Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Hydrologic and edaphic constraints on *Schoenoplectus acutus*, *Schoenoplectus californicus*, and *Typha latifolia* in tidal marsh restoration

Taylor M. Sloey[1,2], Jonathan M. Willis[1], Mark W. Hester[1]

The demand for an improved knowledge base for planning and management of tidal marsh restoration worldwide has become more fully recognized. In the Sacramento-San Joaquin Bay Delta, California, U.S.A., concerns have arisen about the degradation of the Delta and key ecosystem services. One restoration method proposed includes intentionally breaching levees that protect agricultural lands to re-establish a hydrology that encourages tidal marsh development. Our research investigated relevant constraints on vegetation establishment and expansion of key tidal marsh species. We transplanted three macrophyte species (*Schoenoplectus acutus*, *Schoenoplectus californicus*, and *Typha latifolia*) using two transplant types (rhizomes and adults) in locations that varied in hydrologic and edaphic conditions at Liberty Island, a post-levee breach tidal marsh restoration site. Two years of monitoring revealed that transplanted adults outperformed rhizomes. In addition, *S. californicus* exhibited greater survival and vegetation expansion. *S. californicus* vegetation expansion covered a maximum area of approximately 23 m^2, which is two orders of magnitude (OOM) greater than the maximum area covered by *S. acutus* (approximately 0.108 m^2) and three OOM greater than *T. latifolia* (approximately 0.035 m^2). Results suggest that hydrologic regime and degree of soil compaction are influential in controlling vegetation establishment and expansion. Greater vegetation expansion occurred in transplant sites characterized by a deeper surface layer of non-compacted soil in conjunction with shorter durations of flooding. Information derived from this study is valuable to restoration planning in the Delta and other tidal marshes worldwide where these species occur, especially in terms of setting restoration goals and trajectories based on site-specific environmental characteristics.

Key words: environmental filters, hydrology, soil physicochemistry, transplant type

Implications for Practice

- Practitioners performing tidal marsh restoration on legacy agricultural land should be cognizant that historical anthropogenic alterations of the natural hydrology, elevation, and soil physicochemical properties may impede wetland vegetation establish and expansion.
- As transplant performance varies among species and transplant types in response to the hydrologic regime, restoration managers and practitioners should, when possible, incorporate preliminary testing of desired species in field scenarios to better design the restoration project.
- Transplanting desired plant species in tidal marsh restoration sites has the potential to accelerate establishment of wetland structure and function. Enhanced understanding of site-specific constraining abiotic factors will improve our ability to manage ecosystems, improve ecosystem trajectories, and achieve restoration goals.

Introduction

The Sacramento-San Joaquin Bay Delta in California, U.S.A., is an ecosystem of considerable environmental and economic value that has undergone substantial habitat alteration and is in need of large-scale ecological restoration (Atwater et al. 1979). More than 95% of the Delta wetlands were modified after the construction of a 1,700-km levee system for agricultural reclamation (Conomos 1979). Concerns regarding the ecological health of the Delta and its role in California's water supply have prompted planning for large-scale wetland restoration projects (Miller & Fujii 2010). Re-establishment of wetland vegetation is critical in restoring historic ecological functions, including nutrient cycling (Jordan et al. 1989), improved water quality (Simenstad & Thom 1996), and the provision of faunal habitat (Perry & Skalski 2009). The intentional breaching of agricultural levees has been proposed as a restoration technique to

Author contributions: TS, JW, MH conceived and designed the research, and implemented and monitored the field study; TS analyzed the data; TS, JW, MH wrote and edited the manuscript.

[1]Coastal Plant Ecology Laboratory, Department of Biology, University of Louisiana at Lafayette, 300 East Saint Mary Boulevard, Lafayette, LA 70503, U.S.A.
[2]Address correspondence to T. M. Sloey, email tms1574@louisiana.edu

doi: 10.1111/rec.12212
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.12212/suppinfo

re-establish tidal hydrology and facilitate the re-establishment of tidal freshwater wetlands (Simenstad & Thom 1996). Unfortunately, pre-breach environmental data are not available for the Liberty Island restoration site, and limited knowledge regarding the success or challenges of using levee breach restoration techniques is available. Therefore, this research seeks to explore how the environmental factors present at this post-levee breach site may constrain vegetation establishment and expansion.

Liberty Island is a freshwater post-levee breach natural tidal marsh restoration site located in the Sacramento-San Joaquin Delta complex in California. This land parcel was leveed in the early 1920s and farmed for various agricultural crops (Malcolm 1981) until a high river discharge event caused the levee to permanently fail in 1997 (Hart 2010). Since the levee breach, this area has been undergoing a gradual succession to tidal freshwater marsh. Tidal hydrology has been reintroduced; our study area exhibits a tidal range of approximately 1.35 m, depending on the time of year (S. Crooks et al. 2012, Environmental Science Associates, personal communication). As wetland hydrology has been reintroduced, the densely compacted legacy agricultural soil has been covered with a layer of fluvial sediment. Wetland vegetation (primarily *Schoenoplectus californicus*, *Schoenoplectus acutus*, and *Typha* spp., with some *Ludwigia* spp., and *Egeria densa*) naturally re-colonized and expanded, making it a model site for understanding levee breach restoration dynamics (Simenstad et al. 2006). This site can serve as a natural laboratory for elucidating the specific mechanisms that regulate colonization and expansion of the emergent wetland plant community, thereby enhancing our understanding of the efficacy of this restoration technique and ecosystem restoration trajectories.

Lambers et al. (2008) proposed that a species' ability to establish and persist at a site depends on three environmental filters: (1) the ability to disperse to the site, (2) physiological tolerance to the environmental conditions, and (3) biotic interactions. A previous seed-bank assay indicated that the seeds of many species are present in the Liberty Island seed-bank (including the site dominants), but their germination is currently inhibited by the site hydrology, as flooding can limit environmental cues that trigger germination (T. Sloey & M. Hester 2015, University of Louisiana at Lafayette, unpublished data). Similarly, we have observed that expansion of the emergent macrophytes into unvegetated areas is primarily through vegetative reproduction and that substantial areas of intertidal and subtidal mudflats remain uncolonized. Our study design implemented planting, so we therefore focused on the two latter environmental filters (physiological tolerance and biological interactions).

Some of the potential physiological and biological constraints encountered in restoration may be associated with drastic anthropogenic changes to landscape level and local edaphic environmental conditions (O'Neill 1999). Although natural deltaic wetlands tend to be characterized by fluvial sediments that are high in organic matter and pore space (Nyman et al. 1990; Mitsch & Gosselink 2000), in the case of reclaimed wetland restoration sites, the soil physicochemical properties may not be initially suitable for wetland plant establishment due to intensive land use and heavy equipment (Campbell et al. 2002). In addition, previous modifications to the natural hydrology can be problematic for re-establishing ideal tidal wetland hydrology (Lytle & Merritt 2004).

In this study, we utilized a manipulative field-transplant experiment to investigate how environmental factors and biological interactions may limit successful vegetation re-colonization and plant community development in a tidal marsh hydrologically restored by breaching a levee. The information resulting from this research will not only advance the ecological understanding of establishment dynamics of three key species at two transplant types but also provide guidance on the potential success of levee breach restoration techniques, thereby informing and enhancing future restoration efforts.

Methods

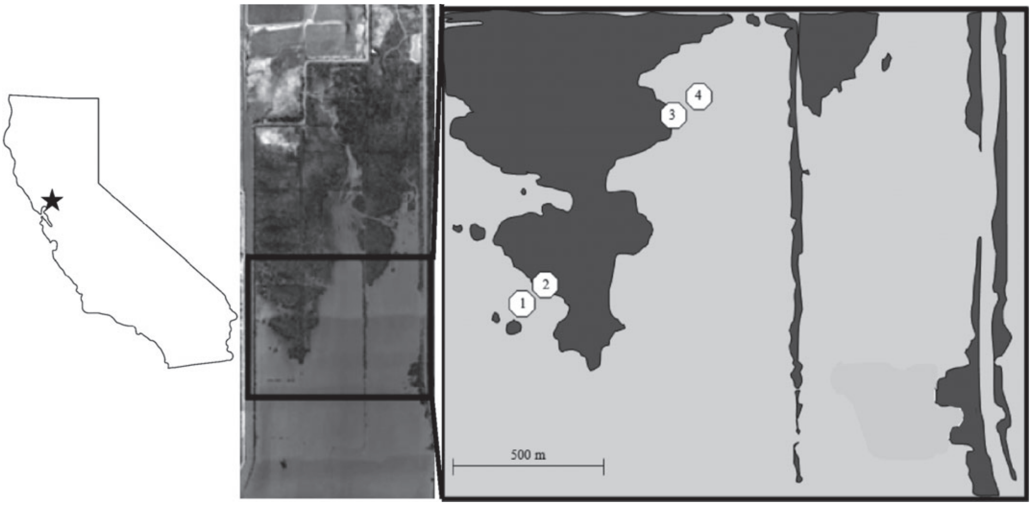
Experimental Design

At the Liberty Island post-levee breach restoration site (38°18′N; 121°40′W), we implemented a factorial design consisting of three species: *Schoenoplectus acutus* (hardstem bulrush), *Schoenoplectus californicus* (California bulrush), and *Typha latifolia* (cattail), two transplant types that represent different life history stages (adults and rhizomes), and four transplant sites. The four transplant sites were located in the western half of Liberty Island and positioned on both sides of a large stand of naturally colonized *S. californicus* tule marsh (referred to as locations West A and West B; Fig. 1). Each of these locations contained transplant plot sites at two different distances from the naturally colonized marsh edge: 1 m (marsh fringe) and approximately 70 m (open water). In each of these four sites, we established eight transplant plots (four adult and four rhizome plots). Each plot consisted of three 0.25 m^2 quadrats, each planted with four individuals of a single species of a single transplant type, which were arranged in a triangular fashion with an open space in the center to allow for observation of biotic interactions between species (Fig. S1, Supporting Information). Placement of species was randomized for each plot. All transplants were planted in June of 2010 and monitored in September 2010, June 2011, and June 2012.

Transplant Preparation and Sampling

Bare-root adult individuals of each species were purchased from a local plant nursery in California. Healthy plants with similar-sized rhizomes were selected. Stems of adult transplants were cut to a length of 0.25 m above the base, whereas aboveground stems were removed from rhizome transplant units. Both transplant types were planted during low tide (non-flooded conditions) at each of the four Liberty Island transplant sites in June 2010 to a depth that just covered the top of the rhizome tissue.

At each transplant plot, we measured edaphic and hydrologic conditions over the 2-year period. We used a hand-held salinity meter (YSI 30; YSI Inc., Yellow Springs, OH, U.S.A.) to confirm freshwater conditions (<0.2 ppt). Real-time kinematic (RTK) surveys were conducted in September of 2010, 2011, and 2012, during which elevation (m NAVD 88) and annual lateral



1. West A Open Water 3. West B Marsh Fringe
2. West A Marsh Fringe 4. West B Open Water

Figure 1. Transplant locations at the Liberty Island marsh restoration site. The star demarks the approximate location of the Liberty Island restoration site in California.

expansion rate were determined at each transplant site. For lateral expansion, the RTK location of the original transplanted unit for each plot and species was determined, as well as the location of the current marsh edge on both sides of the plot (two edge points established for each plot). Each year, the previous marsh edge location was reoccupied and the distance to the current closest linear marsh edge was established as a new RTK point; the distance between those two points was calculated as lateral expansion. All other edaphic conditions were monitored during each sampling period (September 2010, June 2011, and June 2012) unless otherwise stated. We measured soil redox potential at 1 and 10 cm depths using ORP electrodes (Thermo Orion 9179BN; Thermo Electron Corporation, Fitchburg WI, U.S.A.) in combination with a hand-held mV meter (Beckman Φ 265; Beckman Coulter, Brea, CA, U.S.A). Degree of soil compaction was measured with a soil compaction tester (PN 15585-0003D; DICKEY-john Corporation, Auburn, IL, U.S.A) in June 2011 and 2012. At each plot, we took three replicate soil compaction measurements, a total of 24 measurements for each site, from which we defined the depth of soil resistance as the depth that resulted in an abrupt increase in penetration pressure. During each sampling event, two soil cores measuring 5 cm diameter by 15 cm depth were extracted from just outside of each transplant. One soil core was dried at 65°C and weighed to determine soil bulk density (D_b). The other soil core was dried, pulverized using a mortar and pestle, and soil organic matter content was determined as loss on ignition (LOI) (Soil and Plant Analysis Council, Inc. 1999). In addition, soil chemical characteristics were determined using a 1:2 KCl extraction (for ammonium and nitrate–nitrite) and a 1:2 deionized water extraction (for pH, conductivity, phosphorus, and other specific cations) following standard methods (American Public Health Association 2012). Daily hydrologic data were obtained from on-site weather stations at Liberty Island and nearby Rio Vista. Percent time flooding was calculated for May–September 2010 as the hydrology during this time period would exert the greatest influence on the initial transplant survival. Percent time flooding of the soil surface was calculated using the soil surface elevation. Percent time of overtopping of plant material was calculated using the maximum elevation of the top of the plant material (we used soil surface elevation for rhizomes with no aboveground materials, whereas overtopping adults (0.25 m stems height) were calculated by adding 0.25 m to the soil surface elevation. Hydrologic data of hourly means collected from a nearby water level gauge and weather station were provided by a team of hydrologic modelers (S. Crooks et al. 2012, Environmental Science Associates, unpublished data) as part of the larger research project (BREACH III) collaborative effort.

We monitored the transplants during each sampling period for survival, growth, and area of vegetation cover. Plant survival could only be accurately measured in September 2010, after which the transplants expanded and integrated to a point where we could no longer distinguish individual transplants. During each site visit, the live and dead cover were visually estimated by species for each plot. If rhizome units produced no aboveground material, they were considered dead. Each transplant plot was monitored for stem density (number of live stems per 0.25 m^2 quadrat) and stem height (live stems within the 0.25 m^2 quadrat). Total area of vegetative expansion was measured by using the maximum and perpendicular diameters of the spread of vegetation to determine the ellipsoidal area of vegetation, including vegetation extending beyond the quadrat. In addition, over 100 stems of various heights were collected from naturally colonized *S. californicus* located outside of our plots, and measured, dried, and weighed to generate a length/mass regression to estimate plot biomass (estimated by multiplying stem heights by the number of individuals in the plot; Fig. S2). Biomass was not calculated for *S. acutus* or *T. latifolia* due to low survival.

Table 1. Environmental parameters (mean ± SE) at four transplant locations at the Liberty Island, CA, U.S.A., restoration site from 2010 to 2012. Means within the same parameter followed by the same superscript letter are not significantly different ($p > 0.05$).

	Elevation (mNAVD88)	*Flooding Time (%)*	*Soil Redox Potential at 1 cm (mV)*	*Soil Redox Potential at 10 cm (mV)*	*Soil Bulk Density (g/cm³)*	*Depth-to-Soil Penetration Resistance (cm)*	*Soil Organic Matter (%)*
2010							
West A marsh fringe	0.84 ± 0.002^{c}	93.8 ± 0.188^{c}	233 ± 48^{a}	195 ± 47^{b}	0.75 ± 0.02^{eb}	NA	13.4 ± 0.1^{a}
West A open water	0.77 ± 0.003^{e}	98.9 ± 0.212^{e}	171 ± 21^{ab}	188 ± 17^{b}	0.79 ± 0.02^{db}	NA	14.2 ± 0.1^{a}
West B marsh fringe	0.94 ± 0.008^{a}	86.0 ± 0.626^{a}	29 ± 24^{bc}	62 ± 25^{ab}	0.60 ± 0.03^{ea}	NA	13.3 ± 0.2^{a}
West B open water	0.85 ± 0.005^{dc}	92.7 ± 0.434^{dc}	166 ± 13^{ab}	116 ± 25^{ab}	0.69 ± 0.03^{ba}	NA	13.6 ± 0.1^{a}
2011							
West A marsh fringe	0.85 ± 0.009^{dc}	93.2 ± 0.630^{dc}	83 ± 39^{abc}	156 ± 48^{b}	0.81 ± 0.02^{b}	6.3 ± 0.8^{a}	13.2 ± 0.1^{a}
West A open water	0.81 ± 0.008^{f}	96.6 ± 0.637^{f}	195 ± 42^{ba}	203 ± 39^{b}	0.82 ± 0.03^{b}	7.4 ± 0.9^{a}	13.2 ± 0.1^{a}
West B marsh fringe	0.99 ± 0.005^{b}	82.4 ± 0.473^{b}	-87 ± 76^{c}	-84 ± 93^{a}	0.54 ± 0.05^{ac}	14.0 ± 1.7^{bc}	12.9 ± 0.2^{a}
West B open water	0.87 ± 0.005^{d}	91.3 ± 0.45^{d}	116 ± 26^{ab}	174 ± 65^{b}	0.73 ± 0.04^{ab}	13.6 ± 0.9^{bc}	12.8 ± 0.1^{a}
2012							
West A marsh fringe	0.84 ± 0.002^{c}	93.8 ± 0.188^{c}	279 ± 57^{a}	291 ± 26^{b}	0.72 ± 0.08^{ab}	9.1 ± 1.5^{ab}	12.3 ± 0.1^{a}
West A open water	0.77 ± 0.003^{e}	98.9 ± 0.212^{e}	278 ± 39^{a}	257 ± 54^{b}	0.79 ± 0.04^{be}	8.4 ± 1.9^{ab}	11.7 ± 0.2^{a}
West B marsh fringe	0.85 ± 0.006^{dc}	92.7 ± 0.434^{dc}	161 ± 36^{ab}	138 ± 13^{ab}	0.38 ± 0.07^{c}	16.9 ± 2.3^{c}	11.6 ± 0.5^{a}
West B open water	0.94 ± 0.007^{a}	85.9 ± 0.574^{a}	253 ± 44^{a}	222 ± 29^{b}	0.56 ± 0.07^{acd}	27.4 ± 1.4^{d}	13.7 ± 1.5^{a}

Statistical Analyses

Survival of transplants was transformed using ARCSIN square-root transformation to normalize residuals of proportional data (Kery and Hatfield 2003; Gotelli & Ellison 2004). Transformed data were analyzed using a split plot analysis of variance (ANOVA) with both location (West A or West B) and proximity (marsh fringe or open water) being the between-plot factors; transplant type was the within-plot factor and species was the within-subplot factor. The daily percentage of time the soil surface at each plot was flooded, beginning at the time of transplantation, was calculated using the information provided by the aforementioned hydrologic modelers and analyzed using an ANOVA. We were able to calculate the percentage of time the uppermost plant tissue was flooded (overtopped) by factoring in the height of the stem with the elevation. The remaining measured abiotic and transplant response parameters were analyzed as a repeated measures ANOVA with sampling season (June 2010, Sept 2010, June 2011, and June 2012) as the repeated measure. Due to overall low survival, rhizome transplant types were omitted from most transplant response analyses except survival and cover. Analysis of these data was conducted using the general linear model (GLM) procedure of SAS (SAS Enterprise Guide 4.3; SAS Institute, Cary, NC, U.S.A). Huynh−Feldt−Lecoutre epsilon (hereby referred to as H-F-L) univariate tests of hypotheses for within-subject effects are reported for repeated measures analyses. A significance level (α) of 0.05 was used for all analyses. A Tukey post hoc test of pairwise comparisons was conducted to determine significant differences between means.

Results

Environmental Characterization

Differences in elevation, hydrology, and soil physicochemistry were apparent among sampling sites (Table 1). Although RTK surveying techniques typically have a potential measurement error of 3 cm, our results of Liberty Island show that elevation displayed a significant interaction with location, time, and proximity (H-F-L; $F_{[2,56]} = 180.93$, $p < 0.0001$). Elevation tended to be higher near the marsh fringe at West B than West A during the first 2 years, with the West B open water site significantly increasing in elevation over time (Table 1). West B locations were inundated for a shorter percentage of time than the West A locations due to their higher elevation (Table 1). The percent time flooding experienced by the plant tissue (overtopping) of each transplant type also displayed significant differences. Adult transplants protruded into the air from the water, whereas rhizome transplants had no original aboveground biomass, thus adult transplants experienced significantly less overtopping by water than rhizomes (74 vs. 93% time overtopped by water, respectively) ($F_{[1,60]} = 4{,}284.53$, $p < 0.001$) (Fig. 2).

Figure 2. Mean percentage of time water overtops the maximum height of the plant tissue (±SE) during the 4 months following transplantation in June 2010. Means marked by the same letter are not significantly different ($p > 0.05$).

Soil redox potential was related to location ($p < 0.01$), proximity to the marsh shoreline ($p = 0.0166$), and sampling season

Table 2. Survival (%) of each species and transplant type combination at each transplant location. Means followed by the same superscript letter are not significantly different ($p > 0.05$).

	Schoenoplectus acutus		Schoenoplectus californicus		Typha latifolia	
	Rhizome	*Adult*	*Rhizome*	*Adult*	*Rhizome*	*Adult*
West A marsh fringe	0 ± 0^{d}	50 ± 14^{bcd}	31 ± 12^{cd}	44 ± 12^{abc}	0 ± 0^{d}	0 ± 0^{d}
West A open water	0 ± 0^{d}	$75 + 10^{ab}$	25 ± 14^{d}	94 ± 6^{a}	0 ± 0^{d}	0 ± 0^{bcd}
West B marsh fringe	0 ± 0^{d}	$25 + 10^{bcd}$	12 ± 12^{cd}	75 ± 10^{abc}	0 ± 0^{d}	25 ± 14^{d}
West B open water	0 ± 0^{d}	$56 + 19^{ab}$	6 ± 6^{d}	62 ± 16^{a}	0 ± 0^{d}	56 ± 19^{bcd}

($p = 0.0007$). Although soil redox was consistently lower at the West fringe sites and became more reduced over time, soil redox potential was not in the range for sulfate reduction (Sumner 2000) or at levels that are considered to be harmful for *Schoenoplectus* spp. (T. Sloey et al. 2015, University of Louisiana at Lafayette, unpublished data). Soil extraction chemistry from June 2010 showed that ammonium, phosphorus, and potassium concentrations also tended to be higher in the West B locations ($p = 0.0442$). Soil D_b decreased marginally over time (H-F-L; $F_{[2,24]} = 6.2$, $p = 0.14$), most dramatically in the West B locations. Soil D_b tended to be lower on the West B locations ($p < 0.0001$) and along the marsh fringe compared with that on open water ($p < 0.0044$). No significant differences in soil organic matter were detected. Similar to soil D_b, the depth-to-soil resistance increased over time (H-F-L; $F_{[1,12]} = 25.45$, $p = 0.0003$) with a three-way interaction among time, location, and proximity (H-F-L; $F_{[1,12]} = 6.76$, $p = 0.0232$). Depth-to-soil resistance tended to be deeper on the West B locations than that on West A (Table 1).

Transplant Response

We observed significant differences in transplant survival and growth among species and transplant types (Table 2). In September 2010, transplant type had a strong effect on survival ($F_{[1,2]} = 66.61$, $p = 0.0147$), with adult transplants (overtopped by water 74% of the time on average) exhibiting superior survival compared with the rhizomes (overtopped 93% of the time). *Schoenoplectus californicus* exhibited much greater survival ($F_{[2,88]} = 18.56$, $p < 0.0010$) than the other species, and *S. californicus* outperformed the other species at both transplant types ($F_{[2,88]} = 4.80$, $p < 0.0105$). Rhizome transplants of *Schoenoplectus acutus* and *Typha latifolia* exhibited 100% mortality by September 2010. There was also a significant interaction between proximity to the marsh fringe and transplant type ($F_{[2,88]} = 5.63$, $p < 0.0050$), indicating that transplant survival was higher in open water locations for the adults.

Due to high mortality of rhizome transplants, only plots with adult transplants were analyzed for stem density and total area of coverage and vegetative expansion. There were significant interactions between time and proximity (H-F-L; $F_{[4,180]} = 7.91$, $p = 0.0003$), and time and species (H-F-L; $F_{[6,180]} = 94.62$, $p < 0.0001$) on stem density. Regarding total area of coverage, the repeated measures analysis indicated a significant interaction between location and time (H-F-L; $F_{[3,39]} = 4.81$, $p < 0.0470$). Both stem density and area of vegetative coverage showed similar trends; *S. californicus* far outperformed other species. The total area of expansion for *S. californicus* was two orders of magnitude greater than *S. acutus*, and three orders of magnitude greater than *T. latifolia*. *Schoenoplectus californicus* rapidly became the dominant species in the open center plot between species transplants. *Schoenoplectus acutus* transplants showed a general trend toward increasing stem density during the first 3 months, but then declined over the next two sampling seasons. Although *S. acutus* expansion increased in the West B open water site up until June 2011, it regressed by 2012 and died back completely in all sites except for West A fringe. The poor establishment of *T. latifolia* was apparent within 3 months with complete mortality by June 2011. Total area of vegetative expansion showed a significant interaction between time and location (H-F-L; $F_{[3,39]} = 4.42$, $p < 0.0442$), and between time and proximity (H-F-L; $F_{[3,39]} = 78.0$, $p < 0.0001$) with vegetative expansion being greater in the open water sites, especially in the West B open water site (Fig. 3). RTK surveys in each September also showed that annual lateral expansion tended to be higher in the West B locations in areas of higher elevation and lower percent time of flooding (Fig. 4).

Discussion

Our research at Liberty Island provides important information that can assist managers to achieve restoration goals in reclaimed tidal marshes. Although access to historic environmental data before and during the initial levee breach at Liberty Island is limited, our observations of transplanted vegetation suggest two major implications for post-levee breach restoration. First, species and transplant type greatly vary in their ability to survive and expand under given environmental conditions. Second, wetland vegetative expansion at legacy agricultural sites may be inhibited by high soil bulk densities and excessive flooding (i.e. longer durations of inundation). The three-filter framework (sensu Lambers et al. 2008) posits that species distribution and abundance are controlled by dispersal abilities, species physiological tolerance to environmental conditions, and biotic interactions. Although these three factors are equally relevant to understanding species distribution and abundance, a previously conducted seed-bank assay and field observations indicate that although germinable seeds are present in the mudflats at Liberty Island, environmental conditions (likely percentage of time flooded and depth of flooding) inhibit successful germination (T. Sloey & M. Hester 2015, University of Louisiana

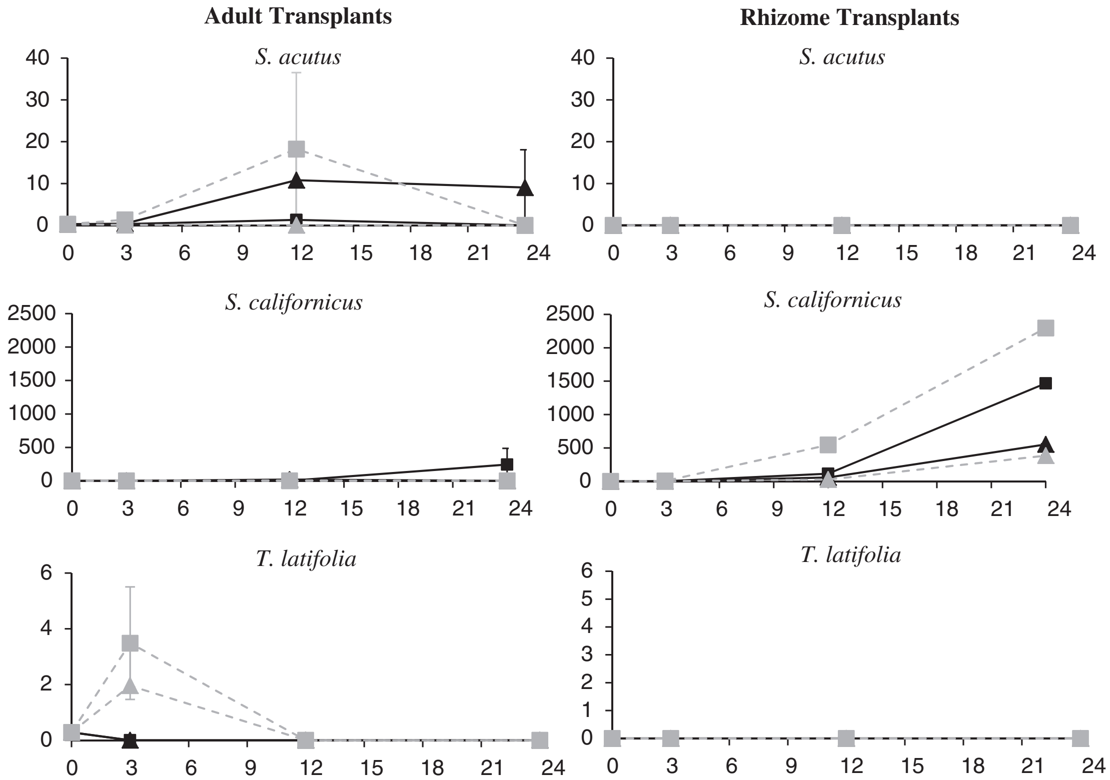


Figure 3. Mean area of vegetation cover (±SE) of transplant areas (by species and transplant type) over 24 months. Black lines represent side West A, whereas gray dashed lines indicate side West B. Squares and triangles denote open water and marsh fringe orientations, respectively. Note that the scale of the *y*-axis differs between species.

at Lafayette, in review). Therefore, our research focused on the latter two filters: the creation of suitable environmental conditions (i.e. hydrology and soil properties) and selection of appropriate plant species and transplant type. Wetland plant species establishment and expansion at Liberty Island under the current conditions are largely constrained to asexual reproduction; De Lange et al. (1998) have also reported the importance of asexual reproduction in other established *Schoenoplectus californicus* marshes. At this particular restoration site, physiological tolerance of young ramets (or transplants) and biotic interactions have become increasingly important in understanding where vegetation can establish and expand as natural colonization and expansion via seed are negligible under the current conditions.

Species and Life History

For all species combined, adults exhibited higher survival than rhizomes with a combination of factors likely responsible for this superior performance. Other studies have shown the importance of emergent stems for increasing survival of *S. californicus* transplants in deep, freshwater lakes (Mallison & Thompson 2010). The presence of stem material protruding from the water enables oxygen transport from the stems to the root system under flooded soil conditions (Langeland 1981), and this enhanced gas exchange may have substantially reduced the flooding stress experienced by the transplants. Clonal plants are well known to have a high propensity for success because of the ability of ramets to share resources (Cook 1983). We have observed that vegetation at Liberty Island is capable of asexually expanding into subtidal elevations. The ability for these expanding ramets to tolerate stressful flooded conditions may be due to their physiological integration with an extensive network of healthy adults from which to gain resources (Eckert 1999).

Differences in establishment success were apparent among species. Although *Typha* spp. are considered to be effective competitors in typical freshwater wetland core habitats (Keddy 2010), *Typha latifolia* was outperformed by the other species at Liberty Island. According to the centrifugal organization model (Wisheu & Keddy 1992), core habitats characterized by benign conditions may favor species such as *Typha* spp., whereas more stressful environments (e.g. flooding, elevated soil bulk densities, and freezing), known as peripheral habitats, favor the occupation by species that are better adapted to specific environmental stressors but may not be dominant due to inferior competitiveness in core habitats. In this case, we observed reduced plant survival and growth in areas that corresponded with higher soil bulk density and longer durations of flooding, suggesting that these environmental conditions may represent a peripheral habitat that favors more robust *Schoenoplectus* spp. over *Typha* spp.

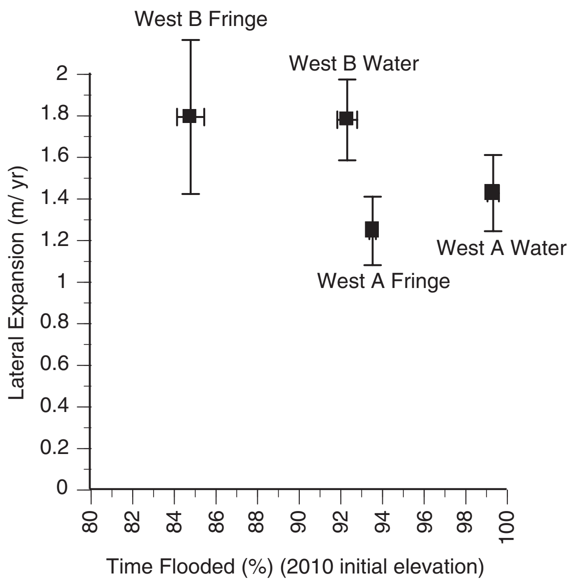


Figure 4. Average annual lateral expansion rates of *Schoenoplectus californicus* (±SE) via rhizomatous growth in relation to percent flooding of the soil surface.

Recreating Proper Hydrologic Conditions

Hydrology is well known to be a key variable in freshwater tidal wetlands as it profoundly influences biogeochemical properties and patterns of species distribution and abundance (Altor & Mitsch 2008). Tidal wetlands are highly dynamic systems with variable hydrologic regimes that exert considerable influence on plant community composition. *Typha latifolia* transplants displayed low initial survival and suffered complete mortality by June 2011, which we believe was the result of high flooding and water flow during an extreme flooding event in the spring of 2011; high mortality was observed in the local *Typha* spp. population. Previous studies have found that *T. latifolia* naturally occurs in shallow water and is restricted to flooding depths less than 80 cm (Grace & Wetzel 1981). A controlled greenhouse study found that *Schoenoplectus acutus* survival is reduced when flooded more than 40% of the time (T. Sloey et al. 2015, University of Louisiana at Lafayette, unpublished data). Interestingly, transplanting efforts in Florida that have implemented the use of *S. californicus* have shown that it can establish in deep submerged zones as long as the vegetation is periodically exposed (Denson & Langford 1982). This study indicated that *S. californicus* can tolerate more severe frequency, depth, and duration of flooding than the other transplanted species, although a greater understanding of species-specific thresholds to inundation would further aid restoration managers.

The overwhelming success of *S. californicus* may also be partially attributed to its stem morphology. *Schoenoplectus californicus* possesses triangular stems, versus the rounded stems of *S. acutus* or flattened leaves of *T. latifolia*. Triangular stems tend to have lower torsional rigidity than round stems and the triangular shape of the stem allows stems to twist with wind movement, reducing drag and preventing stem breakage (Ennos 1993). Thus, species with triangular stem morphologies may be favored under the high wind and wave stress that occurs at Liberty Island. Although we did not directly measure competitive interaction, due to the extensive mortality of *T. latifolia* and *S. acutus*, there is some evidence that *S. californicus* might be capable of displacing *S. acutus*. In June 2011, *S. acutus* exhibited moderate growth and expansion in the West A fringe and West B open water sites. However, by June 2012, *S. californicus* exhibited extremely dominant growth and expansion, whereas *S. acutus* had regressed. We cannot draw definitive conclusions regarding whether this was due strictly to unsuitable abiotic parameters, or if *S. acutus* was shaded out or perhaps outcompeted for nutrients by *S. californicus*, but it is clear that *S. acutus*' occurrence in this location is likely to remain much more limited than *S. californicus*.

Soil physicochemical properties can be a limiting factor on vegetation growth because highly reduced soils can impact multiple plant functions, including photosynthesis (Pezeshki 2001) and nutrient uptake (Koch & Mendelssohn 1989). Soil redox potential measurements in the top 10 cm of soil surveyed at Liberty Island indicated that substantial microbial reduction of SO_4^{2-} to H_2S, a potent phytotoxin, was unlikely (Sumner 2000). Soils across the entire Liberty Island site exhibited higher bulk densities (D_b of 0.6–1.2 g/cm^3) than have typically been reported in other freshwater and tidal marshes (Hammer 1989). A review of regional marshes by Craft (2007) indicated that bulk densities in freshwater California marshes typically range between 0.1 and 0.6 g/cm^3 and are consistently lower than salt marshes. Other studies have found that high soil D_b can act as a physical barrier that impedes rhizome and root expansion, reduces soil porosity, and movement of water, oxygen, and nutrients (Håkansson & Lipiec 2000). Lower soil D_b and deeper penetration depth-to-soil resistance corresponded with locations of optimal transplant expansion at the Liberty Island site.

It is well established that higher availability of nitrogen, phosphorus, and potassium can increase the production of plant species under a variety of conditions (Frost et al. 2009) and also alter species composition (Houlahan et al. 2006). Although ammonium, phosphorus, and potassium were initially higher in the West B locations, this trend was not observed among other sampling seasons, and it is unlikely that soil nutrients are constraining growth at the transplant areas, or at the site in general (M. Hester et al. 2015, University of Louisiana at Lafayette, unpublished data).

Implications for Restoration

Our observations from this transplant experiment have several major implications for restoration practice. It is essential to understand that although the presence of desired vegetation is indicative that reclamation is underway, it does not necessarily indicate that the original ecosystem functions or structure have been restored. To achieve successful restoration, both species composition and abiotic parameters should reflect that of natural, analogous reference marshes. As we observed at Liberty Island, some of the transplanted vegetation was able to thrive; however, the soil conditions were not necessarily reflective of what typically characterizes a freshwater tidal marsh. Although we were unable to sample from local references marshes, our review of literature suggests that soils at Liberty Island are more compacted than would be found at a natural marsh. In addition, the hydrology at Liberty Island appears to impede the survival of two of our transplanted species, and all of the rhizome transplants. Too often, restoration monitoring efforts focus heavily on species diversity and re-occupation by targeted flora and fauna, but neglect to include edaphic conditions and soil development (Ballantine & Schneider 2009). Whenever possible, modifications to establish optimal abiotic conditions should take place prior to a plant establishment effort to maximize the likelihood of restoration success. This modification may manifest itself in the process of ameliorating legacy soils to reflect more wetland-like conditions (i.e. elevation, hydrology, and soil physicochemistry); however, the specific physical conditions required are likely to differ depending on site, desired species, and the individual restoration goals for the site.

Transplanting of vegetation can have successful results in terms of accelerating the re-establishment of desired species and ecosystem structure and function and when the proper species and transplant types are implemented. Selection of the proper species for restoration plantings depends on site-specific conditions and the individual goals of the restoration project. At this particular site, the conditions were comparatively most favorable for *S. californicus* transplant establishment and expansion. Similarly, our work emphasizes that elevation and hydrologic regime have variable impacts on plant establishment depending on the species and age of the plant. Construction of proper hydrologic regime should also be considered on a site- and species-specific basis. Finally, during restoration planning it is also important to consider that the presence of vegetation will likely modify elevation and soil conditions over time. It is generally understood that the successful introduction of vegetation can increase soil organic matter, reduce soil D_b, and as we saw in West B open water site where plant colonization was most successful, increase soil surface elevation. In the case of Liberty Island, restoration managers could not prepare the area for wetland rehabilitation as the levee breach was unintentional. Transplanting adult macrophytes into a restoration site has immense potential for successful re-establishment of target species, and we strongly recommend that restoration managers assess the site's edaphic and hydrologic conditions, as well as thoroughly consider the appropriate species selection to achieve individual restoration goals. The environmental conditions of the site, physiological tolerances of selected species, and biological interactions should be primary concerns for restoration projects, regardless of the location or size of the system being addressed.

Acknowledgments

We extend thanks to the BREACH III team. Funding and support was provided by the California Federal Bay Delta Program, Ecosystem Restoration Program, and University of Louisiana at Lafayette. Field assistance was provided by members of the California Department of Fish and Wildlife. RTK elevation surveys were conducted by Darren Gewant of Environmental Data Solutions. Hydrologic data were obtained from ESA-PWA. Field assistance was provided by Mike J. Dupuis and Christine N. Pickens of the UL-Lafayette Coastal Plant Ecology Laboratory. Finally, we thank Beth Middleton, Rebecca Howard, Paul Leberg, and Scott France for comments and manuscript review.

LITERATURE CITED

Altor AE, Mitsch WJ (2008) Methane and carbon dioxide dynamics in wetland mesocosms: effects of hydrology and soils. Ecological Applications 18:1307–1320

American Public Health Association (2012) Standard methods for the examination of water and wastewater. 22nd ed. American Water Works Association/American Public Works Association/Water Environment Federation, Washington, D.C.

Atwater BF, Conard SG, Dowden NJ, Hedel CW, MacDonald RL, Savage W (1979) History, landforms, and vegetation of the estuary's tidal marshes. Pacific Division of the American Association for the Advancement of Science c/o California Academy of Sciences, San Francisco

Ballantine K, Schneider R (2009) Fifty-five years of soil development in restored freshwater depressional wetlands. Ecological Applications 19:467–1480

Campbell DA, Cole CA, Brooks RP (2002) A comparison of created and natural wetlands in Pennsylvania, U.S.A. Wetlands Ecology and Management 10:41–49

Conomos TJ (1979) San Francisco Bay: the urbanized estuary. Pacific Division of the American Association for the Advancement of Science, San Francisco, California

Cook RE (1983) Clonal plant populations: a knowledge of clonal structure can affect the interpretation of data in a broad range of ecological and evolutionary studies. American Scientist 71:244–253

Craft C (2007) Freshwater input structures soil properties, vertical accretion, and nutrient accumulation of Georgia and U.S. tidal marshes. Limnology and Oceanography 52:1220–1230

De Lange P, Gardner RO, Champion PD, Tanner CC (1998) *Schoenoplectus californicus* (Cyperaceae) in New Zealand. New Zealand Journal of Botany 36:319–327

Denson K, Langford F (1982) Expansion of transplanted giant bulrush in central Florida lakes. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 36:287–293

Eckert CG (1999) Clonal plant research: proliferation, integration, but not much evolution. American Journal of Botany 86:1649–1654

Ennos AR (1993) The mechanics of the flower stem of the sedge *Carex acutiformis*. Annals of Botany 72:123–127

Frost JW, Schleicher R, Craft C (2009) Effects of nitrogen and phosphorus additions on primary production and invertebrate densities in a Georgia (U.S.A.) tidal freshwater marsh. Wetlands 29:196–203

Gotelli NJ, Ellison AM (2004) A primer of ecological statistics. Sinauer Associates, Inc., Sunderland, Massachusetts

Grace JB, Wetzel RG (1981) Habitat partitioning and competitive displacement in Cattails (*Typha*): experimental field studies. The American Naturalist 118:463–474

Håkansson I, Lipiec J (2000) A review of the usefulness of relative bulk density values in studies of soil structure and compaction. Soil and Tillage Research 53:71–85

Hammer DA (1989) Constructed wetlands for wastewater treatment. Lewis Publishers/CRC Press LLC, Boca Raton, Florida

Hart J (2010) Liberty Island: scenes of transition. April–June ed. Bay Nature, Long Beach, California

Houlahan JE, Keddy PA, Makkay K, Findlay CS (2006) The effects of adjacent land use on wetland species richness and community composition. Wetlands 26:79–96

Jordan TE, Whigham DF, Correll DL (1989) The role of litter in nutrient cycling in a brackish tidal marsh. Ecology 70:1906–1915

Keddy PA (2010) Wetland ecology: principles and conservation. Cambridge University Press, New York
Kery M, Hatfield JS (2003) Normality of raw data in general linear models: the most widespread myth in statistics. Bulletin of the Ecological Society of America 84:92–94
Koch MS, Mendelssohn IA (1989) Sulphide as a soil phytotoxin: differential responses in two marsh species. Journal of Ecology 77:565–578
Lambers H, Chapin FS III, Pons TL (2008) Plant physiological ecology. 2nd ed. Springer Science + Business Media, LLC, New York
Langeland K (1981) Bulrush-*Scirpus* spp. Aquatics 3:4–15
Lytle DA, Merritt DM (2004) Hydrologic regimes and riparian forests: a structured population model for cottonwood. Ecology 85:2493–2503
Malcolm RK (1981) The story of Liberty Island. The Oral History Center, Shield Library, University of California, Liberty Farms Company Archives, D-044, Department of Special Collections, University of California Library, Davis, California
Mallison CT, Thompson BZ (2010) Planting strategies to establish giant bulrush. Journal of Aquatic Plant Management 48:111–115
Miller RL, Fujii R (2010) Plant community, primary productivity, and environmental conditions following wetland re-establishment in the Sacramento-San Joaquin Delta, California. Wetlands Ecology and Management 18:1–16
Mitsch WJ, Gosselink JG (2000) Wetlands. 3rd ed. John Wiley & Sons, Inc., New York
Nyman JA, Delaune RD, Patrick WH Jr (1990) Wetland soil formation in the rapidly subsiding Mississippi River Deltaic Plain: mineral and organic matter relationships. Estuarine, Coastal and Shelf Science 31:57–69
O'Neill RV (1999) Recovery in complex ecosystems. Journal of Aquatic Ecosystem Stress and Recovery 6:181–187
Perry RW, Skalski JR (2009) Estimating survival and migration route probabilities of juvenile Chinook Salmon in the Sacramento-San Joaquin River Delta. North American Journal of Fisheries Management 30:142–156
Pezeshki SR (2001) Wetland plant responses to soil flooding. Environmental and Experimental Botany 46:299–312
Simenstad CA, Thom RM (1996) Functional equivalency trajectories of the restored Gog-Le-Hi-Te estuarine wetland. Ecological Applications 6:38–56
Simenstad CA, Toft J, Williams P, Crooks S, Nur N, Herzog M, et al. (2006) BREACH III: evaluating and predicting 'restoration thresholds' in evolving freshwater-tidal marshes, October 27:9
Soil and Plant Analysis Council, Inc (1999) Soil analysis handbook of reference methods. CRC Press, LLC, Boca Raton, Florida
Sumner ME (2000) Handbook of soil science. CRC Press LCC, Boca Raton, Florida
Wisheu IC, Keddy PA (1992) Competition and centrifugal organization of plant communities: theory and tests. Journal of Vegetation Science 3: 147–156

Supporting Information

The following information may be found in the online version of this article:

Figure S1. Example of transplant configuration at a site. The three 0.25 m^2 quadrats make up one plot, plots are separated by 1 m of space. Only one transplant type (rhizome or adults) are used in a plot. Species orientation is sequentially rotated for each plot.
Figure S2. Plot of linear regression of the natural log of dry stem biomass (g) versus natural logged against stem height (cm) of *Schoenoplectus californicus* collected from naturally colonized tule marsh at Liberty Island in September 2010. Estimated biomass per 0.25 m^2 plot was calculated with the following equation: Total biomass = (0.0091 × average stem height) × (average stem density).

Coordinating Editor: Rachel Thiet

Received: 21 November, 2014; First decision: 8 January, 2015; Revised: 10 March, 2015; Accepted: 10 March, 2015; First published online: 24 April, 2015