

Will inundation and salinity levels associated with projected sea level rise reduce the survival, growth, and reproductive capacity of *Sarcocornia pacifica* (pickleweed)?

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ABSTRACT

In the San Francisco Bay Estuary, CA, USA, sea level rise (SLR) is projected to increase by 1.4 m during the next 90 years resulting in increased inundation and salt water intrusion up-estuary. Since inundation and salinity are critical factors that drive vegetation structure and composition in coastal wetlands, we asked whether inundation and salinity levels associated with SLR would reduce the survival, growth, and reproductive capacity of a dominant halophyte, *Sarcocornia pacifica* (pickleweed). We conducted a 4 × 4 factorial greenhouse experiment to examine the effects of a range of inundation periods (25, 50, 75, and 100%) and water salinities (0, 10, 20, 30 psu) on individual *S. pacifica* adults and seedlings. We found that inundation and salinity treatments affected the height of adults and seedlings combined. When examined separately, adult height was negatively affected by inundation ≥ 75%, while seedling height was affected by the interaction of both inundation and salinity. Adult belowground biomass was negatively affected by complete inundation. Seedling aboveground biomass decreased 46% at the highest salinity (30 psu) and belowground biomass decreased at salinities ≥ 20 psu. Adult flower production was not affected by treatments but was reduced by 38% at 30 psu salinity for seedlings. While adult survival was 99%, seedling survival was 56% with greatest mortality at low (25%) inundation, possibly because their roots were more susceptible to desiccation. Vegetation structure of the marsh platform comprised of *S. pacifica* adults will be susceptible to greater inundation rates associated with SLR. Our results suggest that adults may grow less tall, thus altering the vegetation structure and likely the tidal marsh wildlife that rely on these habitats.

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1. Introduction

Tidal marsh plant communities are distributed along salinity and inundation gradients which are largely determined by marsh elevation and tidal inundation rates (Mahall and Park, 1976a, 1976b; Atwater et al., 1979; McKee and Mendelssohn, 1989; Adams and Bate, 1994; Baldwin and Mendelssohn, 1998), tidal channels (Sanderson et al., 2000), and biotic interactions such as plant competition (Pennings and Callaway, 1992; Pennings et al., 2005). At low elevations within a tidal marsh, plants are stressed by excessive inundation and anaerobic conditions affecting productivity and survival (Mahall and Park, 1976a, 1976b, 1976c; Spalding and Hester, 2007). Elevation changes of several centimeters may lead to a shift in plant species and habitat structure of the marsh platform (Mahall and Park, 1976a; Adam, 1990; McKee and Mendelssohn, 1989; Zedler et al., 1999; Baldwin et al., 2001).

Increasing salinity and inundation under projected SLR (Cloern et al., 2011) may affect plant species that are already at their upper limits of physical tolerance and alter their competitive ability. Ultimately, salinity changes may lead to shifts in plant composition, especially in freshwater and brackish tidal marshes that become more saline (Atwater et al., 1979; McKee and Mendelssohn, 1989; Baldwin et al., 2001; Pennings et al., 2005). Changes in salinity in combination with inundation may cause shifts in both plant composition and productivity, and the resulting differences may be reflected in community structure.

Along the Pacific coast of North America, the San Francisco Bay Estuary (SFBE) comprises the largest expanse of remaining tidal marsh in California, despite loss of over 80% of its historic tidal marsh extent (Goals Project, 1999). Recent large-scale (>14,000 ha) tidal marsh restoration projects seek to reverse this habitat loss, ameliorate ongoing threats (Takekawa et al., 2006), and advance the recovery of endemic species (USFWS, 2010). Relative sea-level rise is projected to increase by up to 1.4 m in SFBE during the next 90 years (Heberger et al., 2009) altering inundation and salinity regimes as sea water moves up-estuary. In urbanized coastal areas such as SFBE (Nichols et al., 1986), development may prevent salt

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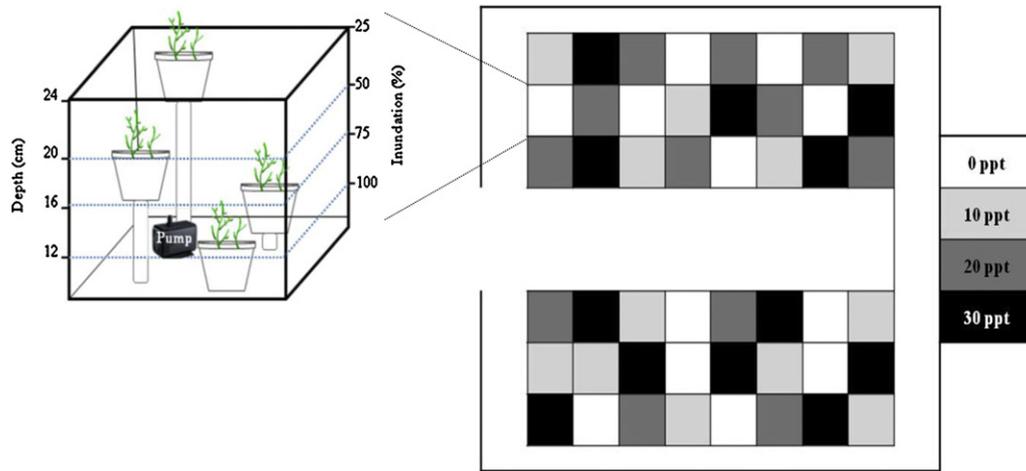


Fig. 1. Randomized block design to examine effects of salinity and inundation on the growth of *Sarcocornia pacifica*. Plants were grown under four salinity (0, 10, 20, and 30 psu) and four inundation (25, 50, 75, and 100%) treatments for 16 total combinations replicated 12 times ($n = 192$). We simulated the 24-h, semi-diurnal tidal cycle found in San Francisco Bay by filling aquaria from reservoir tanks containing the four different salinity levels through pumps controlled by digital timers on a 1.5 h schedule. In each of 48 aquaria, a pot with an adult and a seedling was inundated for 25, 50, 75, or 100% of a 24-h day by elevating it 12, 16, 20, or 24 cm from the bottom. Aquaria were randomly assigned to locations on two benches within a greenhouse at the San Francisco Bay Estuary Field Station in Vallejo, CA and measured throughout the growing season (April–August).

marshes from migrating inland to higher elevations as sea level rises effectively reducing salt marsh zones in a phenomenon known as “coastal squeeze.”

Common pickleweed *Sarcocornia pacifica* (Standley), formerly known as *Salicornia virginica* (plant nomenclature follows eFloras, 2008), is a perennial succulent halophyte that is the dominant species of tidal salt marshes in SFBE (Atwater et al., 1979; Cuneo, 1987; Goals Project, 1999). Interspersed with patches of *Spartina foliosa* in the lower elevations, *Grindelia* spp. near channels, and *Frankenia salina* and *Baccharis pilularis* in higher elevations, *S. pacifica* forms the matrix species of the marsh landscape. In this study, we developed a greenhouse experiment to test whether inundation and salinity expected with SLR would affect the survival, growth, and reproductive capacity of *S. pacifica* adults and seedlings. Our null hypothesis was that elevated salinity and increased inundation or their interaction would not affect the growth of pickleweed.

2. Methods

2.1. Experimental design

We conducted a 4×4 factorial experiment to test the effects of salinity (0, 10, 20, and 30 psu) and inundation (25, 50, 75, and 100%) on *S. pacifica* adults and seedlings in a randomized block design (Fig. 1). We restricted the salinities from 0 to 30 psu, because that is a range commonly observed at our study sites in the northern reach of the estuary. We replicated ($n = 12$) the 16 unique salinity and inundation combinations for a total sample of 192 pots. Salinity and inundation ranges were selected to represent the variation currently observed in SFBE, although future conditions may be more extreme. The greenhouse was located at the U.S. Geological Survey, San Francisco Bay Estuary Field Station in Vallejo, CA, USA (38.11°N, 122.29°W). The greenhouse replicated natural light and temperature conditions while controlling other factors including herbivory that could confound experimental manipulations by affecting plant biomass. Average summer day length was 13.5 h, and high and low temperatures were 24.8 °C and 9.5 °C, respectively (Napa County Airport, 12 km north; <http://www.wunderground.com>).

2.2. Specimen collection

Adult and seedling plants were collected from the Guadalcanal Restoration Project site located 2 km north of the field station (38.12°N, 122.29°W). The restoration site was restored to tidal flow on 31 October 2001, and plants first colonized the site in 2002 (Woo et al., 2009). Plants collected from this single location may not be representative of the entire region, but we are unaware of studies of genetic variation in *S. pacifica* populations within SFBE. Adult plants were collected in April 2003, had woody bases, and were at least one-year old, while seedlings had germinated that year and were less than one-month old (Electronic supplementary material 1).

The plants were gathered from within the marsh plain and were rinsed to remove the soil from their roots. We measured the height, number of branches, and wet weight of each plant, but a preliminary analysis of covariance indicated that they were not related to subsequent growth and thus were not included in further analyses. Soil was collected from several different areas of the restoration site and homogenized in a cement mixer. Our experimental unit was a greenhouse pot ($h = 20$ cm, $r = 12.5$ cm) that consisted of one adult plant and one seedling and filled to the top with homogenized soil. We trimmed adults to a standardized height of 15 cm and maximum root length of 5–8 cm prior to being planted so we could assess treatment effects on monthly growth. Plants were conditioned (daily watering with freshwater) prior to treatment to reduce transplant shock, and we found no transplant-related mortality after one week. Treatments spanned the growing season (April–September), and plants were inspected during monthly height measurements and survival observations (April–August). Survival, number of branches, flower production, and biomass were collected in September. We did not detect any signs of herbivory during monthly measurements and visual inspections.

2.3. Salinity

We filled four 378.5-L plastic tanks with tap water and mixed in Instant Ocean Sea Salt (Aquarium System, Inc., Mentor, OH, USA) to achieve salinities desired for the experimental treatments. The salinity reservoirs were buried underground and covered to reduce sun and heat exposure, and a series of pumps delivered the water to

pots situated in glass aquaria (37.9 L, 25 cm × 25 cm × 30 cm). Four salinity treatments (0, 10, 20, and 30 psu) were replicated in 48 aquaria randomly placed on two greenhouse benches. We checked salinity reservoirs weekly with a refractometer and added fresh water to maintain desired salinity levels.

2.4. Inundation

We simulated a semi-diurnal tide cycle for each of the four salinity treatments with separate sets of pumps controlled by a digital timer. Water levels inside each aquarium were maintained at a base height of 12.5 cm. Within each of the 48 aquaria, four pots were randomly placed on PVC blocks of different heights so that the top of the pot was at 12, 16, 20, or 24 cm and each pot experienced a different inundation regime (Fig. 1). Water from the 0, 10, 20, and 30 psu salinity reservoirs was pumped into each aquarium via black irrigation tubing with a 1.4-A Pony Pump (Proven Pumps, Los Angeles, CA). We used emitters (18.9 L/min) to establish a uniform flow rate regardless of distance from the pump, and water was pumped in for 7 min at 1.5-h intervals.

Each aquarium was equipped with its own 0.3-A fountain pump (Via Aqua Fountain Pump, Commodity Axis, Inc., Camarillo, CA) to pump water out for 1 min at 1.5-h intervals. Each fountain pump was adjusted by hand so that water was pumped out at the same rate and remained at 24 cm for 3 h, 20 cm for 6 h, 16 cm for 9 h, and 12 cm for 12 h during each 12-h cycle. That semi-daily tidal cycle was then repeated using digital timers to simulate a continuous cycle, although we did not alter the inundation pattern to reflect natural variation or changes across 14-day cycles. Thus, daily inundation treatments included 25% (6 h), 50% (12 h), 75% (18 h), and 100% (24 h) (Fig. 1). In relation to tidal datums, the 25% treatment would roughly correspond to inundation at Mean Low Water, 50% at Mean Tide Level, 75% at Mean High Water, and 100% at Mean Higher High Water.

2.5. Data analyses

Soil samples were collected in April 2003 to characterize initial soil conditions (soil texture, organic matter content, and pH) and sent to A&L Western Agricultural Laboratories (Modesto, CA) for analyses. Additional soil samples were collected with soil tins (70 cm³ volume), weighed for both wet and dry soil moisture content, and analyzed for bulk density. In addition, three natural marshes within 10 km were sampled in April 2004 and used to compare bulk density and soil moisture content.

We used repeated-measures ANOVA to assess the main effects of inundation and salinity and their interaction on the combined height of adults and seedlings by pot. If treatment effects were significant, we then examined separate measurements for adults and seedlings to identify differences (see Jutila and Grace, 2002), but we did not control for competitive or facilitative interactions within a pot. In addition, we did not have control pots with adults and zero seedlings or with seedlings and zero adults. However, we tested for interactions by regressing adult versus seedling height. To assess plant growth, biomass, canopy structure, and reproductive potential, we measured maximum height, number of branches (above 15 cm for adults, total branches for seedlings), and number of flowers produced each month. Above- and belowground dry biomass, was collected at the end of the season.

We analyzed the main effects of salinity and inundation and their interaction with analysis of variance (ANOVA: STATISTICA v. 8, StatSoft Corp., Tulsa, OK) and reported the mean ± SE for growth parameters. Data were log₁₀ transformed (above- and belowground biomass, height) or square-root transformed (number of flowers) to meet assumptions of normality and equal variances under Levene's test. A repeated-measures ANOVA was used

to assess treatment effects and interactions on maximum plant heights over time. Where main effects and no interaction effects were detected, differences among treatment levels were compared with post hoc Tukey's HSD multiple comparisons ($\alpha = 0.05$).

We assessed the effects of salinity and inundation on estimated survival (\hat{S}) by applying a Kaplan–Meier, known-fates model (Program MARK; White and Burnham, 1999). We evaluated the relative support for different survival models by month, inundation, salinity, and the interaction of inundation and salinity with Akaike's Information Criterion for small sample sizes (AIC_c; Akaike, 1973). We built a set of a priori candidate models where k was the number of parameters, and the model with the smallest AIC_c was considered to be the most parsimonious (Burnham and Anderson, 1998). We used the differences between the AIC_c value of the best model and other candidate models (ΔAIC_c) to determine the relative ranking of each model and considered all models where $\Delta\text{AIC}_c < 7.0$. We used Akaike weights (w_i) to assess the evidence that the selected model was the best of the candidate models, and we presented the model-averaged estimates for survival.

3. Results

Soil analyses indicated that samples used for experimental treatments were consistent between batches. Soil texture was classified as clayey: 12% sand, 29% silt, and 59% clay. Soil organic matter from the restoration site was $3.4 \pm 0.04\%$, a relatively low content commonly seen at new wetland restoration sites within San Pablo Bay (Woo et al., 2007). Soil pH was slightly acidic at 6.3 ± 0.05 , bulk density was $0.8 \pm 0.01 \text{ g/cm}^{-3}$ and moisture content was $33 \pm 2\%$. Soil samples collected from natural marshes in the northern estuary (19, 20, and 20 samples collected from three marshes in April 2004) had lower soil bulk density ($0.5 \pm 0.02 \text{ g/cm}^{-3}$) and higher soil moisture content ($51 \pm 1\%$), and their organic matter content has been reported at 10–11% (Reynolds and Boyer, 2010).

We detected significant differences in combined height growth of adults and seedlings within a pot under different salinity and inundation treatments, while the interaction term was not significant (Table 1). We found no correlation between adult and seedling aboveground biomass ($R^2 = 0.011$), belowground biomass ($R^2 = 0.005$), and total biomass ($R^2 = 0.004$) that could indicate a competitive effect within pots. Thus, we assumed that competitive or facilitative interactions within pots was negligible and reported results for analyses of adult and seedling growth separately.

3.1. Effects on adults

Inundation had a negative effect on height ($F_{3,174} = 16.12$, $P < 0.001$), although we detected no relationship of height with salinity nor the interaction between inundation and salinity (Table 1). Adults that were inundated the least grew the tallest, especially early in the growing season. Tukey's HSD tests revealed that plants inundated 25% of the time grew significantly taller than those inundated 100% of the time ($P < 0.001$). Plants inundated 50% of the time were also taller than those inundated 75% ($P = 0.030$, Fig. 2). Adults experiencing $\geq 75\%$ inundation were 11% shorter, and by the end of the experiment, plants in 100% inundation were significantly shorter than plants grown in any of the partially inundated treatments (Fig. 2 and Electronic supplementary material 2).

Aboveground biomass was linearly correlated with total biomass (for both adults and seedlings; $R^2 = 0.978$, where total biomass = $1.411 \times$ aboveground biomass). Aboveground biomass was not affected by salinity (Table 1), but belowground biomass was negatively affected ($F_{3,167} = 4.70$, $P = 0.004$) and positively affected by inundation ($F_{3,167} = 4.42$, $P = 0.005$). Belowground biomass was greater in fresh water (0 psu; $4.3 \pm 0.3 \text{ g}$) compared

Table 1

Salinity, inundation, and salinity \times inundation interaction effects on the mean growth (height), biomass, canopy structure (branches), and reproductive potential (number of flowers) of seedling and adult *Sarcocornia pacifica*. Repeated measure ANOVAs were used to examine treatment effects after data were log or root transformed to meet assumptions of normality and equal variances.

Effect	Salinity	Inundation	Interaction
Whole pot			
Height	$F_{15,470} = 3.00 P < 0.001$	$F_{15,470} = 2.42 P = 0.002$	$F_{45,764} = 0.84 P = 0.772$
Adults			
Height	$F_{3,174} = 0.79 P = 0.499$	$F_{3,174} = 16.12 P < 0.001$	$F_{9,174} = 16.36 P = 0.208$
Aboveground biomass	$F_{3,176} = 0.37 P = 0.756$	$F_{3,176} = 0.25 P = 0.858$	$F_{9,176} = 1.06 P = 0.398$
Belowground biomass	$F_{3,167} = 4.70 P = 0.004$	$F_{3,167} = 4.42 P = 0.005$	$F_{9,167} = 1.28 P = 0.250$
Branches (>15 cm)	$F_{3,747} = 4.13 P = 0.006$	$F_{3,747} = 4.54 P = 0.004$	$F_{9,747} = 2.74 P = 0.004$
Flower production	$F_{3,176} = 0.69 P = 0.561$	$F_{3,176} = 0.34 P = 0.798$	$F_{9,176} = 0.73 P = 0.680$
Seedlings			
Height	$F_{3,74} = 7.52 P < 0.001$	$F_{3,74} = 8.39 P < 0.001$	$F_{9,74} = 3.07 P = 0.004$
Aboveground biomass	$F_{3,100} = 5.35 P = 0.002$	$F_{3,100} = 2.21 P = 0.092$	$F_{9,100} = 1.80 P = 0.078$
Belowground biomass	$F_{3,97} = 3.18 P = 0.027$	$F_{3,97} = 0.26 P = 0.857$	$F_{9,97} = 1.24 P = 0.282$
Branches (total #)	$F_{5,59} = 1.49 P = 0.205$	$F_{10,118} = 1.05 P = 0.410$	$F_{35,251} = 1.08 P = 0.354$
Flower production	$F_{1,73} = 10.45 P = 0.002$	$F_{2,73} = 1.83 P = 0.168$	$F_{7,73} = 0.75 P = 0.627$

to 20 psu (3.4 ± 0.2 g) or 30 psu (3.2 ± 0.2 g) salinities (Tukey's HSD, $P < 0.05$). Belowground biomass was greatest under 100% inundation (4.2 ± 0.3 g) compared to 25% (3.2 ± 0.2 g) and 50% (3.2 ± 0.2 g) inundation (Tukey's HSD, $P < 0.05$). Inundation positively influenced belowground biomass ($F_{3,167} = 4.42$, $P = 0.005$), but had no effect on aboveground biomass. There was no interaction between inundation and salinity on above- or belowground biomass (Table 1).

The number of mid-canopy branches (located above 15 cm) was affected by the interaction of salinity and inundation ($F_{9,747} = 2.74$, $P = 0.004$). The number of branches in the mid-canopy was negatively affected by salinity, and those grown in 30 psu had 25% fewer mid-canopy branches than those grown in fresh water. In contrast, inundation positively affected the number of mid-canopy

branches: adults grown in 25% inundation had 9.1 ± 0.6 branches while those grown in 100% inundation had 12.4 ± 0.8 branches. The greatest number of branches was detected in fresh water at 100% inundation (16.5 ± 2.3 branches) and was similar to those grown in intermediate salinity and inundation (20 psu with 75% inundation: 16.2 ± 2.3 branches).

Reproductive potential and survival were not affected by treatment (Table 1). Flower production was not significantly affected by salinity, inundation, or their interaction. Only two plants died while 99% survived during the experiment which precluded testing the relationship of adult survival by treatment. One adult died during July in a 20-psu salinity and 25% inundation treatment, while the second died in August in a 10-psu salinity and 25% inundation treatment.

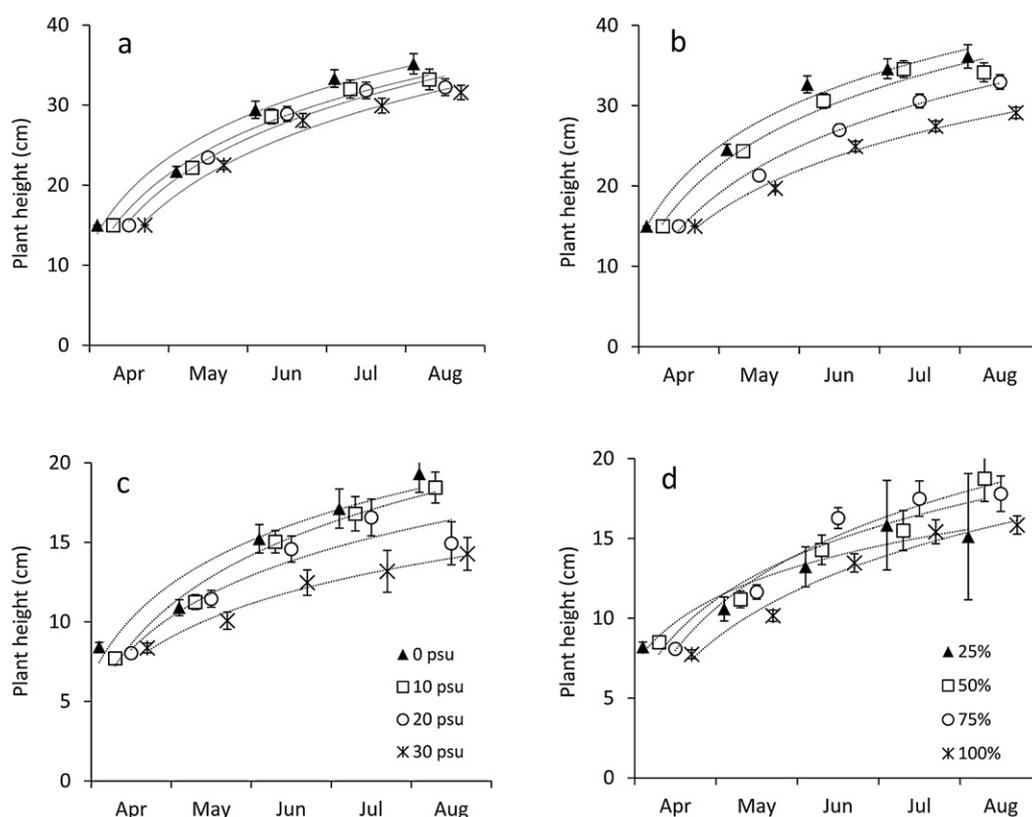


Fig. 2. Effects of four salinity (0, 10, 20, 30 psu) and four inundation (25, 50, 75, 100%) treatments on growth (height, in cm) of *S. pacifica* adults (a and b) and seedlings (c and d) across a growing season (April–August).

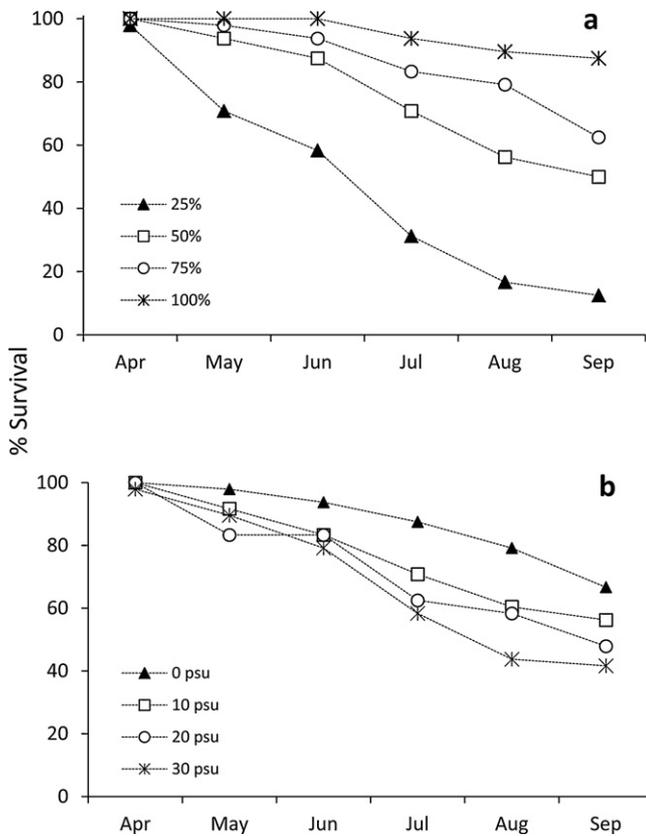


Fig. 3. Differences in survival of *S. pacifica* seedlings during the growing season (April–September) exposed to (a) four inundation periods (25, 50, 75, and 100%) and (b) four salinity treatments (0, 10, 20, and 30 psu) in a greenhouse experiment. Period survival was estimated with a Kaplan–Meier, known-fates model in Program Mark (White and Burnham, 1999).

3.2. Effects on seedlings

Seedling survival was 56% and positively associated with increased inundation while negatively associated with increased salinity. Seedling mortality was greatest (87% mortality) in the lowest inundation treatment (25% inundation; Fig. 3). The top models included the additive effects of month, salinity, and inundation ($w_i = 0.980$, Table 2). The model-averaged probability estimate of survival was $56 \pm 5\%$.

Survival was higher in the first two months ($\hat{S} = 95 \pm 2\%$ for May and $96 \pm 1\%$ for June) than the last three months ($\hat{S} = 85 \pm 3\%$ in July, $86 \pm 3\%$ in August, and $85 \pm 4\%$ in September). Survival was positively related to increased inundation (100% inundation: $\beta = 3.32 \pm 0.48$), and negatively related to increased salinity (30 psu: $\beta = -1.24 \pm 0.36$; Fig. 3). Seedlings subjected to 25% inundation had the lowest rate of survival (Fig. 3). Of those that survived, inundation had no effect on above- or belowground biomass (Table 1).

We detected significant interactive effects of salinity and inundation on seedling height ($F_{9,74} = 3.07$, $P = 0.004$). Mean height was greatest in freshwater and intermediate levels of inundation (0 psu, 75% inundation: 15.6 ± 0.9 cm; 0 psu, 50% inundation: 14.2 ± 0.8 cm; Fig. 2). Height was significantly greater ($P = 0.01$) in freshwater compared with 30 psu (Fig. 2 and Electronic supplementary material 2), and conversely, the shortest seedlings were detected at the highest salinities (30 psu) in each month. Seedlings in freshwater were almost 30% taller (19.0 ± 1.2 cm) than those in the 30 psu salinity (13.4 ± 1.0 cm).

Increasing salinity led to lower aboveground ($F_{3,100} = 5.35$, $P = 0.002$) and belowground ($F_{3,97} = 3.18$, $P = 0.027$) biomass. Seedlings grown in freshwater (0.28 ± 0.04 g) had significantly

greater aboveground biomass than those grown in 30 psu (0.15 ± 0.03 g; $P = 0.024$). Similarly, belowground biomass was greater in fresh water (0.04 ± 0.01 g) compared to 30 psu (0.01 ± 0.00 g; $P = 0.048$).

We did not detect any treatment effects or interactions on the total number of branches (Table 1); however, those grown in fresh water had the greatest number of branches (7.6 ± 0.3 branches). There was a strong, negative effect of salinity on flower production ($F_{1,173} = 10.45$, $P = 0.002$), with a 38% decline from the freshwater treatments to the 30 psu treatment ($P = 0.02$). The number of flowers was not affected by inundation or the interaction of salinity and inundation.

4. Discussion

We found that inundation and salinity affected the height of both adult and seedling pickleweed plants. Assuming that effects of within-pot competition were minimal, our results indicate that adult height was negatively affected with greater inundation, while seedling height was affected by the interaction of inundation and salinity. With increasing inundation, adult belowground biomass decreased, while aboveground and belowground biomass of seedlings decreased with increasing salinity. Adult flower production did not differ by treatment, but seedling flower production was reduced at highest salinities. Almost all adults survived, but seedling survival decreased with increasing salinity with greatest mortality at lowest inundation levels.

SLR projections include short term increase in the productivity of C4 *Spartina* marshes (Kirwan et al., 2009); however, our study does not support this finding for pickleweed, a C3 plant. Shorter adult heights in response to increased inundation from SLR may result in pickleweed becoming more vulnerable to competitive displacement (Pennings and Callaway, 1992; Callaway and Zedler, 1998). Although increased inundation favors seedling survival, the potential for greater inundation with SLR in areas of coastal squeeze will likely result in a loss of overall tidal marsh extent. We found that seedling survival was positively associated with increased inundation and negatively associated with increased salinity.

Since newly developed marshes typically have low levels of soil organic matter (Craft et al., 2003; Woo et al., 2009), they have reduced water-holding capacity. Thus, if SLR leads to marsh migration, seedlings may establish in new areas slower than would be predicted when compared with mature areas with greater soil organic matter. Greater soil salinities in shallow root zones (Anisfeld and Benoit, 1997) may adversely affect subsequent pickleweed growth. Increased salinity also reduces flowering capacity of seedlings, but this effect may be negligible since *S. pacifica* produces a prolific amount of seeds ($>15,000$; Lindig-Cisneros and Zedler, 2002).

The viability of tidal marsh restorations and conservation of current marshes may increasingly rely on their location within the landscape in relation to levees or water control structures and available sediment supply. Sediment management may be a key feature of successful future restoration as use of dredge material may become increasingly important as a tool in marsh creation and upland wildlife refugia (Yozzo et al., 2004).

Identifying environmental thresholds that cause changes in plant growth and structure also defines important thresholds for wildlife habitat (see Takekawa et al., 2006, 2011). Although we focused our study on observed conditions rather than extreme events, we detected distinct morphological and reproductive responses in adult and seedling life stages associated with moderate salinity and inundation levels expected with SLR. If increased inundation results in reduced overall height and decreased canopy cover, it may increase the risk of tidal marsh species to predation or

Table 2

Ranking of candidate models describing results for *S. pacifica* seedling survival (\hat{S}) under varying inundation and salinity treatments, where $\Delta AIC_c < 7.0$. Survival was examined monthly during the growing season at four inundation treatment levels (25, 50, 75, and 100%), four salinity concentrations (0, 10, 20, and 30 psu), and including the interaction term of salinity \times inundation. The null model (intercept only) and full model (all parameters) were also reported.

Model	ΔAIC_c^a	w_i^b	k^c
\hat{S} (Month + Salinity + Inundation) ^d	0.000	0.980	11
\hat{S} (Month + Inundation)	7.819	0.020	8
\hat{S} (Month + Salinity + Inundation + Salinity \times Inundation)	15.402	0.000	20
\hat{S} (Salinity + Inundation)	15.946	0.000	7
\hat{S} (Inundation)	20.960	0.000	4
\hat{S} (Salinity + Inundation + Salinity \times Inundation)	31.166	0.000	16
\hat{S} (Month + Salinity)	74.217	0.000	8
\hat{S} (Month)	76.721	0.000	5
\hat{S} (Salinity)	79.040	0.000	4
\hat{S} (-)	80.975	0.000	1

^a The difference between the AIC_c of a given model and the lowest AIC_c in the set of candidate models.

^b AIC_c weights indicate the likelihood that a given model is the best model in the set of competing models given the data.

^c Number of parameters.

^d Top model; $AIC_c = 478.683$.

drowning (Takekawa et al., 2006). Species that may be particularly vulnerable to reduced vegetation structure are those with limited dispersal ability or high site fidelity, such as the state threatened California black rail (*Laterallus jamaicensis coturniculus*).

In SFBE, the marsh platform is completely submerged during extreme high tide so that only the top of the tallest plants are above water, forming temporary “islands” of refugia for tidal marsh inhabitants. Notable levels of predation have been observed on the state threatened California black rail during these flood events (Evens and Page, 1986). Canopy structure is also important for the reproductive success of tidal marsh birds. Nests placed higher within the canopy to reduce nest failure due to flooding can be more vulnerable to predation because the nests are more visible to predators (Greenberg et al., 2006; Takekawa et al., 2006; Rush et al., 2010). Breeding black rails selected areas of *S. pacifica* that were taller and denser than average (Tsao et al., 2009) and the endangered salt marsh harvest mouse (*Reithrodontomys raviventris*), is dependent on dense, tall *S. pacifica* (Shellhammer et al., 1982) and forbs (Bias and Morrison, 2006). Greater branching of pickleweed that we observed with increased inundation may not provide sufficient cover at heights valuable to protect breeding sites or as high tide refugia (Zedler, 1993).

With salinity intrusion up-estuary, freshwater marshes will likely be converted to brackish marshes, and brackish marshes will be converted to salt marsh (McKee and Mendelsohn, 1989). Shifts in vegetation may lead to changes in productivity, foodweb composition, and habitat structure. Changes in estuarine plant productivity and decomposition rates may lead to cascading effects on food-web support and organic matter inputs to marsh soils that may help marshes “keep up” with SLR (Kwak and Zedler, 1997; Callaway et al., 2007).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.aquabot.2012.03.014>.

References

- Adam, P., 1990. Salt Marsh Ecology. Cambridge University Press, New York, NY, US.
- Adams, J.B., Bate, G.C., 1994. The effect of salinity and inundation on the estuarine macrophyte *Sarcocornia perennis* (Mill.) A.J. Scott. Aquatic Botany 47, 341–348.
- Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In: Petran, B.N., Csaki, F. (Eds.), International Symposium on Information Theory. 2nd ed. Akademiai Kiado, Budapest, HU, pp. 267–281.
- Anisfeld, S., Benoit, G., 1997. Impacts of flow restrictions on salt marshes: an instance of acidification. Environmental Science and Technology 31, 1650–1657.
- Atwater, B.F., Conard, S.G., Dowden, J.N., Hedel, C.W., MacDonald, R.L., Savage, W., 1979. History, landforms, and vegetation of the estuary's tidal marshes. In: Conomos, T.J. (Ed.), San Francisco Bay: The Urbanized Estuary. pp. 347–385.
- Baldwin, A.H., Mendelsohn, I.A., 1998. Effects of salinity and water level on coastal marshes: an experimental test of disturbance as a catalyst for vegetation change. Aquatic Botany 61, 255–268.
- Baldwin, A.H., Egnotovich, M.S., Clarke, E., 2001. Hydrologic change and vegetation of tidal freshwater marshes: field, greenhouse, and seed-bank experiments. Wetlands 21, 519–531.
- Bias, M.A., Morrison, M.L., 2006. Habitat selection of the salt marsh harvest mouse and sympatric rodent species. Journal of Wildlife Management 70, 732–742.
- Burnham, K.P., Anderson, D.R., 1998. Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York, USA.
- Callaway, J.C., Parker, V.T., Vasey, M.C., Schile, L.M., 2007. Emerging issues for the restoration of tidal marsh ecosystems in the context of predicted climate change. Madroño 54, 234–248.
- Callaway, J.C., Zedler, J.B., 1998. Interactions between a salt marsh native perennial (*Salicornia virginica*) and an exotic annual (*Polypogon monspeliensis*) under varied salinity and hydroperiod. Wetlands Ecology and Management 5, 179–194.
- Cloern, J.E., Knowles, N., Brown, L.R., Cayan, D., Dettinger, M.D., Morgan, T.L., Schoellhamer, D.H., Stacey, M.T., van der Wagen, M., Wagner, R.W., Jassby, A.D., 2011. Projected evolution of California's San Francisco Bay Delta River System in a century of climate change. PLoS ONE 6, e24465.
- Craft, C.B., Megonigal, J.P., Broome, S.W., Cornell, J., Freese, R., Stevenson, R.J., Zheng, L., Sacco, J., 2003. The pace of ecosystem development of constructed *Spartina alterniflora* marshes. Ecological Applications 13, 1417–1432.
- Cuneo, K., 1987. San Francisco Bay salt marsh vegetation, geography, and ecology: a baseline for use in impact assessment and restoration planning. Ph.D. Dissertation. Univ. of Calif., Berkeley, Berkeley, CA.
- eFloras, 2008. Missouri Botanical Garden, St. Louis, MO & Harvard University Herbaria, Cambridge, MA. <http://www.efloras.org> (accessed 21.10.11).
- Evens, J., Page, G., 1986. Predation on Black Rails during high tides in salt marshes. Condor 88, 107–109.
- Goals Project, 1999. Baylands Ecosystem Habitat Goals. A report of habitat recommendations prepared by the San Francisco Bay Area Wetlands Ecosystem Goals Project. U.S. Environmental Protection Agency, San Francisco, CA/S.F. Bay Regional Water Quality Control Board, Oakland, CA.
- Greenberg, R., Elphick, C., Nordby, J.C., Gjerdrum, C., Spautz, H., Shriver, G., Schmelting, B., Olsen, B., Marra, P., Nur, N., Winter, M., 2006. Flooding and predation:

- trade-offs in the nesting ecology of tidal-marsh sparrows. *Studies in Avian Biology* 32, 96–109.
- Heberger, M., Cooley, H., Herrera, P., Gleick, P.H., Moore, E., 2009. The impacts of sea-level rise on the California coast. California Climate Change Center Final Paper CEC-500-2009-024-F, Sacramento, CA. 115 pp.
- Jutila, H.M., Grace, J.B., 2002. Effects of disturbance on germination and seedling establishment in a coastal prairie grassland: a test of the competitive release hypothesis. *Journal of Ecology* 90, 291–302.
- Kirwan, M., Guntenspergen, G.R., Morris, J.T., 2009. Latitudinal trends in *Spartina alterniflora* productivity and the response of coastal marshes to global change. *Global Change Biology* 15, 1982–1989.
- Kwak, T.J., Zedler, J.B., 1997. Food web analysis of southern California coastal wetlands using multiple stable isotopes. *Oecologia* 110, 262–277.
- Lindig-Cisneros, R., Zedler, J.B., 2002. Halophyte recruitment in a salt marsh restoration site. *Estuaries* 25, 1174–1183.
- Mahall, B.E., Park, R.B., 1976a. The ecotone between *Spartina foliosa* Trin. and *Salicornia virginica* L. in salt marshes of northern San Francisco Bay. I. Biomass and production. *Journal of Ecology* 64, 421–433.
- Mahall, B.E., Park, R.B., 1976b. The ecotone between *Spartina foliosa* Trin. and *Salicornia virginica* L. in salt marshes of northern San Francisco Bay. II. Soil water and salinity. *Journal of Ecology* 64, 793–809.
- Mahall, B.E., Park, R.B., 1976c. The ecotone between *Spartina foliosa* Trin. and *Salicornia virginica* L. in salt marshes of northern San Francisco Bay. III. Soil aeration and tidal immersion. *Journal of Ecology* 64, 811–819.
- McKee, K.L., Mendelssohn, I.A., 1989. Response of a freshwater marsh plant community to increased salinity and increased water level. *Aquatic Botany* 34, 301–316.
- Nichols, F.H., Cloern, J.E., Luoma, S.N., Peterson, D.H., 1986. The modification of an estuary. *Science* 231, 567–573.
- Pennings, S.C., Bestor-Grant, M., Bertness, M.D., 2005. Plant zonation in low-latitude salt marshes: disentangling the roles of flooding, salinity, and competition. *Journal of Ecology* 93, 159–167.
- Pennings, S.C., Callaway, R.M., 1992. Salt marsh plant zonation: the relative importance of competition and physical factors. *Ecology* 73, 681–690.
- Reynolds, L.K., Boyer, K.E., 2010. Perennial pepperweed (*Lepidium latifolium*): properties of invaded tidal marshes. *Invasive Plant Science and Management* 3, 130–138.
- Rush, S.A., Woodrey, M.S., Cooper, R.J., 2010. Variation in the nesting habits of clapper rails in tidal marshes of the northern Gulf of Mexico. *Condor* 112, 356–362.
- Sanderson, E.W., Ustin, S.L., Foin, T.C., 2000. The influence of tidal channels on the distribution of salt marsh plant species in Petaluma Marsh, CA, USA. *Plant Ecology* 146, 29–41.
- Shellhammer, H.S., Jackson, R., Davilla, W., Gilroy, A.M., Harvey, H.T., Simons, L., 1982. Habitat preferences of salt marsh harvest mice (*Reithrodontomys raviventris*). *Wasmann Journal of Biology* 40, 102–114.
- Spalding, E.A., Hester, M.W., 2007. Interactive effects of hydrology and salinity in oligohaline plant species productivity: implications of relative sea-level rise. *Estuaries and Coasts* 30, 214–225.
- StatSoft Inc., 2001. STATISTICA, Version 6., www.statsoft.com.
- Takekawa, J.Y., Woo, I., Gardiner, R., Casazza, M., Ackerman, J.T., Nur, N., Liu, L., Spautz, H., 2011. Bird communities in tidal salt marshes of San Francisco Bay. *San Francisco Estuary and Watershed Science* 9, 2–24.
- Takekawa, J.Y., Woo, I., Spautz, H., Nur, N., Grenier, J.L., Malamud-Roam, K., Nordby, J.C., Cohen, A.N., Malamud-Roam, F., Wainwright-De La Cruz, S.E., 2006. Environmental threats to tidal marsh vertebrates in the San Francisco Bay estuary. *Studies in Avian Biology* 32, 176–197.
- Tsao, D.C., Takekawa, J.Y., Woo, I., Yee, J.L., Evens, J.G., 2009. Home range, habitat selection, and movements of California black rail at tidal marshes at San Francisco Bay, California. *Condor* 111, 599–610.
- U.S. Fish and Wildlife Service, 2010. Draft Recovery Plan for Tidal Marsh Ecosystems of Northern and Central California. U.S. Fish and Wildlife Service, Sacramento, CA, xviii + 636 pp.
- White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46, S120–S139.
- Woo, I., Dembosz, L.S., Gardiner, R., Takekawa, J.Y., 2009. Early phase tidal marsh progression: the Guadalcanal tidal marsh restoration project. Data Summary Report, U.S. Geological Survey, Western Ecological Research Center, San Francisco Bay Estuary Field Station, Vallejo, CA.
- Woo, I., Takekawa, J.Y., Rowan, A., Gardiner, R., Bernstein, O., Block, G.T., 2007. The Tubbs Setback Restoration Project: Final Report. U.S. Geological Survey, Unpubl. Progress Rep., Vallejo, CA.
- Yozzo, D.J., Wilber, P., Will, R.J., 2004. Beneficial use of dredge material for habitat creation, enhancement, and restoration in New York – New Jersey Harbor. *Journal of Environmental Management* 73, 39–52.
- Zedler, J.B., 1993. Canopy architecture of natural and planted cordgrass marshes: selecting habitat evaluation criteria. *Ecological Applications* 3, 123–138.
- Zedler, J.B., Callaway, J.C., Desmond, J.S., Vivian-Smith, G., Williams, G.D., Sullivan, G., Brewster, A.E., Bradshaw, B.K., 1999. Californian salt-marsh vegetation: an improved model of spatial pattern. *Ecosystems* 2, 19–35.