

# UC Davis

## UC Davis Previously Published Works

### Title

Responses to salinity of *Spartina* hybrids formed in San Francisco Bay, California (*S. alterniflora* × *foliosa* and *S. densiflora* × *foliosa*)

### Permalink

<https://escholarship.org/uc/item/3bw1m53k>

### Journal

Biological Invasions, 18(8)

### ISSN

1387-3547

### Authors

Lee, Alex K  
Ayes, Debra R  
Pakenham-Walsh, Mary R  
et al.

### Publication Date

2016-08-01

### DOI

10.1007/s10530-015-1011-3

Peer reviewed

*Responses to salinity of Spartina  
hybrids formed in San Francisco Bay,  
California (S. alterniflora × foliosa and S.  
densiflora × foliosa )*

**Alex K. Lee, Debra R. Ayres, Mary  
R. Pakenham-Walsh & Donald R. Strong**

**Biological Invasions**

ISSN 1387-3547

Volume 18

Number 8

Biol Invasions (2016) 18:2207-2219

DOI 10.1007/s10530-015-1011-3



**Your article is protected by copyright and all rights are held exclusively by Springer International Publishing Switzerland. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at [link.springer.com](http://link.springer.com)".**

# Responses to salinity of *Spartina* hybrids formed in San Francisco Bay, California (*S. alterniflora* × *foliosa* and *S. densiflora* × *foliosa*)

Alex K. Lee · Debra R. Ayres ·  
Mary R. Pakenham-Walsh · Donald R. Strong

Received: 20 February 2015 / Accepted: 12 November 2015  
© Springer International Publishing Switzerland 2016

**Abstract** San Francisco Bay (SFB), which supports large populations of the California native cordgrass *Spartina foliosa*, has been the recipient of introductions of *S. alterniflora* and *S. densiflora*. Hybrids have arisen between the native and these exotic species. Sterile F1 *S. densiflora* × *foliosa* hybrids have formed numerous times in a number of marshes, while introgressing *S. alterniflora* × *foliosa* hybrids are fully fertile and invaded widely in SFB, especially onto naturally-open low tidal flats by inundation-tolerant hybrids. *Sarcocornia pacifica*, pickleweed, dominates the mid-to-upper marsh zones where the hypersaline conditions that occur during the summer drought, characteristic of this climate, exclude *S. foliosa*. Here we report on two glasshouse experiments investigating the salinity tolerance of hybrid *Spartina*. Some hybrids of both origins grew well and flowered at high salinity levels while the parental species grew

little and did not flower. Our results imply that mid-zone marshes are also vulnerable to invasion by salinity-tolerant *Spartina* hybrids. Herbicide control implemented over the last 10 years targeting both the exotic species and their hybrids have reduced their extent. However, efforts in monitoring and management of exotic *Spartina* and its hybrids must continue as vast areas of tidal marsh restoration are underway and planned in SFB; colonization by *Spartina* hybrids tolerant to inundation and/or salinity will greatly alter restoration trajectories. These concerns are all the more vital given projections of climate change and its effects on salinity and sea level rise in SFB salt marshes.

**Keywords** Global climate change · Hybridization · Restoration · Salinity · Transgression · Salt marsh

## Abbreviations

GCC	Global climate change
ISP	Invasive Spartina Project
ppt	Parts per thousand
<i>S. axf</i>	<i>Spartina alterniflora</i> × <i>foliosa</i>
<i>S. dxf</i>	<i>Spartina densiflora</i> × <i>foliosa</i>
SFB	San Francisco Bay
SLR	Sea level rise

## Introduction

The future survival of salt marsh systems may be at risk on a global scale due to extensive human

Guest editors: Alan Gray and Malika Ainouche/Invasive Spartina.

A. K. Lee  
700 Heinz Avenue Suite 200, Berkeley, CA 94710, USA

D. R. Ayres (✉) · D. R. Strong  
Department of Evolution and Ecology, University of California, Davis, CA 95616, USA  
e-mail: drayres@ucdavis.edu

M. R. Pakenham-Walsh  
Sacramento, CA, USA  
e-mail: marypw1@hotmail.com

modification and global climate change (Thorne et al. 2012). Introduced invasive species are a significant component of human-related modifications, representing a serious threat to ecosystem structure and function. Estuaries are among the most modified and invaded systems on earth (Grosholz 2002) and San Francisco Bay (SFB), CA, USA is perhaps the most invaded estuary in the world, hosting over 230 exotic species (Cohen and Carlton 1998). The cordgrass genus *Spartina* holds several notable examples of salt marsh invaders (summarized in Strong and Ayres 2013) most of them resulting from interspecific hybridization and polyploidy (Ainouche et al. 2009). Five estuaries along the North American Pacific coast are currently host to four introduced species of *Spartina*, and two newly formed hybrid taxa, and more than 20 other estuarine sites are considered vulnerable to exotic *Spartina* invasion (Daehler and Strong 1996). *Spartina* invasions in Willapa Bay, WA (*Spartina alterniflora*) and San Francisco Bay, CA (*S. alterniflora* (2n = 62), *S. anglica* (2n = 120–124), *S. densiflora* (2n = 70), *S. patens* (2n = 40), *S. alterniflora* × *foliosa* hybrids (2n = 62), and *S. densiflora* × *foliosa* hybrids (2n = 65; 3n = 94, 96) see Table 1 in Ayres et al. 2008a for chromosome numbers) have been subject to control efforts at a cost of over \$50 million (Strong and Ayres 2013).

*Spartina alterniflora*, native to the U.S East and Gulf coasts, was deliberately introduced to the SFB for marsh restoration in 1973 (Faber 2000). *Spartina foliosa* is endemic to the North American west coast, ranging from Baja California, Mexico to Bodega Bay, CA (Spicher and Josselyn 1985). Introgressive hybridization between these two species produced an array of plants exhibiting diverse genetic contributions from each parental species (Ayres et al. 1999; Sloop et al. 2010). Aggressive expansion of the hybrid swarm threatened to radically alter the Bay's near-shore ecosystem through both genetic and ecological pathways (Ayres et al. 1999; Grosholz 2002). *Spartina* hybrids are highly fit, propelling rapid sexual and clonal reproduction (Hall et al. 2006). Prodigious hybrid pollen swamping of *S. foliosa* threatened it with local extinction by genetic assimilation (Anttila et al. 1998; Ayres et al. 1999; Hall et al. 2006).

*Spartina densiflora* is native to Chile and Argentina. It was introduced during the sixteenth-century to the Iberian Peninsula in Spain (Castillo et al. 2010), to Humboldt Bay, California in the mid-1800s (Kittelson

and Boyd 1997), and to SF Bay in 1978 (Faber 2000). In its native and introduced ranges it occurs above the lower marsh where the native maritime *Spartina* species grow—*S. alterniflora* in Argentina, *S. maritima* in Spain, and *S. foliosa* in California—likely owing to limitations on seedling establishment due to anoxia (Mateos-Naranjo et al. 2008; Abbas et al. 2012), by the intolerance of adult plants to high inundation (Castillo et al. 2000; Nieva et al. 2001, 2003; Idaszkin et al. 2014), and to possible competition with *S. maritima* in Spain (Castillo et al. 2008).

*Spartina densiflora* plants from Humboldt Bay were planted in Creekside Park, Larkspur, California, along with *S. foliosa* and *S. anglica*, during the park's restoration to tidal marsh in 1978 (Faber 2000). Sterile F1 hybrids mostly between *S. densiflora* and *S. foliosa*, both of which were seed parents, arose (Ayres et al. 2008a). Broadly spreading hybrid plants, like their *S. foliosa* parent, were found in the *S. anglica* zone while plants in mid and especially high positions in the marsh retained more of the tussock character of their *S. densiflora* parent. Like *S. densiflora*, the hybrids were evergreen with a long growing season, while *S. foliosa* loses its tillers in winter. Hybrids were found in 23 of the 32 marshes where both species grew together (Hogle 2011).

Hybridization between native and alien species has been positively associated with invasibility (Lee 2002; Ellstrand and Schierenbeck 2000; Hovick and Whitney 2014). Hybrid invaders pose an extinction risk to native species from interspecific gene flow or introgression (Rhymer and Simberloff 1996; Ayres et al. 2003). Ecological impacts of hybrids are often related to extreme transgressive hybrid traits relative to those of either parental species and these traits can be strongly heritable (Rieseberg et al. 1999). More specifically, in *Spartina*, it has been shown that formation of new hybrid lineages is accompanied by consistent epigenetic alteration (Salmon et al. 2005) associated with transgressive gene expression (Chelaifa et al. 2010) when compared to the parents. On the other hand, non-introgressive F1 hybrids, like sterile *Spartina townsendii* and fertile *S. anglica*, may have fixed hybrid vigor (Comai 2005). In a hybrid-driven invasion, differential tolerances to various biotic and abiotic determinants may be the most significant factor to invasion success (Rieseberg et al. 1999).

The classical paradigm of salt marsh zonation in the SFB estuary holds that the two foundation species are

limited by different abiotic stressors—inundation and salinity (Fig. 1a). The pattern of these stressors in California, and in other salt marshes in Mediterranean climates, is driven by summer drought that results in hypersaline conditions where tidal flood is inadequate to leach salts accumulated through evapotranspiration (Pennings and Callaway 1992). The highly salt-tolerant native *Sarcocornia pacifica* (Mahall and Park 1976a), (“pickleweed” hereafter) dominates much of the hypersaline intertidal zone above approximately mean high water in SFB (Josselyn 1983). The upper distribution of *S. foliosa* overlaps the lower distribution of pickleweed by about 0.5 vertical meter, with *S. foliosa* occupying the zone closest to open water and salt marsh channels (Mahall and Park 1976b). Intolerance to prolonged immersion is thought to exclude pickleweed from lower intertidal zones (Mahall and Park 1976b). *Spartina foliosa* has been hypothesized to be both competition-limited (Hinde 1954) and intolerant of highly saline conditions (Mahall and Park 1976a), preventing substantial encroachment into the pickleweed-dominated zone.

We have already seen the consequences of increased tolerance to inundation in the colonization and rapid spread of *S. alterniflora* × *foliosa* (*S. axf* hereafter) hybrids on open mud flats below the limits of *S. foliosa* inundation tolerance (Strong and Ayres 2013 and references therein). Since 2004, control efforts by the Invasive *Spartina* Project (ISP) have reduced cover of all exotic species and hybrids by 95 % (Rohmer et al. 2014). However, these efforts have been scaled back due to a decline in SFB populations of the endangered California Ridgway’s rail following *Spartina* control (Strong and Ayres 2016), leaving at least 26 occurrences of *S. axf*

hybrids, mostly in the south and central Bay (Ort and Thornton, this volume). *Spartina densiflora* and *S. densiflora* × *foliosa* have been reduced 99 % leaving <120 m<sup>2</sup> in the SFB (Rohmer et al. 2014).

The potential for expansion by *S. axf* and *S. densiflora* × *foliosa* (*S. dxf* hereafter) hybrids into mid-and-upper tidal marsh zones via enhanced salinity tolerance has not yet been examined. As has been shown for *S. alterniflora* (Proffitt et al. 2005), genotypic and phenotypic variation in this key marsh species can influence patterns of recruitment, suppression, and facilitation of other plant species. Cordgrass plants with a higher salinity tolerance than *S. foliosa* can grow further inland into the pickleweed zone and potentially alter marsh structure through these mechanisms.

Salinity, nutrients, and anoxia influence the productivity of *S. alterniflora* (Nestler 1977; Mendelssohn and Morris 2000), *S. densiflora* (Alberti et al. 2010) and *S. foliosa* (Trnka and Zedler 2000). Evidence exists for genetically-based differential response to salinity among populations of *S. alterniflora* (Pezeshiki and DeLaune 1995; Seliskar 1995; Hester et al. 1998, 2001), and *S. alterniflora* exhibits high chloroplast (42 haplotypes) and nuclear diversity in its native eastern US range (Blum et al. 2007). Throughout its range in California *Spartina foliosa* is genetically uniform with only a single cpDNA haplotype (Ayres et al. 2008a) and 1/5th the nuclear genetic diversity of *S. alterniflora* (Sloop et al. 2010). Genetic differences were less important than environmental differences, including salinity, in determining *Spartina foliosa* growth form (Cain and Harvey 1983; Trnka and Zedler 2000). Phenotypic plasticity rather than genetic differentiation accounted for differences observed in *S. densiflora* in the field (Castillo et al.

**Fig. 1** **a** Classic marsh zonation paradigm in SFB (Mahall and Park 1976a, b). **b** Potential zonation pattern alterations due to tolerance of hybrid *Spartina* to inundation and salinity (Mahall and Park 1976a, b; Fig. 6 this study; results, this study)

More Tolerant  Less Tolerant

**A Classic Model**

**Inundation**

*S. foliosa* > Pickleweed

**Salinity**

Pickleweed > *S. foliosa*

**B Potential Zonation**

**Inundation**

some *S. axf* > *S. alterniflora* > *S. foliosa* > *S. anglica* > *S. dxf* > *S. densiflora* > Pickleweed

**Salinity**

Pickleweed > some *S. axf* > some *S. dxf* > *S. alterniflora* > *S. densiflora* > *S. foliosa*



2014). *Spartina densiflora* contained mostly a single cpDNA haplotype (Ayres et al. 2008a; Fortune et al. 2008), and only a single microsatellite locus (out of 8) showed any nuclear variation in SFB (Ayres et al. 2008a).

How great of a threat is hybrid *Spartina* to pickleweed-dominated marsh zones? We hypothesized that hybrid genotypes successfully able to invade the pickleweed zone would possess superior salinity tolerance. We conducted experiments in the glasshouse to test this hypothesis for each hybrid taxa. Specifically we asked: (1) What is the salinity tolerance of hybrid cordgrasses relative to the parental species? (2) How well do hybrid genotypes grow at high salinities? (3) How variable are hybrid genotype responses to salinity?

## Materials and methods

More salt tolerant populations of *S. alterniflora* have been found to have a lower proportion of dead:above-ground tissue, a lower root:shoot ratio in both low and elevated salinity, and a less elevated  $\text{Na}^+:\text{K}^+$  cation ratio; morphological variables such as height and total biomass have been found to be poorer indicators of intraspecific salt tolerance in *S. alterniflora* (Hester et al. 2001). Change in height was the best indicator of salinity tolerance in *S. densiflora* and tiller production declined in salinities over 35 parts per thousand (ppt) (Kittelson and Boyd 1997). Both height and tiller Relative Growth Rates (RGR) were used to evaluate the performance of *S. maritima*, *S. densiflora* and *S. densiflora*  $\times$  *maritima* hybrids in a field transplant experiment in Spain (Castillo et al. 2010); taller plants (the hybrids) had far higher RGR than the shorter plants (parental species). Accordingly, we assessed these metrics and measures in our experiments.

### Experiment 1: *Spartina alterniflora* $\times$ *foliosa*

Twenty-one genotypes were used in this experiment. Clonal fragments from 18 *S. axif* genotypes were collected from Cogswell Marsh in Hayward, California between July and December of 2001. Cogswell marsh is a former salt pond that was restored to tidal action in 1980 and colonized mostly by tidally born seed of cordgrass and pickleweed (Ayres et al. 2008b). One *S. alterniflora* and two *S. foliosa* were also

included in the experiment. The genotypes of all plants were verified by RAPD (Random Amplified Polymorphic DNA) nuclear DNA markers, using methods described in Daehler et al. (1999). Hybrids ranged from 7 to 93 % *S. alterniflora* genetic markers; average hybridity of all plants = 50 %, where *S. alterniflora* = 100 % and *S. foliosa* = 0 %.

Each genotype was eventually separated into nine replications (189 plants total), one plant per pot, using Yolo Fine Sandy Loam as the potting medium, and placed in random positions in nine bins; each bin contained a full complement of genotypes. Fertilizer (GrowMore 4-18-39, no boron, Grow More, Inc., Gardener, CA, USA) was automatically delivered into hose water by a Dosatron (Dosatron International, Clearwater, FL, USA). Pots were partially submerged in freshwater and plants allowed to reach a similar size (3–6 months), after which salinity was raised to three treatment levels for the experiment—10 parts per thousand (ppt), 25 and 40 ppt—with three bins/replications per treatment. The experiment was run for 30 weeks during the spring/summer 2002 growing season at a glasshouse in Davis, CA. During this time the sun's photoperiod ranged from 12 to 15 h, and temperatures were controlled between 14 and 29 °C.

Instant Ocean aquarium salt was used to maintain salinity in the water that submerged potted plants. Salinity was measured using a handheld, temperature-compensated refractometer by Fischer Scientific, and calibrated with deionized water. Deionized water was added into bins to compensate for evaporation and to maintain aqueous salinity at treatment levels. Soil salinity measurements were taken each month as evapotranspiration increased soil salinity throughout the experiment.

Each week, the numbers of living and dead tillers were counted for each plant. Tiller RGRs were calculated by dividing the number of living tillers at each date by the initial number of tillers. At the end of the experiment, plants were separated into inflorescences, living and dead aboveground material, and root + rhizome below ground material and oven-dried for at least 3 days at 55 °C, then weighed for dry biomass. Total biomass was the sum of aboveground and below ground tissue, excluding inflorescences.

Up to 4 g of dried shoot material from the living component of 164 plants was ground in a Wiley mill (40-mesh screen). Twenty-five plants were excluded because of either mortality ( $n = 15$ ) or lack of

sufficient material ( $n = 10$ ). Leaf cation concentrations (ppm) for  $\text{Na}^+$  and  $\text{K}^+$  were determined using inductively coupled plasma atomic spectrometry (ICP-AES) by the DANR Analytical Laboratory, UC Davis, Davis, CA. Leaf cation ratio ( $\text{Na}^+:\text{K}^+$ ) was then calculated.

#### Experiment 2: *Spartina densiflora* $\times$ *foliosa*

Clones from 13 plants were used in this experiment. Clonal fragments from 11 *S. dxf* plants were collected from Creekside Park Marsh, Larkspur, California in December 2002. One *S. densiflora* and one *S. foliosa* plant were also included. All hybrid plants were previously verified by molecular markers and chromosome counts as described in Ayres et al. (2008a). The suite of hybrid plants was of variable morphology, and taken from throughout the elevational range of the marsh. All hybrids were F1 interspecific crosses; however, there were six genotypes distinguished by small variations in nuclear alleles, chloroplast DNA (*S. alterniflora*, *S. densiflora*, *S. foliosa*), or chromosome number (ca 66 vs. ca 95) (see Ayres et al. 2008a for details).

All plants were separated into four replications in four bins for 56 plants total, one plant per pot in Yolo Fine Sandy Loam. Pots were partially submerged in freshwater and allowed to acclimate for 3 months. Each bin contained a complete replication of plants placed in randomized grid positions. After acclimation, water salinity was increased in three of the bins by 10 ppt/week for 10 weeks to challenge the salinity tolerances of genotypes (sensu Hester et al. 1998), ending at 100 ppt at the end of the experiment. The plants in the fourth bin were grown in freshwater during the entire experiment; this single freshwater treatment was not amenable to inferential statistics so these results are portrayed in graphs and tables for comparative purposes. The experiment was run during spring/summer 2003 growing season at a glasshouse in Davis, CA for 11 weeks. During this time the sun's photoperiod ranged from 12.5 to 15 h, and temperatures were controlled between 14 and 29 °C.

Aqueous salinity was established, monitored, and maintained as above.

Each week, the number of living and dead tillers were counted for each plant. Tiller RGRs were calculated as above. At the end of the experiment, plants were separated into inflorescences, living and

dead aboveground material, oven-dried for at least 3 days at 55 °C, then weighed for dry biomass.

#### Supplemental field data

Field data was collected in Creekside Park Marsh to supplement the *S. densiflora*  $\times$  *foliosa* glasshouse experiment. To evaluate fertility, four inflorescences each from five hybrid genotypes and 11 inflorescences from *S. densiflora* were collected and counted for seeds. Inflorescences were separated into florets that were then gently finger pressed on a table to determine the presence of seeds. Viable seeds can be easily felt by this method.

At Creekside Park, a Nikon D50 Total Station was used to measure the relative marsh elevation range of all *Spartina* taxa (*S. anglica*, *S. densiflora*, *S. foliosa*, *S. densiflora*  $\times$  *foliosa*), open mud, and pickleweed. The 2003–2004 field seasons were average rain years.

#### Statistical analysis

Genotype effects in the three treatment replicates (*S. dxf*) and genotype, salinity, and genotype  $\times$  salinity (*S. axf*) were tested by ANOVA using the software JMP 11.2.0. Where needed, normality of the data was improved by transformation (ln, square root) before ANOVA. ANOVA was performed on variables listed in Tables 1 and 2. Tukey–Kramer Honestly Significant Difference (HSD) was conducted for individual variables to determine significant differences between genotype means. The maximum tiller RGR was considered to be the one date that had the highest average RGR; the data associated with this date were evaluated by ANOVA. A repeat-measures ANOVA was used for time-series data on tiller RGR.

## Results

### *Spartina alterniflora* $\times$ *foliosa*

Increasing salinity decreased plant height, biomass, and flowering effort (Table 1; Fig. 2). The height of all genotypes was on average 51 % shorter in high versus low salinity. Under all salinities, the parental species were of similar stature and shorter than most hybrids. Plants at all salinity levels had a high fraction of dead biomass. Increasing salinity decreased total



**Table 1** Summary of statistical analyses evaluating the significance and response ranges for variables measured and calculated in the *S. alterniflora* × *foliosa* experiment

	Treatment effect	Genotype effect	Treatment by genotype	Genotype response range Salinity treatment (avg.)					
	F	F	F	Low		Med		High	
				Min.	Max.	Min.	Max.	Min.	Max.
Height (cm)	83.8**	6.5***	3.5***	21.5	78.7	11.5	65.4	5.5	44.1
Total plant biomass (g)	26.9**	4.4**	1.3	25.1	133.6	8.9	101.9	3.6	76.5
Infl biomass:AG biomass	2.1	5.8***	2.1**	0.08	0.22	0.06	0.19	0.03	0.21
Total # Infls	5.2*	9.6***	1.2	1	12.6	0	10.7	0	9.3
Dead:total aboveground biomass	7.25*	2.5**	1.9**	0.4	0.84	0.37	0.99	0.62	0.97
Tiller maximum RGR	7.86***	2.42***	0.86	0.66	3	0.56	5.27	0.25	2.25
Tiller RGR	0.06	1.84*	0.31						
Time**, Time × Sal.*									
Root:shoot ratio	1.5	6.85***	1.2	0.53	2.92	0.71	2.63	0.76	4.1
Leaf Na <sup>+</sup> :K <sup>+</sup> ratio	1.5	4.2**	1.9*	0.64	1.75	0.44	1.9	0.72	1.83

Genotype 3-2 not included as only 1/9 plants flowered

\* *P* < 0.05; \*\* *P* < 0.01; \*\*\* *P* < 0.001

**Table 2** Summary of statistical analyses evaluating the significance and response ranges for variables measured and calculated in the *S. densiflora* × *foliosa* experiment

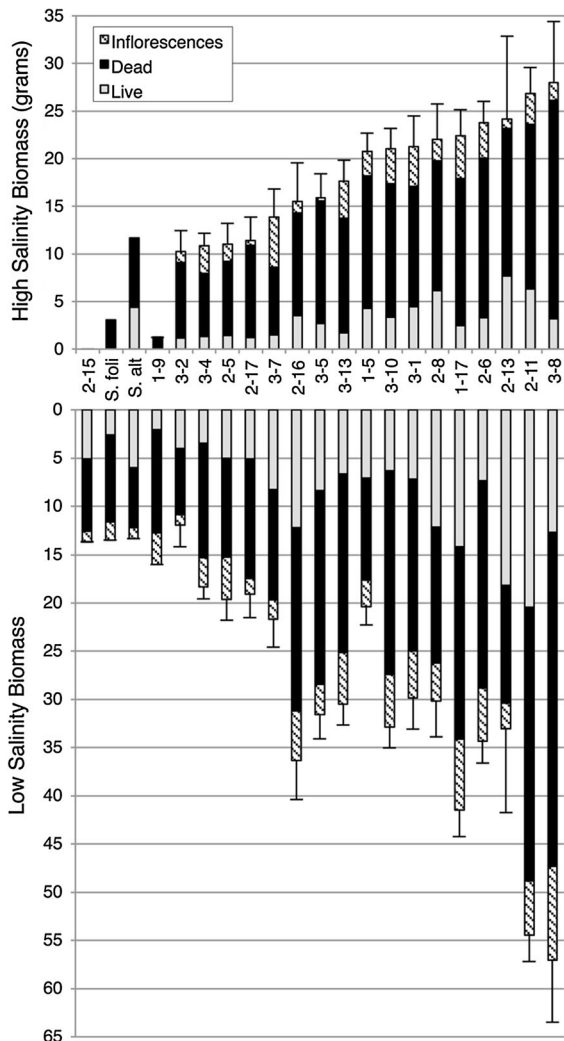
	Genotype effect	Population response range (avg.)			
		Salinity challenge		Freshwater treatment	
		Min.	Max.	Min.	Max.
Height (cm)	11.70***	8.33	106.33	36.00	122.33
Total plant AG biomass (g)	20.69***	10.95	141.83	35.61	354.55
Dead:total AG biomass	5.01***	0.27	0.77	0.01	0.17
Infl. biomass (g)	6.88***	0.01	16.48	0.04	34.03
Infl:total AG biomass	4.20***	0.00	0.19	0.01	0.33
Tiller maximum RGR	1.67	1.32	2.28	1.81	5.00
Tiller RGR	2.88*				
AG aboveground					
Time/salinity	*				
Time × genotype	*				

\* *P* < 0.05; \*\* *P* < 0.01; \*\*\* *P* < 0.001

biomass, but the response varied among genotypes. Parental genotypes, especially *S. foliosa*, were far lower in total biomass than many hybrid genotypes. Increasing salinity reduced the number of inflorescences, and their biomass by 45 %. Despite this, most hybrids were able to flower at the highest salinity; neither parental species did so.

Plants in high salinity conditions had a significantly greater dead:total biomass ratio than those in either low or medium salinity (Table 1; avg. = 0.81 high vs. 0.61 low). *Spartina foliosa* had the highest dead:total biomass at both low and high salinities and

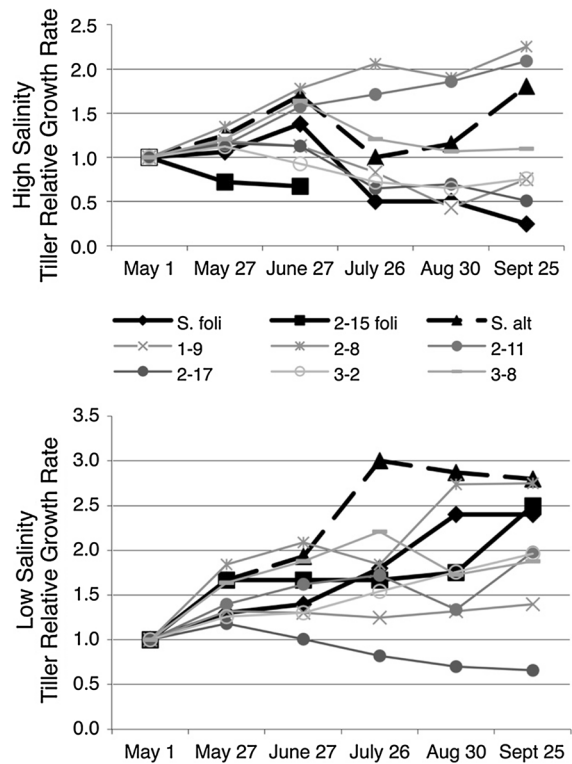
experienced substantial mortality in the experiment while *S. alterniflora* had near the lowest dead:total ratio for both low and high salinity. Root:shoot ratio was significantly affected only by genotype (Table 1); there was high variability between genotypes with genotypes 2–13, 2–15 (*S. foliosa*) and 3–7 having significantly lower root:shoot ratio than many genotypes, while genotypes 2–8 and 2–16 were significantly higher; these ratios were not correlated with growth measures. The cation ratio was insignificantly related to differences in salinity (Table 1) and genotypic patterns were muddled.



**Fig. 2** *Spartina alterniflora*, *S. foliosa*, and *S. axf* hybrid aboveground biomass of dead, living and inflorescences at high salinity (*upper*) and low salinity (*lower*)

The maximum RGRs were reduced 23 % under high salinity, relative to low salinity, and varied between genotypes (Table 1; Fig. 3). The maximum growth rate for the low salinity treatment was 3 months later in the season (September) than the maximum RGR under high salinity (June). Under high salinity, several hybrids continued to grow well into the fall (e.g., genotypes 2–8, 2–11), while some grew poorly (e.g., 1–9, 3–2). Under low salinity, both species had a higher RGR than most hybrids.

Soil salinities were 50–60 % higher than aqueous salinities by the end of the experiment due to evapotranspiration. Maximum soil salinity in the low



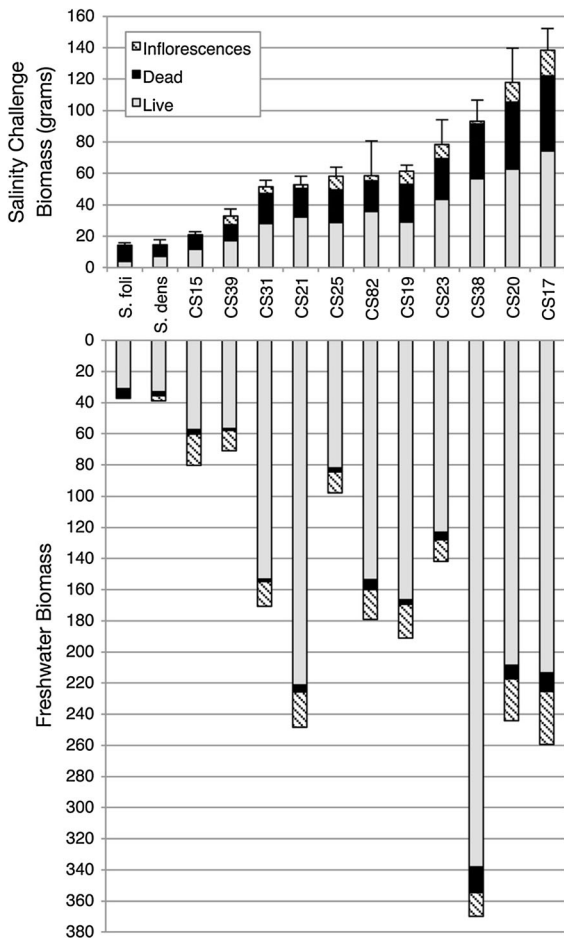
**Fig. 3** Tiller relative growth rate (RGR) of a subset of *S. alterniflora*, *S. foliosa* and *S. axf* hybrids. *Upper figure* is high salinity treatment, *lower figure* is low salinity

(10 ppt) treatment was 25 ppt ± 2, the medium (25 ppt) was 51 ppt ± 3, and the high (40 ppt) was 71 ppt ± 3 by the end of September.

*Spartina densiflora* × *foliosa*

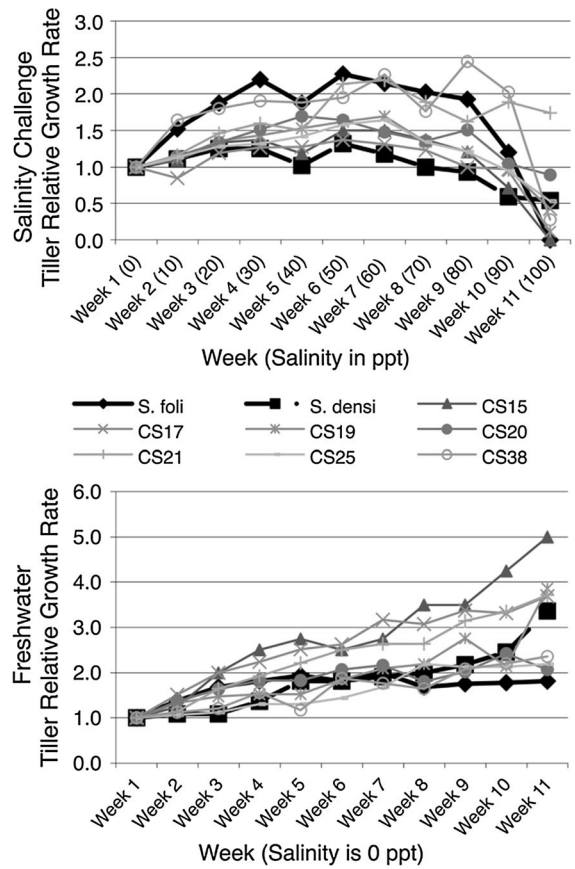
The overall effect of salinity on performance of plants in the salinity challenge was illustrated by comparison to the plants grown in freshwater; plants were shorter, smaller, and flowered less well under increasing salinity (Fig. 4); plants averaged 40 % dead:total biomass compared to 5 % in freshwater; and maximum RGR was at the midpoint of the experiment while the plants in freshwater were still growing well at the end (Fig. 5). Four genotypes grew well under high salinity and in freshwater (CS17, CS23, CS25, CS38), four were consistently poor (*S. densiflora*, *S. foliosa*, CS15, CS17), and a few genotypes only grew well in freshwater (CS19, CS21).

Under the salinity challenge, *S. foliosa* was the shortest genotype, followed by hybrid CS15 and *S.*



**Fig. 4** *Spartina densiflora*, *S. foliosa*, and *S. dxf* hybrid aboveground biomass of dead, living and inflorescences under salinity challenge (upper) and freshwater (0 ppt) (lower)

*densiflora*; four hybrids (CS17, CS20, CS23, CS25) grew twice as tall as the 3 shorter genotypes. This pattern was repeated, generally, in total biomass where *S. foliosa*, *S. densiflora*, CS15, and CS39 grew far less well than hybrids CS17, CS20, CS23 and CS38 (Table 2; Fig. 4). Most hybrids were able to flower under the salinity challenge, while the parental species and two hybrids did not. The plants that performed poorly in height and biomass also contained the highest percentage of dead biomass (*S. densiflora*, *S. foliosa*, CS15, CS17), while the top performers did not necessarily have a low dead:total ratio. Tiller RGR increased for all genotypes until week 6, when aqueous salinity reached 50–60 ppt, and then declined. Intriguingly, *S. foliosa* maintained the highest RGR throughout the experiment and *S. densiflora* had the lowest maximum RGR, while hybrids had mostly



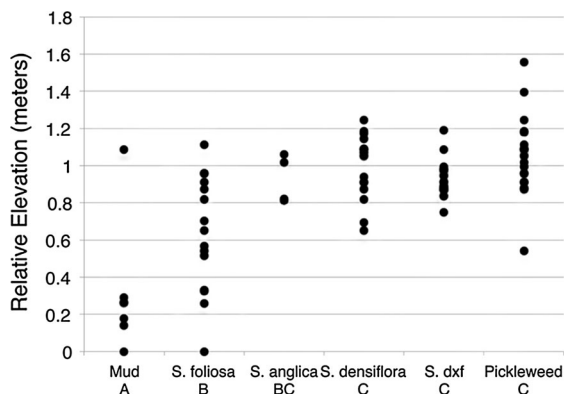
**Fig. 5** Tiller relative growth rates (RGR) of a subset of *S. densiflora*, *S. foliosa* and *S. dxf* hybrids. Upper figure is the salinity challenge; lower figure is freshwater (0 ppt)

intermediate growth rates (differences were not significant). The elevated RGR in this case may be attributable to several small new shoots as opposed to maintenance and growth of existing older shoots. The final soil salinity was 118 ppt  $\pm$  2 for the salinity challenge and 6.4 ppt  $\pm$  0.5 for the freshwater treatment.

Hybrid genotypes did not produce any viable seeds out of the 2064 florets examined, while *S. densiflora* produced 327 seeds out of 755 florets.

Open mud was the lowest point in Creekside Park, followed by *S. foliosa*. *Spartina anglica* overlapped with *S. foliosa* and the mid-marsh locations of *S. densiflora*, *S. densiflora*  $\times$  *foliosa* hybrids, and pickleweed; pickleweed grew highest in the marsh (Fig. 6).

In both experiments the correlation between salinity tolerance metrics (maximum RGR, dead:total,



**Fig. 6** Relative elevations at Creekside Park of open mud, *S. foliosa*, *S. anglica*, *S. densiflora*, *S. dxf* hybrids, and pickleweed; different letters under the location indicate significant difference ( $P < 0.0001$ )

root:shoot,  $\text{Na}^+:\text{K}^+$ ) to each other and to growth measures (height and biomass) was low.

## Discussion

The effect of salinity on height, biomass, flowering and RGR was consistent between experiments; all were reduced with degrees of severity that depended on the genotype. Salinity above 50 ppt became detrimental to tiller initiation of all plants in the *S. dxf* salinity challenge, but to only some *S. axf* hybrids where a few *S. axf* plants continued to grow well into the fall when soil salinities exceeded 70 ppt. The parental species were in the lowest 25 % in biomass in both high and low (freshwater) salinity levels; *S. foliosa* genotypes were the smallest plants overall in both experiments. The season-long RGR analyses, useful for tracking the time course of growth, illustrated that the season of positive growth was cut in half under high salinity with concomitant reductions in biomass accumulation in both systems.

The intermediacy of the *S. dxf* hybrids for RGR under treatment, especially when compared to *S. axf* where the RGR of some hybrids exceeded both parental species at high salinity, may be due to genetic constraints imposed by the genetically uniform F1 nature of these plants, formed from genetically uniform species, versus the introgressive and transgressive nature of some *S. axf* hybrids, infused with genetic variation from the *S. alterniflora* parent. The best performing *S. axf* hybrids tended to have a higher

contribution from *S. alterniflora* (between 43 and 93 %) while the smallest hybrids had the least (<40 %). Even so, pure *S. alterniflora* grew far less vigorously than many hybrids. These results are consistent with a previous glasshouse experiment where *S. axf* hybrids of intermediate hybridity grew best (Fig. 1 in Ayres et al. 2004).

There were no consistent trends between genetic or chromosomal background and performance in the *S. dxf* experiment. Even within an apparently uniform nuclear DNA category, containing ca 66 chromosomes, and having the same maternal species (see Ayres et al. 2008a for details), plants grew well (CS20) or poorly (CS39) in the salinity challenge. Nor were marsh salinity or elevation where the plants grew in nature reliable predictors of performance in the experiment. The range of elevations colonized by *S. dxf* hybrids (Fig. 6) suggests intolerance to inundation, like their *S. densiflora* parent, although some broadly spreading hybrid plants were able to grow into the lower *S. anglica* zone. As well, neither *S. densiflora* nor the hybrids grew in the very high marsh dominated by pickleweed. These tolerance limits imply niches exist for both *S. foliosa*, in the low marsh, and pickleweed, in the high marsh, in *S. dxf* invaded marshes.

Despite the high tolerance to salinity demonstrated by a subset of *S. dxf* hybrid plants, their invasion potential is ultimately constrained by seed sterility. All known *S. dxf* hybrids have been found to be sterile, despite their significant investment in inflorescence biomass. No viable pollen was identified during the experiment, inflorescences collected from the field did not contain any seeds, and no fertile seeds were ever found in glasshouse grown plants (Ayres et al. 2008a and Ayres personal observation). Without fertility no further generations of hybrids can exist.

## Ecological implications of varied salinity tolerance in *Spartina* spp. hybrids

Our work informs the importance of hybrid genotype heterogeneity in driving habitat-dependent invasion patterns (sensu Hacker et al. 2001) throughout much of the elevational range of tidal marshes in SFB. Heretofore, the threat of the *Spartina* hybrid invasion focused on the conversion of naturally-open mudflats and lower marsh into meadows elevated by the sediment accretion abilities of *S. axf* plants (see

review by Strong and Ayres 2013). Our current studies provide the first comprehensive, empirically-based insight on the invasion potential of higher marsh zones by hybrid *Spartina* genotypes that possess the requisite degree of salinity tolerance to promote successful establishment and growth.

We draw three far-reaching conclusions from our results: (1) native *S. foliosa* is the genotype *least* capable of tolerating and growing well under elevated salinity, (2) certain *Spartina* hybrids, especially *S. axf* hybrids, can establish from seed in newly opened tidal marsh and grow well under high salinity; and (3) due to large-scale restoration projects in SFB there *will continue to be* newly opened tidal marsh sites, devoid of vegetation, inclusive of mid-to-high marsh locations well-suited for hybrid *Spartina* establishment. The predictions we make based upon our results are summarized in Fig. 1. Instead of a two-species system (Fig. 1a), in which *S. foliosa* and pickleweed form zones defined by their relative tolerances to inundation and salinity, community development will be radically altered dependant upon the presence of genetically heterogeneous hybrid *Spartina* propagules (Fig. 1b). As hybrid *S. axf* plants occur close by marshes undergoing revegetation (Fig. 1 in Rohmer et al. 2014; Olofson Environmental Inc. and San Francisco Estuary Invasive *Spartina* Project 2013) and former salt pond sites targeted for restoration to salt marsh (see: <http://www.southbayrestoration.org/maps>) those propagules will arrive by virtue of tidal regimes. As some *S. axf* hybrids have higher inundation tolerance and some hybrids have higher salinity tolerance than *S. foliosa*, no niche exists for the native cordgrass in a marsh invaded by *S. axf* hybrids.

#### Considerations for tidal marsh restoration

Natural recruitment processes—seeds arriving via tidal action—were often relied upon in early restoration projects in SFB (Callaway et al. 2007), which resulted in hybrid-dominated swards in the central and south Bay since at least 1989 (Ayres and Strong 2010). Aggressive hybrid control efforts throughout the 2000s in those marshes were correlated with a decline in abundance of the federally endangered California Ridgway's rail (Strong and Ayres, this volume). This led to the curtailment of rigorous control and the implementation of active revegetation in those marshes where hybrid cordgrass had been eliminated.

The ISP Revegetation Program was initiated in 2011, and has since planted tens of thousands of native plants at marsh sites, Baywide (Olofson Environmental Inc. and San Francisco Estuary Invasive *Spartina* Project 2013). Rapid vegetation establishment supports California Ridgway's rail foraging and the creation of nesting and high tide refuge habitat. The two primary species planted by the ISP are *S. foliosa* on mud-flat/marsh plains and tidal benches and *Grindelia stricta* in higher elevation areas. In addition to the re-establishment of *S. axf* hybrids from tidally-born seed in these restored sites, *S. foliosa* ovules are readily pollinated by hybrid pollen, begetting more hybrids (Ayres et al. 2008b). The ISP is continuing hybrid monitoring and limited control efforts to minimize the adverse risks of following a revegetation approach.

#### Effects of global climate change

Adding to the challenge of predicting the outcome of new tidal marsh restoration projects in SFB is the specter of global climate change (GCC), which is expected to have a substantial impact on tidal marshes in SFB (Callaway et al. 2007). Tidal marshes are among the more vulnerable ecosystems in the face of GCC as the key ecosystem drivers of inundation and salinity will be significantly modified over time, as could sediment dynamics such as accretion processes (Thorne et al. 2014). The relative importance of these key drivers may also vary, at a range of scales from geographically (Pennings et al. 2005) to species level (Janousek and Folger 2014).

Large-scale lateral shifts in distribution patterns of dominant vegetation in SFB between 1975 and 2004 are hypothesized to have been driven by human-caused increases in estuarine salinity levels due to freshwater diversion and accelerated sea level rise (SLR) (Watson and Bryne 2012). The most salt-tolerant high marsh species, pickleweed, expanded its coverage likely in response to increased salinity, while the least salt-tolerant species, *Schoenoplectus californicus*, decreased in coverage. *Distichlis spicata* experienced a notable decline in its high marsh distribution, likely in response to increased immersion times. Congruent with these recent observations, longer-term GCC impacts to SFB tidal marshes are predicted to be associated with elevated salinity, though the greater threat is posed by SLR (Callaway et al. 2007). In addition to human-caused increases in estuarine



salinity, such as the contentious “Delta tunnel project” which would divert fresh water from the SF delta and estuary to southern California (Capitol News 2014), GCC is predicted to further augment salinity levels as a result of climate-driven impacts such as less snow and earlier runoff of the Sierra snowpack, and higher sea levels, pushing salinity levels farther inland in the estuary (Callaway et al. 2007). An understanding of how SLR will interact with biogeomorphic processes to further influence elevation of tidal marshes is also critical (Thorne et al. 2014).

Restoration and long-term management of tidal marshes in SFB are unlikely to be able to rely on the classic paradigm of passive tidal marsh zonation: “if you build it, they will come.” First, who is “they?”—desirable native species, or hybrid *Spartina*? Second, what does one build?—a tidal marsh that supports a mudflat-to-high marsh gradient for today, or one that anticipates SLR? Recognition that hybrid *Spartina* poses an invasion threat to a wider gradient of tidal marsh than was previously thought is relevant to the goals of restoration and management of tidal salt marshes. This makes the long-term roles of monitoring and invasive species control all the more critical to salt marsh ecosystem sustainability in SFB.

**Acknowledgments** We thank Krista Hoffman and Pablo Rosso for their contributions to this project, two anonymous reviewers, and the UC Davis *Spartina* Lab for their support. This research was funded by California Sea Grant #27CN to DRS.

## References

- Abbas AM, Rubio-Casal AE, De Cires A, Figuero ME, Lambert AM, Castillo JM (2012) Effects of flooding on germination and establishment of the invasive cordgrass *Spartina densiflora*. *Weed Res* 52:269–276
- Ainouche ML, Fortune PM, Salmon A, Parisod C, Grandbastien MA et al (2009) Hybridization, polyploidy and invasion: lessons from *Spartina* (Poaceae). *Biol Invasions* 11:1159–1173
- Alberti J, Méndez CA, Daleo P, Fanjul E, Silliman BR, Bertness M (2010) Abiotic stress mediates top-down and bottom-up control in a Southwestern Atlantic salt marsh. *Oecologia* 163:181–191
- Anttila CK, Daehler CC, Rank NE, Strong DR (1998) Greater male fitness of a rare invader (*Spartina alterniflora*, Poaceae) threatens a common native (*Spartina foliosa*) with hybridization. *Am J Bot* 85:1597–1601
- Ayres DA, Strong DR (2010) Hybrid cordgrass (*Spartina*) and tidal marsh restoration in San Francisco Bay: if you build it, they will come. In: Ayres DR, Kerr DW, Ericson SD, Olofson PR (eds) Proceedings of the Third international conference on invasive *Spartina*, 2004. San Francisco Estuary Invasive *Spartina* Project of the California State Coastal Conservancy, Oakland, pp 125–126
- Ayres DR, Garcia-Rossi D, Davis HG, Strong DR (1999) Extent and degree of hybridization between exotic (*Spartina alterniflora*) and native (*S. foliosa*) cordgrass (Poaceae) in California, USA determined by random amplified polymorphic DNA (RAPDs). *Mol Ecol* 8:1179–1186
- Ayres DR, Strong DR, Baye P (2003) *Spartina foliosa*—a common species on the road to rarity? *Madroño* 50:209–213
- 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. *Biol Invasions* 6:221–231
- Ayres DR, Grotkopp E, Zaremba K, Sloop CM, Blum MJ, Bailey JP, Anttila CK, Strong DR (2008a) Hybridization between invasive *Spartina densiflora* (Poaceae) and native *S. foliosa* in San Francisco Bay, California, USA. *Am J Bot* 95(6):713–719
- Ayres DA, Zaremba K, Sloop CM, Strong DR (2008b) Sexual reproduction of cordgrass hybrids (*Spartina foliosa* × *alterniflora*) invading tidal marshes in San Francisco Bay. *Divers Distrib* 14:187–195
- Blum MJ, Bando KJ, Katz M, Strong DR (2007) Geographic structure, genetic diversity and source tracking of *Spartina alterniflora*. *J Biogeogr* 34:2055–2069
- Cain DJ, Harvey HT (1983) Evidence of salinity-induced ecophenic variation in cordgrass (*Spartina foliosa* Trin.). *Madroño* 30(1):50–62
- Callaway JC, Parker VT, Vasey MC, Schile LM (2007) Emerging issues for the restoration of tidal marsh ecosystems in the context of predicted climate change. *Madroño* 54(3):234–248
- Capitol News (2014) <http://www.capitalpress.com/stories-of-the-week/20141114/delta-tunnels-the-next-big-water-fight-in-calif>. Accessed 20 January 2015
- Castillo JM, Fernandez-Baco L, Castellanos EM, Luque CJ, Figueroa ME, Davy AJ (2000) Lower limits of *Spartina densiflora* and *S. maritima* in a Mediterranean salt marsh determined by different ecophysiological tolerances. *J Ecol* 88(5):801–812
- Castillo JM, Mateos-Naranjo E, Nieva FJ, Figueroa E (2008) Plant zonation at salt marshes of the endangered cordgrass *Spartina maritima* invaded by *Spartina densiflora*. *Hydrobiologia* 614:363–371
- Castillo JM, Ayres DR, Leira-Doce P, Bailey J, Blum M, Strong DR, Luque T, Figueroa E (2010) The production of hybrids with high ecological amplitude between exotic *Spartina densiflora* and native *S. maritima* in the Iberian Peninsula. *Divers Distrib* 16:547–558
- Castillo JM, Grewell BJ, Pickart A, Bortolus A, Peña C, Figueroa E, Sytsma M (2014) Phenotypic plasticity of invasive *Spartina densiflora* (Poaceae) along a broad latitudinal gradient on the Pacific Coast of North America. *Am J Bot* 101:448–458
- Chelaifa H, Monnier A, Ainouche M (2010) Transcriptomic changes following recent natural hybridization and allopolyploidy in the salt marsh species *Spartina* × *townsendii* and *Spartina anglica* (Poaceae). *New Phytol* 186:161–174



- Cohen AN, Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. *Science* 279:555–558
- Comai L (2005) The advantages and disadvantages of being polyploid. *Nat Rev Genet* 6:836–846
- Daehler CC, Strong DR (1996) Status, prediction and prevention of introduced cordgrass *Spartina* spp. invasions in Pacific estuaries, USA. *Biol Conserv* 78:51–58
- Daehler CC, Antilla CK, Ayres DR, Strong DR, Bailey JP (1999) Evolution of a new ecotype of *Spartina alterniflora* (Poaceae) in San Francisco Bay, California, USA. *Am J Bot* 86:543–546
- Ellstrand NC, Schierenbeck KA (2000) Hybridization as a stimulus for the evolution of invasiveness in plants? *Proc Natl Acad Sci* 97(13):7043–7050
- Faber PM (2000) Good intentions gone awry. *Calif Coast Ocean* 16:14–17
- Fortune PM, Schierenbeck K, Ayres DR, Bortolus A, Catrice O, Brown S, Ainouche ML (2008) The enigmatic invasive *Spartina densiflora*: a history of hybridizations in a polyploidy context. *Mol Ecol* 17:4304–4316
- Grosholz E (2002) Ecological and evolutionary consequences of coastal invasions. *Trends Ecol Evol* 17(1):22–27
- Hacker SD, Heimer D, Hellquist CE, Reeder TG, Reeves B, Riordan T, Dethier MN (2001) A marine plant (*Spartina anglica*) invades widely varying habitats: potential mechanism of invasion and control. *Biol Invasions* 3:211–217
- Hall RJ, Hastings A, Ayres DR (2006) Explaining the explosion: modelling a hybrid invasion. *Proc R Soc B* 273:1385–1389
- Hester MW, Mendelssohn IA, McKee KL (1998) Intraspecific variation in salt tolerance and morphology in *Panicum hemitomon* and *Spartina alterniflora* (Poaceae). *Int J Plant Sci* 159(1):127–138
- Hester MW, Mendelssohn IA, McKee KL (2001) Species and population variation to salinity stress in *Panicum hemitomon*, *Spartina patens*, and *Spartina alterniflora*: morphological and physiological constraints. *Environ Exp Bot* 46:277–297
- Hinde HP (1954) The vertical distribution of salt marsh phanerogams in relation to tide levels. *Ecol Monogr* 24:209–225
- Hogle I (2011) San Francisco estuary invasive *Spartina* Project 2008–2009 Monitoring Report, ed. SFEISP State Coastal Conservancy, 1330 Broadway, 13th Floor, Oakland, CA 94612. Oakland CA. [http://www.spartina.org/project\\_documents/2008-09\\_MonReport\\_ALLwCover.pdf](http://www.spartina.org/project_documents/2008-09_MonReport_ALLwCover.pdf)
- Hovick SM, Whitney KD (2014) Hybridisation is associated with increased fecundity and size in invasive taxa: meta-analytic support for the hybridization invasion hypothesis. *Ecol Lett* 17:1464–1477
- Idaszkin YL, Bortolus A, Bouza PJ (2014) Flooding effect on the distribution of native austral cordgrass *Spartina densiflora* in Patagonian salt marshes. *J Coast Res* 30:59–62
- Janousek CN, Folger CL (2014) Variation in tidal wetland plant diversity and composition within and among coastal estuaries: assessing the relative importance of environmental gradients. *J Veg Sci* 25:534–545
- Josselyn M (1983) The ecology of San Francisco Bay tidal marshes: a community profile. US Fish and Wildlife Service, Division of Biological Services, Washington
- Kittelson PM, Boyd MJ (1997) Mechanisms of expansion for an introduced species of cordgrass, *Spartina densiflora*, in Humboldt Bay, California. *Estuaries* 20:770–778
- Lee CE (2002) Evolutionary genetics of invasive species. *Trends Ecol Evol* 17:386–391
- Mahall BE, Park RB (1976a) The ecotone between *Spartina foliosa* Trin. and *Salicornia virginica* L. in salt marshes of northern San Francisco Bay II. Soil water and salinity. *J Ecol* 64:793–809
- Mahall BE, Park RB (1976b) The ecotone between *Spartina foliosa* Trin. and *Salicornia virginica* L. in salt marshes of northern San Francisco Bay III. Soil aeration and tidal immersion. *J Ecol* 64:811–819
- Mateos-Naranjo E, Redondo-Gomez S, Luque CL, Castellanos EM, Davy AJ, Figueroa ME (2008) Environmental limitations on recruitment from seed in invasive *Spartina densiflora* on a southern European salt marsh. *Estuar Coast Shelf Sci* 79:727–732
- Mendelssohn IA, Morris JT (2000) Eco-physiological controls on the productivity of *Spartina alterniflora* Loisel. In: Weinstein MP, Kreeger DA (eds) Concepts and controversies in tidal marsh ecology. Kluwer, Norwell, MA, pp 59–79
- Nestler J (1977) Interstitial salinity as a cause of ecophenic variation in *Spartina alterniflora*. *Estuar Coast Mar Shelf Sci* 5:707–714
- Nieva FJJ, Díaz-Espejo A, Castellanos EM, Figueroa ME (2001) Field variability of invading populations of *Spartina densiflora* Brong. In different habitats of the Odiel Marshes (SW Spain). *Estuar Coast Shelf Sci* 52:515–527
- Nieva FJJ, Castillo JM, Luque CJ, Figueroa ME (2003) Eco-physiology of tidal and non-tidal populations of the invading cordgrass *Spartina densiflora*; seasonal and diurnal patterns in a Mediterranean climate. *Estuar Coast Shelf Sci* 57:919–928
- Olofson Environmental Inc. and San Francisco Estuary Invasive Spartina Project (2013) San Francisco Estuary Invasive Spartina Project Revegetation Program: 2012–2013 Installation Report and 2013–2014 Revegetation Plan, ed. SFEISP State Coast. Conserv. Oakland, CA. [http://www.spartina.org/documents/ISPRevegetation\\_2012-2013-2014\\_Final\\_111913\\_sm\\_000.pdf](http://www.spartina.org/documents/ISPRevegetation_2012-2013-2014_Final_111913_sm_000.pdf)
- Pennings SC, Callaway RM (1992) Salt marsh zonation: the relative importance of competition and physical factors. *Ecology* 73:681–690
- Pennings SC, Grant M-B, Bertness MD (2005) Plant zonation in low-latitude salt marshes: disentangling the roles of flooding, salinity and competition. *J Ecol* 93:159–167
- Pezeshiki SR, DeLaune RD (1995) Variation in response of two U.S. Gulf Coast populations of *Spartina alterniflora* to hypersalinity. *J Coast Res* 11:89–95
- Proffitt CE, Chiasson RL, Owens AB, Edwards KR, Travis SR (2005) *Spartina alterniflora* genotype influences facilitation and suppression of high marsh species colonizing an early successional marsh. *J Ecol* 93:404–416
- Rhymer JM, Simberloff D (1996) Extinction by hybridization and introgression. *Annu Rev Ecol Syst* 27:83–109
- Rieseberg LH, Archer MA, Wayne RK (1999) Transgressive segregation, adaptation and speciation. *Heredity* 83:363–372
- Rohmer T, Kerr D, Hogle I (2014) San Francisco Estuary Invasive *Spartina* Project 2012 ISP Monitoring and Treatment Report, ed. SFEISP State Coastal Conservancy, 1330 Broadway, 13th Floor, Oakland, CA 94612. Oakland CA. <http://www.spartina.org/documents/>

- Salmon A, Ainouche ML, Wendel JF (2005) Genetic and epigenetic consequences of recent hybridization and polyploidy in *Spartina* (Poaceae). *Mol Ecol* 14:1163–1175
- Seliskar DM (1995) Exploiting plant genetic diversity for coastal salt marsh creation and restoration. In: Khan MA, Ungar IA (eds) *Biology of salt tolerant plants*. Department of Botany, University of Karachi, Karachi, pp 407–416
- Sloop CM, Ayres DR, Strong DR (2010) The rapid evolution of self-fertility in *Spartina* hybrids (*S. alterniflora* × *foliosa*) invading San Francisco Bay, CA. *Biol Invasions* 11:1131–1144
- Spicher D, Josselyn M (1985) *Spartina* (Gramineae) in Northern California: distribution and taxonomic notes. *Madroño* 32:158–167
- Strong DR, Ayres DA (2016) Control and consequences of *Spartina* spp. invasions with focus upon San Francisco Bay. *Biol Inv.* doi:[10.1007/s10530-015-0980-6](https://doi.org/10.1007/s10530-015-0980-6)
- Strong DR, Ayres DR (2013) Ecological and evolutionary misadventures of *Spartina*. *Annu Rev Ecol Evol Syst* 44:389–410
- Thorne KM, Takekawa JY, Elliott-Fisk DL (2012) Ecological effects of climate change on salt marsh wildlife: a case study from a highly urbanized estuary. *J Coast Res* 28(6):1477–1487
- Thorne KM, Elliott-Fisk DL, Wylie GD, Perry WM, Takekawa JY (2014) Importance of biogeomorphic and spatial properties in assessing a tidal salt marsh vulnerability to sea-level rise. *Estuar Coasts* 37:941–951
- Trnka S, Zedler JB (2000) Site conditions, not parental phenotype, determine the height of *Spartina foliosa*. *Estuaries* 23(4):572–582
- Watson EB, Bryne R (2012) Recent (1975–2004) vegetation change in the San Francisco Estuary, California, tidal marshes. *J Coast Res* 28(1):51–63