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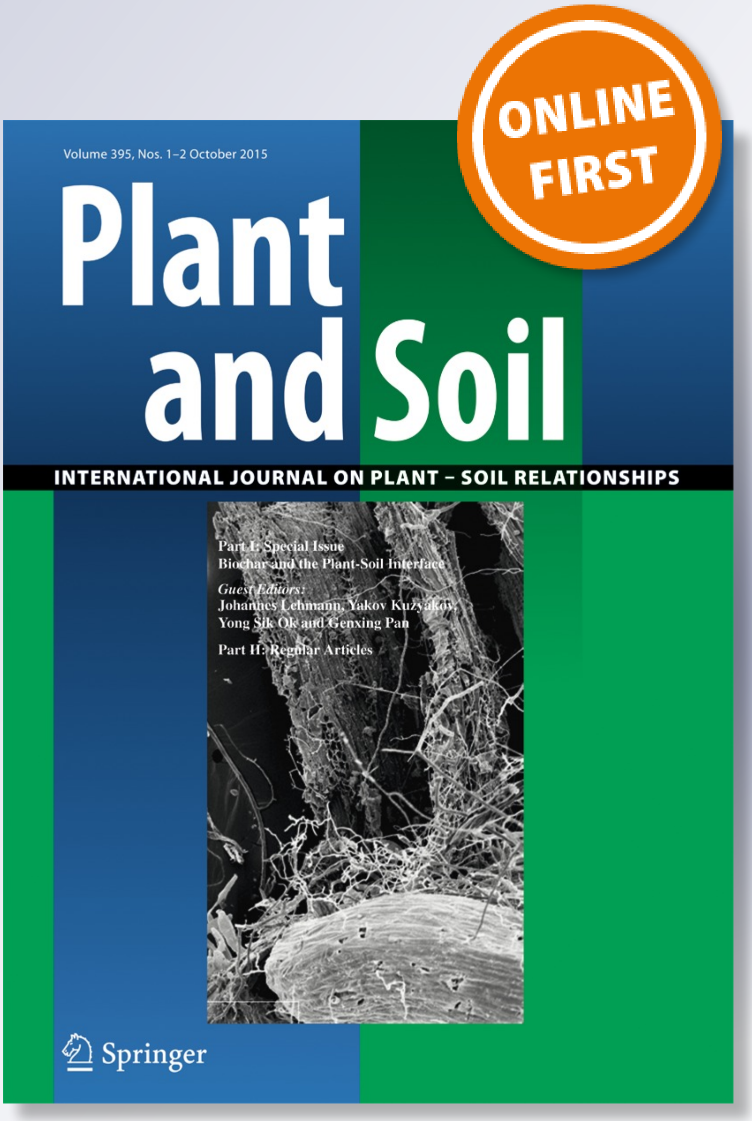

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REGULAR ARTICLE

# Interactions between soil physicochemistry and belowground biomass production in a freshwater tidal marsh

**Taylor M. Sloey · Mark W. Hester**

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**Abstract**
*Background and Aims* The success of tidal freshwater wetland restoration is typically gauged by the re-establishment of characteristics found in reference marshes. Although plant species composition may resemble reference marshes within a few years after the initiation of restoration, return of soil physicochemical properties may take much longer. We investigated soil characteristics in a post-levee breach freshwater tidal marsh restoration site (Liberty Island, California), and the impacts of soil compaction on the survival and growth of emergent macrophytes.
*Methods* In a field study, we examined soil physicochemical properties throughout 50-cm deep soil cores collected from locations at Liberty Island that differed in location and stage of vegetation colonization. In a controlled mesocosm study, we subjected three species that are commonly implemented in restoration plantings (*Schoenoplectus acutus*, *S. californicus*, and *Typha latifolia*) to two levels of soil compaction (control and high soil bulk density) to determine the influence of soil compaction on soil physicochemical properties and macrophyte response.
*Results* Belowground biomass increased and soil bulk density decreased with time since vegetation colonization. The controlled study showed that both *Schoenoplectus* species exhibited greater survival than *T. latifolia*.
*Conclusions* The species explored are capable of ameliorating compacted soil conditions over time; this ability can facilitate the re-establishment of wetland structure and function at restoration sites.

**Keywords** Amelioration · Freshwater wetland · Restoration · Soil compaction

## Introduction

The three-filter framework of ecology emphasizes the importance of abiotic parameters as limiting factors on plant survival and distribution, along with dispersal ability and biological interactions (Lambers et al. 2008). In wetland environments, hydrology is typically considered the most important variable controlling species distribution and abundance (Tiner 1999). We propose that after hydrology, edaphic physical and chemical properties are the most influential abiotic factors related to plant survival and expansion. In wetland ecosystems, complex relationships can exist between soils and vegetation. Optimal plant growth requires the proper combination of biological, chemical, and physical soil

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conditions to facilitate the root system's acquisition of nutrients and water (Barber 1995). Soil nutrients and chemical composition (e.g., essential macronutient and sulfide concentrations) influence plant survival and growth, whereas soil physical conditions (e.g., particle size and soil bulk density) further influence morphological and physiological plant responses. In tidal wetland ecosystems, specific edaphic conditions are highly important to the successful re-colonization of desired wetland vegetation and later successional species (Hammer 1989). Therefore, in addition to the site elevation and hydrologic regime, soil development and soil physicochemical conditions must be considered for successful wetland restoration, creation, and long-term management (Stolt et al. 2000; Ballantine and Schneider 2009).

Restoration efforts often involve reclaiming habitat that has been degraded, developed for other purposes, or was not previously a wetland (Hobbs and Harris 2001). In these cases, re-establishment of the proper abiotic conditions may be impeded by previous land use methods. The use of heavy equipment and intensive agriculture can result in soil compaction (Campbell et al. 2002; Craft et al. 2002; Bantilan-Smith et al. 2009). High soil bulk density produces more intense physical shear strength of substrates (Zhang et al. 2001) and may limit oxygen diffusion and alter microbial processes depending on the severity of compaction and frequency and duration of flooding. Low soil oxygen availability and reduced soil conditions cause numerous stresses to plant life (Pezeshki 2001). including the production of toxic reduced sulfur compounds (Devai and DeLaune 1995). Edaphic conditions influence the growth of species that spread asexually via rhizomatous expansion (Macia and Balsev 2000). Compacted soil can act as a physical barrier to root growth and expansion (Bengough and Young 1993; Bengough et al. 2006; Sloey et al. 2015). Several studies have determined that soil compaction and high soil strength results in reduced root growth and nutrient uptake (Unger and Kaspar 1992). and thicker root diameters (Goodman and Ennos 1999). If root growth is limited, so is the plant's access to nutrients, thus growth impedance or mortality may occur (Dunn and Diesburg 2004). Other morphological responses to soil compaction include an increase in root branching (Vose 1962). increased proportion of adventitious roots (Tang and Kozlowski 1982; Hook 1984). superficial rooting (Schat 1984). and increased production of aerenchyma (Pezeshki et al. 1993; Jackson and Armstrong 1999).

One of the goals of restoration is to re-establish native plant communities such that both above- and belowground processes are on trajectory toward natural wetland structure and function. Therefore, we need to understand the suite of environmental conditions that will facilitate growth of desired species as well as how vegetation colonization can facilitate the formation of those conditions. Other studies have investigated the impacts of invertebrate activity (Dostál et al. 2005). grazing intensity (Gao et al. 2008) and herbivore activity (Ford and Grace 1998) on soil physicochemistry. Similarly, plants are powerful ecosystem engineers, capable of changing and ameliorating their environmental conditions (Tanner 2001). Aboveground plant structures can aid in the accretion of sediments by slowing water flow (Breshears et al. 1998). Belowground plant tissues can contribute to increased soil organic matter, reduced soil bulk density, and increased soil oxygenation (Mitsch and Gosselink 2007). Many studies have explored the interactions between plants and their environmental conditions, as plants are impacted by the environment and have the capacity to change their environmental conditions Gurevitch et al. (2002). This has been studied in agricultural scenarios, finding that perennial crops have a greater capacity to sequester carbon and moderate restrictions on soil respiration than annually harvested crops (Anderson-Teixeira et al. 2013) In wetland creation and restoration scenarios, the degree to which plants alter their environmental conditions is typically relative to the time plants have occupied the area (Craft et al. 1999). The degree to which edaphic properties influence plant establishment, growth, and expansion is an important area of investigation that would benefit by further research.

We conducted an observational field study in a freshwater tidal marsh restoration site that was leveed and converted to agricultural land in the 1920s and farmed until 1997. Additionally, we conducted a mesocosm soil compaction experiment to investigate relationships between soil quality and plant growth. In the field study, we analyzed soil cores from a post-levee breach tidal marsh restoration site. Soil cores were collected from locations that differ in elevation and age of vegetation establishment (a range of two years) to elucidate the effect of the duration of vegetation colonization (a proxy for soil compaction) on soil physicochemical qualities (i.e., bulk density, soil chemistry, and organic matter) and belowground plant growth (depth of root growth and total belowground biomass production). In the manipulative experiment we investigated the effect of soil compaction on three species of freshwater macrophytes (*Schoenoplectus acutus*, *S. californicus*, and *Typha latifolia*) over the span of three months. These species are often used in restoration projects where they are native and are present at Liberty Island, CA. Combined, these studies addressed questions of how edaphic conditions can impact the survival, growth, and expansion of emergent marsh, as well as the role of species as potential ecosystem engineers that influence soil development over time.

## Methods

### Field study

The field study was conducted at Liberty Island, California, USA, (38.308359° N, −121.686974° W) a freshwater tidal marsh restoration site. Liberty Island, along with 95 % of the Sacramento-San Joaquin Delta, has been subjected to hydrologic manipulations (Conomos 1979). Historic wetlands were drained and reclaimed for agriculture. Liberty Island was leveed in the 1920s and farmed until 1997 when portions of the levee collapsed and were not repaired (Hart 2010). Since then, wetland vegetation has been naturally re-colonizing in the area. However, patterns of vegetation growth and expansion, as well as results from a manipulative transplant study (Sloey et al. 2015). suggest the soil physicochemical qualities, specifically high bulk-density, may be limiting natural vegetation establishment and expansion. Natural freshwater wetland reference sites typically exhibit soil bulk densities around 0.2–0.3 g/cm$^3$ (Craft et al. 1999; Ballantine and Schneider 2009). whereas the soil bulk densities at Liberty Island are much higher (0.6 to 1.0 g/cm$^3$) (Sloey et al. 2015). Although wetlands with mineral soils can have soil bulk densities above 0.6 g/cm3, this value is considered a high density for most natural vegetated marshes in this area.

### Soil analysis

Soil cores were collected from a variety of areas colonized by monospecific stands of *S. californicus* at Liberty Island (Fig.1). Sampling sites represented different elevations, hydrology, and wind and wave energy as modeled by ESA consulting (Fig. 1). Hester et al. (2015 in press) determined that lateral expansion of *S. californicus* marsh at Liberty Island ranged between 0.25 to 1.0 m per year. Our sampling of different marsh ages was achieved by extracting soil cores from the naturally colonized marsh interior (~5 m from vegetation/mudflat interface; oldest marsh), marsh edge (~2 m interior from vegetation/mudflat interface; intermediate aged marsh), and from transplant sites (2 years old; youngest marsh) which had been planted in June of 2010. Transplants were only planted on the west side of Liberty Island; therefore, none of the youngest transplant cores were collected from the east side. Ten cores were collected for marsh interior and marsh edge sites each (five from the east, five from the west), whereas four cores were collected from each of four different transplant sites (all from the west).

Aluminum tubes (measuring 12.7 cm in diameter) were inserted 50 cm deep into the soil using a post-driver. Cores were extruded from the soil, using a shovel, and capped on both ends. Some dewatering and minor compaction occurred within the aluminum tubes after the soil was extracted so the tubes were cut to the size of the soil core and kept upright to avoid unnecessary movement or disturbance of soil layers. Cores were shipped over night in an upright position to the University of Louisiana at Lafayette and frozen for further analysis. We adjusted for any compaction that may have occurred during transportation by equally distributing any missing core volume to the surface layers (0–15 cm), as these layers were most likely to condense.

Frozen soil cores were extruded from the aluminum tubing and cut into 2 cm thick increments (disks). Each frozen disk was weighed, dried in a convection oven at 65° C, and weighed again to obtain percent moisture ([wet weight- dry weight/dry weight]*100) and soil bulk density. Each disk was photographed after the drying process. The disks maintained structural integrity and original size after the drying process. Plant material apparent in photos of the disks was analyzed using Image J (National Institutes of Health, Bethesda, Maryland, USA) to determine surface area occupied by plant biomass. Coarse macro-organic plant biomass was removed from the dried disks and weighed, and the soil was pulverized. The soil was analyzed for percent organic matter (OM) using loss on ignition (LOI) (Soil and Plant Analysis Council, Inc. 1999). An average value throughout the entire core was determined for soil OM, soil bulk density, soil percent moisture, and

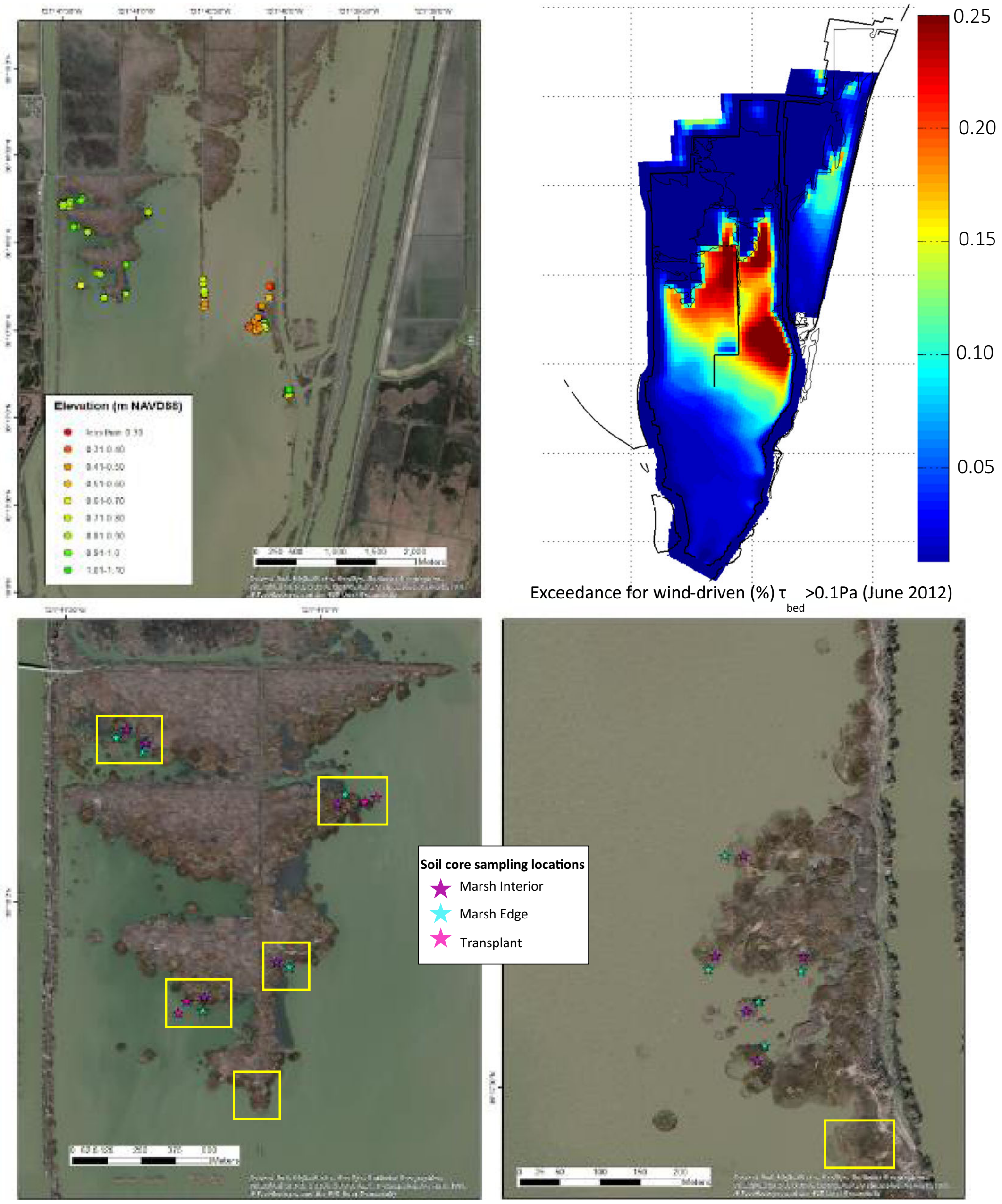

**Fig. 1** Liberty Island, CA soil surface elevation as determined by RTK survey (*top left*), wave energy (*top right*) and soil core sampling sites on the West (*bottom left*) and East (*bottom right*). The hydrologic data and image of wave energy was obtained from modelers at ESA (San Francisco, CA). Yellow boxes outline areas at which stems were collected for the field study

biomass of macro-organic matter and analyzed using a 3-way analysis of variance (ANOVA) to determine the effect of marsh side (west vs. east), exposure (exposed vs. protected), and marsh age (interior/oldest, edge/intermediate, transplant/youngest) on the entire core.

To gain a better understanding of differences between depths in the core, we implemented a split-split plot design to investigate effects of marsh exposure, age, and depth on soil OM, soil bulk density, soil percent moisture, and macro-organic matter. Due to uneven sampling of marsh ages across the marsh because we only collected the transplant aged cores from the west side, we addressed each marsh side (east and west) separately using a split-split plot analysis with marsh exposure and age as between plot factors and depth (0–15 cm, 15–30 cm, and 30–50 cm) as the within plot factor. A Tukey-post hoc test of pairwise comparisons was implemented for each marsh side separately to determine significant differences between means within each measured parameter. A significance level (alpha) of 0.05 was used for all analyses.

### Soil compaction study

A randomized block design was used for a manipulative mesocosm experiment to examine the influence of soil compaction on plant growth. Experimental treatments consisted of three freshwater species (*S. acutus*, *S. californicus*, and *T. latifolia*) and two soil bulk-density treatments (control and compacted) with five replicates of each combination for a total of 30 experimental units.

Soil was obtained from a local soil and gravel distributor in Lafayette, LA, and selected to resemble the sediment profile from samples taken from the Liberty Island restoration site (approximately 30 % sand, 10 % clay, 60 % silt, with 10 % organic matter). Soil particle size distribution of samples from both Liberty Island and the Louisiana distributor were determined using the hydrometer method (Carter 1993). Cylindrical plastic containers measuring 56 cm in diameter and 43 cm in height were perforated at the bottom for water uptake and drainage and filled with the selected soil. A total of 57 and 76 metric liters of soil were used to fill the non-compacted and compacted units respectively; 57 l of soil fit in the planters comfortably without extra force, representing our control units. To achieve a higher degree of compaction, a 11 kg weight (circular and cut to the same dimensions as the planter) was dropped on the soil 10 times from 50 cm height after each 9.5 l of soils was added until the full 76 metric liters were filled. Plants (*S. acutus*, *S. californicus*, and *T. latifolia*) were obtained from a native plant nursery in Eureka, California. Individuals of each species were selected for optimal health and similar rhizome size and stems were cut to a height of 25 cm. In April 2011, each unit was planted with one individual of one species in the center of the container to provide space for rhizomatous root expansion.

The randomized block design was implemented by placing one replicate of each species and degree of compaction treatment combination in a circular water reservoir (50 cm height × 120 cm diameter). The six units were arranged randomly in each reservoir; the five reservoirs were oriented in a straight line running north to south and kept outside at the University of Louisiana at Lafayette's Center for Ecology. Reservoirs were filled with fresh water to 5 cm above the soil surface of the experimental units. Water levels were maintained every two days throughout the experiment, which ran from April to July 2011. Plants were harvested before becoming pot-bound and stressed.

Soil bulk-density was measured in each unit at the beginning and the conclusion of the experiment to observe plant-facilitated changes in soil compaction. Soil redox potential was measured at 1 cm and 10 cm depths every two weeks throughout the experiment using a Pinnacle Calomel reference electrode and a Beckman Φ 265 pH/Temperature/mV Meter. Upon harvest (July 2011), treated individuals were monitored for percent survival (indicated by photosynthetic aboveground biomass), stem height (cm), stem density (number of stems per unit), and expansion in terms of area of vegetative growth (limited to the diameter of the container). Photosynthesis and quantum yield efficiency of photosystem II were determined with a LICOR 6400 Portable Photosynthesis System. All plants were harvested; aboveground and belowground biomass were separated and rinsed of soil. Six representative roots from each unit were collected for analyses of root morphology. RhizoPro was used to determine total length of roots at varying size classes (0.0–0.05 mm, 0.05–0.10 mm, 0.10–0.20 mm, 0.20–0.50 mm, 0.50–1.00 mm, and 1.00–2.00 mm). Root specific gravity was measured using a pycnometer in three representative roots from each unit (Mingshou et al. 2003). Aboveground and belowground plant tissue was dried in a convection oven at 65$^{o}$ C and weighed to determine biomass. Belowground biomass was separated into three classes (adventitious roots, roots, and rhizomes) and analyzed for percent contribution of each root class to total mass.

Soil bulk density and soil redox potential were analyzed to compare changes in soil physicochemical qualities over time and among experimental units using a repeated measures procedure (SAS 2010). The effects of species and soil compaction treatment on the measured dependent variables were analyzed using a two-way

ANOVA procedure with a Tukey post-hoc pairwise comparisons test. Soil pH was log transformed and root class percent of total belowground biomass classes was ARCSINE transformed to normalize proportional data. Due to interspecific variation inherent to the three species of plants, some morphometrics (area of vegetative expansion and belowground biomass production) were analyzed within species. Any dead replicates were removed from all statistical analyses except for mean percent survival.

## Results

### Liberty island field site soil characterization

Analyses of soil cores collected form the Liberty Island field site revealed effects of marsh side, exposure, and age on soil metrics averaged throughout the entire core (Table S1). Separate split-split plot analyses on each marsh side showed that the main effects (exposure, age, and depth) often interacted to affect measured soil metrics (Table S1). A 3-way ANOVA revealed a significant interaction between marsh side and exposure regarding soil percent organic matter (OM) (averaged over the entire core). Overall, soil OM was higher on the west (12.1 ± 0.002 %) compared to the east (10.2 ± 0.003 %). On the east, soil OM was higher in the exposed sites (10.6 ± 0.005 %) compared to the protected sites (9.8 ± 0.004 %), whereas on the west, soil OM was higher in the protected sites (12.8 ± 0.003 %) than the exposed (11.3 ± 0.002 %). The separate split-split plot analyses showed no differences between samples collected from the east, but the west side had a significant interaction between exposure and depth ($P = 0.0080$) with higher soil OM occurring in the protected sites and the top depth.

Analyses on soil percent moisture (Table S1; S2) averaged throughout the entire core showed a significant interaction between marsh exposure and age as percent moisture was highest in soil samples collected from the protected sites for interior (67.2 ± 5.7 %) and edge (61.5 ± 3.8 %) aged sites. Soil percent moisture was significantly lower in protected transplant age (47.2 ± 1.0 %) sites. Soil percent moisture was generally lower in the exposed sites than protected sites, but was similar between marsh interior (56.7 ± 4.1 %), marsh edge (58.3 ± 8.6 %) and transplant (55.9 ± 2.5 %) sites. Split-split plot analyses by side revealed a significant effect of depth on the east with surface (0–15 cm) depths exhibited much higher soil moisture (84.5 ± 8.7 %) than the 15–30 cm (61.1 ± 4.6 %) or 30–50 cm (57.7 ± 5.4 %) depths. On the west, there was a significant interaction between age, exposure, and depth as soil percent moisture tended to be higher in the protected sites, except for the youngest aged transplant sites which had higher soil moisture in the exposed sites. Overall, soil moisture was higher in the surface depths (106.8 ± 10.0 %) compared to 15–30 cm (63.9 ± 4.0 %) or 30–50 cm (43.1 ± 0.9 %) depths on the west side.

Analyses of soil bulk density (averaged throughout the entire core) showed no significant differences between sites (Table S1). The separate split-split plots (Table S2) revealed a significant effect of depth on both the east and west sides as soil bulk density increased with depth (Fig. 2). There was a significant interaction between exposure and age on the west side, though soil bulk density remained relatively consistent within exposure and age classes.

Analyses of the total mass of belowground macro-organic matter for the entire core (Table S1) showed a significant effect of exposure, with more biomass occurring in cores collected from protected sites (24.5 ± 5 g) than exposed sites (14.7 + 3 g). The split-split plot analyses (Table S2) showed no trends on the east side, but the west side showed a significant interaction between marsh exposure and age; the highest biomass production on the west side occurred in the protected marsh edge age sites (Fig. 3).

### Soil compaction study

Initial soil bulk density was significantly greater in the compacted units than non-compacted units. A repeated measures analysis of soil bulk density from start to end time of the experiment elucidated that soil bulk density had increased over time ($P < 0.0001$), becoming more similar between units (Fig. 4; Table S3). Soil redox potential did not significantly change at the 1 cm depth, however, redox potential became more reduced over time at the 10 cm depth ($P < 0.0001$) (Fig. 5; Table S4). At the conclusion of the study, soil redox potential was lower in the compacted units than the non-compacted soils, but not at a level that would result in the formation of toxic sulfides (Sumner 2000).

Plant responses showed differences between species and soil compaction treatment (Table S4; Table 1). Survival differed significantly among species

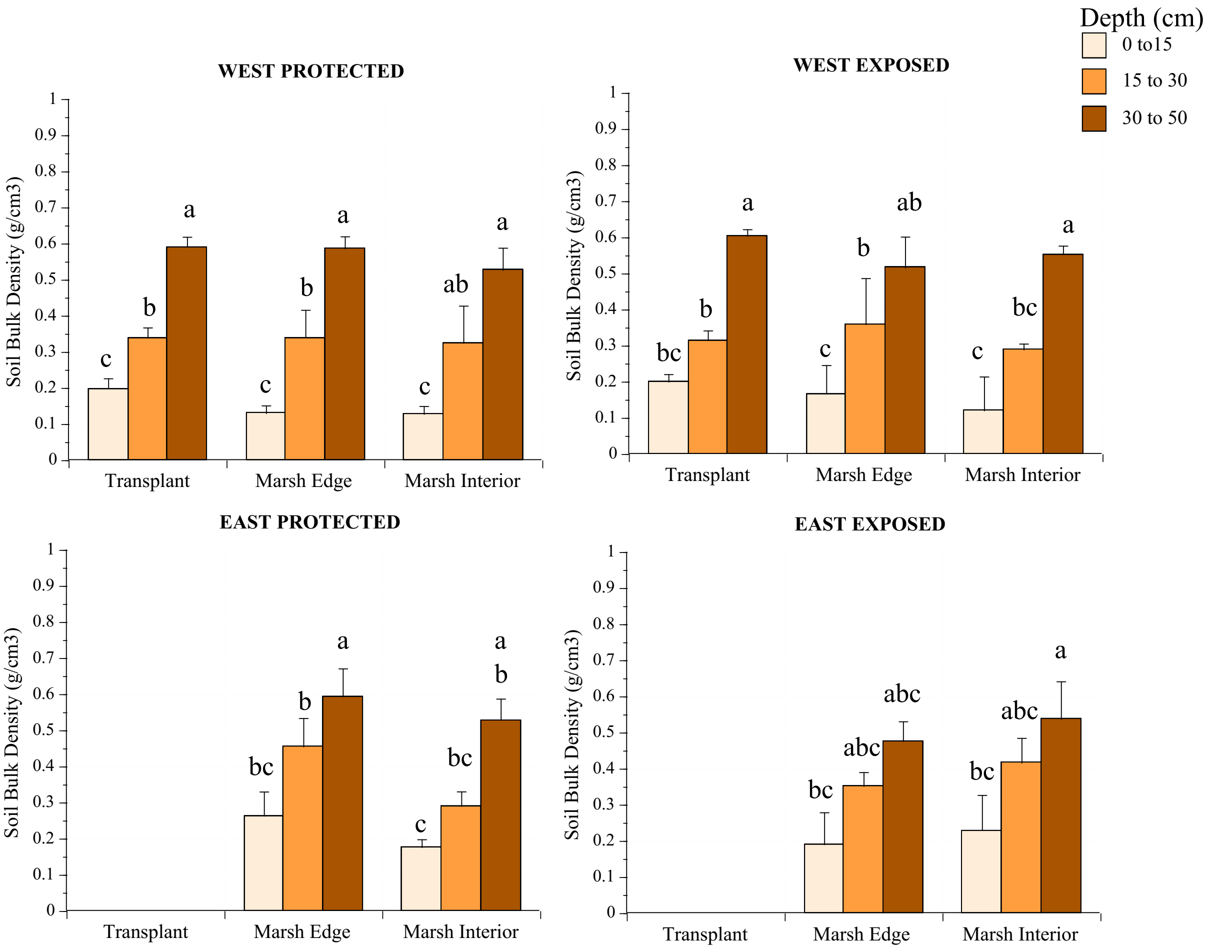

**Fig. 2** Soil bulk density (mean + SE) of soil cores collected from the Liberty Island marsh. Means within the same side (east and west) demarked by the same superscript letter are not significantly different (α = 0.05)

(*P* = 0.0360) with both *Schoenoplectus* species performing relatively similarly and *T. latifolia* exhibiting the lowest survival rates. Regarding stem height, inherent differences were present between species (*P* < 0.0001), with *S. californicus* being the tallest. Interestingly, the compaction treatment had a significant effect on stem height (*P* = 0.0488) with units subjected to higher degrees of soil compaction exhibiting shorter stems. Stem density (number of stems produced) differed between species, being greatest in *S. acutus*, followed by *S. californicus* and *T. latifolia*. A significant interaction between species and treatment is explained by increased stem production in the compacted units of *S. acutus* only. The final area of expansion was significantly greater in *T. latifolia* and *S. acutus* than in *S. californicus* (*P* = 0.0012). Aboveground biomass differed significantly by species (*P* = 0.0012) as *S. californicus* generally produced more aboveground biomass than the other species.

Root morphology was expected to be indicative of plant stress. There was no evidence of significant variation in root specific gravity in response to species or treatment. Total belowground biomass production was significantly (*P* = 0.0007) greater in *S. acutus* than the other species. Soil compaction resulted in significantly (*P* = 0.0471) greater belowground biomass production in all species (Table 1). Regarding differences in root morphology of the selected sub-sample, the total mean length of the representative roots differed significantly between species (*P* = 0.0216) with *S. californicus* roots being longer (214 ± 15 cm) on average than *S. acutus* (152 ± 22 cm) or *T. latifolia* (151 ± 18 cm); however there was no evidence of a significant difference in the percent of adventitious roots present.

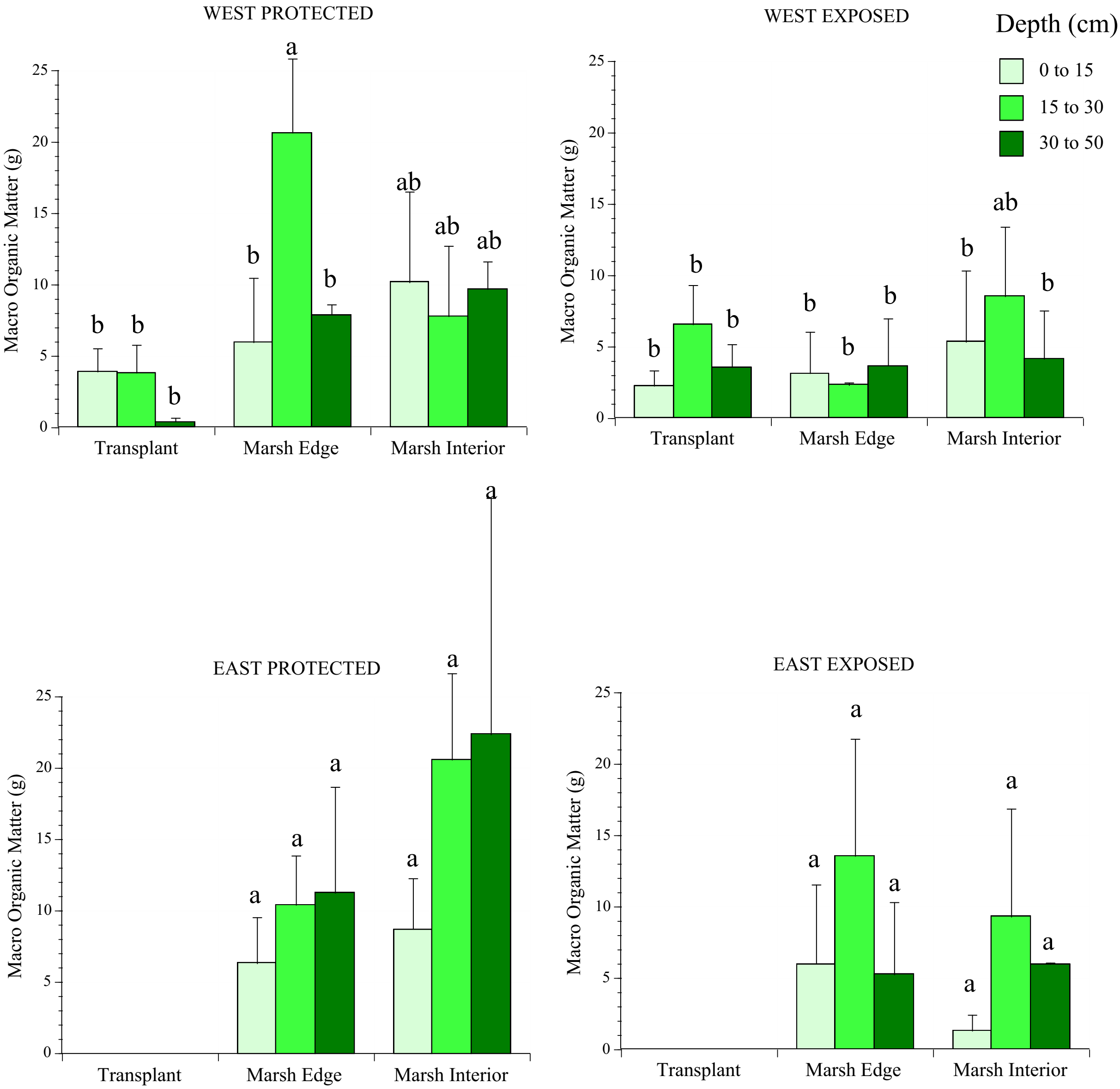

**Fig. 3** Belowground macro organic matter production (mean + SE) of soil cores collected from the Liberty Island marsh. Means within the same side (east and west) demarked by the same superscript letter are not significantly different ($\alpha = 0.05$)

## Discussion

The main goal of restoration is to re-establish natural vegetation and edaphic conditions in an altered ecosystem (National Research Council 1992). however, re-establishment of physical conditions is often constrained by pre-restoration land use practices. Restoration projects and managers are often required to estimate the restoration trajectory, or the timeline of the site's recovery process. However, in many cases, restored or constructed marshes fail to exhibit the targeted natural physical parameters within the monitoring timeline (usually 5–10 years) (Zedler and Callaway 1999). Our research suggests that although the rate of re-establishment of ecosystem structure and function may not be easily or accurately projected from initial sampling, the re-establishment of vegetation can aid in restoring the physical environment to resemble more natural conditions over time.

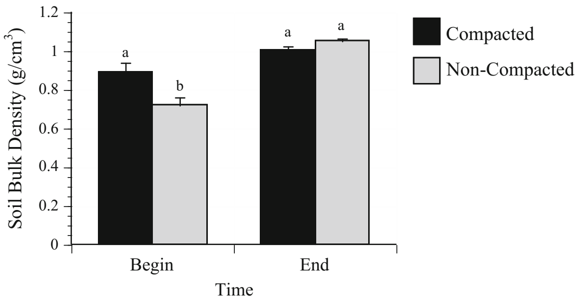

**Fig. 4** Soil bulk density (mean ± SE) of soil compaction experimental units over time. Means demarked by the same superscript letter are not significantly different (α = 0.05)

Extreme soil compaction is a common issue in created or restored wetlands, depending on the substrate type and the use of heavy equipment (Nair et al. 2001). Our initial surveys at Liberty Island in 2010 documented soil bulk densities ranging from 0.6 to more than 1.0 g/cm$^3$, which were significantly higher than the values of 0.1–0.6 g/cm$^3$ typically found in natural California freshwater marshes (Craft 2007; Sloey et al. 2015). Studies have shown that high soil density and soil strength can limit root growth (Laboski et al. 1998) and root elongation (Taylor et al. 1966) in pea plants and cotton respectively. Highly compacted soils also appear to slow the rate of *Schoenoplectus* spp. marsh expansion (Hester et al. 2015, in press; Sloey et al. 2015).

Important interactions exist between vegetation and soil physicochemical properties that can aid in reversing negative impacts of anthropogenic activity on the physical environment. Wetland species can change their environment, ameliorating abiotic conditions for colonization by other species (Tanner 2001; McKee et al. 2007). In created and restored marshes, soil bulk density tends to decrease over time as vegetation colonizes the area (Ballantine and Schneider 2009). A study conducted at Liberty Island that looked at a variety of environmental characteristics along a transect from open mudflat to the marsh interior showed that soil organic matter and plant biomass increased, and soil bulk density decreased with time after vegetation establishment (Hester et al. 2015, in press). The results from our soil core analyses also suggest that more typical marsh characteristics (i.e., reduced soil bulk density and increased belowground macro-organic matter) gradually occurs over time after vegetation colonizes the area. In contrast, a reduction in soil bulk density over time was not evident in the mesocosm study. We believe this discrepancy may be due to the nature of the mesocosm. The soil used in the mesocosms was originally dry and start-time soil bulk density measurements were collected relatively soon after water was added. We believe that the added water caused soil particles in the non-compacted units to further settle throughout the experiment, resulting in higher final soil bulk density. Regardless, the field and mesocosm studies combined showed that even though the rate of growth and expansion may be slowed by soil compaction, the species we tested were able to persist in highly compacted soils, suggesting that the establishment of these species can ameliorate harsh environmental conditions. Results from the mesocosm study showed that all species tested could survive the manipulated soil compaction, and no strong differences were apparent between species regarding their response to soil conditions. However, species differences may aid in selecting the ideal species for restoration scenarios. In amiable growing conditions, *S. acutus* may expand laterally more rapidly than the other species (Table 1), however other studies have reported that *S. californicus* performs better than *S. acutus* or *T. latifolia* when flooded for longer durations (more than 60 % of the day) (Sloey et al. 2015; Sloey et al. in review). Therefore, species selection must consider the environmental setting and goals of the planting effort. Improper environmental setting and/or historical modifications to abiotic conditions can result in unsuitable hydrology, elevation, and seed bank, which can slow the rate of ecosystem recovery (Brown and Bedford 1997; Craft et al. 2002). Our field core collections showed that the east side of Liberty Island exhibited lower soil organic matter; we believe that this is due to the fact that the east side

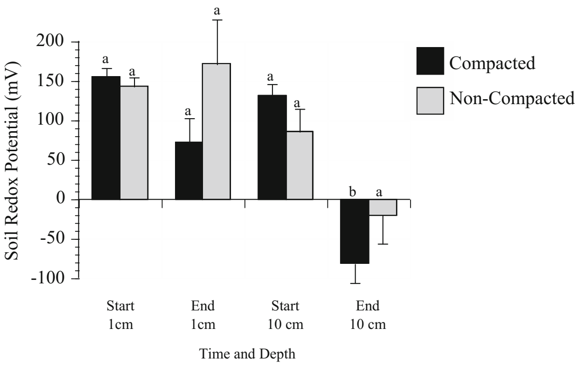

**Fig. 5** Soil redox potential (mean ± SE) of soil compaction experimental units over time. Means demarked by the same superscript letter are not significantly different (α = 0.05)

is lower in elevation (Fig. 1) and flooded for longer durations than the west. Previous work at Liberty Island suggests that the extreme flooding regime on the east side depresses plant productivity and expansion (Sloey et al. 2015; Hester et al. 2015, in press). Factors that inhibit vegetation colonization, such as flooding, may also hinder the re-establishment of natural belowground characteristics, which typically re-establish to reference levels at a slower rate than aboveground characteristics (Zedler and Callaway 1999).

Our findings further emphasize the importance of time in the successful restoration of wetland structure and function. Ballantine and Schneider (2009) conducted extensive surveys of wetlands at various stages of development since initiation of restoration and found that decomposition and aboveground plant litter biomass were important drivers of soil development. Numerous studies advise that restoring soil properties (particularly soil bulk density and soil organic carbon) in restored or created marshes to levels similar to that of reference marshes may take decades or even centuries (Zedler and Callaway 1999; Ballantine and Schneider 2009; Hossler and Bouchard 2010). Our studies show that plant occupation can help to repair modified soils to a more natural state; however, active restoration has shown that human engineering can assist in the reassembly of degraded ecosystems (Suding 2011). Therefore, we recommend that restoration managers take actions to ameliorate soil conditions prior to planting efforts, thus speeding up the process of vegetation recolonization and restoration of natural soil processes. Hamza and Anderson (2005) recommended several practices for reducing soil compaction in agricultural settings including working soil, increasing soil organic matter, and deep ripping in the presence of an aggregating agent. For locations like Liberty Island and similar marshes in the Sacramento-San Joaquin Bay Delta, we recommend that future wetland restoration projects consider tilling or adding topsoil to abandoned agricultural land prior to levee breaching.

**Table 1** Soil characteristics and plant responses (mean ± SE) of soil compaction experimental units

| Species | Treatment | Plant Survival (%) | Stem Height (cm) | Stem Density (#) | Area expansion (cm$^2$) | Aboveground biomass (g) | Total Belowground Biomass | Belowground Biomass (rhizomes) (g) | Belowground Biomass (roots) (g) | Belowground Biomass (adventitious) (g) |
|---|---|---|---|---|---|---|---|---|---|---|
| *S. acutus* | | | | | | | | | | |
| | Compacted | $97 \pm 2^{A}$ | $106.1 \pm 3.3^{C}$ | $101 \pm 2^{A}$ | $1801 \pm 7^{A}$ | $318.5 \pm 13.1^{AB}$ | $778.3 + 57.2^{A}$ | $340.6 \pm 13.2^{A}$ | $299.8 \pm 71.4^{A}$ | $137.8 + 19.9^{A}$ |
| | Non-Compacted | $97 \pm 1^{A}$ | $118.6 \pm 0.9^{C}$ | $73 \pm 5^{B}$ | $1801 \pm 7^{A}$ | $256.4 \pm 15.1^{B}$ | $557.1 + 52.2^{B}$ | $258.9 \pm 23.4^{A}$ | $138.3 \pm 17.3^{AB}$ | $159.8 \pm 32.4^{A}$ |
| *S. californicus* | | | | | | | | | | |
| | Compacted | $100 \pm 0^{A}$ | $155.5 \pm 9.1^{AB}$ | $48 \pm 8^{C}$ | $1440 \pm 108^{B}$ | $403.04 \pm 57.8^{A}$ | $464.3 + 92.5^{C}$ | $197.5 \pm 25.6^{B}$ | $170.7 \pm 42.2^{AB}$ | $96.0 \pm 28.9^{B}$ |
| | Non-Compacted | $97 \pm 1^{A}$ | $169.3 \pm 5.0^{A}$ | $47 \pm 3^{C}$ | $1624 \pm 99^{B}$ | $371.0 \pm 21.3^{AB}$ | $395.5 + 23.8^{C}$ | $211.7 \pm 29.4^{B}$ | $112.3 \pm 15.2^{B}$ | $71.5 \pm 9.9^{B}$ |
| *T. latifolia* | | | | | | | | | | |
| | Compacted | $72 \pm 18^{B}$ | $124.5 \pm 3.9^{C}$ | $20 \pm 2^{D}$ | $1808 \pm 0^{A}$ | $295.6 \pm 21.7^{AB}$ | $431.5 + 68.6^{C}$ | $317.1 \pm 69.4^{A}$ | $102.2 \pm 23.7^{B}$ | $12.3 \pm 6.0^{C}$ |
| | Non-Compacted | $73 \pm 18^{B}$ | $131.1 \pm 11.4^{BC}$ | $15 \pm 2^{D}$ | $1705 \pm 67^{A}$ | $241.1 \pm 10.1^{B}$ | $386.6 + 55.6^{C}$ | $295.1 \pm 42.0^{A}$ | $78.8 \pm 14.8^{B}$ | $12.6 \pm 4.6^{C}$ |

Soil characteristics are averaged over all species as species was not a significant factor. Means within the same parameter followed by the same superscript letter are not significantly different ($\alpha = 0.05$)

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