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The challenge of restoring vegetation on tidal, hypersaline substrates

J.B. Zedler[1,2,4], H. Morzaria-Luna[2] & K. Ward[3]
[1]*Department of Botany and Arboretum. Univ. of Wisconsin-Madison. 430 Lincoln Drive. Madison, WI 53706, USA.* [2]*Department of Botany, UW-Madison.* [3]*Golden Gate National Recreation Area. Building 201. Fort Mason. San Francisco, CA 94123, USA.* [4]*Corresponding author**

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Abstract

Hypersaline tidal wetland restoration sites are challenging to vegetate, and the specific factors responsible for transplant mortality are difficult to pinpoint. Two southern California sites (Tidal Linkage and Friendship Marsh), planted as large field experiments, had differential transplant survival (93% for a 1997 planting at the first site, and 10% for a 2000 planting in the second site). Multiple stresses (high salinity, sediment deposition, algal smothering and animal activity) are implicated as the cause of mortality in the experimental plantings. Greater hypersalinity and sedimentation appeared to be a function of site context, with greater sediment inflows and salt concentration over the larger (8-ha) marsh plain at the Friendship Marsh. Species differed in establishment rates among sites and years; the regional dominant, *Salicornia virginica*, performed best as a transplant and in volunteer seedling recruitment in the Tidal Linkage; hence, it was not planted at the larger site, where it has recruited without assistance. *Frankenia salina* had high survival in the 2000–2001 plantings; this species is also widespread in the region. Our attempts to restore salt marsh plain vegetation in Southern California led to greater appreciation of the importance of environmental stress and stochastic events and their potential for interaction. Hypersalinity and other factors are extremely difficult to ameliorate, especially in large restoration sites.

Introduction

Halophytes are salt tolerant by definition, but salinity still affects their establishment, growth, survival, and reproduction (Waisel, 1972). High salt concentrations can reduce seed germination and initial seedling growth (Callaway and Sabraw, 1994; Callaway and Zedler, 1998; Kuhn and Zedler, 1997; Shumway and Bertness, 1992; Ungar, 1978), as well as the growth of established plants to reproductive stage, whether vegetative or by seed. As plants mature from seed to rhizome-bearing adults, they can become more tolerant of salt (Beare and Zedler, 1987; Zedler et al., 1990); that is, they can ameliorate salinity stress by developing roots that preclude salt uptake, leaves that excrete salts, or tissues that sequester salt in vacuoles that are not sensitive to sodium toxicity (Adam, 1990). They can also avoid the highest salinities, by timing growth to avoid periods of maximum salt stress.

The relationship between halophytes and soil salinity has implications for salt marsh restoration. Establishment in hypersaline sites might be difficult, because most halophytes seem to germinate at higher rates and grow better at salinities well below what they can tolerate (Khan et al., 2001; Naidoo and Naicker, 1992). Establishment opportunities in low salinity sites might also be rare; these environments tend to lack halophytes due to competitive exclusion by faster-growing species, rather than by a lack of tolerance of the physical conditions found in such habitats (Ungar, 1998). So if high salinity limits establishment, and low salinity allows competitors to limit maturation, halophytes should be restricted to habitats that are only occasionally low in salinity, with episodic recruitment followed by persistence via long life spans and/or vegetative reproduction. Noe and Zedler (2001a) offer

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* FAX No: (608) 262 7509. E-mail: jbzedler@facstaff.wisc.edu

support for this hypothesis among high-marsh annuals that germinated in saltpans following cool-season rainfalls that were heavy enough (>3 cm) to lower surface soil salinity. Seedlings thereby avoided salinities of ≥ 70 g L^{-1} (measured in saturated soil pastes). If the regeneration niche (*sensu* Grubb, 1977) is a low-salinity window that follows heavy rainfall, then attempts to establish vegetation in hypersaline restoration sites might be severely constrained by dependence on weather.

Restoration efforts are underway in many Californian-type salt marshes north of the US-Mexico border (cf. Zedler, 2001). This salt marsh type occurs from Point Conception, California, south into Baja California, Mexico. It has a narrow fringe of *Spartina foliosa*, a broad marsh plain dominated by eight halophytes (mostly succulents, notably *Salicornia virginica*), and a high marsh (dominated by *Monanthochlöe littoralis* and *Salicornia subterminalis* = *Arthrocnemum subterminale)* that grades into coastal sage scrub (Ferren, 1985; James and Zedler, 2000; Neuenschwander et al., 1979; Vogl, 1966; Zedler, 1977). Soils are typically hypersaline (>34 g L^{-1}; Ibarra-Obando and Poumian-Tapia, 1991), and most species rely on vegetative reproduction. Seedlings of *S. foliosa* are rarely seen, except after freshwater flooding (Ward, 2000); this species reproduces vegetatively via rhizomes (Zedler et al., 1980). On the marsh plain, *S. virginica* produces some seedlings every year, but major recruitment events are rare, and seldom are all native species seen in seedling stage in the same year. At Tijuana Estuary, *Limonium californicum* and *Atriplex watsonii* both produced exceptionally high numbers of seedlings in spring 1983, when rainfall was heavy and prolonged and soil salinity greatly reduced (Zedler et al., 1992). An even greater salinity-reduction event occurred at the San Diego River salt marsh, due to flooding in January–February 1980 followed by the release of excess freshwater from an upstream reservoir. Monotypic *S. virginica* was replaced by dense stands of *Typha domingensis* (Beare and Zedler, 1987), a shift that was reversed only after several years of hypersaline conditions (JZ, pers. obs.).

If these observations of rare recruitment events represent the norm, the natural diversity of salt marshes might be a result of cumulative responses to multiple establishment opportunities. Over time, common species would recruit frequently while rare species would wait for suitable microsites with substantially lowered soil salinity. In addition to salinity, sedimentation (elevating topography), invertebrate activities (scraping of algal mats), and vertebrate actions (burrowing and sidecasting soil) might create microsites for seedling establishment or, alternatively, reduce opportunities for recruitment via smothering (by sediments or algae) or trampling, grazing and uprooting activities of animals. If the establishment of the full complement of species in a natural marsh is a cumulative process that depends on a range of microsites occurring over long time periods, then our ability to establish diverse vegetation in restoration sites might be seriously compromised by construction plans that call for all species to be planted at once. Conditions might be suboptimal for some desirable halophytes and favorable for some exotics (Callaway and Zedler, 1998; Kuhn and Zedler, 1997).

Here we describe outcomes of two attempts to restore salt marsh vegetation at Tijuana Estuary, a site where sedimentation (up to 2 m of material that has washed in from its agricultural and urban watershed) has reduced wetland area and threatened populations of coastal wetland-dependent species (Zedler et al., 1992). An ambitious restoration plan calls for the excavation of sediments that have accumulated over 200 ha of former wetland to reveal historical marsh plains. In addition, a small area of disturbed upland has been converted to tidal wetland. The restoration program has been designed to occur in modules to be phased over several decades. We report on the first two modules (Tidal Linkage and Friendship Marsh), each of which has been excavated and planted with experimental arrays of greenhouse-grown seedlings of native halophytes.

The Tidal Linkage plantings tested the hypothesis that species-rich plantings would enhance the development of ecosystem functions, comparing assemblages with 0, 1, 3, and 6 species. The efforts to establish the planting treatments are reported here for the first time; other papers report the effects of species diversity on productivity and nitrogen accumulation (Callaway et al., in review; Zedler et al., 2001) canopy development (Keer and Zedler, 2002), and seedling recruitment (Lindig-Cisneros and Zedler, 2002). The Friendship Marsh was designed to test the hypothesis that topographic heterogeneity influences the development of ecosystem functions. Initially, treatments had vertical heterogeneity (replicates with and without a tidal creek network) and horizontal heterogeneity afforded by different assemblages (6 marsh plain species and different combinations of 3-species assemblages), soil amendments (kelp compost + rototilling, rototilling, and control), and nurse plants (i.e. adult plants that provide safe-sites to emerging seedlings, by ameliorating physical and biological stresses Holmgren et al., 1997). Later, following high mortality, the experimental design changed because of insufficient seedlings; we then tested the hypothesis that vegetation would develop differentially in relation to transplant spacing (with the same soil amendment treatments in a two-factor design). In both projects, the plants introduced to the restoration sites were drawn from the same pool of 8 marsh-plain species. The contrasting outcomes of these restoration efforts allow us to speculate on the role of soil salinity, as well as sedimentation and weather conditions, in the survival of transplants and volunteer recruitment of native halophytes.

Materials and methods

Tijuana Estuary (32° 34′ N, 117° 7′ W; Figure 1) is a 1000-ha National Estuarine Research Reserve and is the least fragmented coastal wetland in San Diego County. The estuary is immediately downstream of agricultural fields in the US and the metropolitan area of Tijuana, Mexico, with resulting water quality and sedimentation problems (Ganster, 1998; Zedler et al., 1992).

Tidal linkage

This 0.7-ha restoration site is located in the North arm of Tijuana Estuary, adjacent to natural marsh areas. The Tidal Linkage was excavated to 75–115 cm NGVD (National Geodetic Vertical Datum). We used a 10-m × 100-m intertidal plain alongside an excavated tidal channel for experimental plantings. During excavation, bulldozers encountered and broke up a sandstone hardpan. Fine sediment, salvaged from the construction of a new tidal channel in an adjacent tidal pond, was mixed into the top 20 cm of crushed sandstone and rototilled to improve homogeneity. In April 1997, we positioned 87 experimental plots, each 2×2 m, along the 100-m-long marsh plain that paralleled the tidal channel; each was leveled by hand using a paving trowel, adding channel water as needed to smooth the surface.

Seeds of eight halophytes (Table 1) were collected from Tijuana Estuary in fall and winter 1996, germinated in flats in a greenhouse, then transplanted individually into 5×5-cm peat pots. When seedlings were 4 months old and 5–10 cm tall, they were hardened outdoors and watered with increasingly saline water. We began with a dilute solution of seawater (4 g salt L^{-1}), then increased the concentration every 3–4 days (to 8, 12, and 16 g salt L^{-1}). In between seawater additions, pots were watered with fresh water. We checked soil salinities in pots without plants; when half-strength seawater had been added, soil salinities rose to ≥ 32 g L^{-1}. The hardening process took 2–3 weeks. The seawater was obtained at Scripps Pier in La Jolla, California.

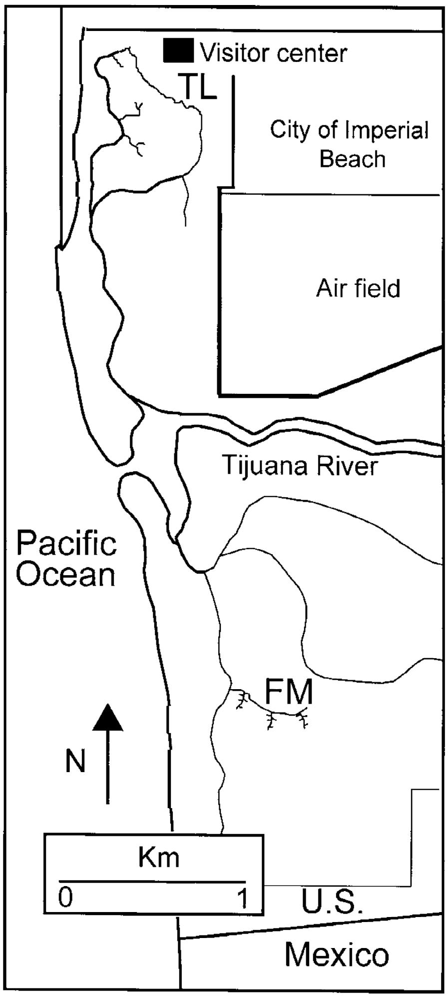

Figure 1. Tijuana River National Estuarine Research Reserve (32° 34′ N, 117° 7′ W). The Tidal Linkage (TL; 0.7 ha) is located near the Visitor Center at the north end of the Reserve and the Friendship Marsh (FM; 8 ha) is found at the South.

Seedlings and peat pots were placed in the experimental plots April 11–21, 1997, with 90 seedlings per 2×2-m plot, spaced 20-cm apart in a 9 × 10 grid. Fifteen plots were left unplanted and 72 plots were planted: 40 with 1 species (5 plots per species

Table 1. Species planted during restoration of the Tidal Linkage and Friendship Marsh in Tijuana Estuary (*indicates species not planted at the Friendship Marsh)

Species	Species
Batis maritima L.	*Salicornia bigelovii* Torrey
Frankenia salina (Molina) Johnston	**Salicornia virginica* L.
Jaumea carnosa Gray	*Suaeda esteroa* Ferren and Whitmore
Limonium californicum Heller	* *Triglochin concinna* Burtt Davy

× 8 species), 16 with 3-species assemblages, and 16 with 6-species assemblages. The 3- and 6-species assemblages were randomly drawn, so the total number of plants per species was not identical but similar (see 'Results'). The plantings were watered intermittently (at least once a week) with freshwater from a hose for two months; subsequently, an irrigation system was installed on the upper edge of the marsh plain with evenly spaced sprinklers. Thereafter, while plants were young, the plots were irrigated daily for 30 min.

We replanted individuals that died with extra seedlings on May 15, June 5, and July 17, 1997. During the El Niño-Southern Oscillation winter of 1997–1998 an extensive growth of algae (*Enteromorpha* and *Ulva* spp.) developed across the restoration site, smothering some seedlings and attracting a flock of coots that damaged the plantings both through their feeding and movement across the site. Seedling mortality was assessed again and plants replaced on January 22 and March 19, 1998. Ultimately, all planted plots had 90 live seedlings. During the first two growing seasons, 1997 and 1998, we found and removed volunteer seedlings of species not planted to a plot, but we left in place those belonging to the prescribed assemblage. Seedling recruitment within plots was quantified at intervals in 1998 and in fall of 1999. In the latter census, we counted only the seedlings present in plots where no conspecifics were planted, because sprouts of vegetatively reproducing species, like *S. virginica*, could no longer be distinguished from seedlings.

Soil salinity was measured in April and June 1997 by collecting soil cores from the top 5 cm and transporting them to the laboratory. Marsh-plain soils are often too dry to allow direct tests of interstitial water salinity; hence deionized water was added to make a uniform saturated soil paste (Richards, 1954). The interstitial water was then expressed through filter paper onto a salinity refractometer. The resulting soil-paste salinities can be substantially lower than maxima that plants experience in the field. Soil texture was measured by the hydrometer method (Gee and Bauder, 1986).

Friendship Marsh

This 8-ha site is located in the southern arm of Tijuana Estuary. In 1999, a layer of sediment, about 2 m thick, was excavated to expose buried salt marsh soil. The site was excavated to an elevation range of 30–80 cm NGVD, with the lower elevation near the tidal channel (mudflat planted with *S. foliosa*) and the higher at the inland margin planted with *S. subterminalis* and other high marsh species. As part of a larger experiment to test the importance of tidal creek networks to ecosystem restoration (Zedler, 2001), the site has six subareas or 'cells' (each ∼1.3 ha), three of which are connected to the main tidal channel by a tidal creek network and three that lack tidal creeks but receive sheet flow from the tidal channel. Tidal flushing was established in February 2000 by connecting the excavated site to an existing tidal channel.

The initial experiment was set up to test effects of assemblage and soil preparation on vegetation development. For our comparison with the Tidal Linkage, we consider only the control plots (no soil amendments), of which there were four per cell (each 1.6 × 1.4-m) for a total of 24 on the marsh plain. These four plots were located near (5 m) and far (13 m) from the creek bank in cells with creeks and in the same positions in cells without creeks.

Soil texture was measured as in the Tidal Linkage. Soil organic matter was assessed as loss on ignition. Sediment accretion was measured using four feldspar marker horizons (Cahoon and Turner, 1989) per cell (total = 24), and soil paste salinity (as above) was measured in plots and across the marsh plain on several dates (see 'Results'). Seedlings were prepared and hardened as for the Tidal Linkage, except that we used 5×5-cm plastic pots that were removed prior to planting. On April 11–13, 2000 seedlings were planted in randomly selected assemblages of 3 species and 6 species, drawn from a pool of 6 species. Either 14 (3-species plots) or 7 individuals (6-species plots) of each species were planted in each plot, for a total of 42 plants per plot (20 cm apart in a 6×7-plant grid). A total of 1008 seedlings were planted into control plots. Survival was assessed on July 7, 2000.

Our first nurse-plant experiment involved the planting of 324 additional seedlings to test the potential of *S. esteroa* to function as a nurse plant. As these were also placed in unamended soil (as for the above control plots), their survival is relevant here. On April 11–13, 2000, plants were placed individually or in clusters of six (2 rows of 3, 10 cm apart) in 3.5×3.5-m plots (4/cell). One individual plot and one cluster plot were placed on each side of the main creek, and in comparable positions for cells without creeks.

Following nearly complete mortality of the plantings (see 'Results'), and lacking enough seedlings to reestablish the above experiments, we designed and established two new experiments (cluster plantings and a second nurse-plant test). We used surplus seedlings that had been held in the greenhouse and transplanted into larger plastic pots that were 5 cm in diameter and 8 cm tall. The few survivors from the initial plantings were removed from the site. On December 20, 2000, we planted seedlings of *Batis maritima*, *Frankenia salina*, *Jaumea carnosa*, *L. californicum*, and *Suaeda esteroa* as clusters in the 1.6×1.4-m plots. Each plot held one individual of each of the five species arranged in a quincunx (i.e., like dots on the 5 die). We varied spacing by placing seedlings 10, 30 or 90 cm from the center plant. Each spacing treatment had two replicate control plots per cell, for a total of 180 seedlings (36 per species) across the entire marsh plain. Survival was assessed on February 9, 2001, approximately seven weeks after planting. Plants that died during the initial months were replaced on March 22-23. Thereafter, on May 17, June 26, August 17, September 15, November 13, and December 14, 2001, survival was assessed and replacements planted on the same dates. Volunteer (unplanted) seedlings were removed during 2000 and 2001 (but not counted) in order to maintain the desired experimental planting treatments.

The second nurse-plant experiment was established in March 2001, planting eight 3.5×3.5-m plots per cell. In each plot, we planted one adult of *L. californicum*, *S. esteroa* and *F. salina* each as individuals (2 m apart) or three single-species clusters of six plants (separated 5 cm); clusters were separated by 2 m. Twenty-five seeds of *Salicornia bigelovii* and 25 of *Triglochin concinna*, collected in 2000, were spread underneath the clusters, the individual plants, and in control plots (no plants), for a total addition of 21 600 seeds. All seeds were covered with squares of burlap fabric to reduce tidal export. Survival of adult plants and recruitment of seedlings were assessed on April 28, May 22–24 (replanting dates), and July 27. After July, we lacked plants to reestablish *L. californicum* and *S. esteroa,* so all survivors of these species that were planted as individuals were replaced with *F. salina*. The experiment shifted to a comparison of three species as individuals vs. clusters to a comparison of *F. salina* as individuals vs. clusters of each of the three species. Survival was assessed on September 01, 2001, and January 28, 2002.

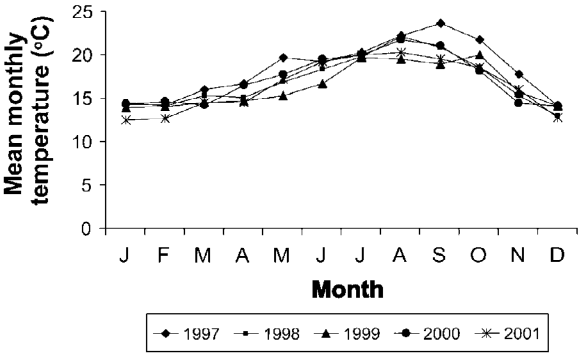

Figure 2. Mean monthly temperature for Lindbergh Field, San Diego 1997–2001. Data from the National Climatic Data Center. NOAA.

Results

Environmental conditions

Weather data obtained from the National Climatic Data Center/National Oceanic and Atmospheric Administration (NOAA) archives (Lindbergh Field Station) indicate that air temperature and precipitation were very similar during the initial plantings of the Tidal Linkage (April 1997) and Friendship Marsh (April 2000; Figures 2–3). Mean daily temperatures averaged about 16.5 °C and less than 2 cm of rain fell in April of both years.

Tidal inundation patterns were similar in April 1997 and April 2000 (Figure 4), with amplitudes characteristic of the season, i.e., considerably less than the 3-m maxima of January and June. The period of time that the marsh plain was exposed during daytime (Fig-

Table 2. Survival of planted seedlings and recruitment of seedlings in experimental plots at the Tidal Linkage. Note that the number planted was unequal due to random selection of assemblages (cf. Lindig-Cisneros and Zedler, in press)

Species	Total planted in 1997	Replanted 1997	% Survival 1997	% Survival Winter 1998	Replanted in 1998	Seedling recruitment (totals in 1998)	Seedling recruitment (totals in 1999)
B. maritima	765	144	81.2	88.2	90	26	8
F. salina	780	5	99.4	76.8	181	2	8
J. carnosa	855	132	84.6	92.3	66	33	33
L. californicum	795	16	98	74.8	200	24	178
S. bigelovii	780	20	97.4	92.8	56	15 978	7586
S. esteroa	810	18	97.8	73.1	218	1668	2685
S. virginica	885	6	99.3	99.8	2	17 703	3445
T. concinna	810	133	83.6	58.1	339	73	8
Totals	6480	474	92.7	82.2	1152	35 507	13 951

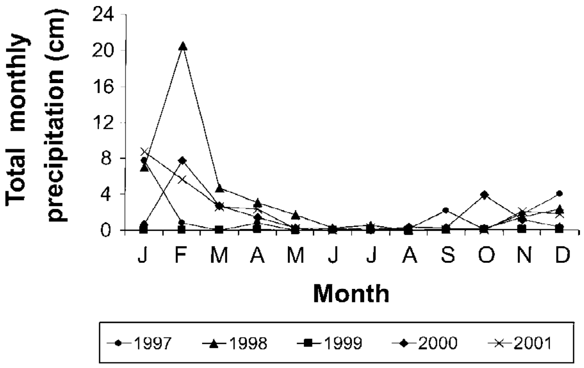

Figure 3. Total monthly precipitation for Lindbergh Field, San Diego 1997–2001 in cm. Data from the National Climatic Data Center. NOAA.

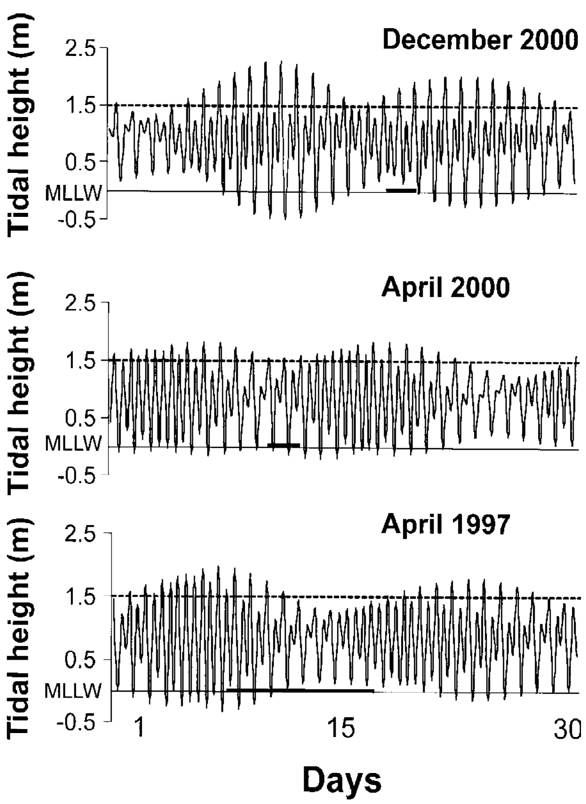

Figure 4. Predicted tides for San Diego Bay Station, April 1997, April 2000, and December 2000 (WXTide32 software ver. 2.7, ©M. Hopper 1998–2000). Dotted line indicates marsh plain elevation at 1.5 m above Mean Lower Low Water (MLLW), equal to 0.9 m above the National Geodetic Vertical Datum (NGVD = 0.6 m MLLW). Thick line on x-axis indicates dates when seedlings were transplanted into the restoration site.

ure 5) gives some indication of evaporation potential and transpiration stress. During both planting times, the entire marsh plain was usually exposed for 6–12 h per day. Higher elevations would have had longer exposure. Note that all are predicted tides.

Tidal Linkage

Initial surveys of the Tidal Linkage marsh plain revealed a sandy substrate (means ± S.E. for all samples: 60 ± 2.1% sand, 20.8 ± 0.9% silt, and 19.2 ± 1.5% clay) with low soil salinities during the planting period (April 1997 mean = 41 ± 0.14 g L^{-1}) and two months later (June mean = 43 ± 1.11 g L^{-1}; Figure 2). Soil organic matter content was not measured, but this was upland subsoil with a low proportion (1:20) of fine dredged material added to improve the

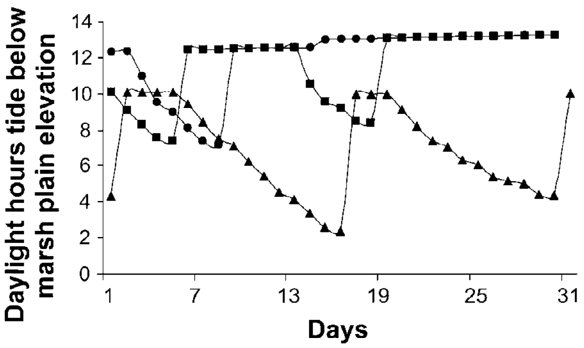

Figure 5. Hours of exposure during daylight, when water levels were predicted to fall below the marsh plain elevation in April 1997 (●), April 2000 (■) and December 2000 (▲). Data from San Diego Bay Station (WXTide32 software ver. 2.7, ©M. Hopper 1998–2000).

nutrient and water-holding capacity. Soils had coarse texture and low organic matter content, and water did not pond on this site.

Transplant mortality was low through the summer of 1997, with 93% of all plants surviving (Table 2). Survival exceeded 80% for all species through fall 1997, with small interspecific differences. *S. virginica* had the highest survival rate (99.3%), and *B. maritima* had the lowest (81.2%). However, during the winter of 1997–98, an algal bloom, a storm sedimentation event, and coot grazing and trampling collectively reduced cover. Nearly 20% of the plants died, including some of every species (Table 2). Most of the mortality occurred at the lower elevation, where plants were covered by both algae and up to 1.5 cm of sediment (Sullivan, 2001). *T. concinna* (58.1% survival) and *S. esteroa* (73.1% survival) were most affected by the disturbances that winter; while *S. virginica* survival (99.8%) was as high as the initial planting.

Following replanting in 1998, all plots achieved high cover, as plants grew in height and expanded laterally (Keer and Zedler, 2002). Seedlings that recruited during 1998 and 1999 were mostly those of *S. virginica*, *S. bigelovii*, and *S. esteroa* (Table 2). Seedlings of the remaining four species accounted for less than 1% of total seedling number for both sampling periods (Table 2).

Friendship Marsh

Initial surveys of the marsh plain surface at the Friendship Marsh revealed a sandy substrate (means for all samples: 75.1 ± 2.3% sand, 17.3 ± 1.7% silt and 7.6 ± 1.1% clay) with extremely high salinity. All soil pastes from the February 2000 samples exceeded the refractometer's 100-g L^{-1} scale. Subsequent soil samples were extremely hypersaline as well (Figure 6). Salinities decreased throughout 2000 and 2001, but the majority of soil pastes still exceeded 40 g L^{-1}. Cumulative sediment accretion determined by feldspar markers ranged from a mean of 0.24 ± 0.01 cm in September 2000, 1.13 ± 0.02 cm in April 2001, and 1.26 ± 0.05 cm in September 2001. That is, most of the sediment accumulated between September 2000 and April 2001, a period with multiple winter storms. During 2001, a thick microbial mat formed on the sediment surface (Morzaria-Luna, pers. obs.), and organic matter on the marsh plain increased from a mean of 3.6 ± 0.1%, in February 2000 to 4.5 ± 0.13%, in February 2001 (Figure 7).

Seedlings planted in April 2000 experienced extremely high mortality (91.2%); that is, only 8.8% of the plants in control plots survived the first weeks after planting (Table 3). No species had a survival rate higher than 18%. Seedlings planted in December 2000 had much higher survival (average = 47.6% for all species). Seven replacement efforts were needed throughout 2001 to achieve our target of 5 plants per plot. The nurse-plant experiment also experienced high mortality, with survivorship for all species of 69.8% in March 2001 and 62.1% in January 2002 (Table 4).

In both the cluster and nurse plant experimental plots and across planting times, there were notable interspecific differences in survival. *F. salina* consistently had high survival rates with 16.4% in 2000, 70.6% in the cluster plantings in 2001, and 75.3% and 81.5% respectively in the nurse plant experiments

Table 3. Survival of seedlings planted on unamended soil in the Friendship Marsh over the 2000 growing season. The number of individuals planted was unequal due to random selection of assemblages. Note that *Suaeda esteroa* was planted in both random assemblages ($n = 210$) and as nurse plants ($n = 324$); the respective survivors were 27 and 30

Species	Total planted	Survivors	% Survival
B. maritima	126	8	6.3
F. salina	140	23	16.4
J. carnosa	196	1	0.5
L. californicum	196	23	11.7
S. bigelovii	140	7	5.0
S. esteroa	534	57	10.7
Totals	1332	119	8.8

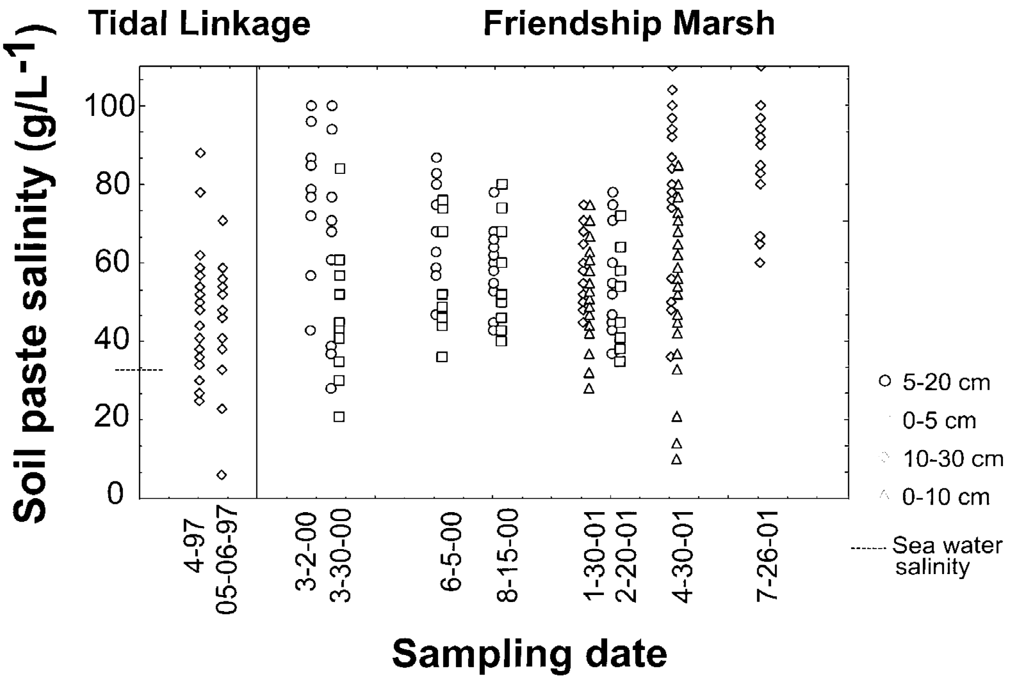

Figure 6. Soil paste salinity (g L^{-1}) taken from unamended plots on the marsh plain of Tijuana Estuary, within the Tidal Linkage (planted in April 1997; salinity sampling dates on left side of x axis) and the Friendship Marsh (planted in April 2000; salinity sampling dates on right side of graph). Sample collection included four different depths.

in 2001 and 2002. *S. esteroa* survivorship was consistently low, at 10.7% in 2000, 29.5% in the cluster plantings in 2001, 68.3% in the nurse plants in 2001, and 44.5% in 2002 (Table 5). Throughout the 2001 surveys, transplants appeared stressed and laden with sediment. We often had to wipe sediment off the leaves in order to determine if plants were alive, i.e., to see if green tissue remained.

Voluntary recruitment was rare during 2001, although we found a few seedlings of *S. virginica*, *S. bigelovii*, and *A. watsonii*. The seedlings of *S. bigelovii* occurred only in plots that had previously been planted with this species in 2000. We found little recruitment from seeds intentionally added to the marsh plain for the nurse-plant experiment during censuses in winter and spring; only 17 of the 10 800 *S. bigelovii* seeds produced seedlings (0.16%), and none of the 10 800 *T. concinna* seeds produced seedlings (Table 5). The burlap used to hold the seeds in place was quickly covered with microbial biofilms and sediment (Figure 8).

Table 4. Survival of seedlings planted in December 2001 as clusters to unamended soil in the Friendship Marsh

Species	Initial planting	Subsequent plantings	% Survival
B. maritima	36	9	80.0
F. salina	36	15	70.6
J. carnosa	36	58	38.3
L. californicum	36	28	56.3
S. esteroa	36	86	29.5
Totals	180	196	47.9

Discussion

Environmental conditions were stressful to transplants

The conditions under which we attempted to establish halophytes were not optimal, even for the most salt-tolerant halophytes. Salt marsh soils in this region are hypersaline year round, even in vegetated, pristine Californian wetlands (Ibarra-Obando and Poumian-Tapia, 1991). The Mediterranean-type climate typically has less than 30 cm of precipitation per year, which falls in a few rainfall events, mostly between November and March. In April, long periods of tidal

Table 5. Survival of seedlings planted as nurse plants to unamended soil in the Friendship Marsh in 2001 and recruitment from added seeds over the 2001 growing season

Species	Initial Mar.	Transplants Replacements through July	% Survival	Initial July	Survivors Jan. 2002	% Survival	Seeds	
							Added seeds Mar 02	No. of seedlings
F. salina	168	55	75.3	216	176	81.5	0	
L. californicum	168	19	89.8	144	73	50.7	0	
S. bigelovii	0						10800	17
S. esteroa	168	78	68.3	144	64	44.5		
T. concinna	0						10800	0
Totals	504	152	69.8	504	191	62.1	21600	17

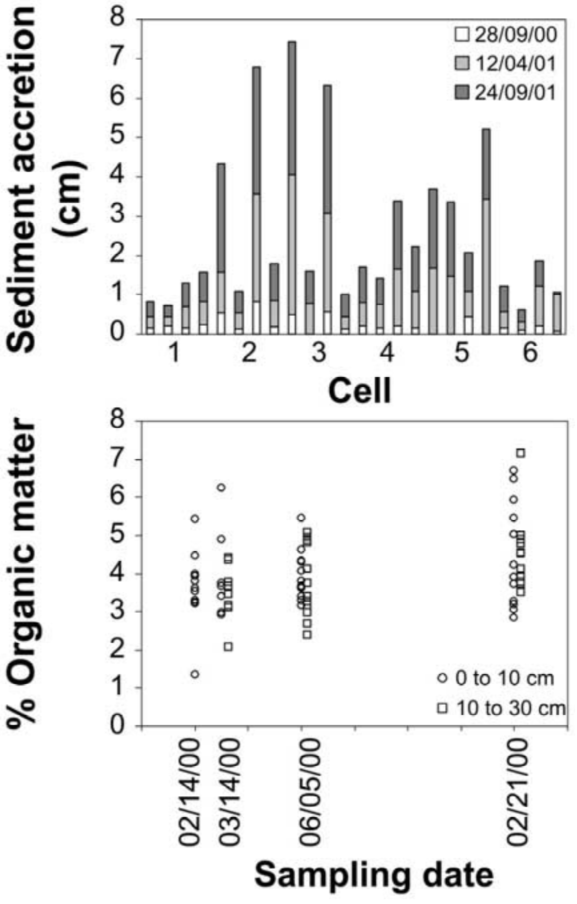

Figure 7. Sediment accretion (measured using feldspar markers) and soil organic matter content (% loss on ignition) and for the marsh plain of the Friendship Marsh, 2000–2001. Top graph shows the spatial variability for the experimental cells from west (1) to east (6); odd-numbered cells have tidal creeks; even do not. Temporal variation is obvious from shading indicating 3 sampling dates. Bottom graph shows the temporal variability in organic matter samples for 4 sampling dates in 2000 and variability within two soil depths (circles vs. squares).

exposure during the daylight hours simplify planting on the marsh plain, but also allow high evaporation from the soil. Planting during the rainy season could reduce desiccation stress, but the risk of flooding and sedimentation is higher, especially where watersheds are large (Tijuana Estuary has a 4452-km^2 catchment). Winter sea storms also make tidal marshes inaccessible by raising sea levels. When tides are low, hot, dry winds, which can occur in any season, bake the sediment and increase stress. There is no risk-free time for transplantation in this region.

Ideally, one would transplant seedlings just before gentle rainfall to reduce stress, but contractors control project completion dates and their schedules reduce choices for timing. While a site might be scheduled for completion by the beginning of the wet season, delays are likely, and seeds cannot be sown until about 17 weeks before planting (allows growth to appropriate size plus 3 weeks for hardening). Projects planted in April will lack benefits of rainfall and can be watered (as at the Tidal Linkage in 1997). Sites with coarse sediment can be amended to improve water-holding capacity. The finer soil at the Friendship Marsh alleviated concerns about drought, but we failed to anticipate inundation stress. Shallow depressions across this large site readily impounded saline water. Every project reveals unexpected constraints on biota.

Sites and species had differential plant-establishment rates

The most striking pattern we report is the large site-to-site difference in initial transplant survival and seedling establishment. The Tidal Linkage was readily vegetated both through plantings and volunteer seedling recruitment. An average of 93.7% of the transplants survived the first growing season, and 80.4% survived the following winter's disturbances (algal bloom, sedimentation, coot grazing and trampling). Plant cover (Keer and Zedler, 2002), biomass (Callaway et al. In review; Zedler et al., 2001) and seedling abundance (Lindig-Cisneros and Zedler, 2002) increased rapidly over the first four years. In contrast, the Friendship Marsh was extremely difficult to vegetate, with extremely low survival in 2000 (8.8%) and only moderate survival in 2001 (47.9%). Neither seedlings nor sown seeds readily established plants on this 8-ha marsh plain.

A second strong pattern is the differential survival of the species we planted. Among the 8 species planted at the Tidal Linkage, *S. virginic*a, a highly-productive perennial, had the highest survival, while *T. concinna*, a succulent monocot with low productivity (Sullivan and Zedler, 1999), had the lowest survival after the winter 1998 damage. At the Friendship Marsh, *F. salina* consistently had higher survival rates; this plant is a perennial subshrub that produces upright stems from rhizomes and can form a dense cover (Sullivan and Noe, 2001). *S. esteroa* survivorship was consistently low in the Friendship Marsh and in the Tidal Linkage after the winter of 1998. *S. esteroa* is a short-lived perennial that does not reproduce vegetatively (Zedler et al., 2001).

Similar differential survival rates were observed at Crown Point restoration project on Mission Bay, which is about 30 km north of Tijuana Estuary. This site had sandy soil (70% sand, 8% clay; Trnka and Zedler, 2000), high survival of planted seedlings and substantial recruitment from volunteer seedlings. Seedlings of 2–4 months in age were transplanted to the site as sod blocks (from 40 × 42 × 4-cm-deep flats). Species had differential survival, declining from *S. virginica* (highest), to *S. bigelovii*, *S. esteroa*, *F. salina*, *L. californicum*, and *T. concinna*. Sullivan (2001) found high mortality of *S. esteroa*, *S. bigelovii*, and *F. salina* where water ponded in two of the five low-elevation blocks. Other studies have found *Salicornia* is better at tolerating hypersaline soils than other marsh species, grows faster, accumulates more biomass and occupies more cover when soil salinity is high (Allison, 1996; Mahall and Roderic, 1976; Pearcy and Ustin, 1984; Zedler and Beare, 1986). After extensive flooding and sedimentation in Bolinas Lagoon, *S. virginica* became established within one year of the disturbance and expanded to occupy more cover than other species (Allison, 1996).

The third pattern concerned recruitment from seed. Only three species, *S. virginica*, *S. bigelovii*, and *S. esteroa*, recruited readily at the Tidal Linkage. Of the seedlings that appeared on the Friendship Marsh plain, virtually all were those of *Salicornia*, both *S. virginica* and *S. bigelovii.* The latter, however, were entirely confined to plots in which *S. bigelovii* seedlings had survived the summer of 2000. At the Tidal Linkage, *S. bigelovii* displayed a similar pattern, recruiting mainly in plots where it had been planted (Lindig-Cisneros and Zedler, 2002). The addition of 21 600 seeds to the Friendship Marsh in 2001 yielded only 17 seedlings. In contrast, *S. virginica* was not planted to the site but was abundant in the adjacent natural marsh. Morzaria-Luna (pers. obs) has documented that *S. virginica* seeds arrive at the site through tidal transport. At Crown Point, the most widespread volunteer recruitment was by *S. bigelovii*, which most frequently produced seedlings in low (0.85 m NGVD) and mid (1.0 m NGVD) elevations, averaging 63% occurrence in 150 sampling plots of 0.25-m^2 area (Sullivan, 2001). Second was *S. virginica* (39%) with seedlings most often occurring at high (1.3 m NGVD) elevation. *S. esteroa*, *B. maritima*, and *J. carnosa* ranked 3rd, 4th, and 5th (17, 12, and 8%), with most of their seedlings occurring in the high elevation. In no case did any species occur in all 50 quadrats that were sampled along an elevation contour. Frequent recruitment by *S. virginica* and *S. bigelovii* and substantially lower but noticeable recruitment by *S. esteroa* were also found at the Tidal Linkage (Table 2). In both sites, the three species with the highest survival of initial transplants also had the most frequent recruitment (Crown Point) or largest numbers of recruits (Tidal Linkage). Because we did not plant *S. virginica* at the Friendship Marsh, and because initial transplant survival was so low, further comparison of rankings would not be meaningful.

Site context appeared to affect environmental conditions

Several stresses relate to site context, i.e., location and size, which could affect rates of water movement and suspended sediment content. The Friendship Marsh is >15 times the size of the Tidal Linkage. The Friendship Marsh is further from the mouth, it is fed by channels that have had sluggist tidal flows for decades, and it has only one inlet, which also functions as its outlet. In contrast, the Tidal Linkage is part of an active hydrological loop; it receives tidal water from both

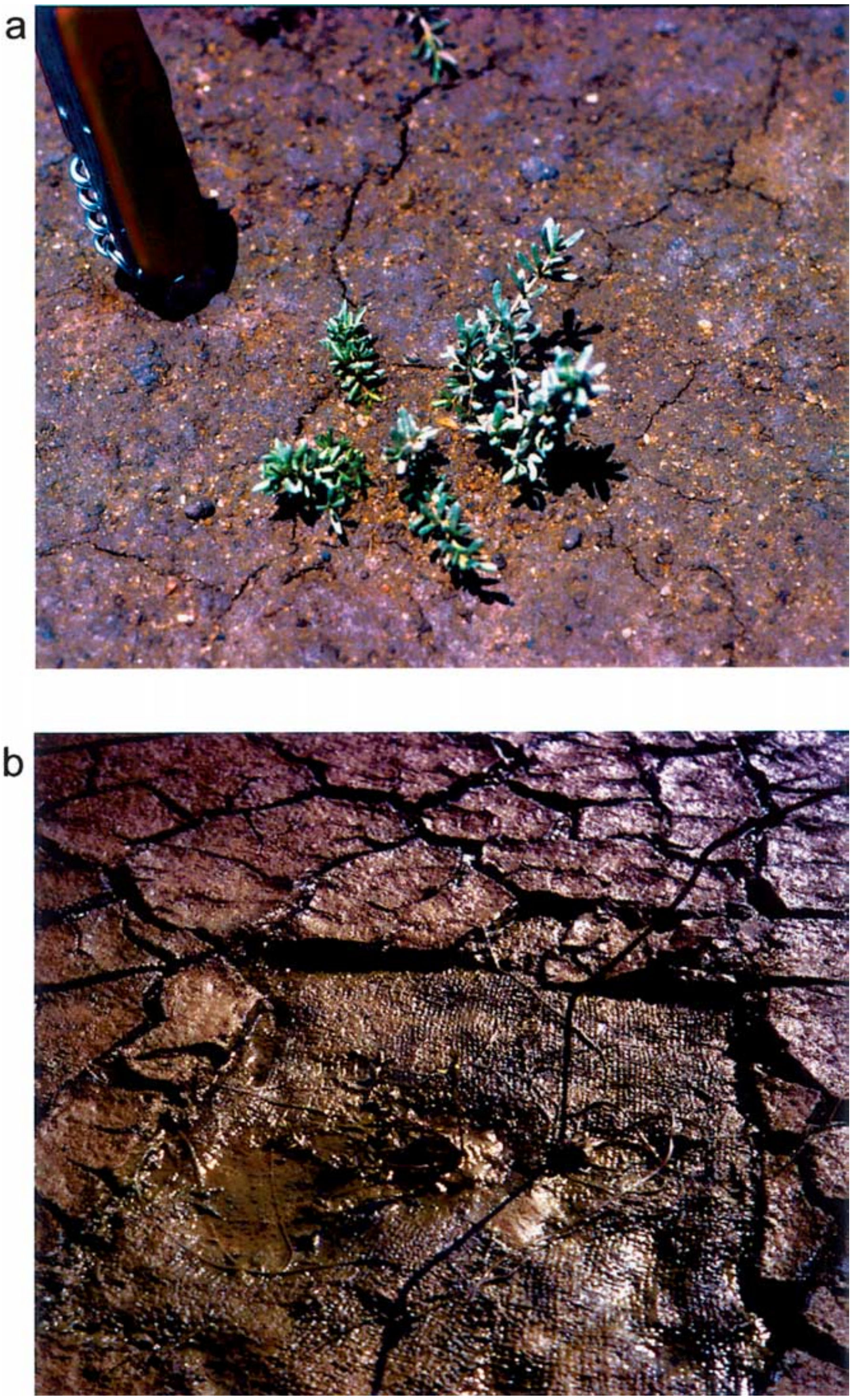

Figure 8. Close up of soil surface at the Tijuana Estuary restoration sites. (a) Single *Frankenia salina* plant in the Tidal Linkage (June 1997). Note healthy plant and coarse soil with developing biofilms. (b) Single *F. salina*, in center of burlap, left of marker flag in the Friendship Marsh (September 2001). Note dark color and cracked surface of soil.

its eastern and western tidal connections (Figure 1). While both restoration sites were connected to channels that were disturbed by the dredging, the mixing and retention of suspended solids in the water column seem more likely at the Friendship Marsh. Water moving into the 8-ha ‘cul de sac’ in the Friendship Marsh floods a much larger marsh plain, and tide water can undergo greater heating and evaporation, while flows are slowed as they move across the plain, increasing sedimentation. In addition, there is less opportunity for throughflow of sediments. Turbid water and a fine layer of sediment covered plants already salt stressed, as water levels rose and fell with the tides.

We attribute a high proportion of the mortality of the December 2000 planting to sedimentation; some plants had been buried by up to a centimeter of sediment by March 2001. *Limonium* and *Jaumea* leaves are especially susceptible to burial, due to their morphology (rosette and trailing flat leaves respectively; Sullivan and Noe, 2001). Sediment deposits might have reduced light interception and clogged stomata. Sedimentation very likely affected germination and recruitment of volunteer seedlings and sowed seeds. In a study of freshwater wetlands, Jurik et al. (1994) found sediment loads as low as 0.25 cm significantly reduced the number of species and total number of individuals recruited from seed bank samples; addition of sediment decreased the number of individuals appearing for most species.

Multiple stresses affected transplant survival

Because our plantings were designed to test the effects of species richness at the Tidal Linkage and effects of tidal creeks, soil amendments, plant spacing and nurse plants at the Friendship Marsh, rather than to compare mortality across sites, we might lack data on important environmental factors that vary between sites and over time. Rainfall, air temperature, and tidal exposure patterns in 1997 and 2001 do not suggest differences due to year (Figures 5–7), but soil salinities indicate a site difference. The low survival of year-2000 transplants at the Friendship Marsh (8.8%) and higher survival (47.6%) in 2001 suggest that the time of planting was important, not just the location.

The first planting at the Friendship Marsh occurred in April 2000, the second in December. The weather was cooler in December; there was some rainfall that month and over 8 cm in January 2001. During the long, warm dry season, marsh plains are fully exposed to evaporation, and during our April planting times, exposure time typically exceeded 10 h per day (Figure 4). It is difficult to avoid transpiration stress and evaporation from the soil (and salt concentration), because daytime low tides are needed for planting. During the rainy season, prolonged rainfall and flooding are necessary to lower soil salinity enough to persist beyond the next high tide (Zedler et al., 1986); but such events are not predictable, in part because flooding is a function of rainfall throughout the watershed. Freshwater flooding has its own hazard, namely sediment influx and deposition (Allison, 1996).

Planting procedures were similar at both sites, except that we used peat pots at the Tidal Linkage and plastic pots at the Friendship Marsh. The disturbance caused by removing plants from the plastic pots might have stressed the younger plants that were transplanted in April 2000. Age of seedlings is a confounding factor (6 months for the initial planting and 14 months for the subsequent experiment) at the Friendship Marsh. The removal of roots from plastic pots was likely less stressful to older plants in December and March of the following year, than to younger plants in April. In addition, the more mature roots could have grown more rapidly to depths with less salt.

We postulate that multiple stresses reduced seedling survival at the Friendship Marsh. The soil salinities we measured explain some of the site-to-site difference in survival, as well as the April vs. December difference within site. Soil-paste salinities were lower at the Tidal Linkage and lower in December than April at the Friendship Marsh. Other stresses we noted concerned sedimentation, algal smothering, and animal activities, but there were many variables that went unrecorded, e.g., soil moisture, waterlogging, soil redox potential, sulfide concentration, soil and water temperature, water percolation rates, and pH. These factors have been shown to change in response to variations in salinity (Baldwin and Mendelssohn, 1998). We propose that both differences in soils (salinity, waterlogging and anoxia) and site context (thermal and sedimentation stresses) cause multiple stresses to transplants, as follows.

First, the sandy soil of the Tidal Linkage (formerly upland subsoil) was well drained, despite our addition of finer sediment from the adjacent tidal pond. The plantings also received freshwater irrigation through the periods when salinity and moisture stress was anticipated (i.e., during the more prolonged daytime low tides). Neither waterlogging or salt crusts were observed at the Tidal Linkage.

While we sampled salinity on only two occasions, we propose that stress was reduced, since irrigation can directly lower salinity, increase soil moisture, cool plants, reduce transpiration, and wash salt and sediment from photosynthetic tissues. Previously Shumway and Bertness (1992) found that watering bare patches of high marsh with fresh water reduced soil salinities and dramatically increased both the emergence and survival of seedlings (i.e., 99 ± 1 seedlings of *Suaeda linearis* in freshwater treatment vs. 59 ± 3 seedlings at 30 g L^{-1}). The newly planted substrate at the Tidal Linkage was light in color but developed a dark surface layer within two months of planting (Figure 8), likely due to algal colonization and sediment trapping. In contrast, the Friendship Marsh soil (formerly buried marsh soil) had 3.6% organic matter at the time of planting. This is relatively high for southern California salt marshes (Langis et al., 1991). The Friendship Marsh surface was dark in color at the time of excavation and likely had higher absorption of solar radiation; thus it was likely warmer and interstitial seawater more prone to evaporation. A salt crust was obvious across the marsh plain during the long exposure periods. Soil salinities were initially high (over 100 g L^{-1}) and have remained high (over 50 g L^{-1}) to date (Figure 2). Tidal water was readily retained in puddles and footsteps (Figure 8), perhaps due to the compression of the organic components of the soil. In addition, we noticed thick biofilms across the marsh surface, with obvious mats of cyanobacteria, diatoms, and other microorganisms; these indicate water retention. While the abundance of microbial mats has not been quantified, the soil organic matter data indicate an increase over the first year of marsh ecosystem development (Figure 7). Collectively, these factors should act to prevent seed germination, and indeed we found very few volunteer seedlings.

If multiple stresses cause transplant mortality and limit recruitment, one might ask how vegetation becomes established in naturally accreting mudflats that gradually become natural marshes. We suggest several possibilities: (1) In nature, it is unlikely that large, open mudflats would suddenly become intertidal, as was the case for both our restoration sites. While this can happen during an earthquake (Vince and Snow, 1984), such occurrences are rare. That is, the restoration context is unusual, and natural patterns of establishment might not apply. The natural model is more likely to be the slow exposure of a narrow band of mudflat as sediments accrete and raise elevations to those suitable for vascular plant colonization. A narrow band might be less prone to concentrate salt, because the tidewater would undergo less heat than when it flows over a broad, hot marsh plain. (2) Vegetative establishment of plants occurs readily in natural marshes, because there are mature plants adjacent to the accreting mudflat that can extend rhizomes or runners onto the bare soil. Excavated sites lack vegetation at their margins, as the bulldozer cuts a 2:1 slope from the upland to the marsh plain. (3) Seedlings can establish at the fringe of a natural canopy, benefiting from shade and lower surface soil salinities (Allison, 1996; Callaway and Sabraw, 1994; Noe and Zedler, 2001b). A large open space will be unshaded, by definition, and prone to hypersalinity. (4) Major recruitment events appear to be episodic, occurring under the more favorable conditions, namely low salinity (Beare and Zedler, 1987; Ward, 2000). It might take decades for a natural marsh to accumulate a dozen halophyte species, just as it might take multiple replantings of a restoration site to get all desired species in place.

The natural, species-rich marshes that we see developed over centuries, and their dense, species-rich canopies are the product of multiple establishment opportunities followed by vegetative expansion. Interspersed in this chronology are various canopy disturbances that create opportunities for recruitment and interspecific interactions, such as wrack accumulation (Valiela and Rietsma, 1995) and flooding events that deposit large amounts of sediment (Allison, 1996). The smothering of plants opens up gaps for recruitment; also, parasitic plants (e.g., *Cuscuta salina*) reduce biomass to levels that increase light penetration and stimulate seedling recruitment (Pennings and Callaway, 1996). Restorationists should not expect to create in a few years what might take decades to achieve. Our attempts to do so led to greater appreciation of the importance of environmental stress and stochastic events and their potential for interaction.

It is extremely difficult to determine the cause of mortality after the fact. While additional soil variables (surface soil moisture, temperature, pH, redox potential, percolation rates) might have allowed us to draw conclusions with more confidence, there is no way to evaluate the effect of plant age or size without experiments designed to do so. We suggest that future experiments test the importance of timing on plant establishment, with continuous recording of soil salinity at multiple depths, moisture, air temperature and humidity, wind speed, and observations of rooting depth. Experimentation with plant age and differential hardening would be beneficial. However, surprises, such as algal smothering and coot trampling, can rarely be anticipated, and at least the latter is difficult to test experimentally. With many unknowns, planting protocols that could ensure 90–100% survival are not possible, but explanations might improve if some environmental attributes are measured more frequently (e.g., monthly measurement of surface salinity). Practitioners are cautioned to anticipate unfavorable conditions by having a reserve of transplants in case multiple efforts are required. Our ongoing experimentation with cluster plantings and alternative spacing should also yield protocols that enhance survival. We expect future modules of the 200-ha restoration plan of Tijuana Estuary to benefit from knowledge generated during these first two modules.

In summary, transplant mortalities that differed by an order of magnitude can be explained by differential stresses from extreme hypersalinity and chronic sedimentation, neither of which is readily predictable or entirely avoidable in salt marsh restoration sites of southern California.

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