Field assessment of environmental factors constraining the development and expansion of Schoenoplectus californicus *marsh at a California tidal freshwater restoration site*

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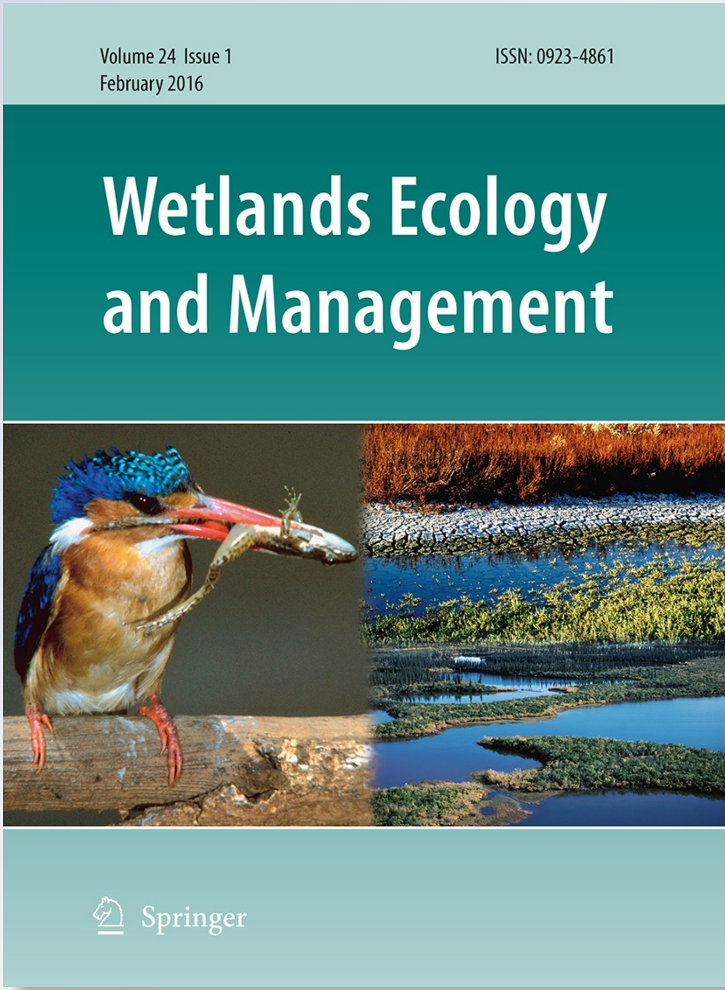

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ORIGINAL PAPER

Field assessment of environmental factors constraining the development and expansion of *Schoenoplectus californicus* marsh at a California tidal freshwater restoration site

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Abstract The effective restoration of wetland habitats requires understanding the establishment requirements, growth responses, and expansion dynamics of targeted plant species. This is particularly true when restoring areas that have been previously managed for other activities, such as agriculture, which can have legacy effects on the local environment. We investigated environmental factors (specifically hydrology and soil physicochemical conditions) that may influence the establishment, growth and expansion of *Schoenoplectus californicus* in a tidal freshwater marsh restoration site in the Sacramento–San Joaquin Delta, California, USA. This study site was previously leveed, drained, and utilized for agricultural production. A 1997 levee breach restored tidal connectivity and wetland vegetation has re-established in portions of the area. Our approach coupled an intensively-sampled transect study in *S. californicus*-dominated marshes with a spatially-extensive survey of *S. californicus* lateral expansion rates and elevation. Lateral expansion of *S. californicus* marsh edge was significantly less in lower elevation areas (0.61 ± 0.04 m NAVD88), whereas the marsh edge at higher elevations (0.84 ± 0.03 m NAVD88) exhibited greater expansion, often at rates greater than 1.0 m year^{-1}. These elevation means correspond to percentages of time that the marsh surface was flooded of 100 and 94 %, respectively. Although marsh edge expansion was influenced by elevation and the resultant hydrology, other factors, such as physical exposure of marsh shorelines and compacted agricultural soils also appear to be important. However, once established, *S. californicus* appears to be able to ameliorate high soil bulk densities over time as the advancing marsh platform develops.

Keywords Bulk density · Elevation · Environmental factors · Hydrology · Lateral expansion · Wetland restoration

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Introduction

Wetlands are important habitat types characterized by a unique interface of water and vegetation that results in specific ecosystem processes, which in turn provide valuable ecosystem services (de Groot et al. 2002). These ecosystem services include the provision of habitat for crucial faunal species, enhancement of water quality, carbon sequestration, and the mitigation of flood water impacts, among others (de Groot et al. 2002; Klemas 2013). However, the value of wetland habitats has only been recognized in the relatively recent past and as a result, expansive areas of historic wetland habitat have been modified for other uses worldwide (Mitsch and Gosselink 2000), including the Sacramento–San Joaquin Delta in California, USA (Bennett and Moyle 1996; Williams and Faber 2001). Because of the substantial alterations that wetland habitats have historically undergone and the significant loss of ecosystem services they provide, there is considerable interest in developing effective and efficient strategies to restore these habitat types (Mitsch and Gosselink 2000; Klemas 2013). However, wetland restoration is unlikely to be successful without a thorough understanding of the tolerance of desired wetland plant species to environmental conditions at restoration sites.

The Sacramento–San Joaquin Bay Delta is the largest deltaic wetland habitat complex on the western coast of the United States (Atwater et al. 1979; Conomos et al. 1985). Importantly, this riverine network is a critical component of California's freshwater infrastructure, providing drinking water for 22 million people and supporting a \$27 billion agricultural industry (Wohl et al. 2012). Further, this area provides habitat for a number of environmentally sensitive faunal species, including Chinook salmon (Perry and Skalski 2009) and delta smelt (Sweetnam 1999). As has occurred with many coastal ecosystems, the Sacramento–San Joaquin Bay Delta has been extensively altered (Diggory and Parker 2011), with over 97 % of the aquatic habitats drained for agricultural use (Bennett and Moyle 1996). Currently, there is great interest in tidal wetland restoration throughout the San Francisco Bay Estuary, including the Sacramento–San Joaquin Bay Delta, with more than 24,000 ha of tidal wetland restoration planned (Williams and Faber 2001). Given that the Sacramento–San Joaquin Bay Delta is projected to also experience substantial alterations due to changing climate (Cloern et al. 2011), the development of a more complete understanding of environmental constraints on the establishment dynamics and productivity of key plant species will be necessary for effective and efficient restoration efforts in this area.

Schoenoplectus californicus is an important plant species in many of the freshwater marshes of the San Francisco Bay Estuary (Watson and Byrne 2009; Vasey et al. 2012). It is native to California and occurs in marshes around the globe (de Lange et al. 1998; Banack et al. 2004; Pratolongo et al. 2008). Although this species produces viable seeds (Sloey et al. in review), in many areas it is believed to spread primarily by fragmentation of rhizomes and asexual tillering (de Lange et al. 1998). This species is well known to be beneficial to many wildlife species, including waterfowl (Kimble and Ensminger 1959) and mammals (Chabreck 1958). *S. californicus* has been reported to occur in areas with soils of high bulk density and high phosphorus concentrations (Richardson et al. 1995) and in areas that are flooded the majority of the time (Ramirez and Anazco 1982; de Lange et al. 1998; Watson and Byrne 2009; Sloey et al. 2015). Because of its wide geographic distribution and flood tolerance, *S. californicus* has been employed for wetland restoration projects in many areas. Denson and Langford (1982) investigated using *S. californicus* transplants in Lake Henry, Florida and observed that after 3 years the transplanted units had expanded from 10 to 160 m^{-2}. A fresh marsh restoration project in Sonoma County, California that employed transplanted *S. californicus* units demonstrated survival of 97 % and substantial increase in stem density after 1 year (Waaland 1995). Although these studies effectively highlight the potential efficacy of using *S. californicus* in low salinity marsh restoration efforts, the range of key environmental conditions, such as flooding depth, under which restoration of this important species can be expected to be successful, is still not fully understood.

The research reviewed above clearly illustrates that *S. californicus* can be employed for wetland restoration applications. However, insights into how *S. californicus* may perform within a restoration context can be greatly enhanced by achieving a better understanding of how environmental conditions influence growth responses and how the plant community interacts with the physical environment as the marsh platform develops. We implemented a dualistic approach incorporating an intensive transect study sampled over several growing seasons with annual, spatially-extensive surveys of marsh edge position and elevation. We sought to characterize *S. californicus* marsh platform (plant/soil) gradients and identify factors that may influence the expansion of *S. californicus*.

Materials and methods

Site description

Liberty Island, California (38.308359°N, −121.686974°W) is a historic wetland area that had been leveed and drained for agricultural purposes in the early twentieth century. In 1997 a non-repairable levee breach flooded the area, thereby re-establishing a freshwater tidal hydrologic regime. Liberty Island is a particularly informative field site as it has been partially recolonized by *S. californicus* and exhibits a gradient of marsh surface elevations and soil physical characteristics, thereby enabling assessment of *S. californicus* dynamics under a range of field conditions.

Transect study

Our transect study was initiated at Liberty Island in May of 2010 to assess how relationships between plant and soil characteristics varied across open mudflat, shoreline, marsh fringe, and interior marsh habitats. Specifically, 1-m^2 plots were established in these four zones with plot centers as follows: open mudflat (plot center approximately 4.5 m out into the mudflat from the marsh edge), shoreline (plot center 0.5 m interior from the marsh edge), marsh fringe (plot center 1.5 m interior to the marsh edge), and marsh interior (plot center approximately 4.5 m interior from the marsh edge) (Fig. S1). Transects were established in marshes on both the west and east sides of Liberty Island. Initial establishment of transects in May of 2010 included five transects on the west side of Liberty Island and three transects on the east side of Liberty Island. In the fall of 2011, two additional transects were installed on the east side of Liberty Island to increase spatial coverage. Also in fall of 2011, one transect each on the east and west sides of Liberty Island were noted to have experienced substantial anthropogenic disturbance; therefore new transects were established laterally from the disturbed transects to replace these. At each transect plot, stem density and average stem height were determined. Standing live biomass was estimated using a regression of stem density and average stem height on live biomass that was developed for Liberty Island (Sloey et al. 2015). Additionally, 5 cm diameter soil cores were collected to a depth of 15 cm for determination of soil bulk density and organic matter content (loss on ignition). A second soil sample was collected to a depth of 15 cm, kept refrigerated, and analyzed for water-extractable pH, conductivity and phosphorus, as well as KCl-extractable ammonium and nitrate-nitrite using EPA approved methods. Depth to soil penetration resistance was determined using a soil penetrometer (15585-0003D, Dickey John) in all plots in fall 2011 and in vegetated plots in fall 2012. We define depth to soil penetration resistance as the soil depth at which the penetrometer displayed an abrupt increase in resistance to further penetration. Soil redox potential was measured using combination redox electrodes in conjunction with a hand-held millivolt meter at 1 cm depths in spring 2010 and at 1 and 10 cm soil depths in fall 2011 and fall 2012. The elevation of all plot centers and the location of the current edge of the marsh were determined as part of a larger Real Time Kinematic (RTK) survey in fall of 2012, described below. Data were analyzed as a factorial ANOVA of location (East, West) and transect zone (open mudflat, shoreline, marsh fringe, and interior marsh) using the appropriate general linear models of JMP 9.0. A priori contrasts were employed to test specific comparisons of interest within the transect zone factor (e.g., open mudflat versus vegetated zones, shoreline versus marsh interior, etc.). Residuals of the data exhibited mild departures from the parametric assumption of normality; however, ANOVA is generally regarded as robust to such deviations (Neter et al. 1990) and therefore transformations were not employed.

Lateral expansion study

To provide greater insight into the effects of marsh surface elevation on *S. californicus* occurrence and lateral expansion rates, we implemented an extensive real time kinematic (RTK) survey of the Liberty Island restoration site. RTK is a satellite-based positioning system that determines X, Y, and Z coordinates with a relatively small error ($\sim$3 cm). Using RTK survey, data points were collected at all transect marsh edges in September 2010, 2011 and 2012, and at additional, naturally colonized marsh edges throughout Liberty Island in September 2011 and 2012. Marsh edges of a companion transplant study (Sloey et al. 2015) were also included in the RTK survey in September 2010, 2011 and 2012, providing high resolution location and elevation data for a total of 257 locations. All survey points were re-occupied during subsequent RTK surveys to detect change in marsh surface elevation. After a survey point (from the previous year) was re-occupied, a new survey point was established at the closest, current perpendicular marsh edge and the linear distance between these points was calculated to determine the annual lateral change (i.e., marsh edge expansion or retreat). To assess the effect of hydrologic regime on *S. californicus* occurrence and lateral expansion rates, the percentage of time marsh surfaces were flooded was calculated using data provided by a local tidal gauge. The linear relationship between marsh surface elevation and lateral expansion rate in the Liberty Island wide survey were evaluated with simple linear regression. Average elevations of marsh edges that were not expanding versus marsh edges that were expanding were compared using one-way ANOVA. Data from marsh edge plots in the transect study and companion transplant study (Sloey et al. 2015) were combined (total of 26 plots) to evaluate the relationships among *S. californicus* lateral expansion rates, estimated biomass, key soil metrics (soil organic matter, bulk density, depth to penetration resistance), marsh surface elevation and percentage of time flooded using principal components analysis in JMP 9.0.

Results

Transect study

No effect of location was detected for *S. californicus* stem density in spring 2010 (see Table S1 for summaries of all ANOVA tests). Further, stem densities of marsh interior and marsh fringe plots were not significantly different from one another in spring 2010. However, stem density was significantly greater on the west side of Liberty Island than on the east side in both fall 2011 and fall 2012 (Fig. 1; $p < 0.05$, $p < 0.05$, respectively). A significant effect of transect zone on stem density was detected in spring 2010, fall 2011 and fall 2012 (Fig. 1; $p < 0.0001$, $p < 0.0001$, $p < 0.0001$, respectively). A very important finding was that by fall 2011 (and continuing into fall 2012), no significant difference in stem density was detectable between marsh interior plots and shoreline plots, indicating that *S. californicus* had expanded into shoreline plots and stem densities had become equitable. Location did not have a significant effect on average stem height in any sampling period. However, in terms of marsh zone, average stem heights were significantly greater in marsh interior plots than in marsh fringe and shoreline plots by fall

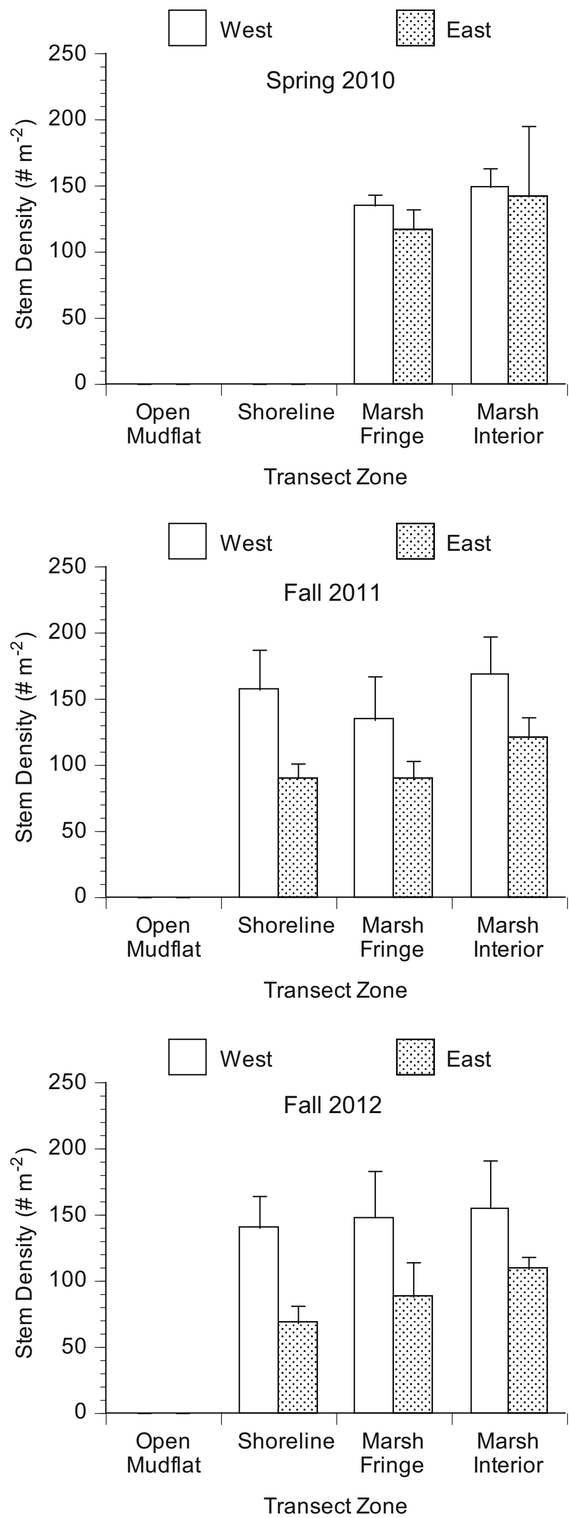

Fig. 1 *Schoenoplectus californicus* stem density (mean ± SE) at different locations, transect zones, and sampling seasons

2012 (Fig. 2; $p < 0.05$). Estimated biomass was not significantly different between the east and west sides of Liberty Island in any sampling season. Although estimated biomass was higher in marsh interior than marsh fringe plots in spring 2010 (Fig. 3; $p < 0.05$), no significant difference was detected among vegetated plots in fall 2011 or fall 2012.

The east side of Liberty Island exhibited a significantly lower elevation than the west side (fall 2012 complete data set; Fig. 4, top panel; $p < 0.001$). Concomitantly with elevation, the percentage of time that the marsh surface was flooded was significantly greater on the east side than the west side of Liberty Island (Fig. 4, bottom panel; $p < 0.001$).

Soil bulk density was significantly higher in unvegetated zones than vegetated zones in spring 2010 (Fig. 5; $p < 0.01$). No significant effect of location was detected for soil bulk density in spring 2010, but in fall 2011 and fall 2012 the east side of Liberty Island exhibited significantly greater soil bulk density than the west side (Fig. 5; $p < 0.01$and $p < 0.01$, respectively). Additionally, by fall 2012 a significant effect of transect zone on soil bulk density was detected (Fig. 5; $p < 0.01$), driven by the open mudflat zone having a greater soil bulk density than the three vegetated zones.

Soil organic matter was significantly higher on the west side of Liberty Island than on the east side in all sampling periods (Table 1; $p < 0.001$, $p < 0.001$, $p < 0.001$, respectively). Soil organic matter tended to be lower in the open mudflat zone than in the vegetated marsh platform, marsh fringe, and shoreline zones in spring 2010 and fall 2011, and became significant by fall 2012 (Table 1; $p < 0.01$). Overall, the west side of Liberty Island tended to exhibit a greater soil depth to penetration resistance in fall 2011 (Table 1; $p = 0.075$). A significant interaction of location and transect zone (Table 1; $p = 0.013$) was detected for resistance to soil penetration in Fall 2011, with resistance to penetration increasing from marsh interior to open mudflat on the east side of Liberty Island, but decreasing from marsh interior to open mudflat on the west side.

Soil ammonium was not significantly affected by location or transect zone in any sampling season and soil nitrate-nitrite was largely below detection for all sampling times (Table 1). A significant effect of transect zone was detected for soil phosphorus in fall

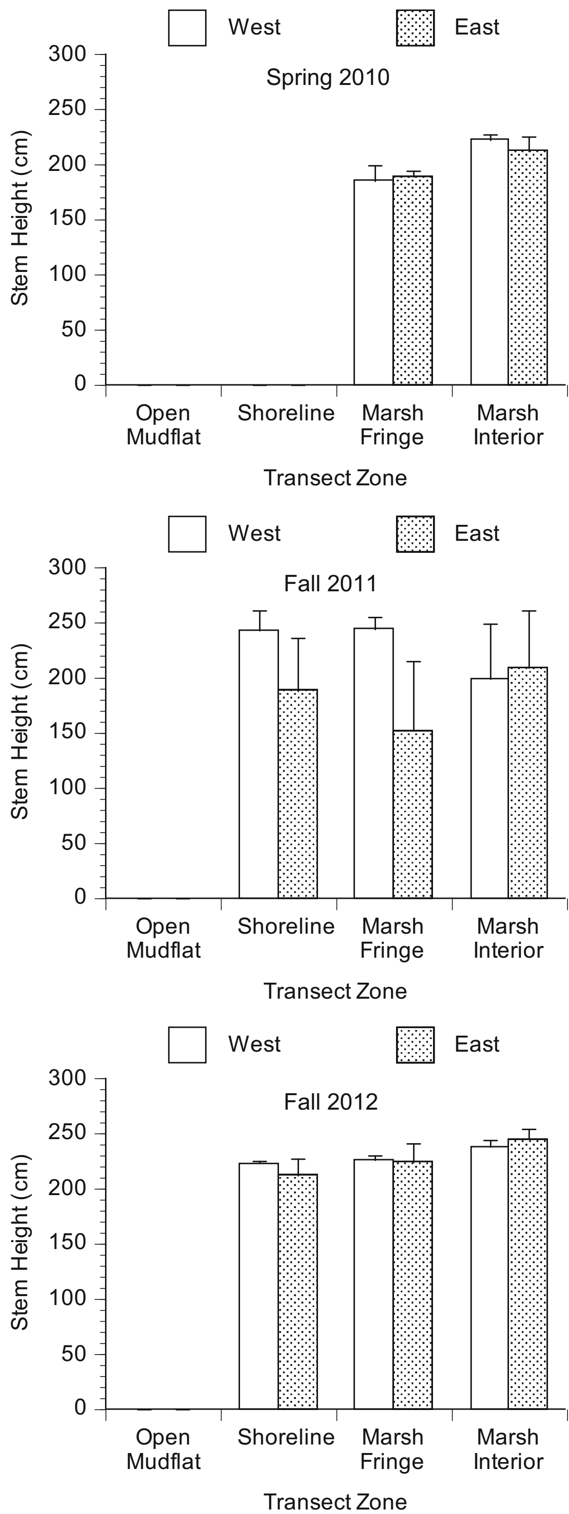

Fig. 2 *Schoenoplectus californicus* stem height (mean ± SE) at different locations, transect zones, and sampling seasons

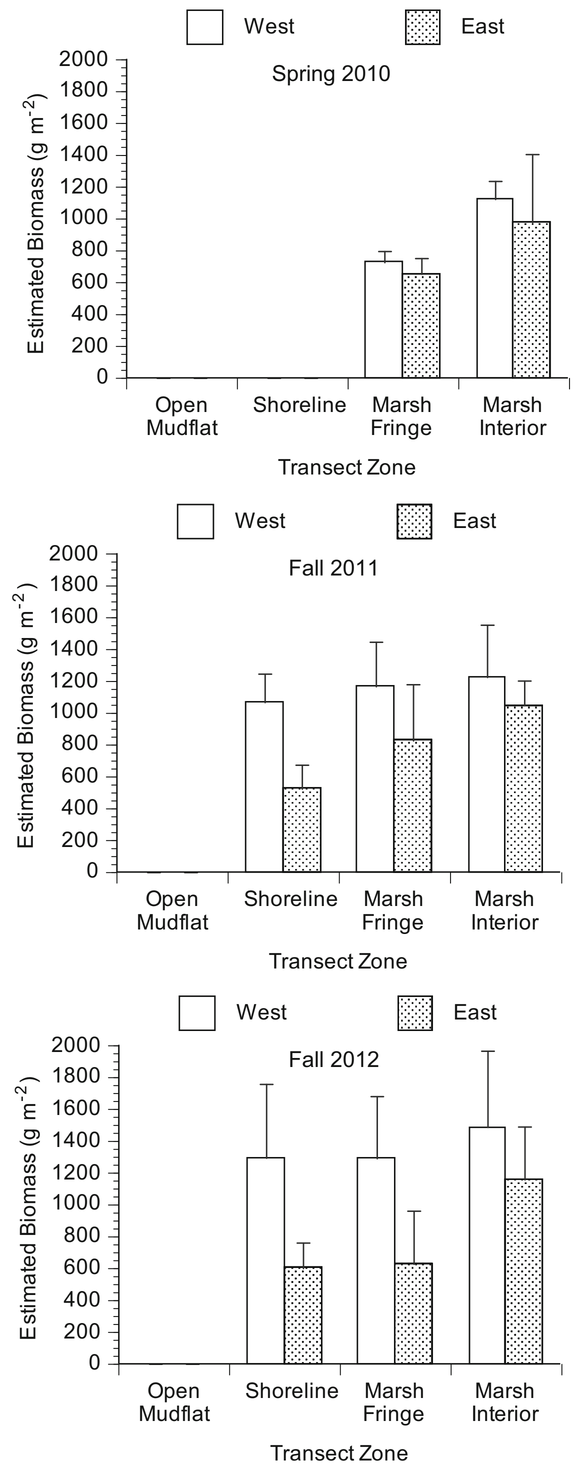

Fig. 3 *Schoenoplectus californicus* biomass (mean ± SE) at different locations, transect zones, and sampling seasons

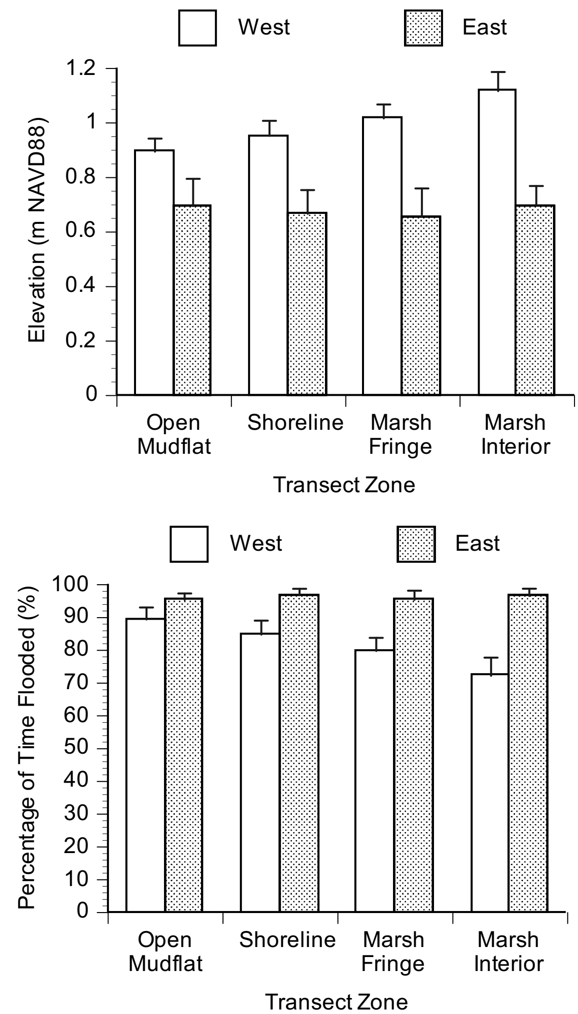

Fig. 4 Fall 2012 plot elevation (*top panel*) and percentage of time flooded (*bottom panel*; mean ± SE) at different locations and transect zones

2011, with the open mudflat having higher soil phosphorus than the three vegetated zones (Table 1; $p < 0.01$). Soil pH was significantly lower on the east side of Liberty Island than the west side in fall 2011 and fall 2012 (Table 1; $p < 0.05$, $p < 0.05$, respectively) and was also higher in the open mudflat zone than the vegetated zones in fall 2011 (Table 1; $p < 0.01$). Soil redox potential at 1 cm was significantly lower on the east side of Liberty Island than the west side in summer 2010 and fall 2011 (Table 1; $p < 0.01$, $p < 0.01$, respectively) No significant

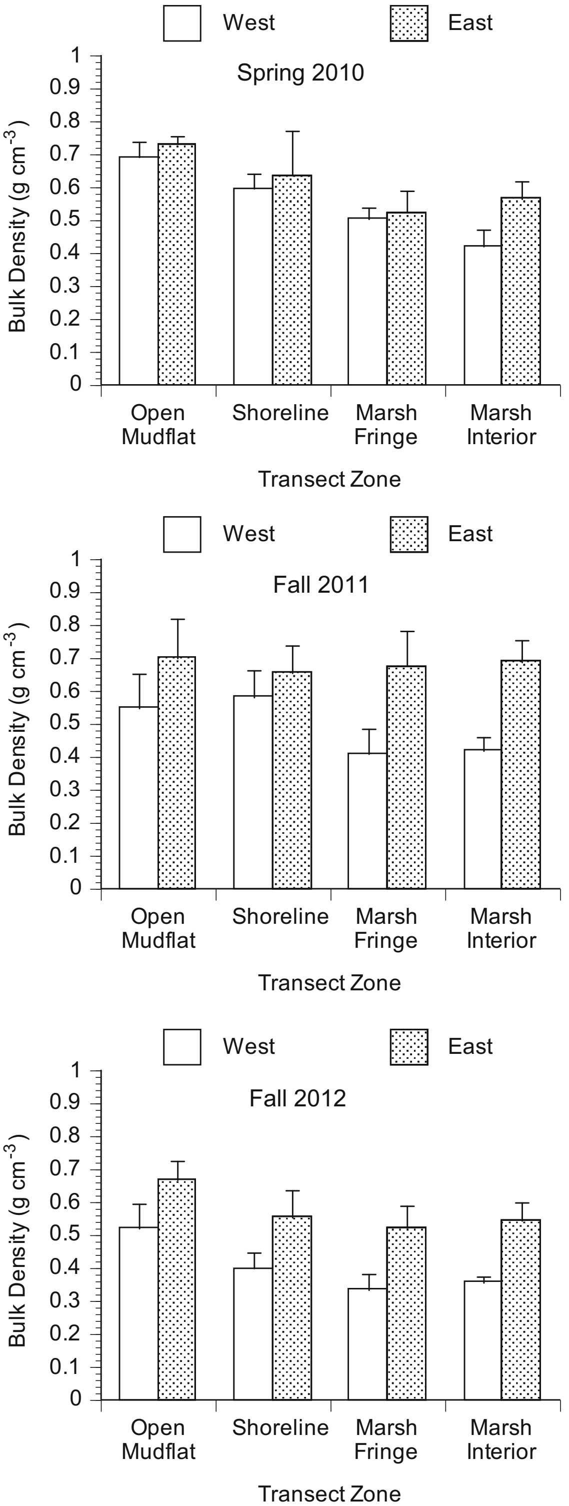

Fig. 5 Soil bulk density (mean ± SE) at different locations, transect zones, and sampling seasons

effects were detected on soil conductivity or soil redox potential at 10 cm in spring 2010, fall 2011, or fall 2012.

Lateral expansion study

The elevations of marsh edges that demonstrated either no expansion or marsh edge loss (mean elevation = 0.61 ± 0.04 m) were significantly lower than marsh edges that had positive rates of lateral expansion (mean elevation = 0.84 ± 0.03 m; $p < 0.001$). These elevation means correspond to a percentage of time the marsh surface was flooded range of 100–94 %. However, a simple linear regression utilizing all 257 survey points of marsh surface elevation on *S. californicus* lateral expansion yielded very little explanatory power (Fig. 6; $R^2 = 0.089$), resulting in a non-significant linear relationship between *S. californicus* marsh edge elevation and lateral expansion, suggesting that additional factors are likely involved in regulating *S. californicus* lateral expansion.

Principal components analysis using marsh edge data from the transect study presented here in conjunction with plots from an associated transplant study (Sloey et al. 2015) revealed the important role of several soil variables in modulating *S. californicus* lateral expansion and also suggest that additional explanatory factors not captured in this study exist (Table 2). The first two principal components extracted during the analysis explained 66.6 % of

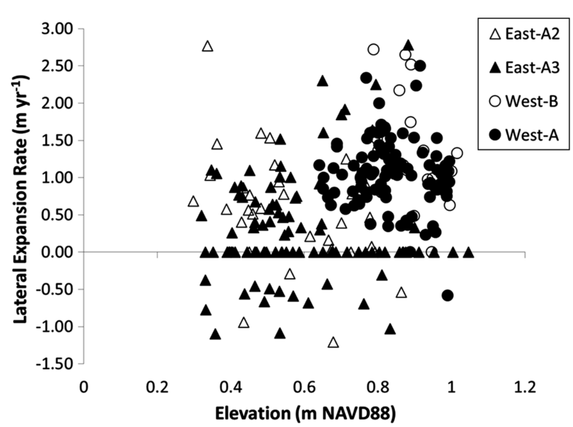

Fig. 6 Scatterplot of marsh surface elevation and lateral expansion rate

Table 1 Key soil metrics (mean ± SE) at different locations, transect zones, and sampling season

Metric	Season	East				West			
		Interior	Marsh fringe	Shoreline	Open mudflat	Interior	Marsh fringe	Shoreline	Open mudflat
Soil organic matter (%)	Spring 2010	7.9 (0.9)	6.5 (2.2)	7.1 (1.1)	7.7 (0.7)	11.6 (0.8)	11.4 (0.6)	11.2 (0.5)	9.8 (0.6)
	Fall 2011	7.2 (0.5)	8 (0.7)	7.2 (0.7)	7.8 (0.5)	10.7 (0.5)	11.3 (1.0)	9.9 (0.8)	9 (0.2)
	Fall 2012	9.6 (0.9)	9.5 (0.6)	8.8 (0.4)	7.2 (0.4)	13 (0.5)	12.8 (0.3)	12 (0.4)	12.2 (0.6)
Soil ammonium (μg g^{-1})	Spring 2010	12.5 (9.0)	15.6 (1.3)	23.2 (7.16)	16.1 (2.3)	10.9 (1.8)	10.3 (1.8)	10.7 (2.4)	11.1 (0.9)
	Fall 2011	22.1 (9.2)	17.1 (4.2)	20.4 (7.4)	19.5 (7.7)	18.8 (4.7)	27.2 (3.5)	30.7 (9.1)	31.0 (5.7)
	Fall 2012	11.8 (6.4)	18 (7.5)	15.1 (7.1)	14.8 (6.1)	18.3 (7.1)	28 (7.0)	15.5 (6.2)	5.2 (2.4)
Soil phosphorus (μg g^{-1})	Spring 2010	0.39 (0.08)	0.26 (0.04)	0.29 (0.03)	0.29 (0.01)	0.30 (0.02)	0.30 (0.01)	0.27 (0.02)	0.23 (0.03)
	Fall 2011	0.09 (0.01)	0.10 (0.02)	0.20 (0.03)	0.22 (0.03)	0.12 (0.04)	0.18 (0.04)	0.27 (0.09)	0.29 (0.05)
	Fall 2012	0.14 (0.03)	0.60 (0.28)	0.16 (0.06)	0.30 (0.16)	0.31 (0.16)	0.18 (0.12)	0.37 (0.26)	0.43 (0.18)
Soil redox potential 1 cm (mV)	Spring 2010	−53.3 (30)	−40 (11)	135 (12)	−24 (9)	26 (21)	26 (36)	30 (44)	1 (18)
	Fall 2011	−72 (48)	−110 (26)	−108 (31)	−83 (14)	−22 (28)	−12 (58)	−82 (28)	−44 (33)
	Fall 2012	14 (37)	86 (31)	96 (33)	68 (27)	66 (33)	68 (8)	83 (12)	87 (20)
Soil redox potential 10 cm (mV)	Spring 2010	NA	NA	NA	NA	NA	NA	NA	NA
	Fall 2011	−54 (35)	−58 (21)	−67 (24)	−52 (14)	−49 (34)	7 (27)	−13 (39)	−145 (52)
	Fall 2012	48 (24)	57 (36)	89 (36)	54 (24)	62 (32)	69 (25)	88 (19)	106 (15)
Soil pH	Spring 2010	7.1 (0.3)	7.7 (0.6)	7.6 (0.6)	8.3 (0.3)	6.9 (0.2)	6.9 (0.2)	6.9 (0.1)	7.5 (0.2)
	Fall 2011	6.9 (0.1)	7.0 (0.3)	7.3 (0.2)	7.6 (0.1)	6.1 (0.1)	6.6 (0.2)	6.7 (0.1)	7.1 (0.1)
	Fall 2012	6.6 (0.2)	6.9 (0.2)	7.2 (0.3)	7.3 (0.3)	5.9 (0.2)	6.3 (0.1)	5.7 (0.1)	6.4 (0.1)
Soil EC (dS cm^{-1})	Spring 2010	173.5 (38.3)	166.0 (18.4)	192.7 (16.6)	129.5 (15.4)	157.4 (42.1)	252.3 (86.8)	191.2 (31.0)	132.0 (20.8)
	Fall 2011	70.8 (10.6)	81.1 (32.5)	51.4 (4.4)	54.7 (7.2)	76.5 (19.3)	45.7 (11.0)	40.4 (7.3)	44.7 (13.9)
	Fall 2012	218.9 (34.2)	146.6 (42.6)	147.5 (60.8)	120.4 (26.4)	257.5 (87.9)	256.8 (50.9)	249.2 (38.5)	131.1 (36.5)
Depth to soil penetration resistance (cm)	Spring 2010	NA	NA	NA	NA	NA	NA	NA	NA
	Fall 2011	9.4 (2.1)	12.4 (4.5)	10.8 (1.2)	25.6 (13.5)	27.8 (3.7)	24.8 (2.7)	16.4 (3.9)	12.8 (3.5)
	Fall 2012	27.9 (8.3)	37.9 (8.7)	35.1 (8.8)	NA	26.3 (2.0)	24.0 (2.6)	20.9 (2.8)	NA

the variation in the data set, with lateral expansion displaying positive loadings on both principal component one (0.426) and two (0.405; Table 2). In addition to lateral expansion, principal component one was associated with strong, positive loadings of marsh surface elevation (0.890) and depth to penetration resistance (0.730), and negative loadings of soil bulk density (−0.473) and especially percentage of time flooded (−0.885; Table 2). Beyond lateral expansion, principal component two was further characterized by a substantial positive loading of estimated biomass (0.857) and negative loadings of soil bulk density (−0.646) and soil organic matter (−0.497; Table 2). Thus, soil compaction, as approximated by soil bulk density and depth to penetration resistance, is an additional factor that, in conjunction with hydrologic regime, appears to regulate *S. californicus* lateral expansion and estimated biomass.

Table 2 Principal component loadings for key vegetation and environmental metrics

Variable	Component 1	Component 2
Lateral expansion	0.426	0.405
Penetration depth	0.730	0.294
Elevation	0.890	−0.297
Organic matter	0.581	−0.497
Bulk density	−0.473	−0.646
Percentage of time flooded	−0.885	0.256
Biomass	0.103	0.857

Discussion

This research has elucidated the role of several environmental variables involved in the modulation of lateral expansion and production of *S. californicus* in a previously leveed and drained wetland after tidal connectivity was restored. In particular, hydrologic regime and soil compaction appear to be important factors constraining both lateral expansion and plant production, whereas soil nutrient levels do not appear to currently limit growth of this species. Interestingly, these findings suggest that additional factors, such as exposure to physical energy, may also modulate *S. californicus* lateral expansion and production (unpublished data). Through studying the vegetation and environmental characteristics of an advancing marsh front, the results from our space for time design also suggest that *S. californicus* can act as an ecosystem engineer and has a bi-directional relationship with environmental conditions. Although the abiotic factors described may initially constrain plant growth, once vegetation successfully establishes in an area it has the potential to influence the physical environment over time (i.e., aboveground biomass exerts a positive influence on sediment deposition, and, in conjunction with belowground productivity and tillering, increases soil organic matter content and decreases soil bulk density), thereby contributing to marsh platform development.

Schoenoplectus californicus has been reported to display a range of productivities depending on the environmental setting. Pratolongo et al. (2008) reported average maximum standing live biomass of 662 g m^{-2} for a *S. californicus* marsh at the mouth of a deltaic system experiencing high physical energy, but 1009 g m^{-2} for a *S. californicus* marsh further inland in a lower energy setting. Under the high nutrient loads typical of treatment wetlands, *S. californicus* has been reported to achieve standing live biomass in excess of 5000 g m^{-2} (de Lange et al. 1998). In this study average estimated biomass for vegetated plots was 1026 g m^{-2}, with 2650 g m^{-2} being the maximum value exhibited by an individual plot, suggesting that these marshes are within the range of productivity expected for natural *S. californicus* marshes. Reflecting this aboveground productivity, average soil organic matter for our transect study was 9.85 %, which is intermediate in the range reported by Pratolongo et al. (2008). This indicates that the developing Liberty Island *S. californicus* marshes are on a trajectory towards natural *S. californicus* marshes, and that accumulation of soil organic matter, a key aspect of the ecosystem service of carbon sequestration, is occurring.

A hydrologic regime that includes some degree of soil inundation is a defining characteristic of wetland habitats and often regarded as the most critical environmental variable modulating plant growth and community development (Mitsch and Gosselink 2000). *S. californicus* has been reported to typically occur in extensively flooded marshes (Richardson et al. 1995; de Lange et al. 1998; Watson and Byrne 2009), but relatively few studies have quantitatively assessed the effect of elevation and resultant hydrology on growth responses of this species in a fashion relevant to deep water restoration efforts. In a recent survey of tidal marsh plant community composition and environmental conditions throughout the San Francisco Bay Estuary, Watson and Byrne (2009) reported that *S. californicus* occurred at a relatively wide range of elevations (approximately −0.75 to 2 m above NGVD). Although the elevation range for *S. californicus* in our Liberty Island-wide survey was narrower (0.30 to 1.05 m NAVD88), it should be noted that the majority of the *S. californicus* populations sampled by Watson and Byrne (2009) occurred at elevations less than 0.75 m NGVD and their higher elevation sampling points where *S. californicus* was found were often associated with levees bordering tidal channels.

Our principal components analysis revealed that although *S. californicus* lateral expansion rate is influenced by elevation, and hence percentage of time flooded, elevation is not the singular linear driver of lateral expansion. The lack of a strong linear effect of marsh elevation on *S. californicus* lateral expansion rate could indicate that hydrologic factors exhibit a relationship to lateral expansion more similar to a step function, or that their effects are further modulated by factors not included in this analysis, such as physical energy exposure or high soil bulk density resulting from legacy compacted agricultural soil. Evidence of a possible step function (or threshold) is provided by the fact that marsh edges that exhibited no lateral expansion or were retreating, had significantly lower elevations (0.61 m NAVD88) than marsh edges that were expanding (0.84 m NAVD88).

Highly compacted soils adversely affect plant growth by reducing soil oxygenation and hampering tillering by roots, whereas low density soils may not provide enough contact with roots for optimal growth (Thompson et al. 1987; Stirzaker et al. 1996). However, vegetation can ameliorate the high bulk densities associated with highly compacted soils through the production of roots, which physically break up soils as well as add organic matter that acts to further loosen soil. At Liberty Island, soil bulk densities tended to be high, which is similar to the findings of other studies where restored marshes exhibit higher soil bulk densities than reference marshes (Wills et al. 2008). Importantly, soil bulk density tended to increase from the interior of *S. californicus* marshes to the open mudflat, indicating that as plants expand into adjacent unvegetated areas they may be decreasing soil compaction, adding organic matter through belowground processes, and decreasing soil bulk density. Further, the principal components analysis conducted on marsh edges revealed a high positive loading of biomass and a moderate positive loading of lateral expansion rate, but a negative relationship between bulk density and lateral expansion on principal component two. Thus, although *S. californicus* appears capable of ameliorating these highly compacted soils over time, high soil bulk densities in mudflats adjacent to the marsh edges may initially have a negative influence on *S. californicus* growth and expansion.

Since wetland restoration sites that have previously been employed for agricultural applications often contain elevated soil nutrients, soil fertility is not typically a direct constraint on plant establishment (Ewing et al. 2012). In this study, concentrations of soil nutrients were generally similar between transect zones, suggesting that sufficient nutrients are available to colonizing vegetation as it expands. Notably, soil nutrient concentrations in the shoreline zone, which was rapidly colonized by *S. californicus*, were not significantly different than open mudflat zones in summer 2010. As expected given the agricultural history of Liberty Island, soil nutrient status does not appear to play a substantial role in constraining *S. californicus* growth. This is similar to findings by other researchers who have reported the occurrence of *S. californicus* under a range of nutrient conditions (de Lange et al. 1998; Neubauer et al. 2012).

Overall, lateral expansion was observed to be occurring along the majority of *S. californicus* marsh edges investigated during the Liberty Island-wide RTK surveys, indicating this ecosystem is on a trajectory towards further development of *S. californicus* marsh. This study identified several key environmental factors that can influence *S. californicus* marsh expansion. Specifically, elevation, hydrology, and soil bulk density appear to exert considerable influence on plant colonization and lateral expansion rates. Our study further provides evidence that once plants successfully establish or vegetatively spread into an area, feedbacks between the plants and soil occur as aboveground production can enhance sediment deposition and in conjunction with belowground production contribute to soil organic matter content and reduce soil bulk density. Achieving a greater understanding of both the abiotic constraints on plant establishment and feedbacks between the vegetation and the environment not only aids wetland managers and restoration scientists in anticipating restoration trajectories based on initial environmental conditions, but may also allow for increased predictability of marsh platform development over time.

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