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# The role of elevation, relative sea-level history and vegetation transition in determining carbon distribution in *Spartina alterniflora* dominated salt marshes

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ABSTRACT

*Spartina alterniflora* salt marshes are among the most productive ecosystems on earth, and represent a substantial global carbon sink. Understanding the spatial heterogeneity in the distribution of both above- and below-ground carbon in these wetland ecosystems is especially important considering their potential in carbon sequestration projects, as well as for conservation efforts in the context of a changing climate and rising sea-level. Through the use of extensive field sampling and remote sensing data (Light Detection and Ranging – LiDAR, and aerial images), we sought to map and explain how vegetation biomass and soil carbon are related to elevation and relative sea-level change in a *S. alterniflora* dominated salt marsh on Galveston Island, Texas. The specific objectives of this study were to: 1) understand the relationship between elevation and the distribution of salt marsh vegetation percent cover, plant height, plant density, above-and below-ground biomass, and carbon, and 2) evaluate the temporal changes in relative sea-level history, vegetation transitions, and resulting changes in the patterns of soil carbon distribution. Our results indicated a clear zonation of terrain and vegetation characteristics (i.e., height, cover and biomass). In the soil profile, carbon concentrations and bulk densities showed significant and abrupt change at a depth of ~10–15 cm. This apparent transition in the soil characteristics coincided temporally with a transformation of the land cover, as driven by a rapid increase in relative sea-level around this time at the sample locations. The amounts of soil carbon stored in recently established *S. alterniflora* intertidal marshes were significantly lower than those that have remained *in situ* for a longer period of time. Thus, in order to quantify and predict carbon in coastal wetlands, and also to understand the heterogeneity in the spatial distribution of carbon stocks, it is essential to understand not only the elevation, the relative sea-level rise rate, and the vertical accretion rate – but also the history of land cover change and vegetation transition.

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## 1. Introduction

Coastal salt marshes are among the most productive ecosystems (Mitsch and Gosselink, 2000) and comprise approximately 25% of the global soil carbon sink (Chmura et al., 2003). These salt marshes can continuously sequester carbon through plant production and burial processes associated with sea-level rise. The rates of atmospheric carbon sequestration in salt marshes are likely an order of magnitude higher than that of terrestrial forests (Bridgham et al., 2006; Nellemann et al., 2009). Further, unlike in other terrestrial systems, a large portion of the primary production is stored in marsh soils (Scott and Greenberg, 1983; Chmura et al., 2003), which is partly resulting from their greater carbon burial rates. However,

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uncertainties exist in the estimates of global spatial extents of coastal salt marshes (Chmura et al., 2003), and their rates of carbon sequestration can vary largely both spatially and temporally (Ouyang and Lee, 2014).

In general, coastal salt marshes are characterized by mild slope terrains and thus span a narrow elevation range above and below mean high water levels. Many studies have reported elevation as an important factor that determines the spatial distribution of salt marsh vegetation communities (McKee and Patrick, 1988; Pennings and Callaway, 1992; Morris et al., 2002; Mudd et al., 2004). In general, lower elevations with optimum growth conditions are characterized by relatively taller and highly productive vegetation communities. However, the distribution of vegetation characteristics and thus above- and below-ground carbon storage over a given area can vary largely depending on different factors including salinity levels and inundation (Kathilankal et al., 2011) that are directly affected by elevation. Thus, an improved understanding on the spatial heterogeneity of salt marsh vegetation distribution, and above- and below-ground carbon stocks, more specifically with respect to the elevation, will enable better understanding and thus improved predictions of the consequences of relative sea-level rise on their future roles as important carbon sinks.

Though these wetland ecosystems have evolved in response to sea-level rise (Pethick, 1981; Delaune et al., 1983), a rapid change in their spatial extent and/or composition can be expected even from a small rise in the relative sea-level (Warren and Niering, 1993; Craft et al., 2009). For example, assumptions of a static landscape (i.e., the topographic surfaces do not move up or down due to subsidence or vertical accretion) inspire predictions that 20–60% of the world's coastal wetlands will submerge in response to sea-level rise during this century (Nicholls et al., 2007; Craft et al., 2009). Among coastal wetlands, tidal marshes are recognized to be highly susceptible to sea-level rise (Kirwan et al., 2010; Mariotti and Fagherazzi, 2013), but how these rising sea-levels will affect ecosystem-scale carbon storage is almost completely unknown (Chmura, 2011), beyond Marsh Equilibrium Model (MEM) estimates (Morris et al., 2002). The current rate of global sea-level rise is reported to be approximately 0.20–0.30 cm per year (Nicholls et al., 2007). While some marshes are accreting vertically fast enough to keep pace with these sea-level rise rates, others are drowning due to local subsidence (e.g., Yeager et al., 2007; Syvitski et al., 2009; Feagin, 2013).

Several studies report that tidal coastal wetlands respond to sea-level rise by migrating landward and/or by accreting vertically (Redfield and Rubin, 1962; DeLuane, 1983; Callaway et al., 1997; Orson et al., 1998; Shaw and Ceman, 1999; Kirwan et al., 2010). Thus, in coastal salt marshes, over relatively long time periods (i.e., several decades), significant changes in above- and below-ground environments could be expected under the influence of relative sea-level rise, increased rates of marsh vertical accretion, and resulting changes in the coastal landscape (Loomis and Craft, 2010). Changes in physical and biotic factors will affect marsh productivity and thus carbon distributions. Due to these reasons, coastal wetland soils are studied extensively to estimate the rates of vertical accretion resulting from marsh sedimentation (Mitsch and Gosselink, 1984; Stoddart et al., 1989), and organic matter accumulation (Callaway et al., 1997; Turner et al., 2004). Further, several other studies link these findings with rates of sea-level rise (Redfield and Rubin, 1962; Orson et al., 1998). Coastal wetland soils are also studied because shallow, open water replaces wetlands if rates of vertical accretion do not keep pace with the rates of submergence (DeLaune et al., 1983; Orson et al., 1998). However, temporal variations in the spatial distribution of salt marshes, as well as the effects of these processes on marsh build up over time and space can vary largely depending on the specific conditions that each wetland experiences.

In this study, through the use of extensive field sampling and remote sensing data (LiDAR and aerial images), we sought to map and explain how vegetation biomass and soil carbon are related to elevation and relative sea-level change in a *Spartina alterniflora* dominated salt marsh on Galveston Island, Texas. The specific objectives of this study were to: 1) understand the relationship between elevation and the distribution of salt marsh vegetation percent cover, plant height, plant density, above-and below-ground biomass, and carbon, and 2) evaluate the temporal changes in relative sea-level history, vegetation transitions, and resulting changes in the patterns of soil carbon distribution.

## 2. Methods

### 2.1. Study area

The study area is composed of tidal salt marshes along several km of shoreline (approximately 10 $km^2$ extent) on the south side of West Galveston Bay on Galveston Island, Texas, USA. West Galveston Bay is a relatively shallow bay, with its deepest portions approximately 3 m deep. It connects to the Gulf of Mexico via San Luis Pass on the southwestern end, and to central Galveston Bay at the northeastern end (Fig. 1). Most (87%) of the shoreline is natural (i.e., not affected by anthropogenic activities such as dredging, dredged material disposal, filling for development (Ravens et al., 2009)). The natural shoreline of West Galveston Bay mainly consists of salt and brackish water marshes (78%). The low marshes (as influenced by daily tides) in our study area were dominated by *Spartina alterniflora*. Most of our sample plots (~80%) were located within the Galveston Island State Park area (Fig. 1). This study area was selected considering the availability of relatively larger, undisturbed, and mono-specific stands of *S. alterniflora,* distributed along the elevation gradient. Over most of the study area, the landward edge of *S. alterniflora* zone is bordered by other low marsh species (i.e. *Salicornia depressa* and *Batis maritime)*, abruptly followed by unvegetated salt pannes, and then by high marsh species.

Soils in our study area are classified as Mustang–Galveston Series (USDA, 1998). These soils occur on nearly level terrain characterized by 0–1% slopes and in depressions on barrier flats including coastal marshes, and tidal flats.

### 2.2. Data

#### 2.2.1. Vegetation height, cover and biomass measurements

Field sampling was conducted from June 4–8, 2012. This time of the year was selected to overlap with the peak growing season of *Spartina alterniflora* as well as the timing of the available aerial images that we used to infer the vegetation cover changes over the study area. *S. alterniflora* although shows a perennial growth habit, shows maximum biomass accumulation rates towards the end of the growing season (Hardisky et al., 1984). For this region growing season continues up to the end of summer (Darby and Turner, 2008).

In locating sampling points, we employed systematic random sampling. First, nineteen transects were established randomly over the study area, (Fig. 1) with each extending from the water line to the landward extent within the *Spartina alterniflora* zone (stopping before the upper reaches of the low marsh dominated by species such as *Salicornia depressa* and *B. maritima*, salt panne species, or the unvegetated salt panne itself). The average spacing between transects ranged from 50 m to 100 m. Second, sample plots (1 m × 1 m quadrats) were located systematically on each transect.

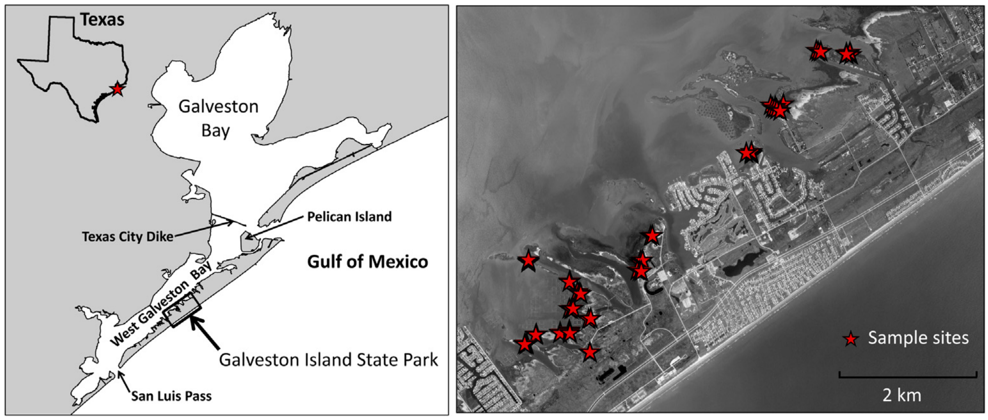


**Fig. 1.** Map of the study area. Sample locations are displayed on high resolution aerial imagery acquired in June 2012.

These quadrats were located only in mono-specific stands of *S. alterniflora*. Systematic sampling along transects was employed to ensure the representation of the gradients of elevation, tidal range, and the heterogeneity in vegetation height and cover that we observed in the field. In locating the sample plots along transects, an average spacing of 15–20 m was maintained. Thus, depending on the width of the *S. alterniflora* zone, there were 3–7 sample plots on each transect.

The percentage of canopy cover within each plot (1 m × 1 m) was estimated visually following the standards of Anderson (1986). To minimize the time and effort in the field data collection, only the plants within the central quadrat of 30 cm × 30 cm were then clipped at the ground surface. As the 1 m × 1 m quadrats were located over homogeneous (in terms of plant height and cover) stands, these central quadrats were well representative of the entire 1 m × 1 m quadrat area. Clipped vegetation was sorted into live plants and dead vegetation/litter. In the laboratory, plant and stem heights of individual plants were measured. Plant height and stem heights were measured from the base to the tip of the longest leaf, and to the base of the leaf sheath, respectively. Numbers of stems per quadrat were also recorded. These measurements were used to derive statistics relating to plot level field vegetation heights and density.

Clipped plants were washed to remove any sediment and then processed and analyzed for vegetation biomass (g dry weight $m^{-2}$) and carbon estimates, separately for live plants and dead plant material. A total of 15 samples were selected to represent the entire study area and were analyzed by combustion/gas chromatography using a Carlo Erba EA-1108 elemental analyzer (CE Elantech, Inc., Lakewood, N.J.) to obtain carbon concentrations in live and dead plant materials.

During field sampling, the central coordinates of sample plots were established using a survey-grade, Global Navigation Satellite System (GNSS) Trimble R2 unit; the Real Time Kinematic (RTK) with infill surveying approach was used, with all points yielding errors less than 4 cm horizontal and vertical. All sampled locations were vertically referenced within NAVD 88 units. We also located a total of 42 reference points (RPs) primarily on salt pannes and other open and distinguishable areas just outside of the *Spartina alterniflora* zones, and at road intersections. At each point x, y, and z coordinates were recorded. These RPs were used to verify location accuracies of the aerial images, relative to their location in the field.

### 2.2.2. Soil sampling

Soil cores were collected from the center of each quadrat after clipping the above-ground material, while not disturbing the soil surface. The rectangular corer (16.4 cm × 16.4 cm width, 25 cm length, with sharpened stainless-steel bottom rim for cutting through roots) was then inserted into the marsh. Once forced into the soil, the corer was extricated with as little disturbance of the cored soil as possible. Soil samples were removed from the corer using a specialized extruder. No obvious compaction of the soil samples was detected. These samples were then divided into 5 cm thick sections and were retained separately for the analysis of soil biomass, carbon and bulk density to evaluate their differences spatially as well as across different soil depths.

To determine soil bulk densities and moisture contents, a known volume of each sample was used. Bulk densities were calculated on the basis of oven-dried weight (at 105 °C for 48 h) and reported in g dry weight/$cm^3$. Separate subsamples of approximately 50 g of soil were used for the analysis of root biomass. Roots were separated using the flotation method (Boutton et al., 1998).

The remaining soil samples were used for soil carbon analyses. Samples were first air-dried, and subsamples were gently crushed and passed through a 2 mm sieve to remove large organic and inorganic fragments, and were then oven dried at 65° C for 48 h. The time required for oven drying was first determined by drying sub-samples until they reached a constant weight. Subsamples of approximately 5 g were ground to a fine, homogenous powder using a mortar and pestle which were cleaned and dried thoroughly between samples to avoid cross contamination. Ground soil samples were placed in a muffle furnace (440 °C for 8 h) to determine the loss of organic matter on ignition ([LOI] ASTM, 2000). A total of 15 samples were then selected for percent carbon analysis. Prior to carbon analysis, all the samples were tested for the presence of soil carbonates (using acidification prior to combustion in elemental analysis) and no carbonates were detected. The relationship between organic carbon determined by LOI and elemental analysis revealed a strong linear relationship (% $C = [LOI * 0.3045] + 0.3671$; Least square regression with $r^2 = 0.97$; $p < 0.0001$; and Root Mean Square Error (RMSE) = 0.17). Using this relationship, LOI results were converted to soil organic carbon percent. Soil carbon concentrations, bulk density values, and depths of the soil sections were used to report soil carbon storage as g carbon/$m^2$ (i.e., soil carbon storage [g carbon/$m^2$] = $\sum$[carbon concentration [g carbon/kg soil] * bulk density [g/$cm^3$] * interval thickness [cm] * 10).

Elemental and isotopic analyses of carbon and nitrogen in soils, vegetation (live and dead), and root samples were conducted in the Stable Isotopes for Biosphere Sciences Laboratory at Texas A&M University using a Carlo Erba EA-1108 elemental analyzer (CE Elantech, Lakewood, NJ, USA) interfaced with a Finnigan Delta Plus isotope ratio mass spectrometer (Thermo

Fisher Scientific, Inc., Waltham, MA, USA) operating in continuous flow mode. We analyzed these values for pooled soil samples from the 0–15 cm depth increment. Subsamples of vegetation (live and dead) and root samples drawn from the same quadrats (15 samples used in soil carbon analysis) were analyzed similarly using elemental analysis for their percent carbon contents. The average percent carbon values (mean of 15 samples) reported for live vegetation, dead vegetation and root biomass were used for the conversion of biomass to carbon.

### 2.2.3. Remote sensing data

High resolution (0.5 m) digital aerial images for June, 2012 were obtained from the National Agricultural Imagery Program (NAIP). These images consist of four (4) spectral bands in blue (428–492 nm), green (533–587 nm), red (608–662 nm), and near-infrared (833–887 nm) regions of the electromagnetic spectrum. The earliest images available for the study area from the NAIP historical data archives were for 1954, and were available in grey scale only. When the RPs collected during the ground survey were overlaid on the 2012 aerial images, the horizontal displacement was less than 0.5 m (one pixel). Thus, we did not attempt to perform any geometric corrections on the 2012 images. However, historical images of 1954 were geo-referenced to the 2012 image using ground control points that were clearly visible on both images. An RMSE of 0.67 m was maintained in geo-referencing the two sets of images, using ArcGIS (version 10.1) software.

We also obtained LiDAR data that were acquired in August, 2006 by the Sanborn Mapping Company, Colorado Springs, CO, through the use of a laser mounted on an aircraft flying at 900 m height. LiDAR data were used to interpolate Digital Terrain Models (DTMs) of 3 m $\times$ 3 m grids. These DTMs were then used to understand the patterns of elevation variation over the study area, particularly within the *Spartina alterniflora* zone. Elevation accuracies of the LiDAR derived DTMs were also evaluated using elevation measurements of the sample points and RPs collected during the ground survey. Surface elevations of the sample locations varied within the range of 0.20–0.57 m, while the marsh extent spans an elevation range from 0 m to 0.8 m. Using 3 m DTMs, three elevation zones were defined as: 1) less than 30 cm; 2) 30–40 cm, and 3) greater than 40 cm. Based on the ground surveyed elevation readings, all the sample locations were then grouped into these respective zones. We defined these elevation zones, in a manner to allow a relatively uniform distribution of sample points among the three zones and also considering the distribution of *S. alterniflora* across the elevation gradient.

Transitions in the dominant vegetation type from 1954 to 2012 were visually evaluated using the two images acquired during 1954 and 2012. Sample locations overlaid onto the two sets of images, revealed that the present day *Spartina alterniflora* locations were historically covered by three different land-cover classes in 1954; 1) *S. alterniflora*-dominated low marsh – LM, 2) salt pannes – SP, and 3) high marsh – HM (Fig. 3). Thus, the changes in the apparent above-ground vegetation cover at each point were reconciled with the records of soil carbon and bulk densities, with reference to soil profile depth.

### 2.2.4. Relative sea level data

Considering the sea level rise rates reported for this region, the mean sea level trends were evaluated using tidal gauge readings of the Galveston Pier 21 station, which is located approximately 15 km from the study area on the northeastern side of Galveston Island (Fig. 1). Data were obtained from the Permanent Service for Mean Sea Level (PSMSL) online data archives (available online at http://www.psmsl.org/). In the dataset, annual mean sea level values have been reduced to a common reference which is defined to be approximately 7 m below mean sea level and is referred to as revised local reference (RLR) datum. This arbitrary choice is made to avoid negative numbers in the resulting RLR sea level values.

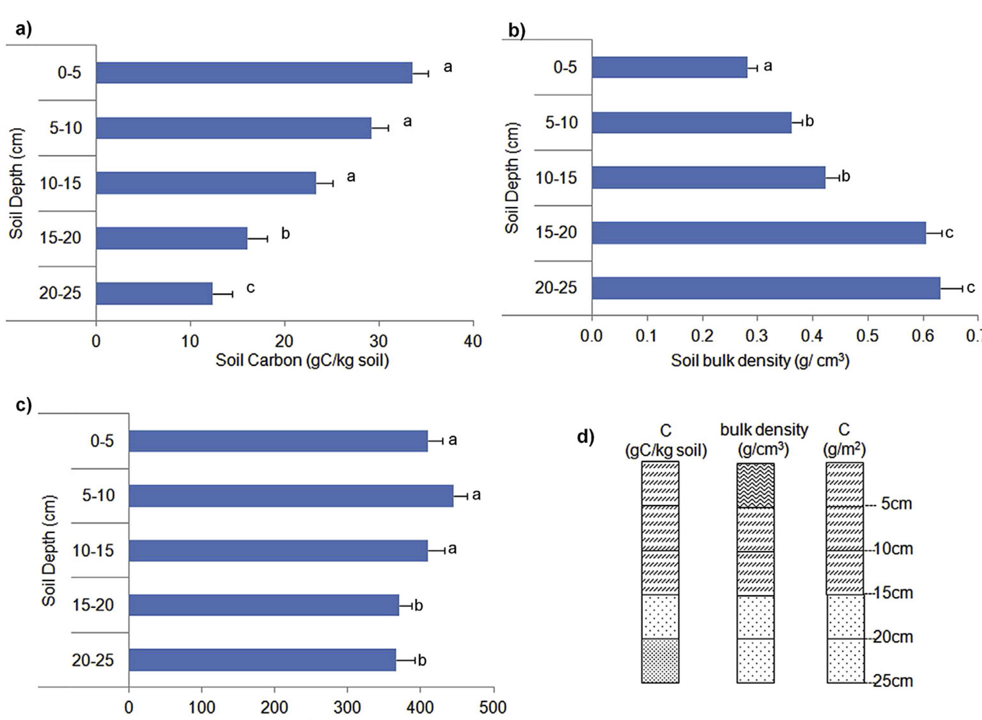


**Fig. 2.** Soil carbon concentration (a), bulk density (b), and soil carbon storage (c) across different depths of the soil profile, and a schematic representation showing the variation of soil properties at different depths of the soil profile (d). Lettering denotes significantly different (p = 0.05) depths.

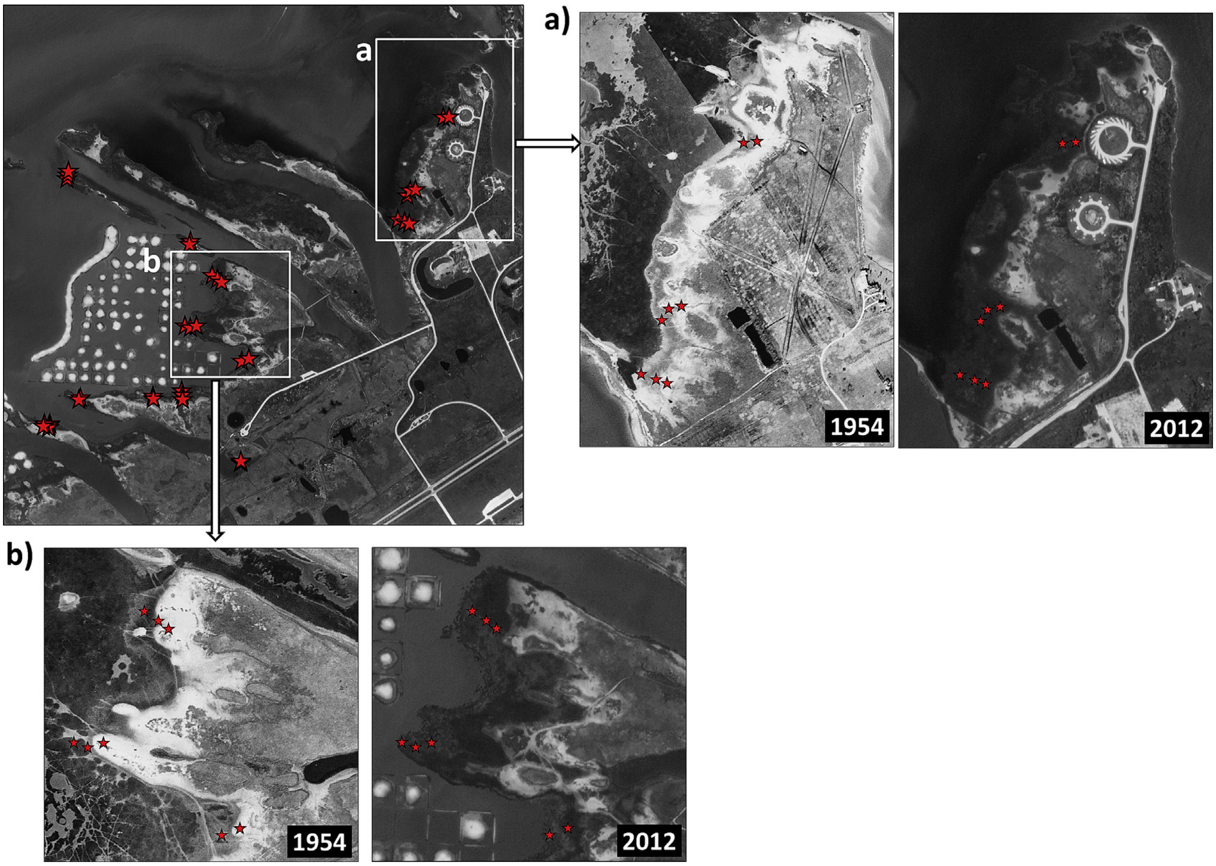


**Fig. 3.** Land cover change during the 58 year time period from 1954 to 2012. Sample points are overlaid on 2012 NAIP imagery (top left). Closer view of the two sample areas to highlight the landward shift of *Spartina alterniflora* low marsh extents and the relative sea-level rise (a & b).

### 2.3. Statistical analyses

Sample points were grouped in to the respective elevation zones identified as <30 cm, 30–40 cm and >40 cm elevation. Significance of the differences in vegetation characteristics and soil properties between these three groups was evaluated using Kruskal–Wallis non-parametric ANOVA. The Kruskal–Wallis test was selected due to the non-normal distribution of some of the parameters. Following the Kruskal–Wallis tests, post hoc comparisons of the means were performed using Mann Whitney u test. This procedure evaluated the significance of the differences in vegetation and soil properties (soil carbon and bulk density) between each elevation zone and soil depth. Post hoc comparisons of mean tests were performed first on all the soil samples to study the general pattern of variation in soil properties across different depths. To evaluate the effects of land cover transitions on the soil properties, this procedure was then repeated separately for each of the three groups defined based on their historical land cover category (i.e., LM, SP, and HM).

## 3. Results

### 3.1. Spatial variations in salt marsh vegetation height, cover, and above- and below-ground biomass and carbon

The mean plant height and stem height of *Spartina alterniflora* in our study area were 44.7 ± 1 cm, and 10.7 ± 0.5 cm, respectively (Table 1). Mean plant height and stem height decreased with increasing elevation, while the percent vegetation cover showed an opposite trend (increased with increasing elevation – Table 1). Plant density, in terms of the number of stems per $m^2$ did not show significant relation to the elevation (Table 1).

Mean above-ground biomass for our study area was 882 ± 36 g dry weight per $m^2$. Live and dead biomass components accounted for 61% and 39% of the total vegetation biomass, respectively. Carbon concentrations (g C/100 g dry weight) in live and dead vegetation components were 41.3 and 34.5, respectively. Live and dead biomass, and thus carbon quantities showed significant differences (Table 1) among the three elevation zones. However each followed an opposing trend along the elevation gradient; live biomass quantities decreased as elevation increased, while dead biomass increased. As a result, the total biomass showed a relatively uniform distribution with respect to elevation.

Soil carbon quantities of the top 15 cm soil did not show significant relation to the elevation (Table 1). Average root carbon storage was 218 ± 17 g carbon/$m^2$, while $\delta^{13}C$ values for soils ranged from −24 to −16‰. In general, $\delta^{13}C$ values increased along the elevation gradient from low to high, and these values were significantly different ($p = 0.03$) among the three sample groups defined based on elevation.

### 3.2. Temporal changes: soil carbon, relative sea-level history and vegetation transition

In general, in the soil profile, organic carbon concentrations decreased with soil depth, ranging from 34 ± 2.0 g C/kg soil at 0–5 cm to 12 ± 1.6 g C/kg soil at 20–25 cm (Fig. 2a). Soil bulk density showed a similar, but opposing pattern (Fig. 2b). As a result of these contrasting patterns in soil organic carbon concentration and bulk density, soil organic carbon storage (g C/$m^2$) was relatively

**Table 1**
Spatial variations of vegetation characteristics and above- and below-ground biomass along the elevation gradient across *S. alterniflora* extent.

| | | All samples | Elevation (cm) | | | Pr>χ2 |
|---|---|---|---|---|---|---|
| | | | <30 | 30–40 | >40 | |
| Plant height mean (cm) | | 45 ± 1.0 | 48 ± 2.0 | 44 ± 1.6 | 43 ± 1.1 | 0.008 |
| Stem height mean (cm) | | 11 ± 0.5 | 14 ± 0.8 | 12 ± 0.9 | 8 ± 0.3 | <0.0001 |
| % cover | | 87 ± 1.9 | 82 ± 3.9 | 84 ± 4.0 | 93 ± 2.0 | 0.009 |
| Plant density | | 356 ± 29 | 351 ± 31 | 360 ± 25 | 344 ± 33 | 0.68 |
| Above-ground C (g/m$^2$) | Live | 219 ± 8 | 251 ± 15 | 222 ± 12 | 200 ± 11 | 0.04 |
| | Dead | 121 ± 11 | 80 ± 11 | 88 ± 16 | 168 ± 13 | 0.0004 |
| | Total | 340 ± 14 | 331 ± 21 | 310 ± 24 | 367 ± 20 | 0.18 |
| Below-ground C | Root C (g/m$^2$) | 218 ± 17 | 258 ± 8 | 216 ± 11 | 197 ± 18 | 0.28 |
| (0–15 cm) | Soil C (g/m$^2$) | 386 ± 13 | 346 ± 20 | 406 ± 17 | 387 ± 30 | 0.22 |
| | $\delta^{13}C_{V\text{-}PDB}$ (‰) | −18.2 ± 0.2 | −18.7 ± 0.2 | −18.1 ± 0.1 | −18.0 ± 0.2 | 0.03 |

constant across soil depth increments (Fig. 2c). However, both soil carbon concentrations and bulk densities showed significant and abrupt change in the profile at a depth of ~10–15 cm (Fig. 2a and b). Further, soil organic carbon stores in the upper 15 cm of the profile were significantly greater ($p = 0.05$) than those below that depth (Fig. 2c). Summing across all depth increments sampled (0–25 cm), these salt marsh soils currently store approximately 1980 g C/m$^2$ (Fig. 2c).

The dominant vegetation zones shifted their spatial locations across the salt marsh extent from 1954 to 2012. The majority of *Spartina alterniflora* dominated low marsh areas that we sampled in 2012 were of a different vegetation type in 1954 (Fig. 3). Nearly 70% of our sample points were located on former salt pannes and high marshes. These observations suggest landward shifts of the salt marsh extent (conversions of salt pannes and high marshes in to *S. alterniflora* low marshes) over this 58 year period. The historical sea level data from tidal gauge readings confirmed rapid sea level rise rates during this period. The overall trend of the sea level rise reported for the period from 1909 to 2013 was 6.35 mm/year ($r^2 = 0.95$), while the highest sea level rise rate was for the decade from 1941 to 1950 at 14 mm/year (Table 2, and Fig. 4). The trend of soil composition across depth, varied in a manner related to each of the three historical land cover types (Fig. 5). For example, for low marsh points (sample points that have been remained as low marshes during the entire period from 1954 to 2012), the 0–5 cm and the 5–10 cm depths were nearly identical in terms of soil carbon concentration and bulk density (Fig. 5). Further, the soil carbon concentrations of these low marsh points decreased more slowly with depth, with a range from 35 ± 4 to 18 ± 4 g C/kg soil. Bulk density slightly increased with soil depth, but only up to ~0.63 ± 0.1 g/cm$^3$. Further, the changes in percent soil carbon and soil bulk density were significant ($p = 0.01$) from that of the adjacent layers only at the depth of 20 cm. Soil bulk density values for individual soil samples in our study area varied over a range from 0.08 to 1.13 g/cm$^3$. These are comparable to previously reported values for coastal salt marsh soils in this region (Callaway et al., 1997) and also in our study area (Feagin et al., 2010).

Low marsh points that have been converted from former salt pannes showed a sudden drop in soil carbon concentration and increase in bulk density at 5 cm and at 15 cm depths (Fig. 5a and b). In this group, the variation in soil carbon concentrations from the surface to the deeper layers was much greater than that of the LM group (i.e. sample points that have been remained as law marshes during the entire period from 1654 to 2012 – LM – Fig. 5a). However, the soil carbon concentrations at the surface (0–5 cm) of former salt panne and low marsh areas were similar; points from either of these land cover history types showed higher soil carbon concentrations as compared to former high marsh areas, more specifically at the soil surface (an approximately 10 g C/kg soil difference in carbon concentrations within 0–15 cm soil layer). These soil parameters in the deeper layers (below 5 cm) did not show significant differences ($p = 0.05$) between the soil cores of former salt panne and former high marsh areas, when comparing the two at similar depths (Fig 5). As compared with the former low marsh areas, the deepest layer of the salt panne was much poorer in percent carbon (about half at the 20–25 cm layer), and moderately higher in bulk densities. The former high marshes had their minimum soil carbon concentrations and maximum bulk density at the 15–20 cm layer, rather than the 20–25 cm layer (Fig. 5a), suggesting a possible transition from a former high marsh into a salt panne, and then finally into a low marsh at the upper layers.

Comparatively, for the top 15 cm of soil, sample points historically covered by low marshes reported relatively higher soil carbon concentrations as compared to the sample points that were converted to low marshes after 1954 (Fig. 5a). Considering the fraction of the soil profile to 25 cm depth, the soil carbon quantities for low marshes, salt pannes, and high marshes were 34.5 ± 3.2, 27.4 ± 2.7,

**Table 2**
Decadal sea level trends for the period from 1909 to 2013. Regression coefficients ($r^2$) and slope values of the linear regression model performed for each decade are given.

| Time period | $r^2$ | Slope (mm/year) |
|---|---|---|
| 1909–1920 | 0.08 | 3.63 |
| 1921–1930 | 0.01 | −0.67 |
| 1931–1940 | 0.15 | 5.15 |
| 1941–1950 | 0.90 | 14.50 |
| 1951–1960 | 0.50 | 9.3 |
| 1961–1970 | 0.23 | 6.40 |
| 1971–1980 | 0.01 | −0.53 |
| 1981–1990 | 0.15 | 4.56 |
| 1991–2000 | 0.02 | −1.32 |
| 2001–2013 | 0.30 | 5.27 |

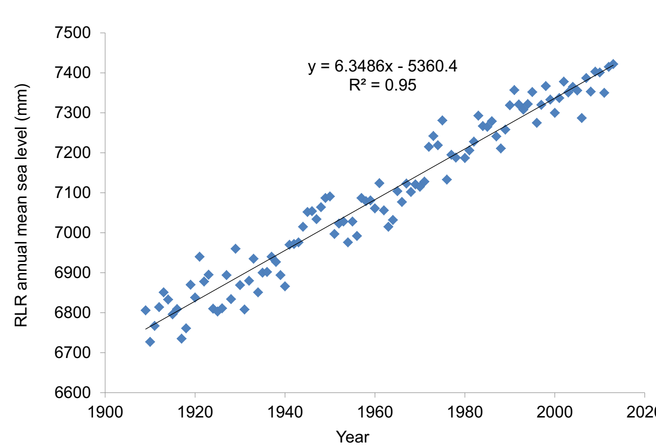


**Fig. 4.** Sea level trends for the period from 1909 to 2013 at Galveston Pier 21 station.

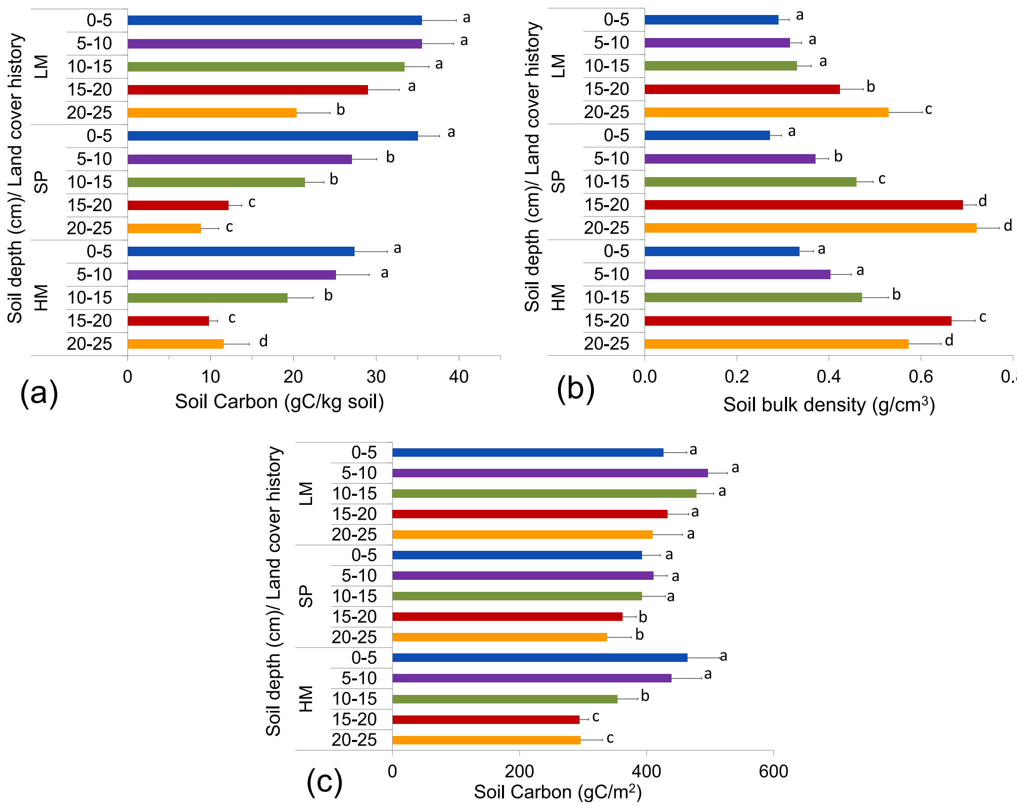


**Fig. 5.** Changes in Soil carbon concentration (a), bulk density (b) and soil carbon storage (c) along the soil profile separately for the three sample groups defined based on the historical land cover identified for each of the sample locations; 1) HM – High marsh, 2) SP – Salt pans, and 3) LM – Low marshes.

and 23.0 ± 1.9 g C/kg soil, respectively. Further, former low marsh areas had the highest absolute quantities of soil carbon (g C/m$^2$) storage at all depths sampled (Fig. 5c).

## 4. Discussion

### *4.1. Spatial variations of salt marsh vegetation cover, plant height, plant density, and above-and below-ground biomass and carbon*

*Spartina alterniflora* vegetation height varies along the elevation gradient, as shown empirically in the present study and in previous studies (Hardisky et al., 1984; Pennings and Callaway, 1992; Castillo et al., 2008). Though our site did not exhibit the typical short versus tall *S. alterniflora* phenotypic expression that is often seen in other studies, we did observe taller plants and stems in lower elevations on the seaward edges of the marsh. Previous findings from *S. alterniflora* report similar findings and explain this variation in plant height distribution using the variations in oxidation potential of the marsh soils along the elevation gradient and with increasing distance from shore line or the tidal creeks (Howes et al., 1981). In our study area, lower elevations were characterized by relatively dense clusters of taller plants as compared to the shorter and relatively drier plants in higher elevations (Table 1). Further, we observed relatively dense accumulations of dry and dead plant material in higher elevations. Increased accumulations of these plant materials contributed to the increased amounts of vegetation cover in the higher elevations regardless of the relatively lower plant densities there as compared to lower elevations (Table 1). Findings from previous studies indicate direct linkages between marsh zonation and the surface elevations. For example, Levine et al. (1998) explained marsh zonation along the elevation gradient resulting from variations in nutrient supply and resource availability. Elevation also plays a major role in determining the direct influence of tidal height, and inundation and thereby the distribution of soil nutrients, suspended sediment supply and sedimentation (Cahoon and Reed, 1995), and anoxic conditions within the marsh environment (DeLaune et al., 1983; Silvestri et al., 2005). Thus, a few cm change in surface elevation can result in a large percentage change in the frequency, duration, and depth of flooding of the marsh surface with direct consequences on plant growth (Reed and Cahoon, 1992) and marsh sustainability (Morris et al., 2002). Several other studies have also shown evidence for direct linkages between elevation and pore water salinity (Moffett et al., 2010). Marsh salinity which is recognized to be an important controlling factor on vegetation distribution typically increases with increasing elevation (Callaway et al., 1997; Zedler et al., 1999) and thus the plants grown in higher elevations may experience increasing physiological stress (Levine et al., 1998) leading to growth retardation and thus decreased biomass accumulation. In addition, the relative importance of each of the edaphic factors that control plant growth can also vary depending on the relative positioning of the marsh on the terrain and thus, the elevation ultimately determine plant zonation patterns (Pennings and Callaway, 1992) reflecting differences in the plant characteristics. Confirming these findings from previous studies, our findings on the above-and below ground biomass distribution along the elevation gradient indicate that the present-day elevation likely is the predominant factor driving above-ground plant characteristics and biomass.

Based on their review, Castillo et al. (2010) report the above-ground biomass of *Spartina alterniflora* in the range of 100–3700 g dry weight/m$^2$. The values reported in our study area varied within the range from 304 to 1452 g dry weight/m$^2$. These values are comparable with the biomass measurements reported for this area. For example, Webb and Newling (1985) reported *S. alterniflora* biomass quantities ranging from 22 to 936 g dry weight/m$^2$ for the salt marshes in the Galveston Bay complex, which includes our study area. Feagin et al. (2011) reported values from a 'healthy' marsh in July, 2010 (a month further into the growing season) within our study area as an average of 1842 g dry weight/m$^2$, with unhealthy marshes considerably lower. Also, Hardisky et al. (1984) reported similar values for *S. alterniflora* salt marshes in the Northern Gulf Coast of the US.

The total biomass carbon (alive + dead) was distributed relatively evenly across elevation. This evenness does not necessarily mean that the processes that occur at low and high elevations are the same. In general, the lower elevations in our study area were characterized by more robust growth with only a few, erect, stems emerging from clumps, while the higher elevations had a short, dense layer of overlapping vegetation canopies consisting largely of dead leaves and stems from the previous season. We observed a greater amount of dead biomass accumulation at higher elevations. Thus, while the total biomass and carbon stocks are relatively evenly-distributed across the elevation gradient and were not significantly different (Table 1) with respect to elevation, newly emerging plants are contributing largely to live biomass at the lower elevations. Tidal gauge readings for this area indicate that the mean tidal range varies from 0.3 to 0.7 m. Thus the increased accumulation of dead plant material in the higher elevations could be attributed to the effect of tidal flux.

Based on data from salt marshes from around the world, Chmura et al. (2003) reported the average soil carbon density of salt marshes as 0.039 ± 0.003 g C cm$^{-3}$. Furthermore, according to their findings, the average salt marsh soil carbon density value for Gulf Coast salt marshes was 0.087 g C cm$^{-3}$. Soil carbon concentrations in this study, when converted using soil bulk densities, yield an average soil carbon density of 0.10 ± 0.02 g cm$^{-3}$. The amount of soil carbon storage is a function of soil carbon concentrations and soil bulk densities. The average soil carbon concentration in our study area was 29 g C/kg soil, while the average soil bulk density within the top 15 cm soil was 0.36 ± 0.3 g/cm$^3$. Soil bulk density values reported in this study are comparable to some previous salt marsh studies (Gosselink et al., 1984; Nyman et al., 1990; Callaway et al., 1997). In general, soils with high mineral matter contents, including upland soils, are characterized by high soil bulk densities. However, in salt marsh soils, organic matter occupies more volume than mineral matter and can lower soil bulk densities (Gosselink et al., 1984; Nyman et al., 1990). Further, salt marsh soils are characterized by increased pore space. For example, Nyman et al. (1990) reported that 88%–96% of the soil volume in the upper 10 cm of marsh soils was occupied by water and air. These factors can collectively contribute to lowering soil bulk densities in marsh soils as compared to upland soils. Thus, regardless of the higher soil carbon concentrations, the marsh soils that are characterized by relatively lower values of bulk densities will result in considerably lower soil carbon storage when expressed in terms of volume (g C/m$^2$). However, to make inferences on their role as carbon sinks, it is necessary to conduct detailed investigations on the entire carbon cycling process within the marsh environment, including the influx or vertical accumulation rate of carbon to these low density soils.

*Spartina alterniflora* is a C4 plant and is characterized by an average $\delta^{13}$C value of −13‰ (Choi et al., 2001). Analysis of *S. alterniflora* vegetation samples in this study returned an average $\delta^{13}$C value of −13.6‰ and −13.7‰ for live and dead plant materials, respectively. However, similar to some previous studies (Haines, 1976; Currin et al., 1995; Choi et al., 2001), our carbon isotopic ratios of marsh sediments revealed relatively greater variability with values ranging from −24‰ to −16‰. Relatively lower $\delta^{13}$C values in marsh soils as compared to that of above-ground vegetation have been explained using different factors: land cover transition from high marsh to low marsh (Choi et al., 2001); energy flow processes within marsh soils (Currin et al., 1995); the presence of marsh benthic algae (−16 to −27.7‰; Fry and Sherr, 1984; Neubauer, 2000) or coastal phytoplankton (−18 to −24‰; Fry and Sherr, 1984; Currin et al., 1995); the presence of C3 plants ($\delta^{13}$C values −35 to −20‰; Kuzyakov, 2006). At our site, it is possible that marsh conversion from former high marsh areas, which do contain C3 plants, to the current low marshes may have contributed to the existence of mixed $\delta^{13}$C inputs to the soils. However, in contrast to this possibility, the mean $\delta^{13}$C value significantly increased with elevation, going from −18.7 to −18.0‰. This trend suggests marine benthic algae inputs as a more likely cause in lowering the mean $\delta^{13}$C value in the soil, with a greater influence at lower elevations where conditions are less dry.

### *4.2. Temporal changes: soil carbon deposition, relative sea-level history and vegetation transition*

The locations of our *Spartina alterniflora* dominated low marsh sample points, relative to the environments present on the historical aerial image of 1954, indicates that over the 58 year period this zone shifted landward. Further, the aerial images suggest that a great deal of marsh area was lost due to submergence (Fig. 3) likely as a result from the combined effects of eustatic sea level rise and land subsidence due to accelerated hydrocarbon and water extraction in this area. Much of the previous work has been devoted to understanding how this zonal migration process is related to relative sea-level rise. As the sea-level rises at a given location, the marsh responds through a coupled vertical accretion process (Morris et al., 2002). Salt marsh accretion is complex, with feedbacks between sedimentary and biological processes (Morris et al., 2002; FitzGerald et al., 2008). Despite variation in these feedbacks across marsh types, many models of marsh accretion predict future marsh drowning and loss resulting from accretionary deficit (Connor et al., 2000; Cahoon et al., 2006; Nyman et al., 2006). Previous findings over this region indicate landward migration of marsh zones to higher elevations (Feagin et al., 2010). When barriers prevent this migration, the marsh is lost, and findings from around the US have indicated a significant loss of coastal salt marshes due to these processes over the last century (Dahl and Stedmann, 2013).

Marsh loss and zonal migration at our study site has been extensive over the last century, and is due to an insufficient mineral sediment supply and vertical accretion rate, as compared to the rate of relative sea-level rise (White and Morton, 1997; White et al., 2002; Ravens et al., 2009). The tidal gauge readings that we detail in this paper revealed a relative sea level rise rate of 6.35 mm/year over the period from 1909 to 2013, while the highest relative sea level rise rates occurred during the two decades from 1941 to 1961 (Table 2). In our study area in the Galveston Island State Park's *Spartina alterniflora* low marshes, Ravens et al. (2009) reported sediment accumulation rates ranging from 0.14 to 0.36 cm per year. More generally in this hydrologic basin, White et al. (2002) reported an average sedimentation rate of 0.5 cm per year, while Yeager et al. (2007) reported a sedimentation rate of 0.16 cm per year for a different wetland in the same region. In our study area, processes driving the accretionary deficit include lowered mineral sediment supply due to the construction of the Texas City Dike, the damming of inflowing rivers, subsidence driven in part by growth fault activation due to water or hydrocarbon extraction, regional autocompaction, and eustatic sea-level rise (White and Morton, 1997). As a result, White and Tremblay (1995) reported a salt marsh loss of about 12% on the Galveston coast between 1950 and 1989, while Glass and Hollingsworth (1999) indicated a loss of 405 ha in Galveston Island State Park (encompassed by our study area) alone between 1930 and 1994. The submergence of the marsh extents along the seaward edge of our study area, and the landward migration of the marsh zones thus confirm the findings of previous studies over the region. For some locations, other phenomena such as hurricanes could also alter the above- and below-ground environments, but the study site was not strongly affected by the two major hurricanes that hit the area during this time period; the site was not overtopped by storm water during Hurricane Alicia (Savage et al., 1984). Further, indicating minimal impacts of Hurricane Ike, for our study area Williams et al. (2009) reported no net accretion or significant erosion following its incidence.

There were two distinct and significantly different layers found in our core profiles: (1) a surface layer to ~15 cm depth characterized by higher soil carbon concentrations and lower soil bulk densities, and (2) a layer below ~15 cm with lower soil carbon concentrations and higher soil bulk densities (Fig. 5a and b). Interestingly, multiplying an average vertical accretion rate of ~0.25 cm per year at this site (from Ravens, 2006), by ~58 years (1954–2012), yields ~15 cm of soil depth – a number that coincides with this transition depth. This transition was particularly evident in the bulk density and soil carbon (g C per kg soil) profiles of the former salt panne and high marsh cores at the 15–20 cm depth interval. However, soil cores of former low marshes did not show this transition in soil carbon or bulk density until the 20–25 cm depth interval. In the above calculation, we assumed conversion of former salt pannes and high marsh areas to low marshes happened immediately after 1954. However, given the varying rates of sea level rise rates reported over this period and the relative positioning of different sample locations on the terrain, each of these salt marsh points may have experienced vegetation transition at different points of time. Thus, further investigations using detailed analyses on land cover change as well as carbon isotope analysis of soil cores will help understanding exact timing of the salt marsh vegetation transitions and their linkages to the relative sea level history.

Even though a considerable amount of research effort has been devoted for understanding the processes of marsh migration, vertical accretion and also to investigate the potential impacts of sea level rise on these processes, (Bricker-Urso et al., 1989; Pennings and Calaway, 1992; Pennings et al., 2005; Moffet et al., 2010), we are not aware of scientific literature that investigated the impacts of marsh migration on the carbon storage ability of salt marshes. While the causes of vegetation zonation within the marsh landscape are both physical and biological, variability in the plant characteristics across these zones are determined in part by their relative positioning on the terrain and edaphic factors including those relating to soil (Pennings et al., 2005). In this work, we attempted to draw the connection between landward migration of marsh zones during this 58 year period and the changes that we observed in the soil profile. Our findings indicate that the effects of vegetation transition from high marsh and salt pannes to *S alterniflora* dominated low marshes were evident in the soil profile and were reflected in terms of the carbon concentrations and bulk densities, leading to considerable changes in the carbon storage. Further, the amounts of soil carbon stored in recently established *Spartina alterniflora* intertidal marshes were significantly lower than those that have remained *in situ* for a longer period of time. Thus, we suggest that in order to quantify and predict carbon in coastal wetlands, it is essential to understand not only the elevation, the relative sea-level rise rate, and the vertical accretion rate – but also the history of land cover change and vegetation transition.

## 5. Conclusions

Our results indicate a clear zonation of vegetation characteristics and the distribution of biomass quantities within the marsh extent. Distribution of biomass quantities within the *Spartina alterniflora* marsh were linked with the elevation, suggesting that flood tides may be exporting material from the lower elevations to the higher elevations over time. In general for the soil profile, the percent carbon decreased with depth, while the bulk density increased. However, both percent carbon and bulk density showed a significant and abrupt change in the profile at a depth of ~10–15 cm. This apparent transition in the soil characteristics coincided temporally with a transformation of the land cover, as driven by a rapid increase in relative sea-level around this time at the sample locations. In general, the amounts of soil carbon stored in recently established *S. alterniflora* intertidal marshes were significantly lower than those that have remained *in situ* for a longer period of time. Our findings indicate that, even though salt marshes can respond to relative sea-level rise by migrating landward, their status as a carbon sink varies as a function of both space and time. Thus, in order to predict carbon in a wetland, researchers need to know not only the elevation, the relative sea-level rise rate, and the vertical accretion rate – but also the history of land cover change and vegetation transition.

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