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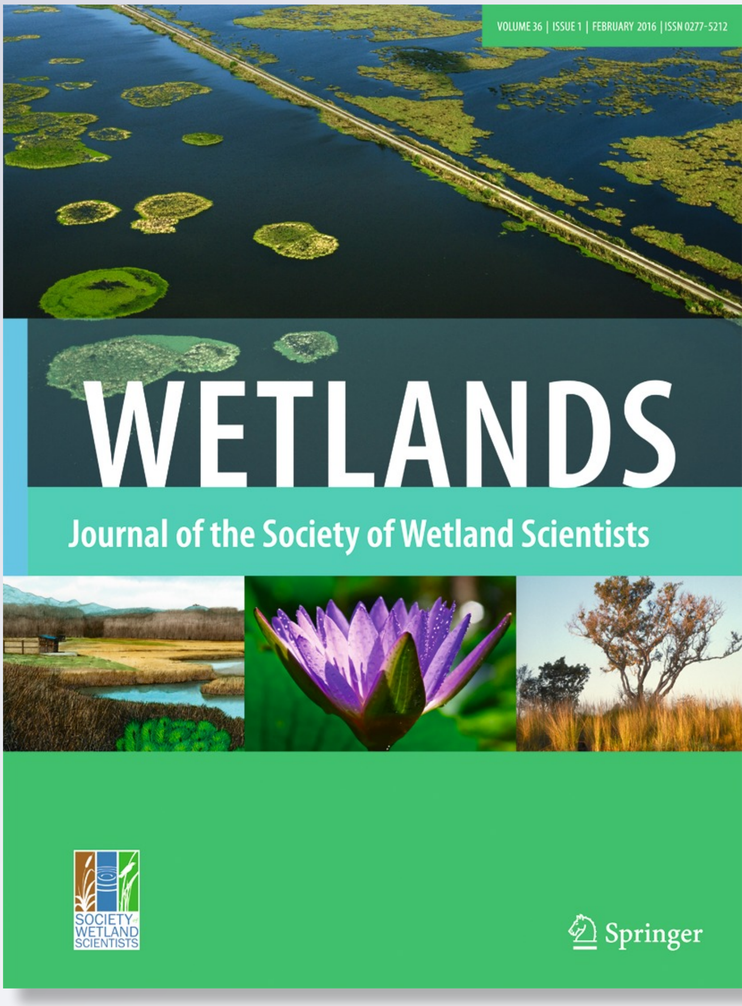

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ORIGINAL RESEARCH

Response of *Schoenoplectus acutus* and *Schoenoplectus californicus* at Different Life-History Stages to Hydrologic Regime

Taylor M. Sloey [1] · Rebecca J. Howard [2] · Mark W. Hester [3]

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Abstract For wetland restoration success to be maximized, restoration managers need better information regarding how the frequency, depth, and duration of flooding affect soil chemistry and the survival, growth, and morphology of targeted plant species. In a greenhouse study we investigated the impact of four different flooding durations (0 %, 40 %, 60 %, and 100 %) on soil physicochemistry and the responses of seedlings and adults of two species of emergent wetland macrophytes commonly used in restoration efforts (*Schoenoplectus acutus* and *Schoenoplectus californicus*). The longest flooding duration, which created more reducing soil conditions, resulted in significantly reduced survival of *S. acutus* adults (34 ± 21 % survival) and complete mortality of seedlings of both species. *Schoenoplectus californicus* adults exhibited higher flooding tolerance, showing little impact of flooding on morphology and physiology. A companion field study indicated that *S. californicus* maintained stem strength regardless of flooding duration or depth, supporting the greenhouse study results. This information serves to improve our understanding of the ecological differences between these species as well as provide restoration managers with better guidelines for targeted elevation and hydrologic regimes for these species in order to enhance the success of restoration plantings and better predict restoration site development.

Keywords Aerenchyma · Flooding · Hydrologic regime · Soil reduction · Stem strength

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✉ Taylor M. Sloey
taylorsloey@gmail.com

1 Coastal Plant Ecology Laboratory, Department of Biology, University of Louisiana at Lafayette, Lafayette, LA, USA

2 U.S. Geological Survey, National Wetlands Research Center, 700 Cajundome Blvd, Lafayette, LA, USA

3 Institute for Coastal and Water Research, Department of Biology, University of Louisiana at Lafayette, Lafayette, LA, USA

Introduction

In tidal wetland environments, flooding regimes influence plant species zonation, patterns of species dispersal, and survival based on the species' individual physiological tolerance to flooding (Jones and Etherington 1971; Weiher and Keddy 1995; Vervuren et al. 2003). Inundated soils and prolonged flooding result in soil oxygen depletion and lowered rates of photosynthesis (Van Bodegom et al. 2008). Wetland plants possess unique adaptations to help tolerate some flooding, including aerenchyma development (Voesnek et al. 2004), changes in root morphology (Sorrell et al. 2000), stem etiolation (Spink and Rogers 1996), and increased alcohol dehydrogenase activity (Messina and Conner 1998). Plant response to the duration of flooding and long-term survival vary considerably depending on species and age of the plant. Depth and duration of flooding can affect seedling mortality (Mandak and Pysek 2001; Elsey-Quirk et al. 2009) as soil oxygenation, soil chemistry, and hypoxic or anoxic conditions may reduce or completely inhibit seedling survival (Wijte and Gallagher 1996). Understanding the effects of specific aspects of hydrology (i.e., frequency, depth, and duration of flooding) on plant establishment, survival, and growth is essential to understanding limitations on vegetation re-colonization.

Flood tolerance characteristics of plants are particularly pertinent in the context of wetland restoration or creation. The dynamic nature of tidal marsh hydrology (i.e. variations in frequency, depth, and duration of flooding) may limit successful establishment and survival of desired wetland vegetation species during the course of restoration (Harper 1977; Galinato and van der Valk 1986). Generally, restoration theory advises that successful wetland restoration or creation can only be achieved after the establishment of the proper abiotic conditions (i.e., hydrologic regime and edaphic conditions) (Middleton 1999). Currently, limited conceptual models exist for marsh development in tidally influenced systems. Williams and Orr (2002) presented a conceptual model showing that colonization of mudflats in salt marsh occurs at approximately mean high water (MHW). Additionally, a review by McKee and Patrick (1988) explained that salt marsh intertidal zonation is dependent on tidal datum. However, because different plant species have different flooding tolerances, these thresholds need to be refined for specific plant species, as well as plant age, and the hydrogeomorphic setting of the wetland. Therefore, it is important to refine this conceptual model for key species of different marsh types and site specific applications.

Re-establishment of vegetation in tidal-marsh restoration sites promotes multiple ecological functions, including provision of animal habitat, protection of shorelines, sediment accretion, primary production, nutrient uptake, carbon sequestration, and enhancement of water quality (Simenstad and Thom 1996). *Schoenoplectus acutus* and *S. californicus* are widely distributed throughout the Americas and parts of the South Pacific (USDA/NRCS 2012). They are ideal species for use in restoration efforts in regions where they are native because they can reproduce both sexually and asexually, provide the aforementioned ecological functions, and are tolerant to general freshwater tidal marsh conditions (Watson and Byrne 2009; USDA/NRCS 2012). Although these species can tolerate some flooding, the species' tolerance thresholds for frequency or duration of inundation is not clearly defined at any life history stage. Little research has been conducted on these plant species to refine their ecology and physiological tolerances to stressors despite their large geographic distribution and expansive applicability for freshwater wetland restoration and creation.

We examined the response of *S. acutus* and *S. californicus* to different hydrologic regimes in both controlled greenhouse conditions and in the field. The objective of this study was to determine the optimum flooding regime for the two *Schoenoplectus* species and life stages to improve and inform restoration. Information from these studies can aid in minimizing restoration expenditures and maximizing efficiency of species placements in future wetland restoration and creation projects.

Materials and Methods

Greenhouse Study

Schoenoplectus acutus and *S. californicus* rhizomes were purchased from a native plant nursery in California, U.S. in February 2013 and transplanted to a greenhouse facility in Lafayette, Louisiana, U.S. (30.304206 N, −92.009775 E). An evaporative cooling system along one greenhouse wall maintained air temperatures below a maximum of 35 °C under ambient light conditions. Plant rhizomes were allowed to grow in Sta-Green ™ top soil for 12 weeks until the experiment initiation. Seedlings were germinated from seeds collected from a freshwater tidal marsh restoration site at Liberty Island, California, U.S. (38.308359 N, −121.686974 E). The experiment was initiated on 7 May 2013, when the seedlings were 8 weeks old. Adults were selected for similar sized rhizomes and consisted of a single ramet with two stems cut to 25 cm in height. Seedling transplants also had two stems that were 1.5–2.0 cm tall. Each plant (hereafter called units) was planted in individual 18.9 L buckets, perforated at the bottom and along the top to allow for uptake and drainage of water without scouring the soil surface. The bottom of the bucket was lined with 5 cm of course gravel, and the rest was filled with a mix of topsoil and clayey soil collected from an abandoned catfish pond located at Cade farm (University of Louisiana at Lafayette) as it more closely resembled the soil profile and particle size distribution of our reference field site at Liberty Island than commercial soil alone. Each unit was pre-treated with 30 g of Osmocote® (14–14-14) slow release fertilizer to avoid potential nutrient depletion.

We used a split-split plot on a randomized block design consisting of two transplant types (whole plot) representing different life history stages (seedlings and adults), two plant species (subplot) (*S. acutus* and *S. californicus*), four tidal flooding durations (sub-subplot) (0 % time flooded and not inundated, 40 % time flooded at a flooding depth of 20 cm, 60 % time flooded at 40 cm depth, and 100 % time flooded at 60 cm depth) with 5 replicates (blocks) of each. The split plot was separated by transplant type so that all species and flooding combinations of a single transplant type shared a tidal mesocosm. Units were blocked perpendicularly to the east/west light gradient.

Plant units were arranged in a large fiberglass cylindrical tank (91 cm height × 122 cm diameter). Different tidal flooding durations were achieved by elevating units on cinderblocks (Fig. 1). Each tank was elevated off the ground and connected by PVC tubing to its own reservoir of water (a cylindrical plastic tub measuring 61 cm height × 122 cm diameter with a covered top to reduce algal growth). Using a magnetic drive pump (MD 32, Zoro Tools Inc., Illinois) and gravity drainage, freshwater was continuously circulated between the experimental tank and the water reservoir to create a semi-diurnal tide with two high tide and two low tide events every 24 h. Tidal cycles for each of the five blocks were set five minutes apart to avoid overloading the electrical system, but the effect of this time difference is considered negligible. The selected percent time flooding and corresponding depths of maximum flooding were based on hydrologic data

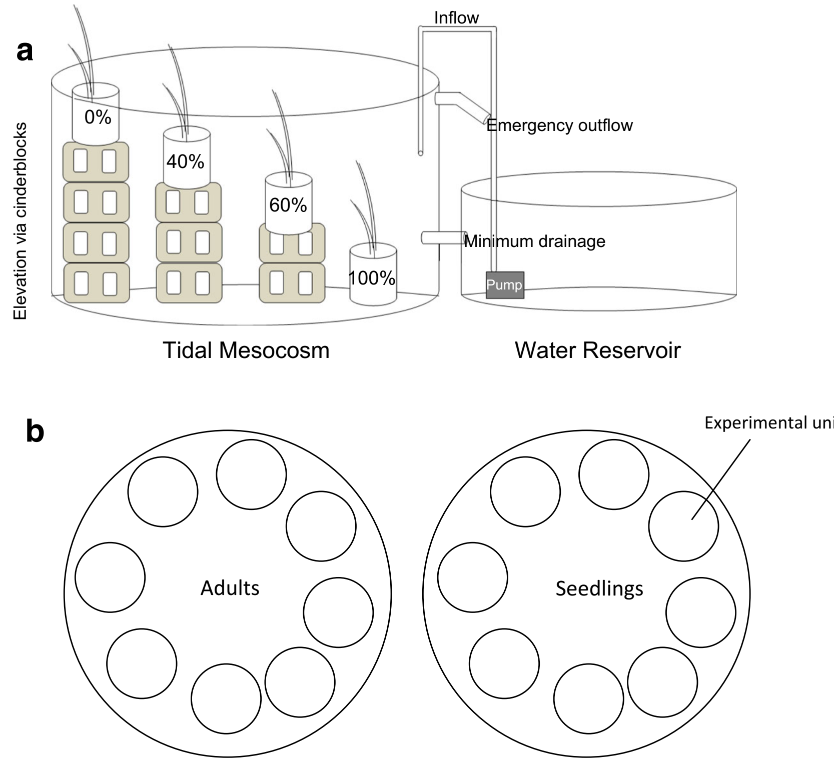

Fig. 1 Diagram of tidal mesocosm showing **a** percentage of time flooded (shown on diagram) based on the percentage of time the soil surface of each unit was inundated, and **b** one experimental block in the split-split plot; transplant type (adult or seedling) represents the whole plot. Each tank contained four pots (experimental units) of each species (*S. acutus* and *S. californicus*). The greenhouse contained five blocks consisting of two tanks each, for a total of 10 tanks and 80 experimental units

extracted from tidal gauges at Liberty Island, California (Table 1). The overall tidal range at this field site was 1.35 m.

Units were monitored at one week, two weeks, and then monthly through 6 September 2013, for percent survival of standing biomass (as indicated by percent green living material of total biomass in each experimental unit), stem density and stem height. Soil redox potential was measured at 1 cm and 10 cm depths of each unit during each monitoring event using ORP electrodes (Thermo Orion 9179BN, Thermo Electron Corporation, Wisconsin). At the conclusion of the study, pore water was extracted from the top 15 cm of soil using a syringe with tubing attached. Pore water was analyzed for concentration of total sulfides using a Thermo Orion ion selective electrode (ThermoFisher Scientific, Massachusetts).

A subset of adult stems (2 stems for each test) was removed and immediately analyzed for stem strength and internal cross-sectional air space (aerenchyma formation). Stem strength was measured at the base, middle, and tip sections of the stem using a tool to obtain the modulus of elasticity, or *E* (Albert et al. 2013). As *E* increases, the stem is less likely to be pulled out of shape or bent with the stress of weight. Cross sections from the tip, middle, and base sections of collected stems were dyed with Tolluidine blue and photographed under a dissecting microscope. Photos of the cross sections were analyzed using Image J ™ software to measure the total area of each cross section and total area of open space (aerenchyma). The area of cross-sectional aerenchyma was averaged across the stem sections to obtain a single mean for the entire stem, as stem section was not a significant factor. Plants were harvested and processed for root specific gravity using pycnometers. A subset of 10 live roots were collected from adult plants and analyzed for root morphology using WinRHIZO image analysis (Regent Instruments Inc., CAN). Roots were measured for the percent of total root length at varying size classes (0–0.05 mm, 0.05–0.10 mm, 0.10–0.20 mm, 0.20–0.50 mm, 0.50–1.0 mm and 1.0- > 2.0 mm). Finally, plant biomass was dried and weighed for total above- and below-ground biomass and mass of inflorescences.

We implemented a mixed effects split-split-plot analysis of variance in SAS (SAS Institute, Inc 2010), with transplant type as our between plot factor, species as the within-plot factor, and flooding duration as a sub-plot factor, to test the effects of these factors on response variables (soil redox potential at 1 cm and 10 cm depths, pore water sulfide concentration, plant survival,

Table 1 Percent time of flooding and water level ranges at mean higher high water (MHHW), mean tide level (MTL), and mean lower low water (MLLW) at Liberty Island, CA

Tidal Datum	Max Depth of Flooding (relative to soil)	Percent Time of Day Flooded
MLLW	+0.01 m	9.47 %
MTL	+0.62 m	75.20 %
MHHW	+1.2 m	99.18 %

stem density, stem height, total aboveground biomass, total belowground biomass, mass of inflorescences, and area of cross-sectional aerenchyma) with a Tukey post-hoc test of pairwise comparisons to determine significant differences between means. Stem strength was tested in adults only. The effect of flooding duration, species, and stem section on stem strength was analyzed using a three-way ANOVA with Tukey post-hoc test. Root morphology was only tested in adults, the effect of flooding duration and species on the percentage of root length at given size classes was analyzed using a two-way ANOVA. For all statistical analyses, $p < 0.05$ was considered significant and all interactions between main factors, including all possible two-way and three-way interaction, were examined.

Field Study

We also sampled the stem strength of *S. californicus* growing in a freshwater tidal marsh restoration site located at Liberty Island, California. Stems were collected in May 2014 from each of eight zones that vary in elevation and wave/wind exposure (Fig. 2). Elevation of these zones was taken in September 2012 using a Trimble real time kinematic (RTK) survey using a rover (NAVD 88; Geoid 2009a). Percent time flooding ranges between 60 and 100 % of the time at this site, depending on elevation and season (Hester et al. 2015). Local hydrology and wave/wind exposure information was provided by hydrologic modelers at Environmental Science Associates (San Francisco, CA). In each zone, stems were collected from each of two proximities to the established marsh, one on the marsh edge/mudflat interface and the other from 5 m into the marsh interior. This was replicated two times at each site, for a total of at least 4 stems per zone, a total of 32 stems in total. Stems were cut at the base and placed in plastic tubes to protect the stems from damage. Stems were transported back to an indoor lab for testing of stem strength (methodology explained above, see Albert et al. 2013). The effect of marsh zone (defined by elevation and wind/wave exposure), proximity (interior and marsh edge), and stem section (tip, mid, base) on stem strength was analyzed for statistical significance ($\alpha = 0.05$) using a split-split plot design with marsh zone as the between-plot factor, proximity as the between-plot factor and stem section as the sub-plot factor.

This field site selected was part of a comprehensive study to assess *S. californicus* marsh expansion (Hester et al. 2015) and transplant success in restoration scenarios (Sloey et al. 2015). Unfortunately, *S. acutus* was not present within our sampling area footprint, but was present within the greater restoration project area. Limited information exists regarding *S. acutus* stem strength, but a study by Sloey and Hester (unpublished data) found that when subject to wind stress, *S. acutus* and *S. californicus* stems break (lodge) at similar percentages.

Results

Greenhouse Study

Flooding duration affected soil redox potential and sulfide concentration. Soils were significantly more reduced with increased flooding at 1 cm ($F_{3,48} = 34.59$, $p < 0.0001$) and 10 cm depths ($F_{3,48} = 27.05$, $p < 0.0001$) (Table 2; Table S1). Soil redox potential values among units exposed to constant inundation fell into the range that sulfate reduction may occur (less than -100 mV). Consequently, concentration of sulfides was significantly higher in the interstitial pore water of units flooded for longer durations ($F_{3,48} = 22.80$, $p < 0.0001$), though these sulfide concentrations were relatively low (< 3 ppm) (Table 2; Table S1).

Plant responses to flooding duration indicated interesting species and transplant type differences. Seedling survival was lower than adults at all flooding durations and decreased with increased durations of flooding resulting in a significant interaction between transplant type and flooding duration ($F_{3,48} = 13.84$, $p < 0.0001$). Adult survival, however, was decreased only at 100 % flooding (Table 2; Table S1). Stem production was greater among *S. acutus* in regard to species, and adult plants in regard to plant age, and units subjected to shorter durations of flooding, as shown by a 3-way interaction between transplant type, species, and flooding duration ($F_{3,48} = 12.01$, $p < 0.0001$) (Table 2; Table S1). Flooding duration did not affect stem production in *S. californicus* adults. *Schoenoplectus californicus* adults grew taller ($F_{3,48} = 6.19$, $p = 0.0012$; Table S1) and produced more biomass ($F_{3,48} = 26.19$, $p < 0.0001$) under all flooding levels compared to *S. acutus*. For seedlings of both species and *S. acutus* adults, stem height and biomass production decreased with increasing duration of flooding; however, *S. californicus* adults showed the opposite trend of increased height with increased flooding duration (Table 2; Table S1). Production of inflorescence biomass was higher in *S. acutus* than *S. californicus*, but *S. acutus* adult inflorescence biomass production was impeded by longer durations of flooding, whereas *S. californicus* showed no impact of flooding on inflorescence biomass production ($F_{3,48} = 39.81$, $p < 0.0001$; Table 2). Seedlings did not produce reproductive structures throughout the duration of our study. Increased flooding generally led to reduced belowground biomass production, except for *S. californicus* adults, which showed no discernible impact of flooding ($F_{3,48} = 8.75$, $p < 0.0001$; Table 2).

Stem strength in adult plants showed a significant 3-way interaction between species, flooding duration, and stem section ($F_{6,685} = 3.47$, $p = 0.0022$) (Table S2; Table S1). Although *S. acutus* exhibited larger overall *E* values than *S. californicus*, it is important to recognize that the value of E is partially driven by stem radius; because *S. californicus* stems were thicker than those of *S. acutus*, the value of E was lower. Stems of *S. acutus*

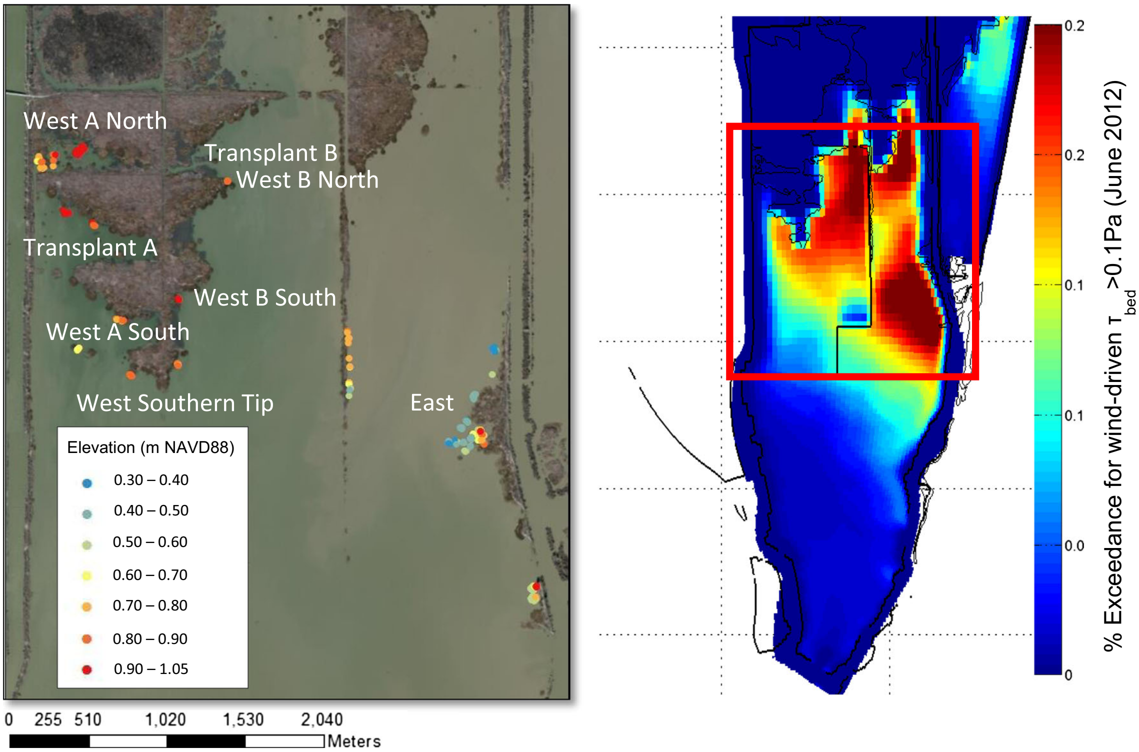

Fig. 2 Liberty Island surface elevations as determined by RTK survey (left) marked with the eight *S. californicus* collection zones and Liberty Island wave energy (right)

(at all sections) appeared less rigid when subjected to longer durations of flooding (Fig. 3). *Schoenoplectus californicus* stems, in contrast, were strongest with intermediate flooding. Calculations of the percent aerenchyma (cross sectional air space) in stems showed that longer durations of flooding resulted in a significantly greater percent of cross-sectional stem space consisting of aerenchyma ($F_{3,25}$ = 9.05, p = 0.0003) (Table 2, Table S1, Fig. 4). Analysis of root morphology showed a significant effect of species at the 0.1–0.2 mm ($F_{1,29}$ = 26.38, p < 0.0001) and 0.50–1.0 mm ($F_{1,29}$ = 139.29, p < 0.0001) (Table S3). There was a significant effect of flooding duration at the 0.20–0.50 mm ($F_{3,29}$ = 5.97, p = 0.0027) class and a significant interaction between the two effects at the 1.00–2.00 mm ($F_{3,29}$ = 3.52, p < 0.0274) class. Trends indicate that longer durations of flooding correlated with a higher percentage of total root length at smaller diameters in *S. californicus* (p < 0.0001) but showed no impact on *S. acutus* (Fig. 5).

Field Study

Schoenoplectus californicus stems collected from the Liberty Island, California field site revealed that stem strength differed among stem section ($F_{2,52}$ = 14.89, p < 0.0001), with the tips exhibiting the strongest stems relative to diameter, followed by mid-section and base (Table S4, Fig. 6). Note that the base sections were able to support more weight overall than the tip and mid sections, but the calculation of E is dependent on diameter. There was no significant effect of proximity (p = 0.8694) or zone (p = 0.8562) on stem strength.

Discussion

Hydrology, referred to as the master variable controlling wetland plant species zonation, plays an influential role in determining which species and ages of plants can successfully establish and survive (Tiner 1999; Mitsch and Gosselink 2007), and Casanova and Brock (2000) reported that the duration and frequency of flooding has more influence on plant species establishment compared to depth of flooding. *Schoenoplectus acutus* and *S. californicus* co-occur throughout much of the western and southern United States (USDA/NRCS 2014), but our understanding of the differences between these species in regard to tolerance thresholds to flooding duration was limited. Our research has defined the flooding tolerance thresholds for these species, which has implications for improving our understanding of competitive interactions in plant associations. This information can be used to maximize restoration efforts in terms of planting the proper species at the proper ages depending on the site hydrology and elevation. Our finding that *S. californicus* exhibits superior stem strength regardless of environmental conditions suggests

Table 2 Soil physicochemical and plant responses (mean ± SE) as a function of plant age, species, and percent of time the soil surface of the greenhouse experimental unit was flooded. Significantly different means ($p < 0.05$) within the same parameter column are indicated by different letters

Transplant Type	Species	Flooding Duration (%)	Soil Redox Potential at 1 cm depth (mV)			Soil Redox Potential at 10 cm depth (mV)			Sulfide concentration n pore water (ppm)			Plant Survival (%)			Stem Density (# of stems per unit)		
Adult	***S. acutus***	**100**	−140.1	±	72.2A	−195.3	±	73.7 A	2.61	±	1.18 A	34	±	21A	2.4	±	1.6 A
		60	−25.9	±	52.7B	−73.5	±	47.8 B	0.52	±	0.27 B	95	±	2B	44.8	±	10.4 B
		40	48.3	±	41.4B	−75.6	±	42.9 B	0.25	±	0.14 B	88	±	7 AB	43.2	±	7.1 B
		0	191.5	±	20.6 C	90.0	±	14.6 C	0.04	±	0.03 B	86	±	9 AB	57.4	±	9.3 B
	S. californicus	**100**	−218.7	±	17.9 A	−271.9	±	15.2 A	2.92	±	1.18 A	100	±	0 B	11.6	±	1.4 A
		60	−36.1	±	21.5 B	−75.5	±	19.9 B	0.55	±	0.04 B	99	±	1 B	12.4	±	1.1 A
		40	−4.8	±	53.9 B	−41.3	±	17.3 B	0.06	±	0.03 B	90	±	8 AB	10.8	±	1.7 A
		0	297.2	±	70.6 C	201.2	±	88.4 C	0.02	±	0.01 B	93	±	4 AB	10.6	±	0.7 A
Seedling	***S. acutus***	**100**	−108.8	±	86.1 A	−107.8	±	107.6 A	3.05	±	0.77 A	0	±	0 A	NA	±	NA
		60	17.5	±	37.5 B	−130.2	±	55.2 B	0.31	±	0.07 B	40	±	24 A	2.4	±	1.6 A
		40	−24.4	±	44.7 B	−41.9	±	47.1 B	0.49	±	0.35 B	80	±	20 B	8.0	±	2.8 A
		0	129.1	±	54.4 C	119.0	±	28.8 C	0.09	±	0.02 B	100	±	0 B	8.6	±	0.6 A
	S. californicus	**100**	−144.3	±	38.5 A	−210.2	±	53.6 A	1.97	±	0.75 A	0	±	0 A	NA	±	NA
		60	19.7	±	41.2 B	29.3	±	70.1 B	0.51	±	0.14 B	20	±	20 A	1.0	±	1.0 A
		40	103.9	±	24.5 B	52.0	±	24.9 B	0.12	±	0.03 B	100	±	0 B	4.4	±	0.5 A
		0	165.7	±	40.5 C	76.1	±	27.9 C	0.06	±	0.03 B	100	±	0 B	9.0	±	3.6 A

Transplant Type	Sulfide concentration n pore water (ppm)	Stem Height (cm)			Total Aboveground Biomass (g)		Total Belowground Biomass (g)			Inflorescence Biomass (g)			Area of Cross-sectional Aerenchyma (%)		
Adult	1.18 A	32	±	21 A	±	4.1 A	6.8	±	4.3 A	0	±	0.00 A	23.8	±	4.6 A
	0.27 B	87	±	3 A	±	10.3 B	96.3	±	25.5 AB	8.46	±	1.79 B	8.8	±	1.9 AC
	0.14 B	87	±	2 A	±	4.3 B	121.5	±	25.6 B	13.30	±	0.67 B	5.7	±	1.2 BC
	0.03 B	76	±	3 A	±	5.4 B	258.3	±	69.4 C	19.44	±	1.78 B	5.9	±	1.3 BC
	1.18 A	217	±	20 B	±	13.8 C	131.6	±	28.5 B	0.20	±	0.07 A	25.6	±	3.1 A
	0.04 B	181	±	3 BC	±	13.3 BC	185.6	±	27.0 B	0.26	±	0.26 A	23.3	±	2.9 A
	0.03 B	162	±	10 BC	±	3.4 B	127.7	±	10.6 B	0.10	±	0.06 A	7.3	±	1.5 C
	0.01 B	129	±	9 C	±	2.9 B	127.3	±	17.4 B	0.02	±	0.02 A	6.4	±	1.3 B
Seedling	0.77 A	0	±	0 A	±	0 A	0	±	0 A	0	±	0 A	NA	±	NA
	0.07 B	22	±	15 AB	±	16.6 A	3.4	±	2.5 A	0	±	0 A	22.7	±	21.6 A
	0.35 B	39	±	19 AB	±	21.7 A	9.2	±	3.5 A	0	±	0 A	16.2	±	3.5 A
	0.02 B	60	±	4 B	±	2.6 A	12.9	±	1.1 A	0	±	0 A	18.8	±	3.3 A
	0.75 A	0	±	0 A	±	0 A	0	±	0 A	0	±	0 A	NA	±	NA A
	0.14 B	10	±	10 AB	±	2.4 A	0.8	±	0.8 A	0	±	0 A	15.0	±	8.6 A
	0.03 B	32	±	8 AB	±	2.5 A	7.1	±	1.7 A	0	±	0 A	9.7	±	3.9 A
	0.03 B	57	±	18 AB	±	12.6 A	8.8	±	2.3 A	0	±	0 A	0.5	±	0.2 B

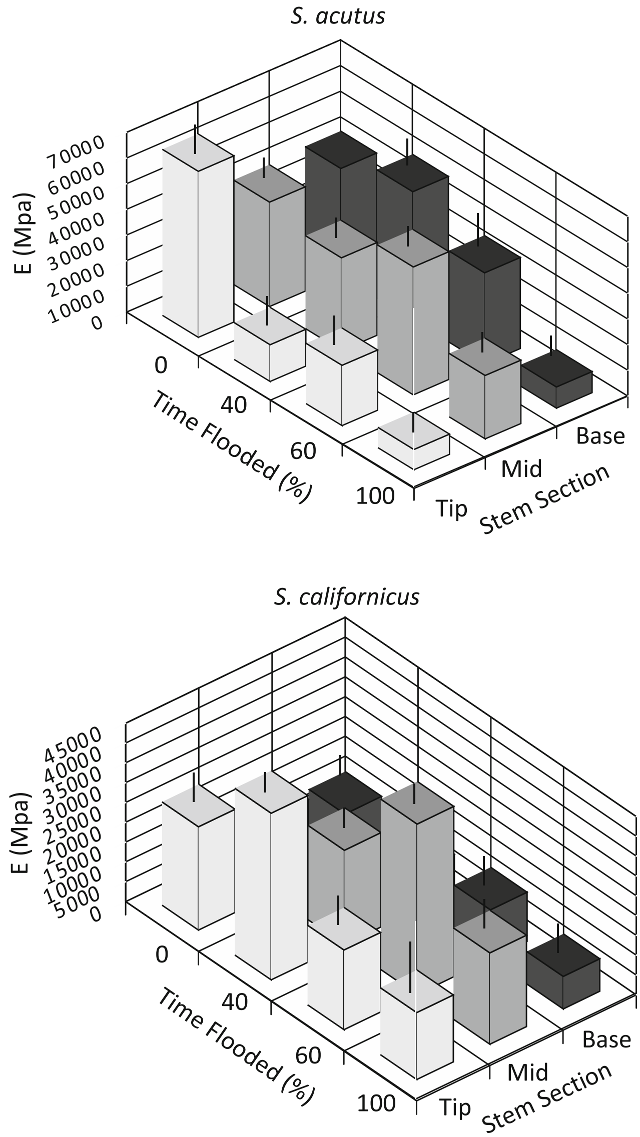

Fig. 3 Stem strength, as expressed as the modulus of elasticity (E), (mean ± SE) of *S. californicus* and *S. acutus* stems. Stems strength was determined for tip, middle, and base sections of the stem as a function of the percentage of time the soil surface of the experimental unit was flooded

that it is an excellent species for establishment in high energy tidal environments under a variety of flooding regimes. Additionally, this research has implications for informing management decisions and improving the science and practice of mitigating wave erosion of earthen levees with vegetation, which also provides marsh habitat. We want to emphasize that for successful wetland restoration/creation, managers and designers should focus not strictly on a target elevation, but rather, on what elevation is needed to achieve a target hydrology (specifically the frequency of flooding and the percentage of time flooded). Additionally, it is important for restoration managers to understand that despite the best conceptual models, each species and age of transplant has a unique range of tolerances to environmental stressors.

Wetland restoration and mitigation efforts are often unsuccessful when they fail to recreate the proper hydrogeomorphology or recognize that the wetlands are part of larger landscapes (especially tidal and coastal wetlands) (Zedler 1997; Whigham 1999). Our study provides specific information for restoration managers to create the proper hydrogeomorphic conditions to facilitate successful restoration of tidal *Schoenoplectus* spp. marshes. Regarding soil physicochemistry, constant inundation resulted in more severely reduced soils, reaching the −100 mV range where sulfate reduction can occur (DeLaune and Reddy 2005). However, for the duration of this experiment, reduction resulted in the production of sulfides at low concentrations (around 0.09 mM), probably due to the lack of sulfates in the fresh water used in the experiments. Sulfide concentrations were therefore unlikely to have a detrimental effect on the plants (DeLaune et al. 1983; Sloey et al. 2015). Regardless, this study shows that the duration of flooding has a strong impact on the severity of soil reduction and therefore, wetland restoration managers should focus on creating elevations for species where the hydrologic regimes and tidal sequences result in sulfide production within the limitations of the target species.

Beyond altering soil chemistry, flooding can impede plant growth by reducing plant exposure to light, oxygen, and photosynthesis, as well as altering the plant's physiology and growth (Crawford 1982). Constant inundation may be too stressful for young seedlings with little carbon storage (i.e., relatively low root/rhizome mass) and small stems that cannot emerge from water to survive, as evidenced by 100 % mortality in seedlings of both species. Sloey et al. (2015) found that *S. californicus* and *S. acutus* transplants that possessed emergent stems at the time of planting performed better under flooded field conditions than rhizome transplants that had no aboveground biomass. *Schoenoplectus* spp. have also been observed to be able to colonize deeper waters (flooded 100 % of the time) at the Liberty Island restoration site via vegetative propagation (Hester et al. 2015 in review). Clonal plants are physiologically integrated and able to share resources, thus allowing the individuals that make up a larger genet to survive in conditions that a lone ramet could not (Eckert 1999). Overall, adult survival and growth was superior to seedlings. Yet, observations of the adults revealed important differences between species. Although *S. acutus* and *S. californicus* are closely related taxonomically and similar in morphology, their tolerance to flooding, and therefore fundamental niches, separate these species. Percent time flooded greater than 60 % resulted in a significant decrease in survival for *S. acutus* adults, yet did not decrease survival in *S. californicus*. This information has important implications for planting and distribution strategies for

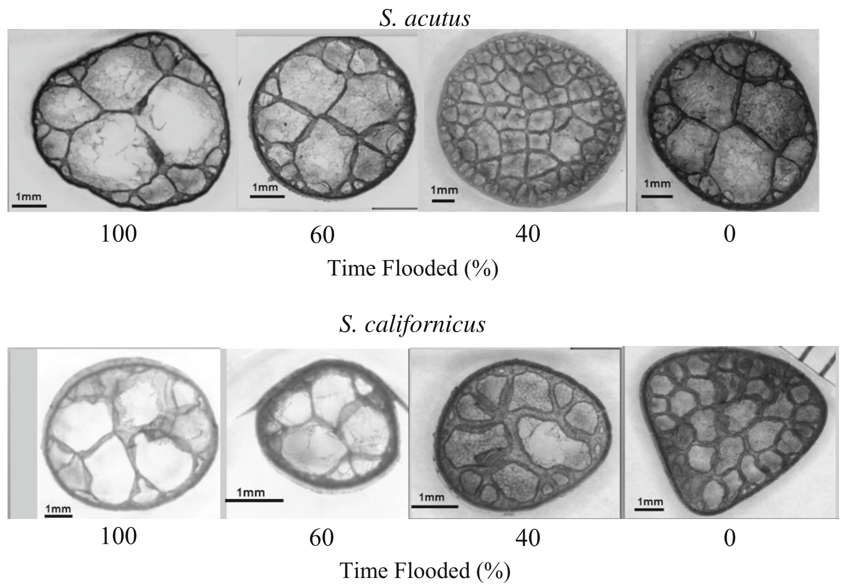

Fig. 4 Images of representative cross sections as a function of percentage of time the soil surface of the experimental unit was flooded. Area of aerenchyma formation was measured as the white, open air space within the stem cross section

restoration efforts. If *S. acutus* is a desired species for implementation, the soil surface at a restoration site must be exposed to air for some portion of the day. To maximize successful establishment of individual ramets at the sensitive seedling stage of both species, our results suggest a minimum exposure of 40 % of the day, although *S. californicus* adults can tolerate longer flooding durations.

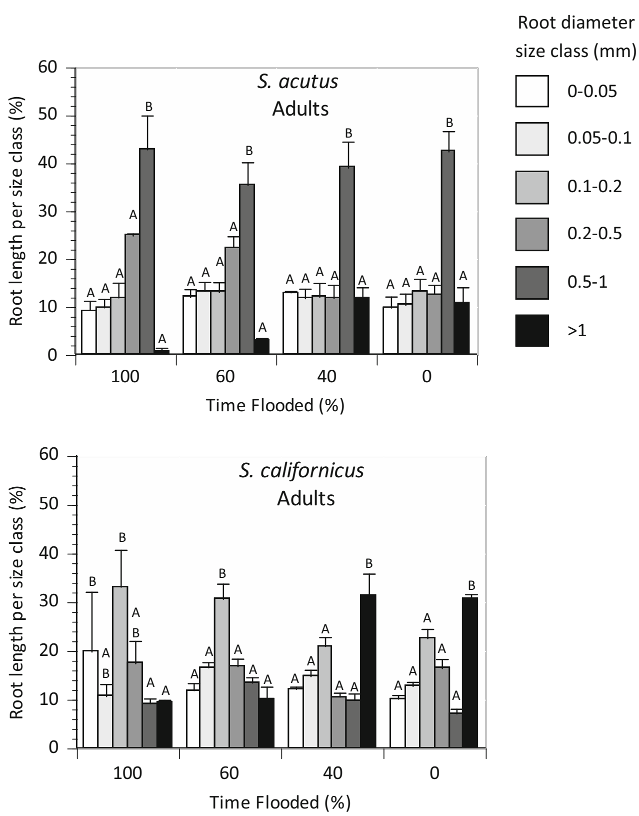

Fig. 5 Percent of total root length per size class of adult *S. acutus and S. californicus* (mean + SE) as a function of percentage of time the soil surface of the experimental unit was flooded. Means marked with different letters indicate statistically significant differences ($p < 0.05$)

Physiological responses to flooding differed among species. We witnessed evidence of both compensatory responses and harmful effects of flooding stress. To cope with the stress of waterlogging, flood-adapted plants produce ethylene which promotes stem elongation (etiolation), aerenchyma formation, and growth of adventitious roots (Dat et al. 2004). Etiolation is a common stress response among submerged plants (Blom and Voesenek 1996) and has been shown to decrease stem strength and contribute to lodging, or bending, of plants (Beatty 1964). We observed a non-significant ($p = 0.0516$) trend that stem height decreased with increased flooding among seedlings of both species and the *S. acutus* adults, however the opposite (and significant) trend was exhibited in *S. californicus* adults (Table 2), suggesting an etiolation response by *S. californicus*. Often plants that etiolate do so at the expense of biomass thus resulting in taller but more fragile stems (Beatty 1964), but *S. californicus* did not exhibit reduced biomass. Both species showed that the area of aerenchyma in stem cross-sections increased with prolonged flooding. The formation of aerenchyma is a common adaptation among wetland plants that facilitates transport of oxygen between shoots and roots in oxygen depleted environments (Jackson and Armstrong 1999). Analysis of root size classes showed that increased flooding resulted in a proportional shift toward smaller roots (<0.2 mm) in *S. californicus* due to the promotion of adventitious roots. Studies on other species have documented that the formation of adventitious roots improves the overall survival of the plant after flooding (Sartoris and Belcher 1949; Kramer 1951). *Schoenoplectus acutus* did not show these positive compensatory growth patterns, indicating it is more susceptible to the negative effects of flooding than *S. californicus*.

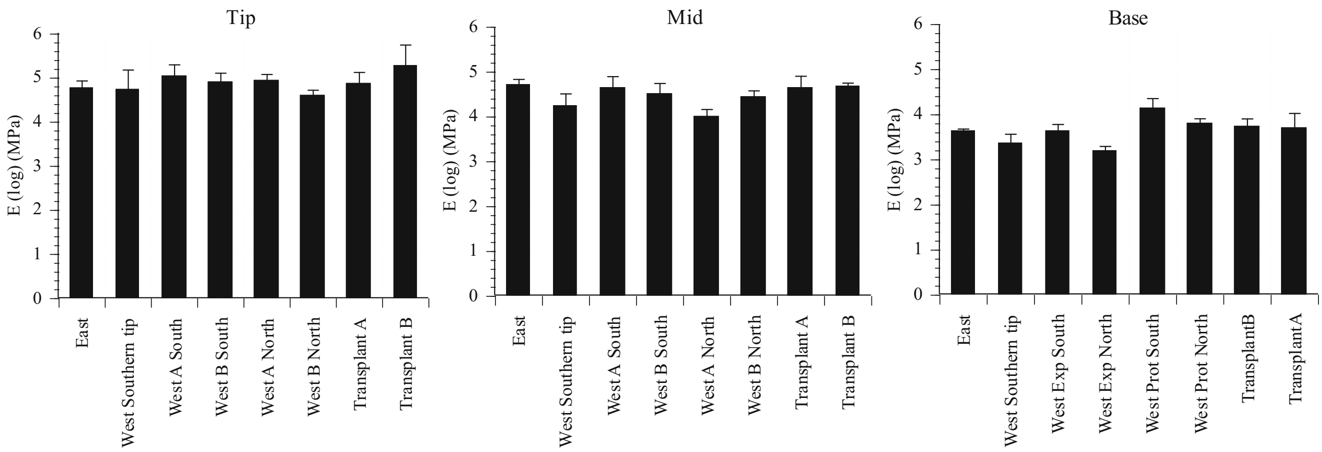

Fig. 6 Stem strength, expressed as the modulus of elasticity (log E), (mean ± SE) of *S. californicus* collected from natural marsh edge and transplant sites at Liberty Island, CA (see Fig. 2). Stems strength was determined for tip, middle, and base sections of the stem

Survival, growth, and biomass production were reduced in *S. acutus* units subjected to longer durations of flooding. Inflorescence biomass production was generally low in all *S. californicus* units. For *S. acutus*, increased flooding duration resulted in lower inflorescence biomass production, which suggests that not only does prolonged flooding limit the vegetation expansion of *S. acutus*, but could potentially limit long distance dispersal by reducing the seed rain. Stem strength of *S. acutus* adults was reduced under flooded conditions, especially when flooded 100 % of the time. In contrast, *S. californicus* stem strength did not appear to be impacted by flooding, as shown in both the controlled greenhouse experiment and field collections. Tidal wetlands are typically exposed to high wind and wave energy, and tall stemmed plants such as *Schoenoplectus* spp. are subject to lodging (Tanner 2001). Our field study supports the notion that *S. californicus* stems maintain rigidity regardless of abiotic conditions. Whereas we might have predicted that plants growing on the east side of Liberty Island would have weaker stems due to longer durations of flooding, we observed a non-significant trend showing that stronger stems were present on the east, where duration of flooding and wind and wave energy were most severe. Studies have reported that the stems of riparian plants have higher tensile strength when they possess larger cross sectional areas and are conditioned to moving water as opposed to stagnant water (Boeger and Poulson 2003; Bociąg et al. 2009). The larger diameter and unique triangular shape of *S. californicus* stems may contribute to its strength, but more empirical research is needed to address these questions. *Schoenoplectus californicus* exhibited many qualities that suggest it may be a more suitable species for implementation in freshwater tidal wetlands, exhibiting stronger evidence of stress compensation and flooding tolerance compared to *S. acutus.*

The results of our study provide informative guidance for future restoration of tidal marshes using *Schoneoplectus* spp. by using a controlled, manipulative mesocosm experiment that imposed a series of hydrologic regimes on adults and seedlings of two *Schoenoplectus* species. Restoration sites can differ in a variety of environmental characteristics, including the site-specific differences in the relationship between elevation and the resultant hydrologic regime. Managers should be encouraged to include a scientific component within the restoration framework, such as small scale test plantings prior to project-wide planting efforts to refine their knowledge of how the target species may respond to site-specific environmental conditions, particularly depth and percentage of time flooded. This type of information can enhance the efficacy of the restoration and improve predicted rates of plant establishment and expansion across elevation gradients of the site.

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