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Dynamics and Ecosystem threats of Bidirectional Cordgrass Hybridization in San Francisco Bay

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SEA GRANT FINAL REPORT

Dynamics and Ecosystem threats of Bidirectional Cordgrass Hybridization in San Francisco Bay

PROJECT GOALS

Hybrids between alien cordgrass, *Spartina alterniflora*, introduced in the 1970s, and native California cordgrass, *S. foliosa* are a menace to the ecology of San Francisco Bay, spreading to aggressively invade open mud, displacing native species, hindering flood control, navigation, and other uses of this habitat. We proposed to determine the key elements of the ecology of the hybrid cordgrass invasion: ecological amplitude of parental species and hybrids, dynamics of seedling movement and recruitment, and broad spread of hybrids around the Bay and up the Sacramento Delta. Our previous field and molecular work suggested that vigorous hybrids grow taller and more densely than either parental species; they should have greatest competitive abilities and tidal range. To experimentally compare ecological amplitudes among cordgrass plants, we measured vegetative vigor and sexual reproduction of cordgrass genotypes planted in common gardens on the intertidal plane. To identify essential components of seedling recruitment, we planned to characterize seed movement on the tides, persistence in the soil seed bank, and germination and establishment of cordgrass genotypes in experimental field plots. To document the rate and extent of the spread of hybrids around the Bay, we annually surveyed and genetically characterized cordgrass seedlings and plants in marshes where hybrids were established as well as previously un-invaded marshes.

GOALS ACCOMPLISHED

COMMON GARDEN EXPERIMENT

The purpose of this experiment was to characterize ecological amplitudes of cordgrass hybrids by establishing common gardens on the intertidal plane. Common garden experiments are a mainstay of evolutionary ecology, with a long tradition in plant ecology (Clausen et al, 1948). These plantations allow the separations of environmentally-induced, phenotypic variation from genotypic variation. By planting individuals of diverse genetic backgrounds in a common garden, genetically-based traits are revealed and natural selection can be measured. The distinct, strong physical and chemical gradients of salt marshes could create steep selection gradients and promote rapid evolution of local specialization on a fine scale (Antonovics and Bradshaw 1970). Salinity, oxygen, and inundation period vary over short distances along the tidal gradient in a salt marsh and are sufficiently harsh to select strongly for the most adapted plants.

In these gardens, we planted arrays of genotypes in different relevant environments. We measured establishment, vegetative growth, and sexual reproduction. Two independent variables were included, “environment treatment level” (3 treatments) and “genotype treatment level” (15

genotypes). The environment treatment levels were: an upper elevation, in a *Spartina-Salicornia virginica* marsh terrace with natural vegetation, an upper elevation with the natural vegetation removed by mowing, and a lower tidal elevation, below the level of native vegetation, in open mudflat. The upper level gardens were centered 0.25 m above MHHW, and the lower elevation was on naturally open mud, centered 0.75m below the edge of the natural vegetation. Each environmental treatment level was replicated three times, amounting to 9 gardens total. The gardens were arranged along the ecotone in the Cogswell Marsh at Hayward Regional Shoreline Park. We installed 2 salinity wells in each garden to monitor soil salinities throughout the experiment.

Three genotypes from each of 5 distinct, genetically-based groups (= 15 genotypes) were vegetatively propagated at a greenhouse on the UC Davis campus, in November 2001. The genetic groups were *S. foliosa* and *S. foliosa*-like plants (4% avg. hybridity, where 0% = *S. foliosa* and 100% = *S. alterniflora*); *S. alterniflora* and *S. alterniflora*-like plants (89% avg. hybridity); hybrids similar to F1 genotypes (44% avg. hybridity); and 2 additional distinct hybrid groups, H1 (41% avg. hybridity) and H2 (52% avg. hybridity) (see Ayres et al, 1999 for a discussion of “percent hybridity” and description of the molecular methods). The genotypes included 2 pure *S. foliosa* and 1 pure *S. alterniflora* (Table 1). All plants were characterized by RAPDs (Random amplified polymorphic DNAs) and prior performance in the field at Cogswell Marsh (Zaremba, 2000). The plants encompassed the range of genotypes and morphologies found among cordgrass plants at this marsh. We used only Cogswell genotypes to avoid enriching the site with more genetic variation. Each of the total 15 genotypes was replicated, by clonal propagation, twice. This yielded 30 plants in each garden. Identical sets of genotypes were planted in each garden. Due to excessive mortality in the upper gardens where pickleweed had been removed, likely due to very high salinity (Fig. 1), we re-planted the upper gardens in March 2003, and monitored them during the growing season. By the 2004 growing season, plants in the mud flat gardens had grown together and upper terrace gardens were invaded by surrounding cordgrass and the experiment was ended.

The dependent variables were survival, growth, clonal expansion, and fecundity of cordgrass, and these were monitored for the duration of the experiment. All surviving cordgrass will be killed at the conclusion of the experiment. The expected results will be performance traits as a function of hybridity and garden treatment level.

Genetic Affiliate	Average Hybridity	Plant labels	Notes
SF	4%	C2-15, C3-4, C3-13	2 are pure <i>S. foliosa</i>
H1	41%	C3-2, C3-5, C3-7	
F1	44%	C2-5, C2-6, C3-10	none are F1s
H2	52%	C1-17, C2-8, C2-11	
SA	89%	C2-13, C2-16, C3-1	1 is a pure <i>S. alt.</i>

Table 1. Descriptions of plants used in the common garden experiment.

Results

Salinity Salinity varied widely seasonally and between treatments (Fig. 1). In spring, after winter rains had rinsed salts from the soil, salinities in the 3 garden treatments were at their lowest points and reflected the ambient estuary water salinity of 28 ppt. The mudflat gardens maintained ambient salinity levels under 35 ppt throughout the season, while the terrace gardens became more saline as the summer drought progressed and reached maximum levels of 45 - 50 ppt in the fall. This increase was especially pronounced where pickleweed (*Salicornia virginica*) had been mowed.

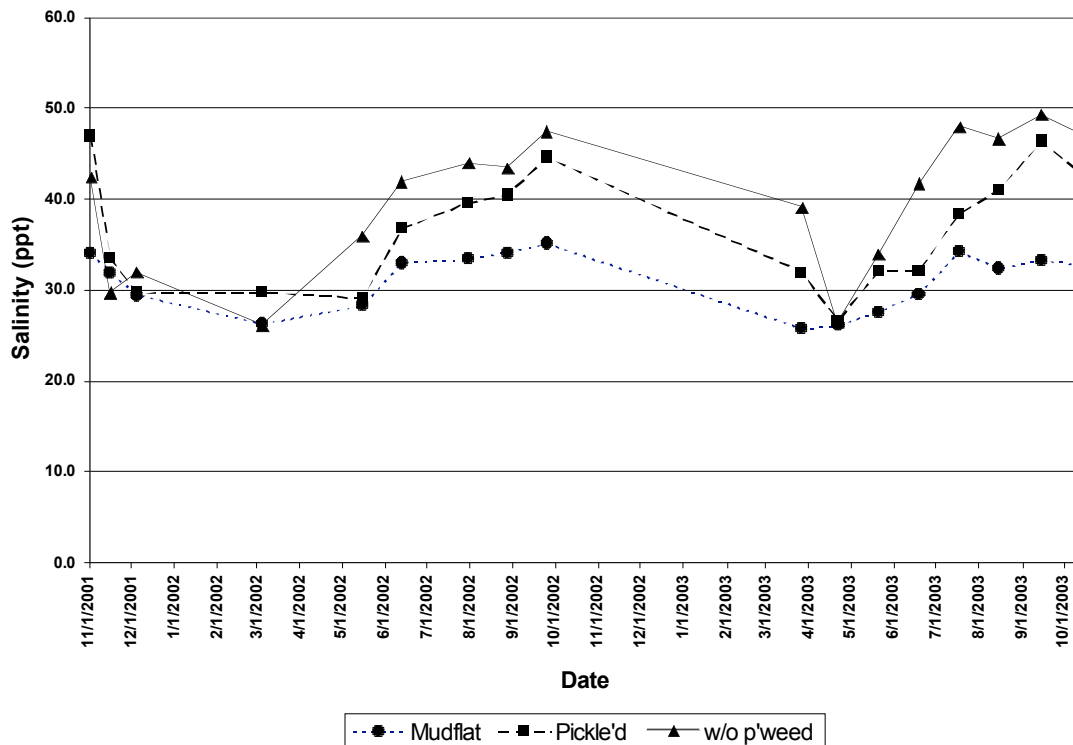


Fig. 1. Seasonal variation in salinity (ppt) in 3 common garden treatments; open mudflat; upper terrace with pickleweed (=Pickle'd) and upper terrace with vegetation mowed (= w/o p'weed).

Plant Response. Plant growth, as assessed by stems and lateral spread, varied widely among treatments ($P < 0.001$), genotypes ($P < 0.001$), and genetic affiliates ($P < 0.01$) (Fig. 2). Compared to the terrace, plants in mudflat gardens produced over 14-times the number of stems (37 vs 2.6), stems that were almost twice as tall (12 vs 7 cm), and plants expanded laterally 8-times more widely (53 vs 6.6 cm) in their first season of growth. Within the upper terrace gardens, the absence of *Salicornia virginica* (Savi) resulted in twice as many stems (3.8 vs 1.4) and a 5-fold increase in lateral spread (11 vs 2.2) compared to plants growing in vegetated gardens.

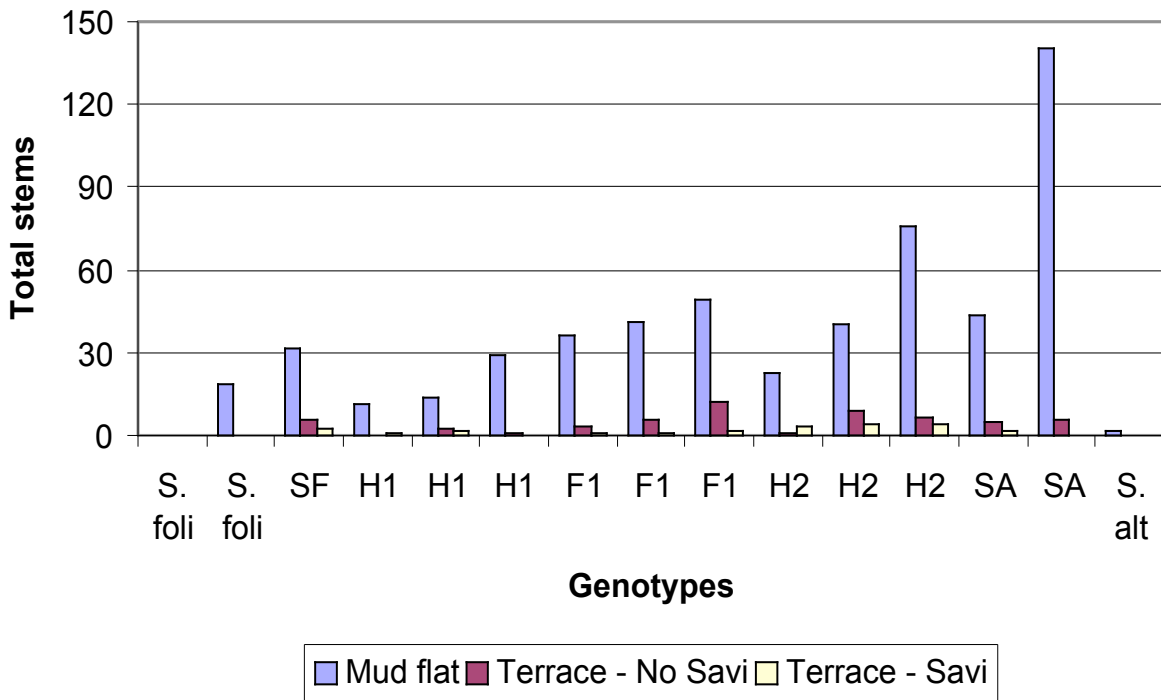


Fig. 2. Total stems (average per plant) at the end of the first season as a function of genotype, genetic affiliate, and treatment.

In general, plants in the genetic affiliates of F1, H2, and SA grew 2-3 times better than plants in the categories SF and H1, producing more (19 vs 6.3) and taller (11.3 vs 4.75 cm) stems, and spreading more widely (28.4 vs 12.6 cm). The 3 individuals from the parental species grew poorly under all conditions.

Under the favorable mudflat environment, these differences became more pronounced by the end of the second season as the F1, H2 and SA plants had 40 - 80 more stems, and had spread 30- 60 cm more widely than plants in the H1 and SF categories (Figs. 3, 4).

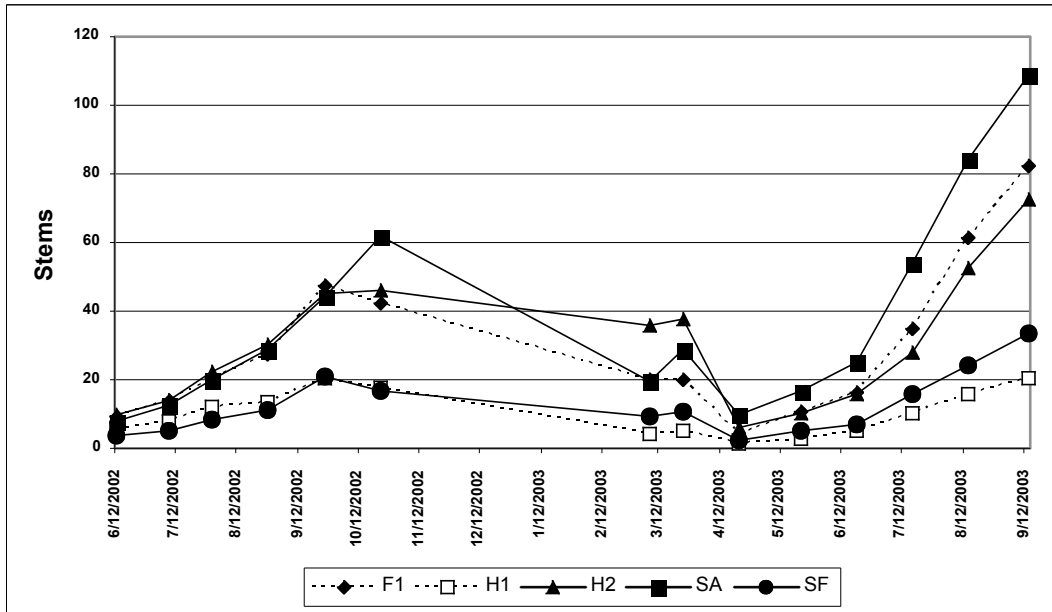


Figure 3. Total living stems per plant by genetic affiliate (F1, H1, H2, SA, SF; see text for explanation).

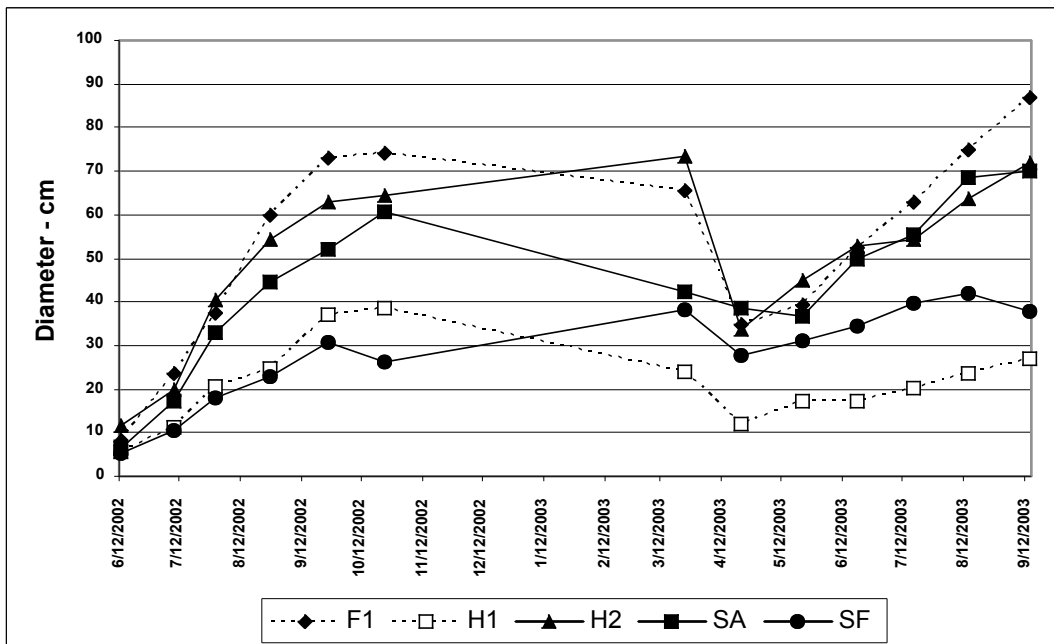


Figure 4. Plant diameter at widest dimension; plants categorized by genetic affiliation.

Growth Patterns From a small handful of stems, plants quickly produced new above- and below-ground stems (laterally growing rhizomes) in open mudflat, reaching peak size in the fall (Figs. 3 and 4). Above-ground stems died back in the winter, while under-ground stems (rhizomes) generally did not. As growth was resuming in late March of 2003, Canada geese were observed feeding in the gardens, and there was ample evidence (goose scat and closely cropped *Spartina* stems) of their continued foraging until the middle of May. Plants losses were more than just the cropping of above ground stems, as plant diameters shrunk indicating that rhizomes may have died. Plants did not recover their previous years' growth until July or August, with plants in SA and H1 taking the longest to recover. Preferential feeding by Canada geese on *S. foliosa* over hybrid cordgrass has been observed in marshes in San Francisco Bay (T. Grosholz, pers. comm).

Conclusions

Open mudflat, despite experiencing greater tidal inundation, was a far more favorable environment for cordgrass growth than the adjacent *Salicornia*-dominated terrace - even when the *Salicornia* was removed. Peak growth of cordgrass in mudflat, where salinity never exceeded 35 ppt, occurred when salinity in the upper gardens was steadily increasing to above 45 ppt. This suggests that salinity is a potent inhibitor of cordgrass growth. Competition by *Salicornia* further suppressed cordgrass growth in the terrace gardens. We conclude that cordgrass invasion of open intertidal mudflats by vegetative growth will occur much more rapidly than invasion of established *Salicornia*-dominated marshes.

This invasion potential is not equal among cordgrass genotypes, however. Neither parental species did well in any garden; in the mudflat gardens 10 out of 12 *S. foliosa* plants had died and only a single (out of 6 plants) *S. alterniflora* plant was alive by the end of the second season. Plants in the genetic category H1, in addition to SF, grew poorly, while many hybrids in the other categories grew very well. If natural selection favors cordgrass plants with rapid lateral expansion, then greater-than-exponential population growth can result. This phenomena has been demonstrated in a theoretical model (Hall, Hastings, and Ayres, in review).

SEEDLING RECRUITMENT

Seed bank assessment.

Squares of fiberglass window screening (0.25 x0.25 m) were anchored to the substrate using aluminum landscape staples in September 2001, prior to cordgrass and *Salicornia virginica* seed shattering. Ten sites were located on open intertidal mud immediately adjacent to a terrace 0.75 m higher of mixed *Sa. virginica* / *Spartina* vegetation where another 10 sites were chosen. Using clippers we removed vegetation within the upland plots. In March 2002, a square-nosed shovel was used to lift the squares plus 2-3 cm of substrate from under the screen. The below screen portion contained seed older than the past season; the material from on top of the screen contained the seed shed the previous fall. Each upper and lower sample was placed in individual trays in the greenhouse and fertigated (fertilizer + irrigation) daily to maintain a water level just short of the top of the soil block. Emerged seedlings were censused for several weeks until no more new seedlings were found.

Results

We observed sediment deposition on the mud flat seed bank plots during the fall and winter, however, when we collected the plots in the spring very little material remained on top of the mesh, and no seedlings germinated from these newer sediments in either marsh location. *Salicornia virginica* was the most abundant seedling found in the older sediments, and was over 12 times more abundant in sediments taken from the existing *Salicornia* marsh terrace than from open mud flat (Table 2). No *Spartina* seedlings were observed.

Table 2. Plant species per m² (SE in parentheses) germinating out of marsh sediments collected below (older) or above (newer) a mesh screen from mud flat or an elevated terrace in the marsh. There were no *Spartina* seedlings.

Plant species	<u>Mud flat sediments</u>		<u>Terrace sediments</u>	
	Older	Newer	Older	Newer
<i>Salicornia virginica</i>	19.2 (24.0)	0	246.4 (102.4)	0
<i>Atriplex</i> sp.	0	0	3.2 (6.4)	0
<i>Triglochin</i> sp.	4.8 (9.6)	0	0	0

Seed Movement/Seed Trapping.

We proposed to assay the import, export, and within marsh movement of *Spartina* seed using standing nets fixed to the soil surface and floating nets (see Huiskes et al 1995 for full description of methods). Nets were placed at three stations along a marsh transect; the tidal flat, within the *Spartina* lower marsh, and in the *Salicornia-Spartina* upper marsh. Nets were positioned and retrieved to sample both flood (via a small boat) and ebb tides (on foot). We constructed seed traps, and sampled seeds at 5 trapping stations (4 traps each) along 2 major marsh channels in Cogswell Marsh on 4 dates in fall 2001. Material collected from traps on Nov. 1 and Nov. 15 was placed on soil in pots in the greenhouse and kept moist. Germinated seedlings were counted one month later.

Results

No seeds were trapped during the two October trapping efforts. Over 1,500 *Salicornia* seeds/seedlings were tallied from the traps in November, but only single *Spartina* seed was found on Nov. 1 and no *Spartina* seed was recovered on Nov. 15. To summarize the patterns of seed dispersal for *Salicornia virginica*: 4-times more seed was recovered Nov. 15 than Nov. 1 (63.9 vs 14.4 seeds per trap; $P = 0.04$); most seed was recovered from the mudflat traps than mid- or upper marsh traps (48.1 > 42.8 > 30.2 seed per site per trap, respectively; ns); more seed was recovered from outflow traps vs incoming water traps (float out = 46.4; soil out = 62.3; float in 35.5, soil in = 12.7 seeds per trap; ns).

Conclusions

While this technique has been used to determine patterns of *Spartina anglica* seed movement in the Netherlands, and perhaps *Salicornia* seeds in our experiment, it was not an

effective technique to assess movements of *Spartina* seed at Cogswell Marsh. Perhaps *Spartina* seed shatters later in the year, when shorter day length and unfavorable tides precluded our assessment; however, in the end, this was a labor intensive technique (comparable to a challenge on the TV series “Survivor”) that returned no meaningful data.

Seedling occurrence and establishment

We proposed to examine the conditions required for successful seedling germination and early growth, and to follow the fate of new recruits. We created bare plots by clipping (1 m²), and left unmanipulated plots in vegetated and open mud flat habitats, adjacent to our common gardens, in each of the first 2 years of this grant. During each spring, we monitored the plots for naturally occurring *Spartina* seedling appearance, and planned to measure survival, growth, and hybridity level for 2-3 seasons. Results from Eastern marshes have found that seedling success in open patches in the lower marsh is high; this suggests one avenue by which native *S. foliosa* marshes may be invaded.

Results - original proposal

No *Spartina* seedlings were ever observed in any of our permanent plots. After the first springs’ observations, we performed the following additional experiments. To determine whether the lack of *Spartina* seeds and seedlings was due to a delivery or removal problem (the seed doesn’t arrive or arrives but is washed away) or rapid seedling mortality, we initiated 2 pilot studies fall 2002. To get around the delivery problem, we placed 100 *S. foliosa* seeds under squares of fiberglass window screen which were anchored to the substrate. We placed these trapped seed plots adjacent to our common gardens both on the mudflat and in the *Salicornia/Spartina* upper marsh. Prior to germination in April 2003, the screen was removed, and *Spartina* seedling germination and survival was monitored. To determine whether seed was deposited and then removed by tidal action (as we observed in our seed bank experiment), we constructed seed traps out of aluminum pans (disposable large (“Turkey”) roasting pans) and cobbles. The idea was that material carried into the pans would filter to the bottom and be protected from tidal action by a 10-15 cm deep layer of cobbles. We collected the material trapped under the stones and placed it in conditions favorable for germination to determine the composition of delivered seed.

Results - first modified proposal

The “trapped seed” technique worked and we observed seedling germination in April 2003, at which time we removed the screens. The seedlings in the open mudflat plots mostly disappeared within 2 weeks, presumably due to tidal action; the seedlings in the upper vegetated plots slowly turned yellow and brown and were completely dead by June, plant symptoms consistent with mortality due to high salinity (based on our personal observations of cordgrass seedling death under high salinity in greenhouse experiments).

We placed the trapped material from the aluminum pans in a greenhouse, supplied fresh water, and made observations for germinating seedlings for several weeks. No *Spartina* seedlings were observed.

In spring of 2003, we began searching long stretches of Bay shoreline for *Spartina* seedlings. We found long stretches of shoreline devoid of *Spartina* seedlings and aggregations of

seedlings near established clones. We mapped the clones and seedlings and have begun microsatellite-based genetic studies (with our newly developed microsatellite markers) to determine whether the near-by clone is in fact the parent (by self-pollination) of the aggregations of seedlings.

Conclusions - SEEDLING RECRUITMENT

Seed dispersal and seedling establishment do not form regular patterns in marshes and mudflat in Cogswell Marsh, making small permanent plots, small seed traps, and small seed bank assessments ineffectual techniques in this marsh, and possibly this system. We overcame the “dispersal problem” by trapping seed and found that all seedlings were lost either to tidal action on the mudflats or killed by excess salinity on the terrace. While it is possible that some hybrid seedlings may have survived in these situations, we have tentatively concluded that these situations are not the most likely regeneration niches for cordgrass.

On the eastern US coast, *S. alterniflora* seedlings establish in disturbance patches within established marshes. This is the most favorable environment regeneration niche there as summer rains rinse the soil of salts, the mid-marsh position offers protection from tidal action, and the lack of existing vegetation provides a non-competitive environment. On the western US coast, however, this mid-marsh habitat may be lethal to seedlings due to high soil salinity during the summer drought. We conclude that understanding the dynamics of recruitment by hybrid cordgrass in San Francisco Bay requires us to find areas where active seedling recruitment is occurring and infer the processes underlying the event. This research is underway and will be reported in the PhD thesis of Ms. Christina Sloop, and in peer-reviewed publications.

HYBRID SPREAD

Working with our collaborators at the California Coastal Conservancy, this work was completed and a paper published (Ayres DR, Smith DL, Zaremba K, Klohr S, Strong DR. 2004. Spread of exotic cordgrasses and hybrids (*Spartina* sp.) in the tidal marshes of San Francisco Bay. *Biological Invasions*. 6: 221-231.). The abstract of this paper follows:

Four species of exotic cordgrass (*Spartina* sp.) occur in the San Francisco estuary in addition to the California native *S. foliosa*. Our goal was to map the location and extent of all non-native *Spartina* in the estuary. Hybrids of *S. alterniflora* and *S. foliosa* are by far the most numerous exotic and are spreading rapidly. Radiating from sites of deliberate introduction, *Spartina alterniflora* and hybrids now cover ca 190 ha, mainly in the South and Central Bay. Estimates of rate of aerial increase range from a constant value to an accelerating rate of increase. This could be due to the proliferation of hybrid clones capable of rapid expansion and having superior seed set and siring abilities. The total coverage of 195 ha by hybrids and other exotic cordgrass species is slightly less than 1% of the Bay’s tidal mudflats and marshes. *Spartina anglica* has not spread beyond its original 1970’s introduction site. *Spartina densiflora* has spread to cover over 5 ha at 3 sites in the Central Bay. *Spartina patens* has expanded from 2 plants in 1970 to 42 plants at one site in Suisun Bay. *Spartina* seed floats on the tide, giving it the potential to export this invasion throughout the San Francisco estuary, and to estuaries outside of the Golden Gate. We found isolated plants of *S. alterniflora* and *S. densiflora* in outer coast estuaries north of the Bay suggesting the likelihood for the San Francisco Bay populations to found others on the Pacific coast.

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