

Declining Diversity in Natural and Restored Salt Marshes: A 30-Year Study of Tijuana Estuary

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Abstract

Between 1974 and 2004, Tijuana Estuary's natural salt marsh underwent pulse disturbance (an 8-month nontidal period in 1984), which caused the sudden loss of two short-lived halophytes (*Salicornia bigelovii* [Sb] and *Suaeda esteroa* [Se]) and rapid dominance of a productive native succulent (*Sa. virginica* [Sv]), plus ramp disturbance that led to gradual codominance by *Jaumea carnosa* (Jc) (another productive succulent) by 1994. Species richness was high in 1974 (4.2 species/0.25-m² plot), low in 1984 (1.4 species), and not fully recovered by 1994 (3.7 species) or 2004 (3.9 species). Restoration efforts (reseeding former habitat and excavating and planting new sites) did not recover the populations of Sb or Se. In a 1997 project, plantings of these and six other native halophytes survived initially, but by 2005, short-lived species were lost and Sv and Jc dominated, as in

the natural marsh. In a 2000 restoration site, planting mortality was high for five species, but Sv recruited voluntarily and dominated by 2005. We attribute recent vegetation changes to frequent catastrophic storms, flooding, and sedimentation, which contrasted strongly with the benign conditions of decades prior to 1974. Sediment blocked tidal channels in 1984 and gradually elevated the marsh plain, degrading the diverse salt marsh and hindering efforts to restore it. Future restoration efforts will require even greater control over sediment inflows plus contouring sites to include natural topographic features that appear critical to sustaining high species richness and evenness.

Key words: catastrophic sedimentation, halophytes, long-term study, plantings, pulse and ramp disturbances, *Salicornia virginica*.

Introduction

Coastal California supports a high diversity of imperiled species (Chaplin et al. 2000). Conservationists in this and many other urbanized regions depend on a finite number of small nature reserves to sustain biodiversity, but they cannot expect the biota to be constant when environmental conditions are not (Pickett & White 1985; Botkin 1990; Byrd & Kelly 2006; Laegdsgaard 2006). Sea level rise, storms, bluff failures, and tectonic uplift are all potential agents of catastrophic and noncatastrophic change (sensu Platt & Connell 2003). Sustaining a regional species pool along dynamic and increasingly developed coastlines is thus a huge challenge. The sudden loss of species can usually be linked to a "pulse" disturbance (short term and intense; Bender et al. 1984) that convinces managers to take specific restoration action (i.e., restore prior conditions). With a "press" disturbance (prolonged) or "ramp" disturbance (steady increase; Lake 2000), species loss might not even be detected. If gradual changes occur, they might be either a successional replacement pattern or a response to an external stressor (Holling & Meffe 1996).

To determine if and when restoration is needed, diversity loss due to pulse or ramp disturbances needs to be distinguished from natural successional change. The task is difficult without "before-after, control-impact" data (Osenberg et al. 2006). Where such monitoring is lacking, one can still compile available data, identify key changes in diversity, hypothesize cause and effect, test relationships, and suggest restoration actions.

Here, we explore responses to pulse and ramp disturbances during 30 years of salt marsh studies in Tijuana Estuary. The earliest data (1974) followed a benign period, whereas later data included loss of tidal influence in 1984 and frequent floods thereafter. We describe both sudden and gradual changes in vegetation and identify diversity losses in response to stressors that operate at variable rates. These losses were not reversed by the four restoration approaches (restoring tidal influence, reintroducing lost species, excavating and densely planting a 0.7-ha site, and excavating and sparsely planting an 8-ha site), but field experiments explained changes and suggested improvements to restoration efforts.

Methods

Study Site and Context

The tidal marshes of the Californian biogeographic province extend from Point Conception (lat 34.4°N, long -120.5°W)

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south along the Baja California peninsula of Mexico (Ferren et al. 1996), and vegetation is species rich relative to more northern sites (Macdonald & Barbour 1974). Losses of wetland area and quality have imperiled at least 24 plant and animal species (Ferren 1985; Zedler et al. 1992).

Tijuana Estuary (lat 32.6°N, long -117.1°W; Fig. 1) lies just north of the U.S.–Mexico border, where the Tijuana River meets the Pacific Ocean. As the largest (approximately 1,000 ha) and least fragmented salt marsh in San Diego County, California, it sustains populations of three federally listed endangered species (Light-footed clapper rail [*Rallus longirostris levipes*], California least tern [*Sterna antillarum brownii*], and Salt marsh bird's-beak [*Cordylanthus maritimus* ssp. *maritimus*]) and one state-listed endangered bird (Belding's Savannah sparrow [*Passerculus sandwichensis beldingi*]). The site is protected as a U.S. FWS Wildlife Refuge, a CA State Park, a National Estuarine Research Reserve (since 1982), and a Ramsar Wetland of International Importance (since 2005).

The majority (73%) of the estuary's watershed lies in Mexico (Zedler et al. 1992). The City of Tijuana contributes raw sewage spills and sediments from steep slopes, whereas both the United States and Mexico discharge urban and agricultural run-off to the estuary. Even though mean rainfall is low (<30 cm/yr), flash floods and sea storms import sediments from the river and dunes and bury salt marsh plants and alter populations of intertidal invertebrates and fishes (Desmond et al. 2002). The region's least disturbed reference site is in San Quintin Bay, Baja California (approximately 320 km south of Tijuana Estuary; Zedler et al. 1999).

Indicators of Flooding

Precipitation data for San Diego's Lindbergh Field were accessed from <http://www.wrcc.dri.edu/cgi-bin/cliMONtpr.pl?casan>. These data are for rainfall years July through June. Streamflows of Tijuana River at the U.S.–Mexico



Figure 1. Tijuana Estuary in southwestern San Diego County, California. (A) Map showing transects as red bars, mostly in the northern arm (Oneonta Slough) of the estuary. The Tidal Linkage restoration site is north of the northernmost transect. (B) January 2005 air photo provided by NEOS Ltd., showing the stormwater detention basins, sediment plumes, and the Friendship Marsh. (C) September 2005 aerial photo of Friendship Marsh (courtesy: NEOS Ltd.), with intended habitats labeled. The mudflat accreted sediment and was invaded by Sv (52% cover); the cordgrass plantings (Sf plugs at 2- and 4-m spacings) coalesced (97% cover), whereas the marsh plain supported only 21% cover (mostly Sv).

border were obtained from the International Boundary and Water Commission Web site (<http://www.ibwc.state.gov/wad/ddqtjrib.htm>) for 1962–2004 and from the Western Water Bulletin (vol. 1950–1961) for earlier years. The monthly streamflow data were summed as million cubic meters per rainfall-year.

Vegetation and Elevation Data

We used several datasets to assess compositional change: biomass aboveground in 1976 (Winfield 1980); extensive sampling of plant cover by species in 1974, 1984, 1994, and 2004 (cover estimated as <1, 1–5%, 5–25%, 25–50%, 50–75%, or 75–100%); and intensively sampled permanent transects (12 at 20 m long) from 1989 to 2004 along elevation contours, with cover assessed as line intercepts (Table 1). All plot data were from 0.25-m² circular plots.

Extensive sampling began in 1974 (February–March and August–September) as a survey from high to low elevation (Fig. 1; Zedler 1977). Three transects (36, 40, and 43) represented the northern arm of the estuary. At 2-m intervals, plots were placed at a random distance of 1–20 m perpendicular to the transect. Elevations were measured with a Wild Automatic Level until 2004, when we used a Leica 530 global positioning system with approximately 5-cm accuracy (but higher precision within transects). In August 1976, Winfield (1980) sampled aboveground biomass in 46 randomly placed plots near transects 30 and 31. Plants were separated by species and oven-dried at 80°C. Twenty-seven plots fell within the 60- to 79-cm elevation range (the modal elevation in his data). In 1984, we placed plots at 5-m intervals along transects near six benchmarks (5, 28, 30, 32, 37, and 43; Zedler et al. 1992). In 1994, we sampled three transects (near benchmarks 28, 30, and 43) and added a north–south transect parallel to (and 2 m west of) a line of trestles that supported a sewer pipe in the 1960s. In 1989, we established permanent 20-m transects in three habitats (cordgrass, marsh plain, and high marsh) and four sites: Peninsula (near benchmark 28), Original (near benchmark 31), Tributary (near benchmark 43), and Old River (in the southern arm of the estuary). Transects were parallel to elevation

contours and were sampled annually from 1989 to 2004, recording hits of plant species within 10-cm intervals. In 2004, we sampled transects at eight benchmarks (2, 5, 28, 30, 34, 37, 43, and 49).

To compare vegetation over 30 years, we selected data (the two most commonly encountered 10-cm elevation classes) that represent the marsh plain, rather than a specific elevation range, specific transect locations, or resampled plots. The 20-cm elevation range that represented the marsh plain in 1974 was 60- to 79-cm National Geodetic Vertical Datum (NGVD). Marsh plain plots fell between pure *Spartina foliosa* (Sf) species and high marsh species (*Salicornia subterminalis* [Ss] [= *Arthrocnemum subterminale*] and *Monanthochloe littoralis* [MI]). Comparable plots totaled 191 in 1974, 75 in 1984, 27 in 1994, and 77 in 2004. The marsh plain had elevated to 70- to 89-cm NGVD by 2004. Patterns reported were robust to sample size. The 1994 data were most limited ($n = 27$), but cover data for 14 species sampled with $n = 27$ vs. 61 plots were highly correlated ($r = 0.80$, $p < 0.01$, degrees of freedom [df] = 12). An additional 72 plots near the trestle fell within the 60- to 79-cm range, but these were often trampled, and 15 plots had pure *Sa. virginica* (Sv), indicating such disturbance. Despite this, cover data for 14 species sampled near the pilings were highly correlated with those of other transects ($r = 0.95$, $p < 0.01$ for $df = 12$). For consistency with sampling in other years, we used the 27 plots to represent 1994.

We compared species richness per plot. We calculated an importance value (modified to identify dominants as those with above-average species dominance index [SDI] [Frieswyk et al. in press], which averages mean cover, tendency toward high cover [degree to which species are usually present with high cover], and the inverse of the number of species that co-occur in a plot):

$$SDI = (THC + MSS + MC)/3,$$

where THC = tendency toward high cover = (the number of times a species has the highest cover)/(total occurrences); MSS = mean species suppression = inverse of plot

Table 1. Datasets for natural and restored marshes at Tijuana Estuary.

Location	Project	Years	Data Type
Natural (mostly in Oneonta Slough)	Extensive sampling in plots	1974, 1984, 1994, and 2004	Cover classes by species in 0.25-m ² plots (all plots were circular)
	Biomass sampling	1976	Biomass in 0.25-m ² plots
	Intensive sampling along lines	1989–2004	Cover by species as intercepts by 10-cm intervals along a transect line
Restored	Tidal Linkage (completed in 1997)	1997, 2002, and 2005	Cover classes by species in 0.25-m ² plots and along transect lines
	Friendship Marsh (completed in 2000)	1997–1999 2004 and 2005	Survivorship and recruitment of plantings Cover in belt transects on aerial photos Survival of plantings and cover along transects

richness = $1/(\text{number of species in a plot})$; and MC = mean cover = average of midpoints of percent cover classes.

The most frequent species are analyzed and those with above-average SDI considered dominants. Species with high cover and few associates are called monotypes, and those with high cover but many co-occurring species are called matrix species. Monotypes and matrix species are of primary interest here, although other forms of dominance can be identified (Frieswyk et al. in press).

Frequency of occurrence data was relativized to compare results across sampling methods, but we did not compare cover data for plots versus lines because of their different biases. Averaging midpoints of cover classes underestimates species with continuous cover as 88%, whereas line intercepts correctly assess 100% cover (10 hits/m) but overestimate sparse canopies (one branch crossing the line yields 10% cover). Errors also differ ($\pm 25\%$ for visual estimates; $\pm 10\%$ for line intercepts).

Salt Marsh Soil Salinity

We collected the top 10 cm of soil from each 0.25-m² plot and each 20-m permanent transect (at 3/transect). In 1974, we measured conductivity (EC_{25}) after diluting soil to make a standard soil paste (Richards 1954). Results were converted to salinity in grams per liter by comparing the conductivity of soil saturated with seawater (Zedler 1977). From 1984 to 1996, we measured in situ pore water salinity in gram per liter by expressing a drop of interstitial water onto a refractometer (PERL 1990). From 1997 to 2004, we dried and ground the soil samples and then added deionized water to form a saturated soil paste (Richards 1954); we then expressed the resulting soil water onto the refractometer. We compared the in situ and soil paste methods in 1999, when we noted increased soil salinity for three of the four marsh plain transects. Although the two methods were positively correlated ($r^2 = 0.65$, $n = 20$), we refrain from detailed comparisons across methods.

Restoration

Efforts in the Natural Marsh. Restoration began in 1984 with dredging to restore tidal flushing after a lengthy permitting period. Oneonta Slough channel was deepened with a dragline and sand pushed by bulldozers to reform the dunes. The mouth was reopened in mid-December 1984. When *Sa. bigelovii* (Sb) and *Su. esteroa* (Se) did not recover, we experimentally reintroduced both species (in 1998) by seeding with and without clearing the overstory (Vivian-Smith 2001). When neither species recovered, larger efforts were initiated, and restoration proceeded by converting upland to intertidal elevations.

The Tidal Linkage. In 1997, the Reserve excavated a highly disturbed upland to create a small (0.7 ha) marsh

plain and tidal channel. The goal was to provide salt marsh habitat and enhance tidal flushing in the northern arm of Tijuana Estuary. The excavated channel connected Oneonta Slough to three tidal ponds that historically served as sewage lagoons for the City of Imperial Beach (Zedler et al. 1992).

We planted the south marsh plain as an experiment to distinguish species that need to be planted from those that colonize readily (Lindig-Cisneros & Zedler 2002) and to determine if ecosystem functions would be accelerated by planting species-rich assemblages (Keer & Zedler 2002; Callaway et al. 2003). The experiment had five blocks and fifteen 2 × 2-m plots/block. In April 1997, we planted treatments with zero, one, three, or six native halophyte species, randomly drawn from the regional pool of eight marsh plain halophytes (excluding the parasitic *Cuscuta salina* and species of lower and higher elevations). Planted treatments had 90 seedlings spaced on a 20-cm grid. Due to randomly drawn assemblages, the eight species contributed nearly equal numbers (approximately 790 plants/species) to the site. Plantings nearly covered the marsh plain, leaving only narrow paths and 15 unplanted controls. Shortly after planting, the site was opened to tidal influence.

In December 2002, after six growing seasons, Morzaria-Luna (2004) sampled 20 of the 2 × 2-m planting plots (five replicates of planting treatment) for cover by species, using 0.25-m² circular plots. On 10–11 November 2005, after nine growing seasons, we resampled the site, using one hundred and one 0.25-m² plots. The total area sampled was more than 4% of the planting area.

The Friendship Marsh. The Reserve excavated 1–2 m of sediment in the southern arm of the estuary to expose a former salt marsh plain. The 8-ha kidney-shaped site was built as an experiment to test the effect of incising tidal creek networks. A 2-m-wide channel fed tidal water into three creek networks and three adjacent areas (cells) without a creek network. Each cell was graded to support mudflat near the main channel, a cordgrass zone, and a marsh plain. At the upper margin of the excavation site, high marsh shrubs were planted next to a 1-m-high berm designed to prevent sediment inflows during catastrophic flooding. Contractors planted Sf, using plugs in 2- and 4-m grids, and we planted the marsh plain sparsely with five species in clusters and introduced a few Sb seedlings.

The Friendship Marsh was opened to tidal flushing in February 2000 and rapidly experienced heavy sedimentation (materials were 15% sand, 65% silt, and 20% clay; Wallace et al. 2005). The geomorphic evolution of the site was documented by Madon et al. (2001), Wallace et al. (2005), and Larkin (2006). We censused Sf cover remotely using aerial imagery because we were denied entry following sightings of the Light-footed clapper rail. We censused marsh plain plantings on foot. Most transplants died (Zedler et al. 2003), so we re-planted our remaining

seedlings (*Batis maritima* [Bm], *Frankenia salina* [Fs], *Limonium californicum* (Lc), *Jaumea carnosa* (Jc), and *Se* at equal numbers (108 plants/species, for a total of 540 plants distributed in experimental plots across the 8-ha site) in dense clusters (10, 30, or 90 cm apart) by December 2000. Each cluster had one plant of each of the five species. O'Brien and Zedler (2006) quantified early survival of plantings (in 2001–2002), and we recensused all 108 plots in July 2004. Also in July 2004, we sampled plant cover (intercept method) in the three middle cells of the Friendship Marsh using transects of 40 m/cell (=120 m). In November 2005, we sampled all six cells with transects in the middle of the marsh plain and 10 m into the marsh from the upland berm (50 m/cell 300 m \times 2 transects = 600 m).

We assessed whole-site plant cover via true-color orthorectified photographs taken during low tide in April 2004 and September 2005 (obtained in digital format from Neos Ltd. Photographs). Five 5-m-wide, east–west belt transects were placed as follows: center of mudflat, center of cordgrass, and three through the marsh plain. Transects were 453–632 m long, depending on marsh width. Within each transect, an experienced interpreter (C. B. Frieswyk) delimited continuous patches of vegetation at least 0.25 m² and calculated their area using ArcMapTM 9.0 software (ESRI, 2004). As quality assurance, Frieswyk's data for the April 2004 photo matched a more extensive interpretation by K. Wallace.

Data Analysis

Statistical analyses (*t* tests, analysis of variance) employed JMP 6 (SAS Institute, Cary, NC, U.S.A.). Analysis of similarity used PRIMER 5 (Clarke & Warwick 2001). Because the data taken at decadal intervals employed different plot layouts, different transects over time, and dif-

ferent number, we present summaries of occurrence and cover and refrain from overanalysis. The annual monitoring data from 1989 ff. are from the same permanently marked transects; for those, changes are not samples but complete descriptions that are compared directly.

Results

Environmental Changes

Rainfall, Streamflow, and Sediment Inflows. Rainfall data from San Diego averaged 25.3 cm/rainfall-year (July through June) for 1950–2004, but most of the high rainfall years occurred after vegetation sampling began in 1974 (Fig. 2). These local data do not necessarily indicate all floods because the watershed is large (448,323 ha), and rainfall events further upstream often contribute to flooding.

Annual streamflows at the U.S.–Mexico border (approximately 8 km upstream of the estuary) also indicated more frequent flooding after sampling began in 1974 than before (Fig. 2). The 5 years with greatest flow rates were 1982–1983, 1980–1981, 1992–1993, 1994–1995 and 1997–1998. Next in rank were 1977–1978, 1978–1979, 1990–1991, 1987–1988, and 1951–1952. Of these, the 1993 flooding was the most catastrophic, as the river cut a new channel just upstream of the estuary, eroding away one house and several fields and discharging substantial sediment into the estuary (data in Cahoon et al. 1996). Only one flood year preceded the 1974 vegetation sample. In fact, annual streamflow was 42.5 times higher for the 30 years following our 1974 sampling of vegetation than for the preceding 24 years ($\bar{X} \pm \text{SE} = 102.7 \pm 41.3$ vs. 2.4 ± 1.01 million m³/yr, respectively; *t* test, unequal variance: *p* = 0.02).

Major flood years were corroborated by monthly streamflow (volume/second; not shown), with flows greater

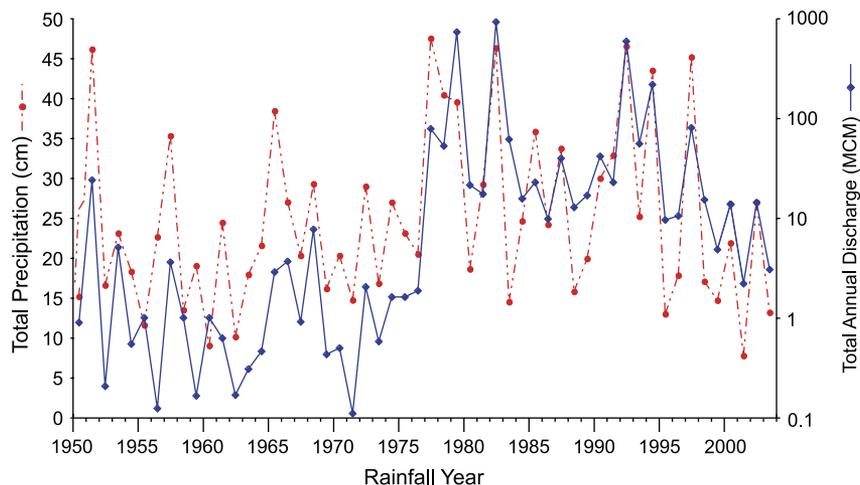


Figure 2. Total precipitation (cm) per rainfall-year (July through June) recorded at Lindbergh Field, San Diego, California, and total annual discharge (million cubic meters) per rainfall-year, as measured in Tijuana River at the International Boundary. Note that the right y-axis is a logarithmic scale.

than 460 m³/second in January 1980, February 1980, March 1983, January 1993, and March 1995; all other rates were less than 150 m³/second. Also, annual streamflow per San Diego rainfall increased after 1974 ($\bar{X} \pm \text{SE}$ for streamflow/precipitation were 0.08 ± 0.02 before 1974 and 2.66 ± 2.66 for 1974 ff.; *t* test, unequal variance: $p = 0.009$).

Impacts of flooding on salt marsh vegetation can be beneficial (temporary lowering of soil salinity; Zedler 1983) or detrimental (sedimentation elevating the marsh plain by 5–10 cm). Recent flows down Goat Canyon were sufficient to justify an \$8 million sediment detention system in the United States (Fig. 1B). All three basins overflowed in November 2004, just before construction was completed, and they required reexcavation in 2005 and 2006. The Friendship Marsh accreted an average of 0.5 cm/yr from 2000 to 2004 (Wallace et al. 2005), which was exceeded by the deposition of 4.5 cm during catastrophic storms of winter 2004–2005 (PERL, unpublished data).

Estuary Mouth Closure. Following strong landward winds in 1983, Oneonta Slough filled with sand, tidal flushing became sluggish, and beach sand blocked the river mouth. Tidal flushing ceased in April 1984 at the beginning of the salt marsh growing season. The next 8 months had neither tidal influence nor rainfall. Water salinity rose to 60 g/L, and salinity in the top 10 cm of soil in the cordgrass marsh averaged 105 g/L (approximately three times of seawater; Zedler et al. 1992). Mortality of *Sf* was widespread, and by October 1984, former tidal pools had dried, cracked, and developed salt crusts. *Sv* was replacing *Sf* by the end of the 1984 growing season, and data from three soil pits documented extreme hypersalinity. Below 40 cm depth, pore water salinities were less than 60 g/L and pH 8.0, but in the top 10 cm of soil, the salinity range was 84–120 g/L and pH ranged from 4.0 to 5.0. On the marsh plain, surface soils were dry and cracked and salinities were more

than 100 g/L (Zedler et al. 1992, 2001) until the mouth was reopened in December 1984.

Marsh Plain Elevation and Rising Soil Salinity. In 1974 and 1984, the marsh plain was 60- to 79-cm NGVD. In 1994, the marsh plain plots averaged 8.7 ± 1.20 cm higher in elevation, although the mode was still 60- to 79-cm NGVD. By 2004, the modal elevation had shifted to 70- to 89-cm NGVD, that is, the marsh plain elevated at least 10 cm during the study period.

The marsh plain surface is usually hypersaline, especially during the rainless season (typically April through October) when salt marsh plants are most active. In 1974, soil paste salinity ($\text{EC}_{25} \pm \text{SE}$) was $18,507 \pm 342.8$ $\mu\text{mhos/cm}$ in February–March and $28,248 \pm 337.5$ in August–September (42 g/L pore water and 64 g/L, respectively, using conversions in Zedler 1977). Having changed salinity-measuring methods in 1989 and again in 1997, we emphasize changes during periods with the same methods. Soil salinity rose in both the cordgrass and the marsh plain habitats (Fig. 3). The largest increase was near the Peninsula (cordgrass and marsh plain transects) from 1997 onward, following the April 1997 completion of the Tidal Linkage project. As intended, tidal flushing increased in the north arm, but increased tidal flows were not the only cause of increased soil salinity because salinity of the Old River transect also rose and it was far from the influence of the Tidal Linkage.

The gradual increase in salinity of marsh plain transects is consistent with sediment accumulation (Cahoon et al. 1996; Weis et al. 2001; Ward et al. 2003), which elevated the marsh plain and allowed salts to concentrate (Fig. 3). The four cordgrass transects show a similar pattern, with a gradual increase that became more rapid post-1997. Soil salinity for the high marsh (not shown) remained stable, a consequence of limited tidal influence and less opportunity for sedimentation (Cahoon et al. 1996).

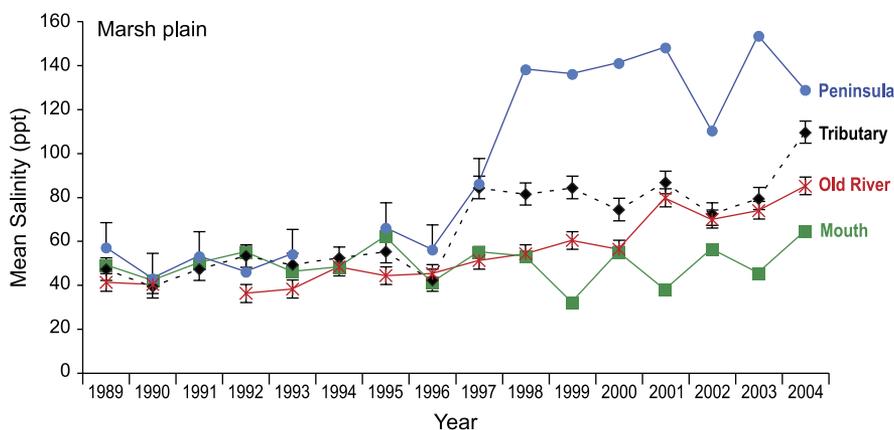


Figure 3. Soil salinity monitored along four marsh plain transects (Peninsula, Original, Mouth, and Old River). Data are mean salinities (ppt = parts per thousand = g/L; $n = 3$) obtained from soil pastes after oven drying the soil samples; error bars are standard errors; some for the Mouth site are hidden by the square symbol.

Changing Vegetation in the Natural Marsh

The early vegetation data indicate a diverse salt marsh, both in number of species and in evenness of species cover. (Note: species are referred to by their initials in Table 2). Four species are of special interest due to subsequent changes in distribution and cover: Sb and Se are short-lived species and Sv and Jc are perennials. In 1974, Sb was widespread, as were Bm, Sv, and Jc, but none averaged more than 32% cover prior to the 1978 flood (Table 2). All four occurred above and below the marsh plain in 1974, but their highest frequencies of occurrence were on the marsh plain (60–79 NGVD). Only one species (Sb) was dominant in 1974 (Table 3).

Winfield's 1976 0.25-m² plots averaged 4.2 ± 0.29 species with a mode of 5 (Table 2). Sv occurred 23 times but contributed only 9.6% of total biomass; Sv contributed over half the biomass of only two plots. Sb had the highest biomass in three of the plots, with more than 300 g/m². The most prominent species was Jc (24 occurrences and over half the biomass of 12 plots). These data show that Sv could behave as a subordinate among diverse vegetation and that Jc and the annual Sb could dominate at the 0.25-m² scale.

During the 1984 nontidal drought, species richness dropped to about one-third the 1974 level (Tables 2 & 4). Five species exhibited rapid declines in both occurrences and cover: Sb, Se, Fs, Bm, and Jc. Subsequent searches located only two small patches of Sb and widely scattered Se (J.B.Z., personal observation). At the same time, Sv rapidly became a monotypic dominant (Table 2) and remained so through 2004 (Table 4). Jc was not identified as a dominant until 1994, but it formed a matrix, coexisting with other species.

All decade-to-decade comparisons of cover by species were significantly different at $p < 0.001$, except at 1994–2004 ($p = 0.053$; analysis of similarities [ANOSIM statistic R]). Recovery from the 1984 pulse disturbance was thus incomplete, with little change since 1994. Species richness dropped in 1984 and then nearly recovered (Tukey–Kramer honestly significant difference [HSD], $q = 2.58$, $\alpha = 0.05$, $\bar{X} = 1.5 < 3.7, 3.9, \text{ and } 4.2$), whereas Shannon's index suggested lower diversity in 1994 and 2004 than in 1974, even though Se and Sb were virtually absent in the 1984–2004 data.

The 1989–2004 data from four marsh plain transects suggested minimal effect of catastrophic flooding on Sv

Table 2. Relative biomass in August 1976 (each species as a total of the mean dry weight; from Winfield 1980) and occurrences and mean cover of species, 1974–2004.

Code	Biomass (g/m ²), 1976	Frequency of Occurrence (%)				Mean Cover (%)			
		1974	1984	1994	2004	1974	1984	1994	2004
Sf	48.9	30.9	13.3	3.7	28.6	21.1	11.7	0.1	4.8
Sb	70.8	91.1	0.0	0.0	2.6	31.1	0.0	0.0	0.9
Se	24.0	31.4	0.0	0.0	0.0	6.2	0.0	0.0	0.0
Cs	0.0	2.1	0.0	22.2	13.0	1.1	0.0	8.4	0.5
Sv	75.5	67.5	80.0	100.0	94.8	13.1	47.3	58.4	35.5
Bm	107.1	80.1	28.0	66.7	64.9	14.8	5.3	11.1	13.1
Jc	406.7	64.9	14.7	70.4	72.7	21.9	2.2	40.4	50.9
Fs	1.1	31.4	5.3	59.3	62.3	11.9	0.5	7.7	18.9
Tc	20.5	9.9	1.3	25.9	40.3	10.6	0.0	5.8	10.4
Ds	1.1	6.8	1.3	11.1	1.3	3.2	0.0	3.5	0.0
MI	31.6	1.6	0.0	7.4	2.6	1.3	0.0	0.7	0.0
Lc	0.0	5.2	0.0	3.7	3.9	6.3	0.0	0.1	0.1

All are native species and are listed in order of low to high elevation preference. All data are from a 20-cm elevation range that represents the marsh plain; all were collected using 0.25-m² circular plots. Sample sizes (n) and marsh plain elevations are given in Table 4. Species codes (except those defined in text) are: Cs, *Cuscuta salina*; Ds, *Distichlis spicata*; Sv, *Sa. virginica* = *Sarcocornia pacifica*.

Table 3. Dominant species based on SDI (Frieswyk et al. in press).

Year	Dominant	THC	MSS	MC	SDI	Form
1974	Sb	0.41	0.32	0.28	0.34	Matrix
1984	Sv	0.85	0.73	0.48	0.69	Monotype
1994	Sv	0.81	0.54	0.71	0.68	Monotype
	Jc	0.57	0.22	0.13	0.31	Patchy
2004	Sv	0.32	0.34	0.39	0.35	Monotype
	Jc	0.80	0.26	0.51	0.52	Matrix

SDI = (THC + MSS + MC)/3, where THC = tendency toward high cover (usually in top cover class), MSS = mean species suppression (few neighbors in a plot), and MC = mean cover. Dominance form is called monotype when THC, MSS, and MC are all high; matrix when only MSS is low; and patchy when only THC is high.

Table 4. Summary data for marsh plain vegetation.

Data	1976 (Biomass)	1974 (Cover)	1984 (Cover)	1994 (Cover)	2004 (Cover)
Modal elevation (=the marsh plain) as "cm NGVD"	60–79	60–79	60–79	60–79	70–89
N for marsh plain	27	191	71	27	77
Maximum species richness	7	10	3	6	6
Mean species richness	4.22	4.23	1.44	3.7	3.87
SE species richness	0.29	0.12	0.09	0.23	0.14
No. plots with pure Sv	0	0	31	1	1
Shannon's diversity index	1.580	1.772	0.909	1.528	1.596

Data for 1976 are for August biomass (from Winfield 1980). Data for 1974, 1984, 1994, and 2004 are for percent cover, as in Table 1. All data were collected from 0.25-m² circular plots.

and rapid but brief drops in Fs, Jc, and Bm cover during the 1993 flood year and increased abundance of *Triglochin concinna* (Tc) after 1995 (Fig. 4). Sv also increased dominance in cordgrass transects that supported 90% cover of Sf from 1989 to 1995 but gradually shifted to Sv dominance in 2000; there, Sf gradually declined to 35% cover in 2004, whereas Sv rose to 90% cover in 2001, sustained through 2004 (PERL, unpublished data). Sv also increased in the high marsh (where Ml and Ss had the highest cover) during 1993 and Sv sustained approximately 20% cover for the next 11 years (PERL, unpublished data).

Restoration at the Tidal Linkage

Planting the eight marsh plain species as random assemblages resulted in near-equal densities in April 1997 (Table 5). Year 1 survival was high (>80%) for all species, and survival to year 2 was greater than 73% for all but Tc (58%) (Lindig-Cisneros & Zedler 2002). Sv, Sb, and Se contributed more than 99% of the seedlings in the first 2 years; Sb produced approximately 16,000 seedlings in 1998

(nearly as many as Sv) and was the top recruiter in 1999 (Lindig-Cisneros & Zedler 2002). Se contributed approximately 1,700 seedlings in 1998 and 2,700 in 1999. Early recruitment by Sb and Se did not predict the long-term outcome, however. By December 2002, Sv and Jc were emerging as dominants, and Tc and Sb were already rare (Table 5). Mean species richness was $4.8 \pm 0.3/0.25\text{-m}^2$ plots. Our November 2005 resample recorded 10 species, with mean richness of only 2.82 ± 0.12 ; Sv and Jc were the most frequent species at the end of the ninth growing season. In 2005, Sv and Jc were monotype and matrix dominants, respectively (Table 6). Fs, Lc, and Bm were subdominant. Two restoration targets were especially rare; we found no Sb in sample plots, although it was still on site, and seven occurrences of Se (Table 5).

Restoration at the Friendship Marsh

Although much of the restoration site became extremely hypersaline after exposure to tidal flushing (Zedler et al. 2003), dense plantings of Sf spread vegetatively to fill the

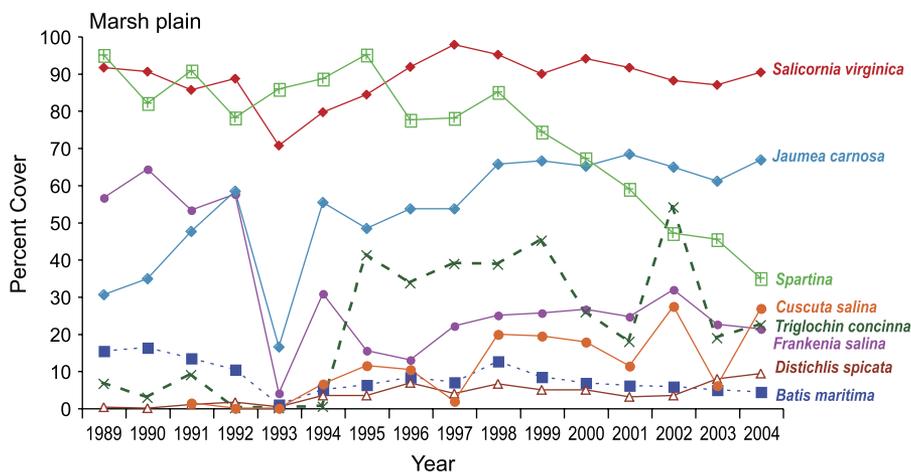


Figure 4. Vegetation change along four marsh plain transects (as shown in Fig. 3) from 1989 through 2004. Data are mean percent cover (intercept method).

Table 5. Initial plantings in eighty-seven 2 × 2-m plots in the Tidal Linkage, resampled in December 2002 and November 2005 using 0.25-m² circular plots.

Species	1997		2002				2005			
	Total Planted	Relative no Planted	% Frequency	Relative Frequency	% Cover	Relative Cover	% Frequency	Relative Frequency	% Cover	Relative Cover
Bm	765	11.8	30	6.2	4.0	2.7	21	7.4	2.2	2.4
Cs			10	0.2	0.3	0.2	9	3.2	0.1	0.1
Fs	780	12.0	65	13.5	23.1	15.3	48	17.2	8.2	9.0
Jc	855	13.7	70	14.6	29.9	19.8	61	21.8	29.0	31.7
Lc	795	12.3	85	17.7	14.3	9.5	36	12.6	2.3	2.5
MI			5	1.0	0.8	0.5	2	0.7	<0.1	0.1
Sb	780	12.0	3.6	4.2	5.4	3.6	0	0.0	0.2	0.2
Se	810	12.5	80	16.7	13.4	8.9	7	2.5	0.4	0.4
Sf			5	1.0	0.1	0.1	<1	0.4	0.1	0.1
Sv	885	13.7	100	20.8	58.0	38.5	96	34.0	49.0	53.5
Tc	810	12.5	10	2.1	1.6	1.0	1	0.4	<0.1	<0.1

The December 2002 data ($n = 20$) were collected by Morzaria-Luna (2004). The November 2005 data are from this study ($n = 101$).

Table 6. Dominant species and their form of dominance in two restored marshes sampled in 2005.

Site	Species	THC	MC	MSS	SDI	Form of Dominance
TL	Sv	0.68	0.49	0.49	0.55	Matrix/monotype
	Jc	0.63	0.29	0.35	0.42	
FM	Sv	0.43	0.30	1.00	0.58	Monotype

Tidal Linkage (TL) was 9 yr old and Friendship Marsh (FM) 6 yr old (counting growing seasons as “years.” Like an “importance value,” the SDI averages the tendency toward high cover [THC], mean cover [MC], and the inverse of species richness [MSS]; species of high frequency that have above-average SDI are considered dominant [Frieswyk et al. in press]).

cordgrass zone with 76% cover in April 2004 and 97% cover in September 2005 (Fig. 1B; Table 7). In contrast, most of the April 2000 plantings of halophyte seedlings died (Zedler et al. 2003). The second planting (5 halophyte species in 108 plots in December 2000) began with equal numbers (one seedling of each per plot) that consistently declined. Survival to September 2005 ranged 10-fold, from 7.4% for Se to 75.9% for Bm. Survival rates for the five species had virtually the same ranking in 2005 as in 2002 (Table 8; O'Brien & Zedler 2006). Every species declined in abundance (no signs of recruitment), and surviving plants were slow to expand vegetatively. If average mortality rates continue, Jc, Lc, and Se could be extirpated by 2007, followed by Fs by 2010.

Table 7. Vegetation cover (% cover along 5-m-wide belt transects) at the Friendship Marsh determined from analysis of aerial images (digital imagery courtesy of NEOS Ltd).

Habitat	April 2004	September 2005
Mudflat	12.16	52.71
Cordgrass	76.48	96.83
Marsh plain (overall average)	8.45	21.39
Near cordgrass	13.82	24.10
Middle	5.86	21.72
Near high marsh berm	5.74	18.40

Sv colonized the site without being introduced. By September 2005, it dominated the mudflat and provided most of the 21% cover on the marsh plain (Table 7). Between April 2004 and September 2005, the mudflat more than quadrupled in cover, mostly due to Sv colonization and vegetative spread (J.B.Z., personal observation). In November 2005, the marsh plain supported 29.3% cover of Sv and 2.5% cover of Sb, based on line intercepts. Virtually all the Sb were encountered near the berm, where Sv cover averaged only 14% and where shallow depressions covered 58% of the transect. After six growing seasons, less than 30% of the sparsely planted marsh plain was vegetated, in contrast to 97% of the heavily planted cordgrass zone. Sv was a dominant with monotype form.

Table 8. Survival of five species established as equal numbers (total = 108/species) by December 2000 in the Friendship Marsh.

Species	% Survival to 2002	% Survival to 2005
Bm	83.3	75.9
Fs	75.0	51.9
Jc	55.6	21.3
Lc	62.0	22.2
Se	30.6	7.4

The data for fall 2002 are from O'Brien and Zedler (2006) and the data for fall 2005 are from this study.

Discussion

Diversity loss is obvious when rapid, but easily missed or confused with successional changes when species shifts are slow. Over the past 30 years, diversity changed rapidly and slowly as Tijuana Estuary experienced both pulse and ramp disturbances (Bender et al. 1984; Lake 2000). The strongest pulse disturbance was inlet closure, which lasted 8 months and coincided with a period of no rainfall. The marsh plain dried and salinized, and many plants and animals experienced high mortality. The endangered Light-footed clapper rail recovered within a few years (Zedler et al. 1992), but short-lived plants did not.

From 1978 through 2004, flooding was a frequent pulse disturbance. As a result, cumulative sedimentation operated as a ramp disturbance that elevated the marsh plain and led to increased soil salinity. Vegetation responses to ramp effects were subtle, in part because drought and flood pulses are very different disturbances (Lake 2000) and in part because of sequencing. Salt marsh diversity was already depleted by drought when frequent floods began spreading sediments over the marsh plain. Two productive succulents, Sv and Jc, were poised to gain dominance through vegetative expansion and enhanced growth. The consequences of shifts in species numbers and abundance are substantial for a region where only 10% of coastal wetland area remains. Diversity loss in Tijuana Estuary was taken seriously, and costly restoration was implemented to compensate for the effects of increased storminess.

We use the results of long-term monitoring and multiple restoration efforts to suggest (1) how diversity developed prior to 1974; (2) how diversity was lost in both natural and restored salt marshes; (3) the difficulty of predicting future events; and (4) how diversity might be restored. The following narrative fits the facts, although more complex explanations could involve ecosystem attributes for which there are no data (e.g., soil microorganisms, diseases, contaminants).

How a Diverse Salt Marsh Develops

In 1939, Purer (1942) described Tijuana Estuary as "largely undisturbed by human activity." She noted that Sv was the most abundant plant in the salt marsh, occurring by itself next to tidal channels and in mixtures at higher elevation (presumably the marsh plain) with Ml, Se, Lc, and Bm. Her observations were qualitative and she did not mention Sb. Our 1974 data were the first to quantify species richness and abundance, and they characterize conditions following more than 20 years with no record of a major river flood or extended estuary mouth closure. On average, 4.2 species co-occurred at the 0.25-m² scale on the marsh plain. Sv was widespread but not dominant (Zedler 1977). Only the annual Sb achieved dominance. At the time, Tijuana Estuary was similar to Volcano Marsh, in San Quintín Bay (lat 30.4°N, long -115.95°W), which has no river and a deep ocean inlet

that sustains tidal flushing (Neuenschwander et al. 1979; Alvarez-Borrego & Alvarez-Borrego 1982). The marsh plain of Volcano Marsh averaged 4.7 species/plot in 1996 ($n = 224$; Zedler et al. 1999) and 5.22/plot when a second annual species of *Salicornia* was distinguished ($n = 216$; Morzaria-Luna et al. 2004).

The persistence of Sb and Se at Tijuana Estuary, Volcano Marsh, and other wetlands in the region (Zedler et al. 2001) suggests that diversity developed in the absence of catastrophic sedimentation events or during many decades after such events. Like the succession model, perennials can slow recruitment of short-lived species and can also persist where the canopy is sparse (Lindig-Cisneros & Zedler 2002). One hypothesis is that short-lived species persisted where wrack smothered perennials (Bertness & Ellison 1987; Hartman 1988) or trapped and mulched seeds. The wrack effect, however, does not explain the broad distribution of Se at Tijuana Estuary in the 1970s or at Volcano Marsh (Zedler et al. 1999). A second hypothesis (Zedler et al. 2001) is that Sv, Tc, and Sb coexist via facilitation (i.e., Tc reduces N available to Sv and then shares N with Sb as the ephemeral leaves of Tc decay in summer when the annual has the greatest N demand). Recent work supports facilitation where N is limiting, that is, Tc accumulated N belowground and shared ¹⁵N with neighbors in the Friendship Marsh (Morzaria-Luna 2004). A more general hypothesis, which we favor, is that Se and Sb persist indefinitely in microhabitats where competitive perennials are subdued (refuges sensu Platt & Connell 2003). In French salt marshes, for example, shallow depressions (20 cm deep) sustain the annual *Suaeda maritima* (Tessier et al. 2002). In Californian salt marshes, Se and Sb likely have unique refuges because these two species are not positively associated (Zedler 1977). Refuge for Se includes creek edges, where side lighting could stimulate germination. The refuge for Sb appears to be shallow depressions that retain water and broad marsh plains that drain sluggishly. In the 1970s, Tijuana Estuary had a broad band of waterlogged soil just inland of cordgrass, where the perennial canopy (mostly Bm) was open and wet enough to support both Sb recruitment and high algal productivity (Zedler 1980).

How Diversity Was Lost in the Natural Marsh

Five species declined rapidly during the 1984 nontidal period (Sb, Se, Fs, Bm, and Jc) as soils dried and pore water salinities rose to greater than 100 mg/L (Zedler et al. 1992). We attribute the sudden loss of Sb and Se to shallow root systems (Sullivan & Zedler 1999), which could not track the declining water table. The perennials Fs, Bm, and Jc were also affected, but all recovered by 2004. In contrast, the short-lived Sb and Se did not recover. By April 1984, Sb and Se seeds had already germinated and any ungerminated seeds would have had to survive through December 1984. If there had been a seed bank, the next adequate rainfall event would have

stimulated germination (Noe & Zedler 2001); however, only one occurrence of Sb (in 1986) and one of Se (in 1987) were recorded in annual observations from 1985 to 1988 (PERL, unpublished data).

Competition with Sv likely impeded recovery of Sb and Se. In greenhouse microcosms, neither Sb nor Se was highly productive or a strong competitor (Sullivan et al. in press). When grown in three-species assemblages with either Sv or Jc, the shoot biomass of Sb was reduced more than 70% than when growing alone. When grown in six-species assemblages (all with Jc and most with Sv as well), shoot biomass of Sb was reduced more than 80% (Sullivan et al. in press).

Sv rapidly gained dominance during 1984, presumably by growing deep roots. We found Sv roots at 60 cm depth in two soil pits and 75 cm in a third pit late in 1984; pore water salinities were lower at these depths (PERL, unpublished data). With high survival and access to groundwater, Sv was poised to dominate vegetatively. Its broad tolerance of environmental conditions is evidenced by its occurrence in virtually every coastal salt marsh in the Californian region (Macdonald & Barbour 1974).

Sv clearly benefited from recent disturbance events, and its tendency to form monotypes challenges efforts to restore diversity. Even the catastrophic flood of 1993 barely reduced Sv cover. Compared to Jc, Sv is taller and its dense photosynthetic branches can remain above water and oxygenate its roots during inundation. In contrast, the shorter, horizontal-leaved Jc is vulnerable to both inundation and sediment deposition.

We found rapid changes following pulse disturbances (1984 drought and 1993 inundation and sedimentation) and more gradual changes accompanying the ramp disturbance of marsh plain elevation and increasing salinity. The responses to drought are similar to those of a diked Californian salt marsh (Punta Banda, near Ensenada, Mexico), also studied in 1984. Ibarra-Obando and Poumian-Tapia (1991) documented elevated soil salinity and similar changes in diversity. In fact, most southern California coastal salt marshes have lost diversity in response to frequent or prolonged loss of tidal influence and sedimentation from increasingly disturbed watersheds (e.g., Mugu Lagoon; Onuf 1987 and Los Peñasquitos Lagoon; Greer & Stow 2003). Sv, Fs, and usually Jc are virtually all that remain (Zedler et al. 2001), likely responding to increased elevation, increased salinity, and loss of refuges for short-lived species, as reconstructed for Tijuana Estuary.

How Diversity Was Lost in the Restored Marshes

Early Restoration Actions. Restoration of tidal flushing in 1984 did not recover the diverse salt marsh of the 1970s. Reconnecting the estuary to the ocean restored tidal influence but not short-lived halophytes. Because Sb and Se did not recover on their own, we introduced 2,000 seeds of each species in 1998 in an experiment \pm seeds and \pm removal of the Sv canopy. Only 435 Sb and

2 Se seedlings resulted, and none persisted to 2000 (Vivian-Smith 2001; Morzaria-Luna 2000, UW-Madison, personal communication). Sv removal improved recruitment, but we were not allowed to create large open spaces in this endangered bird nesting habitat.

Tidal Linkage. The initial high survival (>90%) of all eight planted species did not ensure their persistence to year 9 (2005). Se and Sb dropped out and Sv and Jc became dominant, just as in the natural marsh. The cause, however, was different, as the 1997 plantings postdated both the 1984 and the 1993 catastrophic events. Se and Sb experienced El Niño rainfall in 1997–1998 and both recruited more than 1,000 seedlings. Sb seedlings occurred primarily in unplanted plots and in pure Sb plots (Lindig-Cisneros & Zedler 2002), but numbers dropped to near zero once canopies closed. Se also recruited many seedlings, but only a few plants remained in 2005.

Sv emerged as a dominant by 2005, when its cover averaged 49%. In pure Sv plots (0.25 m²), this species left only 6.0% bare space, and where Sv cover was high, species richness was low ($r = -0.435$, $p < 0.01$). Jc spread vegetatively and became dominant (29% cover in 101 plots and 47% cover in the 62 plots where it occurred), but Jc cover was independent of species richness ($r = -0.041$). Sv tended to form a monotype, whereas Jc formed a matrix.

We suggest that Sb and Se were outcompeted because there were no shallow depressions to subdue Sv. We had troweled each plot smooth to create replicate experimental plantings. Soon after planting, Sv became the top biomass producer (Callaway et al. 2003).

Friendship Marsh. Diversity was not restored by three types of introductions at this 8-ha site (Sf plugs, five-species clusters, and patches of Sb seedlings). The most effective were Sf plugs, which created a monotype (as intended) for nesting by clapper rails. Initial differences between 2- and 4-m grids disappeared by year 6 (2005), when the cordgrass zone had approximately 100% cover of Sf. The Light-footed clapper was seen there in 2005–2006, but nesting was not confirmed.

The marsh plain was intended to support diverse halophytes, but none of the cluster plantings (Bm, Fs, Jc, Se, and Lc) thrived. The soil became extremely hypersaline (Zedler et al. 2003), and it took several plantings to achieve 108 live plants/species by December 2000. Thereafter, repeated sedimentation events covered leaves, and all five species experienced steady mortality. Only Se recruited offspring—a few seedlings occurred along the wrack line near the berm in March 2006. We do not expect Bm, Fs, Jc, or Lc to persist beyond 2010.

The patches of Sb recruited seedlings into bare spaces, like a fugitive species (Bertness et al. 1992). Many persisted in shallow depressions formed by wind and wave action (Wallace et al. 2005); however, the 2004 storms filled the shallower pools in the western half of the site. As Sv expands vegetatively, the plant canopy will slow the wind and wave

action, roots will stabilize the soil, and pool formation will cease. With sediment accreting at a mean rate of 1.3 cm/yr (Wallace et al. 2005), the topography will continue to flatten.

Sedimentation elevated both the mudflat (intended to remain bare for shorebird feeding) and the marsh plain (intended for diverse halophytes). Sv was not planted, but it established large clones from seed brought in by tides (Morzaria-Luna & Zedler 2007). Sv seedlings and clones were obvious in year 4. Unexpectedly, the highest sedimentation rates (up to 2.50 cm/yr; Wallace et al. 2005) were on the mudflat, where Sv cover expanded to approximately 50% by 2005. On the marsh plain, Sv recruited widely and formed monotypic patches. Sf normally grows best next to open water (Zedler et al. 1999), but here it is bounded by higher elevations that are stabilized by Sv. A pair of storms could easily fill the cordgrass zone—the first filling the Goat Canyon basins, as in 2004, and the second discharging silt and clay into Friendship Marsh. Sv would then replace Sf, as has happened with sediment accretion in the natural marsh.

In summary, the loss of diversity in two restored marshes matches that in the natural marsh, but for slightly different reasons. In the natural marsh, pulse and ramp disturbances interacted to accelerate compositional change, whereas in the restored marshes, sedimentation filled shallow depressions, favoring the regional dominant.

The Difficulty in Predicting Future Events

Based on disturbance history, the future will be hard to predict. At Chesapeake Bay's Otter Point Creek, the highest sedimentation rates (3.9–48.0 cm/yr, which greatly exceeded the pre-1700 rate of 0.05 cm/yr and the 0.60 cm/yr after Europeans cleared the land) coincided with forest clearing and four major storms between 1840 and 1880 (Hilgartner & Brush 2006). Storms exacerbated erosion, and sedimentation shifted estuarine marsh to shrubs and riparian vegetation (Hilgartner & Brush 2006). Likewise, Tijuana Estuary's recent storms interacted with increasing land use. As the City of Tijuana grew from 341,000 people in 1970, 462,000 in 1980, and 747,000 in 1990 to 1,309,634 in 2000 (Ganster 2000), steep canyons were developed and unvegetated slopes became vulnerable to mudslides. Future impacts of storms will depend, in large part, on land use in Mexico and storms, neither of which is easy to predict.

The sequence of events is also important. The 1984 tidal closure occurred during a drought year. In future times, tidal closure could be followed by moderate rainfall, and impounded freshwater could drown Sv, as seen by Ferren (1985) in Carpinteria Marsh (near Santa Barbara, CA). Alternatively, heavy rainfall could produce enough river flow to reopen a closed inlet. Then, freshwater inflows could convert hypersaline vegetation to brackish marsh, as seen by Greer and Stow (2003) in Los Penasquitos Lagoon, north of San Diego.

In addition, sea level rise will interact with both land use and disturbance sequencing. Current trends of diver-

sity loss might become reversible if sediment delivery slows and detention basins become more effective and if frequent storms are a temporary phenomenon (Bromirski et al. 2003) rather than a response to global warming (Houghton et al. 2001). Although sediment accretion levels at the Friendship Marsh (0.5 cm/yr average from 2000 to 2004 to 4.5 cm in 2004–2005) have been extreme for Tijuana Estuary (Zedler 1983; Weis et al. 2001; Ward et al. 2003; Wallace et al. 2005) and for salt marshes in general (Cahoon et al. 1996), future sedimentation could counter increased rates of sea level rise (currently <0.02 cm/yr; Munk 2002). Although we cannot predict the future in detail, we can suggest how restoration efforts can accommodate pulse and ramp sedimentation.

Implications for Practice: How Diversity Might be Restored

As in most efforts aimed at restoring diversity, those at Tijuana Estuary and other southern California salt marshes (Entrix et al. 1991; www.scwrp.org) will benefit from experimental approaches and long-term commitments. Our study shows that restoration requires more than contouring sites, planting native species, and reintroducing tidal flushing. To counter pulse and ramp sedimentation, we recommend that:

- Restoration efforts accelerate to keep rare species (e.g., Sb, Se) from becoming endangered.
- Restoration efforts mimic natural topographic heterogeneity (e.g., tidal creeks and depressions) to include microhabitats that subdue dominant plants.
- Innovative tools be tested to create heterogeneous topography (e.g., C. Cornu of South Slough National Estuarine Research Reserve in Oregon used dynamite to cut complex meandering creeks at low cost and minimal disruption).
- Excessive sedimentation be capitalized upon by overexcavating sites to mudflat elevation, allowing creeks to form naturally as sediment accumulates.
- Small islands be left on the mudflat and planted with dense, species-rich clusters to trap sediments and “grow the marsh plain” horizontally.

Overall, we recommend that new approaches be tested in an adaptive restoration framework, with replicated treatments, monitoring, analysis, interpretation, and dissemination of findings, so that the next 30-year history of diversity restoration can benefit from more systematically collected data.

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