

AMERICAN JOURNAL OF Botany

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Source: *American Journal of Botany*, Vol. 71, No. 3 (Mar., 1984), pp. 348-355

Published by: Botanical Society of America

Stable URL: <http://www.jstor.org/stable/2443494>

Accessed: 10/07/2009 14:03

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A STUDY OF THE SEED BANK OF A SALT MARSH IN NORTHERN SAN FRANCISCO BAY¹

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ABSTRACT

Abundance, species composition, and distribution of buried seeds in a San Francisco Bay salt marsh were studied by collecting soil samples in October and February and observing seedling emergence in the greenhouse. Results were compared with existing vegetation patterns and field germination. Average numbers of buried viable seed down to a 5-cm depth were 380/m² in October and 700/m² in February, with field germination averaging 118/m². *Salicornia virginica* dominated the seed bank in the greenhouse and in field germination. Most other marsh species were present in the seed bank but numbers of seeds were low. A significant correlation was found between highest species diversity and proximity to channels. The nature of this low-diversity, low-density seed bank reflects dominance of long-lived perennial species, seed dispersal patterns and selective environmental pressures.

SEED BANK RESERVOIRS are often a critical aspect of the dynamics of a particular vegetation. Work on wetland seed banks has shown a variety of responses depending upon the location and type of environment. Prairie glacial marshes experience long-term variability in hydrologic conditions and their regeneration following drawdown depends upon the persistent nature of their seed banks (van der Valk and Davis, 1976, 1978). On the other hand, freshwater tidal marshes in New Jersey, which experience diurnal fluctuations in water level but long-term relative stability, exhibit a seed bank in which most species germinate in early spring when the soil begins to warm (Leck and Graveline, 1979; Parker and Leck, in press; Leck and Simpson, pers. commun.).

Few studies have been conducted on salt marsh seed banks. Milton (1939) collected soil cores along the riverbank of an estuary in Wales and found that the dominant species, *Glyceria maritima*, *Juncus maritimus*, and *Festuca rubra*, had very few viable seeds in the soil while other species were well represented in the buried seed flora although scarce in the surface vegetation. He also found that the salt marsh seed bank was dominated by annual species in comparison with low numbers of seeds from perennials. These patterns of lack of corre-

spondence between seed bank and dominant surface vegetation and of predominance of annuals are also common to many terrestrial studies (Chippindale and Milton, 1934; Oosting and Humphreys, 1940; Major and Pyott, 1966; Livingston and Alessio, 1968).

Ungar and Riehl (1980) studied an inland salt marsh in Ohio where the surface vegetation showed distinctly segregated species patterns which were related to soil salinity. Species distributions changed from year to year as soil salinity varied with yearly rainfall patterns. They found seeds from the dominant species of each zone throughout the marsh and concluded that the seed bank provided the potential for changes in vegetation zonation as soil salinity levels changed.

The objectives of the present study were to characterize the size, species composition, relative abundance and distribution of the buried seed flora of a well-established salt marsh in San Francisco Bay. California salt marshes have predictable daily and seasonal environmental changes with relatively constant vegetation structure and composition. Our intention was to examine the dynamics of the seed bank in this stressful but relatively stable habitat. The assumption that the species distribution observed along the bay front and along main channel systems can be correlated with patterns of tidal flow was used as an initial hypothesis to detect seed bank distribution patterns and field germination.

MATERIALS AND METHODS—This study was conducted at the China Camp State Park salt marsh in Marin County, California (Lat. 38°00'N, Long. 122°30'W). China Camp marsh

¹ Received for publication 18 February 1983; revision accepted 15 November 1983.

We wish to thank the California Department of Parks and Recreation for permission to work at China Camp State Park and Drs. Michael Josselyn, Curt Davis, and Mary Leck for help with the project and manuscript.

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covers an area of approximately 180 ha along the southwest end of San Pablo Bay (northern San Francisco Bay) (Fig. 1). The climate is temperate with an average mean in January of 8.76 C and in July of 19.1 C (data from Howell, 1970). Rainfall is moderate, averaging 700 mm/yr with all but 20 mm falling between October and April (Mahall and Park, 1976b). The growing season extends from late February through October. The existing vegetation at China Camp is typical of a mature west coast salt marsh community, dominated by perennial halophytes and with a low overall species diversity. *Spartina foliosa* is the dominant species from 0.34 to about 1.0 m above MLLW (mean lower low water) while *Salicornia virginica* dominates the vegetation from this elevation up to the approximate line of the highest tides, 2.1 m above MLLW. About half a dozen other species including *Distichlis spicata*, *Grindelia humilis*, *Limonium californicum*, *Jaumea carnosa*, and *Frankenia grandifolia* are found commonly along channels above MHW (mean high water), which is approximately 1.8 m above MLLW in this part of San Francisco Bay (Pestrong, 1972), and along the marsh periphery.

The area of the marsh chosen as a study site covers roughly 6,000 m² and was selected as a representative, undisturbed area with no direct freshwater inflow from the landward side. Sampling transects were set up perpendicular to one of the large main channels dissecting the marsh. The channel is a natural feature, with extensive meanders at the back reaches of the marsh, and is large enough to provide significant water flow. Seven transects were set up at 5, 25, 50, 100, 200, 300, and 450 m from the Bay edge (considered as the *Spartina*/mud-flat interface) (Fig. 1). Sampling locations were marked off at distances of 0.25, 0.5, 0.75, 1.5, 3.0, 5.0, 10.0, and 15.0 m from the edge of the channel bank along each transect. Elevations of sample locations ranged from 0.91 m above MLLW at the 5-m transect to 1.95 m above at the 300-m transect, with a rise of 0.86 m within the first 50 m from the Bay.

On October 20–22, 1981, soil samples were collected at each of the sampling sites. Using an aluminum sampling frame, a block of soil 20 × 20 × 5 cm deep was marked off, the soil removed with a trowel and placed in a labeled plastic bag. Coarse surface litter was removed before collecting the soil. In the *Spartina* zone (5-m transect) the presence of a large number of mussels (*Ischadium demissum*) and rhizomal material made sampling a discrete block of soil extremely difficult; therefore, a volume of soil equivalent to a 20- × 20- × 5-cm block

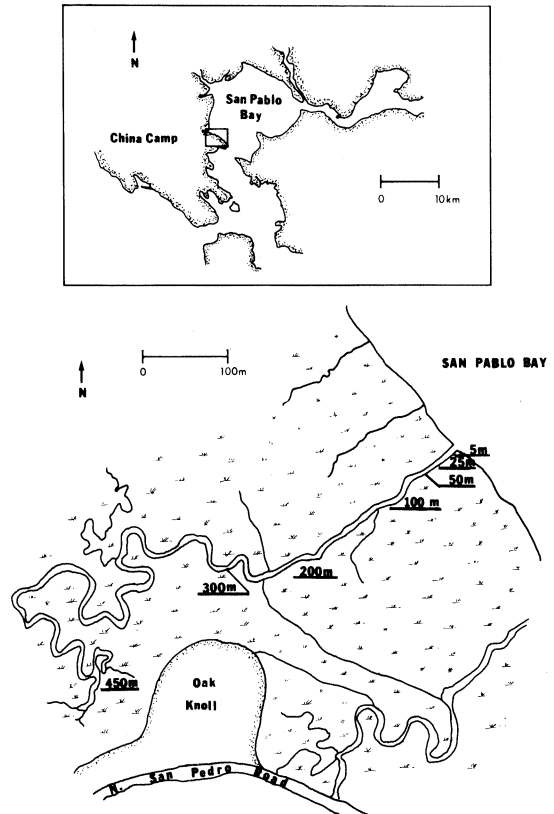


Fig. 1. Map indicating location of China Camp salt marsh (top) and study site (bottom).

was removed within the sampling area or directly adjacent. The samples were stored at 5 C for 4–5 days and then taken to the greenhouse. Each was broken into small chunks, rhizomes, sticks and other extraneous material removed, and the soil placed upon a 3-cm substrate of moistened sterile potting soil (1/3 sand, 1/3 perlite, 1/3 peat moss) in 25- × 25-cm perforated greenhouse flats. *Spartina* transect samples, being very wet and clayey, were rinsed directly from the plastic bags onto the potting substrate and then spread evenly over the surface. The 56 sample flats were placed in random order on a greenhouse bench and thoroughly watered with fresh tap water. It has been noted by various researchers (Chapman, 1960; Rozema, 1975; Ungar, 1978) that fresh water stimulates germination of most salt marsh species. Six flats of sterile potting soil were placed among the marsh samples to act as a check on contamination from greenhouse species. Flats were watered at least once daily to keep soil moist at all times. They received natural photoperiod and lighting (with a low of 9 hr of daylight/day in December to a high

TABLE 1. *Species emerging in the greenhouse from soil samples collected at China Camp salt marsh in October 1981*

Species	Total no.	Rel. abund. % ^a	Freq. % ^b	Avg. no./m ²
<i>Salicornia virginica</i>	821	96.7	96.4	367.5
<i>Distichlis spicata</i>	14	1.6	12.5	6.3
<i>Jaumea carnosa</i>	7	0.8	8.9	3.1
<i>Frankenia grandifolia</i>	2	0.24	3.6	1.0
<i>Polygonum aviculare</i>	2	0.24	1.8	1.0
<i>Gnaphalium luteo-album</i>	1	0.12	1.8	0.5
<i>Cyperus esculentus</i>	1	0.12	1.8	0.5
<i>Grindelia humilis</i>	1	0.12	1.8	0.5
<i>Atriplex patula</i> var. <i>hastata</i>	1	0.12	1.8	0.5
Total no. of seedlings:	850			

^a Percent relative to total number of germinated seedlings.

^b Percent of sampling locations in which species germinated (a total of 56 locations).

of 13 in April). Temperatures ranged from about 13 to 31 C.

On January 25 and February 1–4, 1982, soil samples were again collected from the field sample locations. These were processed as before; photoperiod ranged from 11.5 hr/day in February to 15 hr/day in mid-June, with temperatures from 15.5–32 C.

Germination from the October samples was observed over a 5.5 month period; February samples were observed for 4 months. Seedlings were marked, counted weekly, and numbers and species were recorded. Species not identifiable by the end of the experiment were transplanted and allowed to grow until positive identification could be made. Several of the species did not flower during the course of the experiment; their identification was based on comparison of vegetative characteristics with herbarium or field specimens. Species were identified using Munz and Keck (1968), Howell (1970), and Mason (1957); Dr. J. T. Howell of the California Academy of Sciences tentatively identified several immature specimens. Nomenclature follows that of Munz and Keck (1968).

In order to test the reliability of seedling emergence in the greenhouse as an indication of total viability of seeds in the soil, two further methods were used with the October samples to find out if there were ungerminated viable seeds remaining in the soil. Four subsamples of 100 ml by volume (measured by water displacement) from the 25-m/5-m, 50-m/15-m, 100-m/3-m, and 200-m/10-m plots were placed in 600-ml flasks, water added to make a total volume of 400 ml, and the mixtures agitated

on a gyratory stirrer for 2 hr at medium speed. The slurry was then poured gently over a substrate of sterile potting medium in 10- × 15-cm flats. The four flats were placed on a greenhouse bench with two sterile soil controls and watered daily with fresh water.

In the second procedure 100 g of soil were subsampled out of one flat from each transect (a total of seven subsamples) and filtered through a 0.1-mm mesh sieve. The material retained was air dried, placed under a binocular dissecting microscope, and visually searched for seeds which were then removed and identified from Mason (1957).

To compare greenhouse germination with field germination, field plots were set up in December to monitor seedling emergence. Along each of the 7 from-bay transects, 3-m transects were measured off parallel to the channel at 0.5, 5, and 15 m from the channel bank. Five randomly chosen 20- × 20-cm plots were marked along each 3-m line and the number of seedlings germinating within each plot was recorded approximately biweekly from late February (when the first seedlings appeared) through mid-June. In order to compare germination results with the existing vegetation, a field survey was made on May 26–28 at each from-bay transect. A 10-m line was laid out at 0.5, 5.0, and 15.0 m from the channel edge at each of the 5- to 450-m transects and percent cover of all species recorded.

Field sampling in both October and February was designed to test for the effects of: 1) distances from the bay, and 2) distances from the channel on seed distribution. In order to test for these two effects, a model I, two-way analysis of variance (*F*-test) was used, with 6 df for from-bay distances, 7 df for from-channel distances, and error df = 42. Multiple range analysis (*Q*-test) was used to compare sample means where *F*-tests were significant. A pairing-design "*t*"-test (5 df, *t* = 2.57 at 0.05 probability) was used to compare seed distribution at distances 1.5 m or less from the channel with those 3 m or more away. Since the 5- and 25-m transects were at an elevation below mean high water, it was assumed that tidal influence was exerted relatively equally at all points along the transects from the channel; therefore, these two transects were excluded from the "*t*"-test. All statistical methods follow Zar (1974).

RESULTS—*October sampling*—Table 1 summarizes the results of greenhouse germination for soil samples collected in October. A total of 850 seedlings of nine species germinated. *Salicornia virginica*, with 821 seedlings, constituted 96.7% of the total and was present in

TABLE 2. Species emerging in the greenhouse from soil samples collected at China Camp salt marsh, February 1982; * indicates introduced and/or weedy species

Species	No. of seedlings	Rel. abund. %	Freq. %	Avg. no./m ²
<i>Salicornia virginica</i>	1,464	92.3	100.0	651.8
<i>Rumex crispus</i> (?)*	56	3.5	33.9	25.0
<i>Distichlis spicata</i>	31	1.7	32.1	12.1
<i>Typha</i> sp.	5	0.32	7.1	2.2
<i>Baccharis pilularis</i> var. <i>consanguineus</i>	4	0.25	7.1	1.8
<i>Chenopodium</i> sp. (?)*	11	0.7	1.8	4.9
<i>Frankenia grandifolia</i>	2	0.13	3.6	0.9
<i>Atriplex patula</i> var. <i>hastata</i>	2	0.13	3.6	0.9
<i>Cyperus esculentus</i> *	2	0.13	3.6	0.9
<i>Grindelia humilis</i>	1	0.06	1.8	0.5
<i>Scirpus robustus</i>	1	0.06	1.8	0.5
<i>Cyperus eragrostis</i>	1	0.06	1.8	0.5
<i>Sonchus asper</i> *	1	0.06	1.8	0.5
<i>Sonchus oleraceus</i> *	1	0.06	1.8	0.5
<i>Polypogon monspeliensis</i> *	1	0.06	1.8	0.5
<i>Jaumea carnosa</i>	1	0.06	1.8	0.5
Umbelliferae	1	0.06	1.8	0.5

96.4% of the samples. The next most abundant species were *Distichlis spicata*, with 14 seedlings or 1.6% of the total (48% of the non-*Salicornia* seedlings), and *Jaumea carnosa*, with seven individuals, 0.8% of the total (24% of the non-*Salicornia*). Six of the nine species are found within the immediate study area or along the marsh periphery; the other three are weedy species which have not been recorded from this area (see Day and Follette, 1981). Two of the 56 flats had no germination.

The mean number of germinating seedlings for all sample sites was 380/m² ± 68.9 SE. The mean number of *S. virginica* seedlings for all sites was 368/m² ± 71.1 SE, with a range from a transect average of 63/m² at the 5-m transect to a transect average of 1,375/m² at 25 m. The total number of seedlings at any one sample ranged from 0 to 2,300/m².

Two-way analysis of variance (*F*-test) to test for the effects of distance from the bay and from the channel on germination numbers showed no significant differences in seedling numbers at the various distances from the channel but did show a significant (*P* < 0.01) difference in seedling numbers at varying distances from the bay. Multiple range analysis (*Q*-test comparing sample means of from-bay transects) showed that the 25-m transect had significantly greater seedling numbers. Significantly higher (*P* < 0.05) numbers of seedlings occurred next to the channel, however, when transects below MHW (5 and 25-m transects) were not included in the analysis (pairing-design "t"-test run on samples within 1.5 m compared to those 3–15 m from the channel).

In general, seedling numbers of non-*Sali-*

cornia species were too small to allow valid statistical analysis, although there were some clear trends in distribution. Of 29 seedlings, 18 were evenly distributed in the transects below MHW (15 at 5 m, 3 at 25 m) and 10 of the remaining 11 seedlings were from samples collected within 0.75 m of the channel. The exception was an *Atriplex patula* var. *hastata* seedling in the 200-m from-bay, 5-m from-channel sample; this species had been found growing in the field at this location as well (see field germination results below). *Distichlis spicata* germinated almost exclusively in samples from the 5-m transect (12 of 14 individuals).

Thorough mixing of five subsamples with water and subsequent repotting yielded one *Salicornia* seedling from the 25-m/5-m flat after 8 wk. Seed sieving yielded 62 seeds of two species, *Salicornia virginica* and *Polygonum aviculare*, 80% of the former in the 25-m/0.5-m sample and 97.3% of the latter (36/37 seeds) in the 100-m/0.75-m sample, the same location where the two seedlings of *Polygonum* germinated in the greenhouse. Less than 10% of the 25 *Salicornia* seeds appeared to be viable, most being flaccid and empty. *Polygonum aviculare* seeds appeared viable from outward condition.

February sampling—A summary of germination data for the February soil collections is given in Table 2. A total of 1,586 seedlings was recorded; of these 1,464 or 92.3% were *Salicornia*, which occurred in 100% of the sample flats. The second most abundant species was *Rumex crispus* (tentative identification based on comparison with field specimens) with

TABLE 3. Numbers and species of seedlings germinating in the field at three from-channel distances along each of seven from-bay transects. Data from five replicate plots were pooled for each site. S = *S. virginica*, D = *D. spicata*, R = *R. crispus* (?), A = *A. patula* var. *hastata*, G = *G. humilis*

Meters from bay	Meters from channel			Total	% of total
	0.5	5.0	15.0		
5	27 S 1 D	36 S	27 S 3 D	94	19
25	23 S 1 D	108 S 3 D	88 S 5 D	228	46
50	4 S	2 S	1 S	7	1
100	1 S 1 G	1 S	1 R	4	1
200	5 S 6 R	9 S 2 D 27 R 1 A	0	50	10
300	8 S 44 R 2 A	13 S 1 R	2 S	70	14
450	24 S 3 R	3 S	13 S	43	7
Total	150	206	140	496	
% total	30	42	28		

56 individuals, 3.5% of the total and a frequency percent of 33.9. The mean number of total seedlings per sample was $700/\text{m}^2 \pm 92.8$ SE; *Salicornia* seedlings averaged $652/\text{m}^2 \pm 92.4$ SE, ranging from a transect average of $213/\text{m}^2$ at the 100-m transect to $1,366/\text{m}^2$ at the 25-m transect. Total germination at individual sites ranged from $25/\text{m}^2$ to $3,175/\text{m}^2$. Of the 17 total species germinating, 8 have been found within the study area, 5 along the marsh periphery, and the remaining 4 species are either found remote from the study area but within the state park or are not recorded from the area. *Cyperus esculentus* is not recorded as occurring in Marin County (Howell, 1970).

Analysis of variance of the February sampling data showed no significant differences among sample means since the data were highly variable. It appears, as in the October samples, that seedling numbers in the 5- and 25-m transects were affected by tidal flow from the bay front rather than by overflow from the channel. Although not significant statistically, the number of *Salicornia* seedlings was higher in the 25-m transect than at any other, as was true in the October samples. *Distichlis spicata* was again found predominantly in the 5-m transect (48.4% of the *Distichlis* total), though it had a broader distribution range than in the October samples. *Rumex crispus* was found

TABLE 4. Field germination compared to seedlings emerging from greenhouse soil samples collected in February 1982, China Camp salt marsh. Numbers are average no./m² at each transect location

Meters from bay	Field seedlings	% of total	Greenhouse seedlings	
			seedlings	% of total
5	157	19	372	8
25	380	46	1,425	29
50	12	1	506	10
100	7	1	256	5
200	83	10	459	9
300	117	14	856	17
450	72	9	1,081	22
Total avg.:	118	100	Total avg.:	708 100

near the channel bank occurring almost exclusively in the 200-m (35.7%) and 300-m (50%) from-bay transects and at distances 0.25–1.5 m from the channel bank (85.7%). Of the 120 non-*Salicornia* seedlings, those from the 50–450-m transects were generally found in sites within 1.5 m of the channel (70/82 seedlings, $P < 0.05$, pairing-design “*t*”-test), while 15% were in the 5-m and 17% in the 25-m transects, scattered across all from-channel distances.

In comparing October and February samples, it can be seen that the total germination in February (1,586 or $700/\text{m}^2$) was almost twice that of October (850 or $380/\text{m}^2$), while species numbers nearly doubled, from 9 to 17. Seedling numbers of non-*Salicornia* species increased fourfold from 29 in October to 120 in February. In both sample collections *Salicornia* was the most numerous species. Distribution patterns related to from-bay and from-channel distances were similar in both collections.

Field germination and vegetation survey—Earliest field germination was observed in late February with a peak from mid-March to mid-April. The total number of seedlings germinating in the field plots was 496 or $118/\text{m}^2 \pm 26.8$ SE. Five species germinated (Table 3): *Salicornia virginica* (79.6% of the total, 53.3% frequency), *Rumex crispus* (16.5% of total, 16.2% frequency), *Distichlis spicata* (3.0% of total, 8.6% frequency), *Atriplex patula* var. *hastata* (0.5% of total, 2.9% frequency), and *Grindelia humilis* (0.2% of total, 1.0% frequency). All of these species germinated in the February sample collections in the greenhouse.

For field seedling numbers there were no statistical differences for from-bay or from-channel distances although these data suggest

TABLE 5. Percent cover of species at from-bay and from-channel points

	From-bay elevation		From-channel distance (m)*			
	Ht. (m) above MLLW		>1.5 (MHW)	0.5	5	15
	<1	1 > 1.5				
<i>Spartina foliosa</i>	99.3	2.6				
<i>Salicornia virginica</i>	0.6	96.6	87.7	67.5	95.5	100
<i>Scirpus robustus</i>		0.6				
<i>Distichlis spicata</i>			5.7	13.2	3.9	
<i>Frankenia grandifolia</i>			5.0	14.7		
<i>Rumex crispus</i>			1.0	2.9	0.8	
<i>Grindelia humilis</i>			0.3	0.8		
<i>Jaumea carnosa</i>			0.2	0.5		
<i>Atriplex patula</i> var. <i>hastata</i>			0.1	0.4		

* For vegetation >1.5 m above MLLW.

some correlation between numbers of seedlings and proximity to channel banks at several transect locations. The distribution of *Salicornia* seedlings in the field plots was similar to the greenhouse germination, the highest number (58%) occurring in the 25-m transect. *Rumex crispus* was found almost exclusively in the 200- and 300-m transects in the field seedling counts (40% and 55% of the total *Rumex*, respectively). Of 105 field monitoring locations, 32 or 30.5% showed no seedling germination at any time. Table 4 shows the relationship between field seedling numbers and greenhouse germination at comparable locations.

Salicornia germination peaked in late March to early April, while *Distichlis* and *Rumex* peaks were in early and late May, respectively. By mid-June mortality for *Salicornia* was over 96% and *Distichlis* mortality was 67%. Seventy-five percent of *Rumex* seedlings survived well into June but by late summer most of the plants were dead. A survey of field plots in mid-October showed no survival of any species except one. The only species germinating and surviving to maturity in the field plots was *Atriplex patula* var. *hastata*; total number of seedlings was quite small but all survived to maturity.

The from-bay vegetation pattern was in agreement with Mahall and Park (1976a) (Table 5), *Spartina foliosa* dominating near the bay below MHW with a rapid transition to a *Salicornia virginica* marsh near and above MHW. There was a clear pattern of species diversity within 1 m of the channel at elevations above MHW (Table 5 from-channel data represent only transects above MHW), while *Salicornia* dominated the vegetation (90–100% cover, usually 100%) at distances 5 m or more away from channels or the marsh periphery.

DISCUSSION—Maximum densities of buried seeds in a San Francisco Bay salt marsh ranged

from 2,100–3,175/m² while average densities were 380/m² (October) and 700/m² (February). These were low numbers and an order of magnitude less than those found in freshwater marshes and most temperate terrestrial soil studies. Leck and Graveline (1979), for example, recorded up to 32,430 seedlings/m² in their soil samples from a freshwater tidal marsh, while van der Valk and Davis (1978) reported average seedling densities of up to 42,615/m² in a prairie glacial marsh.

Our salt marsh was dominated by seven perennials and two annuals (Table 5) and, in contrast to Milton's (1939) salt marsh study, the seed bank corresponded well. *Salicornia virginica*, the principal marsh dominant and a perennial, constituted over 92% of the seed bank in both sampling periods. While perhaps underrepresented, most of the other perennial dominants were present and ordered reasonably well in proportion to their cover (Tables 1, 2). The patchy distribution of these species along channels within extensive *Salicornia* vegetation may have resulted in their underrepresentation in a random sampling procedure. Only *Spartina foliosa* and *Limonium californicum* were absent. *Spartina* has low seed viability in several San Francisco Bay marshes (Crispin, 1976); Zedler (1982) has rarely observed *Spartina* seedlings in southern California marshes. Although not found in our samples, *Limonium* was observed to have high seed set and seedlings were found near parent plants.

The February results differed in several ways from those of October, with increases in density, diversity, and proportion of annuals. These differences reflect seed set and dispersal by wind and water prior to sampling. Most of the species found in the seed bank begin flowering in summer, peaking and setting seed in mid- to late fall. Additionally, with the exceptionally high rainfall of the 1981–82 winter (more than twice

the yearly average) and consequent high runoff from the north bay rivers, it seems likely that seeds of freshwater and terrestrial species were washed down off neighboring slopes or floated from freshwater sources into the China Camp marsh and collected in the seed bank. While many of the non-resident species which grow near the marsh have propagules designed for aerial transport (e.g. *Baccharis*, *Sonchus*), the intra-marsh distribution of these and of the freshwater marsh species (*Typha*, *Cyperus*) also suggest runoff and flooding tidewaters. Flood-wrack with seeds and seedlings on top was found distributed along channels and the bay front. Most of the seeds of non-resident species were found in samples from within these areas (5-m and 25-m transects or within 1.5 m of channels). Tidal import of seeds has been found to be of importance in other Bay marshes (Atwater et al., 1979; Josselyn and Perez, 1981) and most of the China Camp marsh species have seeds which float for long periods (Hopkins, 1982).

Atwater et al. (1979) noted that, other than *Spartina foliosa* and *Salicornia virginica*, "additional species on tidal-marsh plains typically grow in scattered patches next to sloughs, natural uplands and man-made levees." Our observations confirmed this diversity pattern, extending it to areas along natural tidal channels (Table 5). This zonation pattern, which can be correlated with potential tidal dispersal of seeds, is also correlated with a number of factors which influence seed germination and successful seedling establishment, e.g., reductions in soil salinity and in waterlogging, increased disturbance (Parker, unpublished). Both salinity and excessive waterlogging can be critical in seedling establishment (Chapman, 1960; Rozema, 1975; Mahall and Park, 1976c; Ungar, 1978) and both of these factors are moderated next to channels.

Germination in the field followed the pattern of species diversity along channels (Table 3). Eighty-five percent of all field germination occurred either next to channels or along the bay front below MHW. Above MHW there was a consistent decline in seedling number with distance from the channel. While most germination occurred along the bay front, high germination rates were followed by almost 100% mortality by early June due to a combination of tidal submersion and high siltation. Only one species survived at any location to maturity and seed set.

The most abundant of the five species germinating in the marsh, *Salicornia virginica*, is variously reported as having abundant seedlings in cleared patches (Hinde, 1954; Zedler, 1982; Josselyn, pers. commun.) or being rare

or nonexistent (Onuf, unpubl. manuscr. cited in Zedler, 1982). In our study area, capacity for producing seedlings in the field was moderate (94/m²), but there was no survival through the summer and very few seedlings were seen colonizing bare patches. *Distichlis*, *Rumex*, and *Grindelia* seedlings were more persistent than *Salicornia* but showed a similar lack of growth and survival. The larger seedlings of the annual *Atriplex*, on the other hand, survived to maturity in all sample plots. Many of the marsh species do not rely on seedling establishment but reproduce extensively by vegetative means. Since most of the marsh species are long-lived perennials, a few successful seedlings could ensure the long-term survival of the species in the community.

The seed bank of this salt marsh was remarkable for several reasons. The degree of correspondence with the dominant species (88% of the site dominants in the seed bank) was higher than in any other study known to us where perennials are the dominants. Nearly absent from our samples were seeds of the opportunistic annual marsh species (*Salicornia europaea*, *Cotula coronopifolia*, *Spergularia marina*, *Polypogon monspeliensis*) which completely dominate nearby marsh restorations (personal observations; Josselyn and Perez, 1981). Even though their seed densities have been found as high as 70,000/m² in these other marshes, only *Polypogon* was found in our undisturbed marsh and at low density and frequency. Most of the diversity of the seed bank occurred along the bay front and along the channels. This distribution primarily reflected tidal movement but also local seed source. Overall diversity was low, as were the densities of seeds, although both increased from October to February samples. There seems to be no strong selection for a persistent seed bank, but instead, high germination in early spring corresponding to release from high soil salinities. On the other hand, field germination and survival were low. The seed bank of this salt marsh does not appear to play a role in the vegetation dynamics similar to that in other wetlands where annuals dominate or disturbance is a characteristic (van der Valk and Davis, 1976, 1978; Leck and Graveline, 1979; Keddy and Reznicek, 1982; Parker and Leck, in press). The China Camp seed bank appears to be a low density, low diversity source for the occasional establishment of new individuals in this long-lived perennial-dominated marsh.

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