankenia salina (Molina) Jtn.	*	*	*	12.5%	4.7%

density of sand vs. organic-rich silty clays (Brady and Weil 1999), which was the original substrate in the marsh. The sediment fans were also characterized by lower soil moisture that decreased with increasing proximity to the upland. Lower soil moisture was correlated with high sand content, which has low water holding capacity.

Along the wetland-upland gradient, soil salinity on the sediment fans decreased significantly with increasing elevation and proximity to the upland. The fans' high sand content may contribute to the maintenance of low saline conditions since sandy soils do not bind well to salts, and salts may easily leach from sandy slopes when upland freshwater runoff flows through. The original, poorly drained silty-clay marsh soil located below the layer of sand may also serve as a relatively impervious layer that impedes vertical flow of upland freshwater, leading to the development of a freshwater lens perched above saline soils. The hydraulic force of upland water flow as it moves laterally through the sand layer may prevent salt water from intruding into the lens, also maintaining freshwater conditions (Brady and Weil 1999).

In April, NO_3-N and NH_4-N concentrations were generally higher on the reference sites than on the

Table 8. One-way ANOVA results showing differences in average percent cover of pickleweed, cattail, and arroyo willow for 2002, 2003, and 2004. Means and standard deviations are provided. Bold value represents significantly different mean based on Tukey-Kramer HSD test. Degrees of freedom are in parentheses.

	Pickleweed	Cattail	Arroyo willow
2002	31.6 ± 40.5	**17.2 ± 32.1**	11.7 ± 26.4
2003	26.6 ± 38.8	7.2 ± 20.6	14.1 ± 27.8
2004	24.9 ± 36.2	4.0 ± 14.3	11.6 ± 21.1
F statistic	0.919 (2, 341)	9.979 (2, 341)	0.361 (2, 341)
P value	0.400	**<.0001**	0.697

sediment fans. It is likely that high sand content influenced low nutrient levels on the sediment fans. Sandy soils do not retain nutrients well because of low cation exchange capacity and organic content (Brady and Weil 1999), and nitrogen concentrations were significantly negatively correlated with percent sand. However, some limited soil water sampling suggested that water from upland farms carried high nitrate loads to the sediment fans, with some soil water readings as high as 70 mg/l NO_3-N (Byrd, unpublished data). In addition, long-term monitoring of nitrate in Elkhorn Slough has shown a trend of high nitrate input levels (Caffrey et al. 1997).

Environmental Gradients. Differences in salinity and soil moisture between sediment fans and reference sites are also evident when studying their change along an elevation gradient. There was no gradient difference between reference and fan sites in any situations except one: tidal sites in the spring. However, for a given elevation, there was a multiplicative difference in salinity and moisture between the fan and reference sites for all cases. In both seasons, levels of salinity and moisture were greater on the reference sites than the sediment fans for any given elevation.

Our ability to compare reference sites and sediment fan sites directly was limited because the reference sites did not receive freshwater flows, while the fans received inputs of both freshwater and sediment. Interpretation of historical aerial photographs revealed that pickleweed was the dominant vegetation below drainages before sediment fans formed (Dickert and Tuttle 1980, Byrd et al. 2004). These historical conditions provide evidence that vegetation changes occurred as a result of sedimentation. Historical soil properties on the sediment fan sites may have differed from reference site conditions because of greater freshwater inputs; historical salinity levels were probably lower and soil moisture levels may have been higher than on reference sites. Elevation, bulk density, and soil texture were likely similar because of the proximity of the sites. Differences in soil nitrogen between the two sites would have been influenced by historical land use.

Plant Community Distribution

The distribution of plant communities reflects the changing environmental conditions on the sediment fans along the wetland-upland gradient. Classification trees were useful for discriminating environmental differences among plant communities without the need to meet assumptions of normality and equal variance. Through this analytical method, we identified environmental thresholds that separated one plant community from another, as well as interactions among variables. The results indicated the environmental conditions in which each species existed and also whether a species may be located within a range of conditions or within a well-defined setting. According to the classification trees, arroyo willow was located in soil with year-round low salinity, low soil moisture, high bulk density, low nutrients, and high elevation. Environmental conditions in which cattails were found included fluctuating salinity, low nutrient levels, percent sand greater than 30%, soil moisture greater than 20% in the spring, and elevations lower than arroyo willow but similar to that in pickleweed communities. Pickleweed on sediment fans were located in areas with percent sand less than 30%, lower bulk density, higher nutrient levels, and high saline conditions. Reference sites had higher salinity levels and soil moisture than pickleweed sites and lower percent sand and bulk density.

Varying classification accuracy levels among species do not necessarily reflect the success of the CART classification algorithm. Instead, different accuracy levels demonstrate that, while some species may exist within a narrow environmental range, others may be present along a range of environmental conditions. For example, arroyo willow data points fell within the willow class more often than pickleweed or cattail data points fell within their respective classes. This difference in accuracy illustrates that the arroyo willow was restricted to a much more well-defined environmental range than the other species.

Arroyo Willow Establishment. Classification tree analysis of the cattail/willow transition suggested the presence of an environmental threshold that limits willow expansion. Generally, these limitations included elevation of at least 1.8 meters, spring soil moisture less than 20%, and salinity less than 3 dS/m. Average willow elevation varied by about 0.5 meter, depending on whether the site was tidal or non-tidal and had subsided. The elevation thresholds predicted by CART appear to apply to willows present in the higher tidal areas. (Willows were found at lower elevation ranges in the subsided areas).

These edaphic restrictions match well with what is known about willow species habitat requirements. Willows are salt-intolerant pioneer species that establish on sandy, sparsely vegetated, newly formed fluvial deposits. Seedling survival depends on year-round soil moisture, and willows have been found to be highly efficient in nutrient uptake (McBride and Strahan 1984, Sacchi and Price 1992, Karrenberg et al. 2002). While our classification results place soil moisture at less than 20% as a habitat requirement, soil moisture was lower among willows than cattails because of their higher elevation and greater sand content. Where seedlings established, soil moisture was probably present year-round or the depth to the water table was not great. Also, the willows may utilize high concentrations of nitrate in runoff water as it flows through the fan, despite the low soil nitrogen levels.

In this study, the main indirect effect of the edaphic and topographic changes in the Elkhorn Slough salt marsh was loss of pickleweed-dominated salt marsh and invasion of cattails and bulrush followed by expansion of arroyo willow. Land that once supported salt-tolerant species has become suitable for salt-intolerant species that can tolerate dry soil in at least the top 30 centimeters.

Models for Species Distribution and Succession. One paradigm for zonation of marsh plants states that the upper limits of distributions are set by competition in relatively low-stress environments and that lower limits are set by tolerances to harsh physical conditions (Snow and Vince 1984, Bertness 1991a, Bertness 1991b, Pennings and Callaway 1992). Pickleweed can grow along a range of salinities and has shown optimal root growth in low salinity conditions (Barbour and Davis 1970). Also, it has relatively high tolerance to flooding, which enables it to exist in lower marsh elevations (Pennings and Callaway 1992). However, at higher elevations where salinity and soil saturation are at optimal conditions, its competition with cattail prevents further expansion in the upland direction.

It is unclear whether cattails and bulrush established at the same time as arroyo willow on newly deposited sediments or if one plant community preceded the other. We hypothesize that allogenic succession occurred on the sediment fans in a manner similar to successional processes on river floodplains. As subsequent alluvial deposits created a new substrate with different edaphic and topographic properties, conditions became suitable for new species to establish (Drury and Nisbet 1973). The continued disturbance by alluvial deposition would have limited facilitation among species (Connell and Slatyer 1977). Species distributions were likely driven initially by habitat suitability and transition zones were determined by competition.

Cattails have been known to invade salt marshes and other wetlands under many circumstances. Cattails, especially the hybrid *Typha* × *glauca* can be invasive because of its clonal growth, rapid uptake of nutrients that facilitates opportunistic growth (Woo and Zedler 2002), tolerance of salt (Wilcox 1986), and a range of water depths (Waters and Shay 1992). Its rapid vegetative expansion, along with its vigor and efficient use of nutrients, allows *T.* × *glauca* to form single species stands (Woo and Zedler 2002). Cattail may be more successful where sediment accumulation is high (Werner and Zedler 2002), and large nutrient loads may not be required for cattail invasion. Cattails and other freshwater species have taken over native species in salt marshes where freshwater flows occur over two to three months in the spring, allowing for germination and seedling establishment (Beare and Zedler 1987, Greer and Stow 2003).

In Elkhorn Slough, soil salinities were low within the cattail community but became quite saline by August. Spring freshwater flows may have lasted long enough for cattails to establish on the sediment fans and expand out into the marsh. Spring soil salinities in the pickleweed community on the fans were significantly higher than within the cattails; this difference may have been the limiting factor controlling the location of the transition between the two species. Willows invaded to the point at which low, year-round salinity levels could sustain them. If sediment were to build further out into the marsh and obtain a sufficient elevation, we predict that willows would follow this progradation of sediment deposition.

Plant Community Changes. There was virtually no difference in average cover among pickleweed, cattail, and arroyo willow over three summers except that cattail cover decreased between 2002 and 2003. However, on some transects, we observed the death of cattail and the corresponding recovery of pickleweed. On the sediment fans, freshwater flow from upland farms moves laterally from year to year as sediment loads obstruct stream channels and the stream shifts sideways across the fan from one side to the other. We observed that cattails grew more robust when present in the direct flow of freshwater, and the location of greater cattail biomass shifted from year to year. As flows changed direction, sections of the fans that had previously supported cattails may have dried out and become more saline, preventing cattails from returning. Also, elevation may have lowered as cattail rhizomes decomposed, and lack of competition from cattails may have enabled pickleweed to recover. We did not observe any cases of willow dieback or movement of cattails into the willow grove. In summary, over three years, we noted a dynamic interaction between pickleweed and cattail that was possibly influenced by interannual variation in environmental conditions. This interaction suggests that there is possibility for salt marsh recovery where cattails are now dominant. However, once willows have been established, their deep root system probably stabilizes the sediment fans and prevents salt marsh recovery.

CONCLUSION

Increased sedimentation within a hydrogeologic setting defined by highly erodible sandy soils and steep topography led to a shift in the type of wetland located downhill of agriculture. A location that once supported salt marsh vegetation now supports arroyo willow groves as topographic and edaphic properties have changed. The hydrogeologic setting played a part to this change, as the contribution of upland sandy soils likely facilitated the emergence of new edaphic properties, including lower salinity, lower soil moisture and reduced soil nutrients. The Elkhorn Slough Foundation, Natural Resources Conservation Service and the Monterey County Resource Conservation District are actively working with farmers to reduce soil erosion and off-farm sediment (USDA-NRCS 2002, USDA-NRCS and RCDMC 2004). Findings from this study emphasize the importance of continuing efforts by these groups to estuarine conservation in central California.

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