Geomorphic influences on the contribution of vegetation to soil C accumulation and accretion in *Spartina alterniflora* marshes

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Abstract. Salt marshes are important hotspots of long-term belowground carbon (C) storage, where plant biomass and allochthonous C can be preserved in the soil for thousands of years. However, C accumulation rates, as well as the sources of C, may differ depending on environmental conditions influencing plant productivity, allochthonous C deposition, and C preservation. For this study, we examined the relationship between belowground root growth, turnover, decay, above-and belowground biomass and previously reported longer-term rates of total, labile, and refractory organic C accumulation and accretion in *Spartina alterniflora*- dominated marshes across two mid-Atlantic, US estuaries. Tidal range, long-term rates of mineral sedimentation, C accumulation and accretion were higher and salinities were lower in marshes of the coastal plain estuary (Delaware Bay) than in the coastal lagoon (Barnegat Bay). We expected that the conditions promoting high rates of C accumulation would also promote high plant productivity and greater biomass. We further tested the influence of environmental conditions on belowground growth (roots + rhizomes), decomposition and biomass of *S. alterniflora*. The relationship between plant biomass and C accumulation rate differed between estuaries. In the sediment-limited coastal lagoon, rates of total, labile and refractory organic C accumulation were directly and positively related to above- and belowground biomass. Here, less flooding and a higher mineral sedimentation rate promoted greater above-and belowground biomass, and, in turn, higher soil C accumulation and accretion rates. In the coastal plain estuary, C accumulation rate was related only to aboveground biomass, which was positively related to the rate of labile C accumulation. Soil profiles indicated that live root and rhizome biomass was positively associated with labile C density for most marshes, yet high labile C densities below the live root zone and in marshes with high mineral sedimentation rates and low biomass signify the potential contribution of allochthonous C and preservation of labile C. Overall, our findings illustrate the importance of sediment supply to marshes both for promoting positive plant-C accumulation-accretion feedbacks in geomorphic settings where mineral sediment is limiting, and for promoting allochthonous inputs and preservation of labile C leading to high C accumulation and accretion rates in geomorphic settings where sediment supply is abundant.

1 Introduction

Salt marshes are among the most productive ecosystems on Earth where over half of the annual plant biomass production can occur belowground in the form of rhizomes and roots (Valiela et al., 1976; Gallagher and Plumley 1979; Schubauer and Hopkinson 1984). Plant biomass, especially belowground biomass, is considered to be a primary contributor to soil organic matter and carbon (C) sequestration in marshes (DeLaune et al. 1983a; Nyman et al. 2006). High rates of plant productivity coupled with relatively slow rates of decomposition allow a net accumulation of plant-derived C over time. Important feedbacks among aboveground plant structure, such as stem density, sediment deposition, elevation, above-and belowground productivity, and burial of organic matter promote both C accumulation and accretion, allowing some resilience to relative sea level rise (Kirwan and Megonigal 2013). Belowground productivity alone may contribute to an estimated 3.0 mm/yr of vertical accretion, based on a theoretical maximum belowground production of 2,500 g/m^2/yr for *Spartina alterniflora* (Morris et al. 2016). For British coastal marshes dominated by different species, autochthonous production has been estimated to contribute 0.2 to 1.0 mm/yr (Allen 1990; French 1993). Variation in plant productivity due to differences in environmental conditions, therefore, may account for a significant portion of the variability in rates of marsh C accumulation and accretion. For *S. alterniflora* marshes, which naturally occur along the Atlantic and Gulf coasts of the U.S., roots and rhizomes of marsh plants are estimated to comprise up to 90% of organic input (Howes et al. 1985). Accretion rates above the local organic production, must be due to allochthonous sources of C and sediment (Morris et al. 2016). Yet, it is unclear whether local plant organic matter input is constant across geomorphic settings that experience a range of environmental conditions and sedimentation rates. Local environmental conditions such as hydrology, salinity, sediment availability, and soil properties are predicted to play a key role in influencing relationships between biotic processes and rates of C accumulation and accretion (Haslett et al. 2003). Despite knowledge of bio-physical feedbacks governing C accumulation and accretion, and the recent emphasis on the efficiency of salt marshes in sequestering C, fine-scale controls of marsh C accumulation are still poorly understood (Connor et al. 2001, Chmura et al. 2003, Mcleod et al. 2011). These fine-scale controls may account for a large portion of the spatial variability in C accumulation rates in marshes (e.g., Mcleod et al. 2011; Ouyang and Lee 2014). Of the numerous studies that have separately quantified plant productivity or biomass and soil carbon accumulation rates, few have examined relationships between plant growth, decay, and biomass in concert with soil C accumulation and accretion. In addition, understanding these relationships across natural systems is extremely important as multiple abiotic conditions will determine the ability of marshes to accumulate and store C and adjust their elevation relative to sea-level.

While *insitu* plant biomass production may be a major C source, non-plant derived (e.g., edaphic algae) and allochthonous C deposition also contributes to carbon accumulation in marsh soil. Some have suggested that allochthonous C may be a more important component of surface sediments, while the accumulation of plant-derived C from root productivity becomes more important at depth (Santilan et al. 2013). The relative magnitude of allochthonous versus autochthonous carbon inputs may also differ within and among marshes depending on rates of deposition (mineral and organic) and environmental conditions that regulate *insitu* productivity and decay. Higher tidal range, greater supply of mineral nutrients and sediments, and lower salinities are conditions that are all predicted to enhance both plant productivity and soil C accumulation (Mendelssohn and Kuhn 2003; Craft 2007; Kirwan and Guntespergen 2010). Across geomorphic settings of estuaries, from deltas to coastal lagoons, physical and abiotic factors often co-vary with potential consequences for C sequestration and even vulnerability to relative sea-level rise. Microtidal marshes in coastal lagoons, for example, are considered particularly vulnerable to relative sea-level rise due to limited sediment supply, weak and limited tidal movement for sufficient sediment transport and surface deposition leading to a reliance on *insitu* organic matter production for accretion (Reed et al., 2008; Kirwan & Guntenspergen 2010; Ganju et al., 2017). In contrast, marshes in geomorphic settings with high rates of mineral sedimentation such as those near river deltas may have greater magnitudes of both allochthonous C deposition and autochthonous plant C inputs (e.g., Craft et al. 2007). In tidal marshes of Australia, for example, soil C stocks in fluvial environments containing finer-grained sediments were approximately double the C stocks in marshes of marine sandy estuaries (Macreadie et al. 2017). Higher contributions of allochthonous C and greater preservation of plant-derived C likely influenced greater soil C accumulation in fluvial versus marine geomorphic settings (Saintilan et al. 2013; Kelleway et al. 2016). Similarly, in marshes of a coastal plain estuary, soil C accumulation and accretion were greater than in marshes of a coastal lagoon (Unger et al. 2016). In these systems, C accumulation rate was strongly and positively related to the rate of mineral sedimentation. The strong positive relationship between mineral sedimentation and C accumulation rates implied that mineral sediment availability influenced greater plant-derived C inputs, greater allochthonous C inputs, and/or greater C preservation.

Stable C isotopic signatures have shed some light on the relative importance of different C sources in marsh soil. A comparison of δ^{13}C in soils of mineral-rich and organic marshes showed a depletion of plant-derived δ^{13}C signatures in mineral marsh soils and strong signal of local plant δ^{13}C in organic marsh soils (Middleburg et al. 1997). Preferential decomposition of labile C, which is enriched, with more negative δ^{13}C values, relative to *Spartina* tissue and preservation of refractory lignin, which is depleted relative to *Spartina* tissue, may partially explain the overall shift in δ^{13}C in mineral-rich marshes (Benner et al. 1991). Another mechanism potentially causing the depletion of δ^{13}C signatures relative to local plant tissue is a greater allochthonous C input consisting of organic matter sorbed onto mineral particles, estuarine phytoplankton, microphytobenthos and non-local macrophytes (Middleburg et al. 1997). Though labile soil C may be derived from algal sources, it is also possible that the environmental conditions in mineral-rich marshes stimulate *insitu* plant productivity and inputs of labile plant C. Mineral sedimentation, for example, tends to be positively related to C accumulation (Chmura et al. 2003; Unger et al. 2016) and also creates favourable conditions for plant growth (DeLaune et al. 1990; Mendelssohn and Kuhn 2003). Specifically, mineral sediment input can increase marsh elevation, supply a physical substrate for root growth, supply inorganic nutrients, raise the redox potential, and promote the precipitation of sulfide with iron and manganese to form non-toxic compounds (DeLaune et al. 2003). Regardless of the source, labile organic C can be more abundant in marshes with higher rates of mineral sediment deposition, and ultimately drive total C accumulation rates (Unger et al. 2016).

The goal of this study was to examine the relationship between autochthonous plant-derived C inputs and longer-term labile, refractory, and total organic C accumulation rates in short-form *Spartina alterniflora* marshes. In a previous study, we found rates of C accumulation to be significantly greater in marshes of a coastal plain estuary, Delaware Bay, USA than marshes of an adjacent coastal lagoon, Barnegat Bay (Unger et al. 2016). Total organic C accumulation rates were positively associated with rates of mineral sedimentation and labile C accumulation. Refractory C accumulation was similar across marshes averaging 78 ± 5 g/m^2/yr (Unger et al. 2016). The sources of the C fractions were unknown. For this study, we tested the hypothesis that rates of *S. alterniflora* belowground productivity were greater in marshes of the coastal plain estuary than in the marshes of the coastal lagoon, where a higher water table, higher salinity, and lower rates of sediment deposition were predicted to limit root and rhizome growth. We predicted that patterns of belowground productivity and turnover would mirror those of longer-term total and labile organic carbon accumulation rates across marshes and estuaries. Our hypothesis would be supported if environmental conditions that promoted C accumulation such as high rates of mineral sedimentation and, potentially, high tidal range and low salinity also promote high belowground biomass production. Further, we examined the role of belowground decay in explaining spatial patterns of C accumulation. We hypothesized that the amount of organic material remaining following 20 months of belowground decomposition would be greater in marshes with higher C accumulation rates. For this, the conditions that promote high rates of C accumulation may also promote the preservation of C particularly in the upper soil column where much of the decay of labile organic matter occurs (Hackney and de la Cruz 1980; Hackney 1987; Morris and Bowden 1986). Ultimately, the net amount of belowground biomass (C fractions greater than ~1 mm in size) was predicted to be directly and positively related to the density of C in the soil profile and C accumulation rate. Similarly, above-and belowground biomass was predicted to be positively related to soil C accumulation. Finally, because plant productivity and decay processes as well as overall plant structure (e.g., height, stem density, biomass) have been shown to be tightly regulated by abiotic factors, we examined the influence of local environmental conditions (i.e., water level, salinity, soil nutrient status, and sediment deposition rates) on *S. alterniflora* growth, decay and biomass across marshes and estuaries.

2 Methods

2.1 Study sites

Six marshes in two estuaries along the Mid-Atlantic coast of the United States, Barnegat Bay and Delaware Bay, New Jersey were the focus of this study (Fig. 1). The two estuaries and marshes therein varied in geomorphic setting and therefore, tidal range, hydrology, salinity, sediment availability, and nutrient concentrations also varied. The Delaware Bay is a large coastal plain estuary extending 215 km from the head-of-tides to the bay mouth at the Atlantic Ocean. Tidal amplitude is approximately 1.5 m at the mouth and increases up-estuary modulated by estuary and tidal channel geometry. Barnegat Bay is a shallow coastal lagoon extending 62.7 km along the coast of New Jersey, separated from the Atlantic Ocean by a barrier island apart from two inlets. Barnegat Bay experiences a relatively small tidal amplitude ranging from 20 to 50 cm depending on location in the bay (Defne and Ganju 2014). Mean salinity ranges from 18 to 25 with lowest salinities in the northern part of the bay farther from the inlets and also near Toms River (Kennish 2001). Across the two estuaries, marshes ranged from being along a large tidal tributary with relatively low salinity (Maurice River, MR, in Delaware Bay) to a back-barrier marsh (Island Beach State Park, IB) in Barnegat Bay, which has been converting from *S. alterniflora* to shallow open water between the parallel mosquito ditches over approximately the last decade, likely due to a lack of drainage through the ditches (pers obs). All six marshes had some level of mosquito ditching. Reedy Creek (RC) marsh in northern Barnegat Bay had interior ponds which have been expanding in size over time. Of the six marshes in the study, MR had the highest freshwater input and the highest longer-term mineral sediment, total organic C and labile C accumulation and accretion rates (Unger et al. 2016). RC and IB in Barnegat Bay, had the lowest rates of accumulation and accretion, while Channel Creek (CC) to the south had larger mineral sediment input and was intermediate in accumulation and accretion rates to RC and IB and those in Delaware Bay (Unger et al. 2016). Accretion rate in Barnegat Bay marshes (0.28 ± 0.06 cm/yr) over the last 50 – 100 years was less than the rate of relative sea-level rise over approximately the same time period (0.41 cm/yr; NOAA, Tides and Currents; *in* Boyd et al., 2017). In Delaware Bay, salt marsh accretion rate (0.70 ± 0.26 cm/yr) exceeded the rate of local relative sea-level rise over the same time period (0.34 cm/yr, NOAA, Tides and Currents). Study locations have also been described in Elsey-Quirk 2016; Unger et al., 2016 and Boyd et al., 2017.

2.2 Experimental design

In each of the six marshes, five plots were established along a transect of increasing distance from the marsh/estuary boundary. Transects ranged from 270 to 2970 m with shorter transects in smaller marshes (generally in Barnegat Bay) and longer transects in marshes along larger tidal channels (in Delaware Bay). This transect-based study design, rather than replicate plots in close proximity, was employed to capture a range of within-marsh variation, while also stratifying by short-form *S. alterniflora*. Belowground ingrowth and litterbag decomposition studies were employed at each of the five plots (n = 5). Vegetation structure (i.e., stem density and shoot height and above- and belowground biomass) was measured at three of the five plots (nearest, middle and farthest from the estuary). Belowground biomass was determined from 2-cm depth sections from half of a 15.2-cm diameter soil core. The other half of the core was used for analysis of soil properties, C (total organic, labile, and refractory) and nitrogen concentrations, and ^{137}Cs and ^{210}Pb-activity (*reported in* Unger et al., 2016; Boyd et al., 2017). Organic C (labile, refractory and total) accumulation rates, with which we examined relationships with plant processes and properties (present study) were previously published in Unger et al. 2016. C accumulation rates were calculated using ^{137}Cs-based accretion rates published in Boyd et al. 2017.

2.3 Environmental conditions

2.3.1 Marsh elevation, hydrology and salinity

Elevations of the plots were collected using a Leica GS-14 (NJ NAD83, Geoid 12A). A minimum of three GPS survey points were collected on the marsh surface at each plot. Two water level/conductivity recorders (In-Situ 5000 vented) were installed in each of the six marshes from August 2012 to October 2013. Probes were placed in each marsh near and far from the estuary approximately 5 m from the location of two of the five belowground ingrowth and litterbag plots and two of the three standing biomass and soil core plots. Probes were installed in slotted wells to a depth of 70 cm. Water level and conductivity were recorded every 15 and 30 minutes, respectively. Elevation of the marsh surface around each well was also collected. Water levels were referenced to the marsh surface, while elevations were referenced to the North American Vertical Datum 1988 (NAVD88).

2.3.2 Soil properties

Soil cores were collected for testing relationships between belowground biomass and previously reported soil C accumulation (*in* Unger et al., 2016) and accretion rates (*in* Boyd et al., 2017). PolyCate tubes 15.2 cm in diameter and 110 cm long with a sharpened bottom edge were used to collect soil cores. Cores were taken back to the lab and sectioned into 2-cm depth sections. Physical and chemical analyses were conducted on half of each 2 cm section. Soil bulk density (g/cm^3), percent organic matter, total organic C, refractory and labile C, total nitrogen, and radiometric analyses were conducted and is reported in Unger et al., 2016 and Boyd et al., 2017. The remaining half of each 2-cm depth was rinsed and sieved for belowground biomass (see below).

2.4 Vegetation parameters

2.4.1 Belowground growth and turnover

Belowground growth rate (g DW m^{-2} yr^{-1}) was measured at five locations in each of the six marshes using rates of root and rhizome growth into flexible mesh bags filled with a 1:1 mixture of unfertilized top soil and peat moss (i.e., ingrowth technique; McKee et al., 2007; n = 5). Ingrowth bags were constructed of flexible crawfish sack material with a mesh size of 6.3 x 3.2 mm, and, when filled, were 5 cm diameter and 15 cm length. Four ingrowth bags were deployed in each of the five plots and sequentially harvested approximately every four months from April 2013 to October 2014 to calculate belowground (root + rhizome) ingrowth rate. The four bags were deployed 50 cm apart in each plot and all bags were installed vertically into 15 cm deep cored holes. Accumulated root and rhizome mass was dried at 60°C to a constant weight. All of the roots and rhizomes in ingrowth bags were live based on color and structural integrity. Belowground turnover was calculated by dividing ingrowth (g m^{-2} yr^{-1}) by live root and rhizome biomass (g m^{-2}; Section 2.4.3). Ingrowth typically underestimates absolute rates of belowground productivity, and therefore, both absolute productivity and turnover will be underestimated. However, our goal was to examine relative responses to varying environmental conditions (Valiela et al., 1976; Graham and Mendelssohn 2016).

2.4.2 Belowground decay

Belowground decomposition of macro-organic matter was estimated using the litterbag technique. Litterbags (20 x 10 cm) made of 1 x 1 mm window screen mesh were filled with 9 g wet weight of macro-organic material comprised of coarse roots and rhizomes in a live to dead ratio of 1:3. Organic material was subsampled from all soil cores (Section 2.4.3) and combined as a composite sample. Five replicate 9 g wet weight samples were dried at 60°C to estimate initial dry weight. Four litterbags were deployed horizontally 10-cm below the surface in each of five plots approximately 2 m from ingrowth bags in each of the six marshes (n = 5). Litterbags were placed in Delaware Bay marshes on 12 December (DN), 13 December (MR), and 9 January (DV). Litterbags were deployed later in BB marshes (13 February (RC), 29 March (IB), and 8 April (CC)) because of the difficulty of accessing these sites in the months following Hurricane Sandy, which made landfall within 115 km of the marsh study sites on 29 October 2012. Once deployed, litterbags were collected sequentially over the same ~20 month period of ingrowth study for determination of mass loss over time. Percent of the original dry mass remaining at the end of the study period was determined.

2.4.3 Biomass

Aboveground biomass was harvested from three plots within a 0.25 m^2 quadrat where soil cores for radiometric dating, C analysis and belowground biomass were also collected. In the lab, stems were rinsed of mineral matter, counted, and measured for height. Belowground biomass from half of each 2 cm soil section was rinsed to remove all mineral sediment and separated into size classes of coarse and fine organic material. Coarse organic matter, comprised primarily of stem bases and rhizomes, were further sorted into live and dead categories based on color and rigidity. A sieve with a 2 mm mesh size retained coarse material and a sieve with a 1 mm mesh size retained fine organic matter, which could not be easily separated into live and dead components. All above- and belowground biomass was dried to a constant weight in a 70°C drying oven. Dry weights were converted to a g m^{-2} basis and depth profiles were constructed. For analysis, belowground biomass in each core was summed to two depths in the soil profile. One was to each respective ^{137}Cs peak, accounting for biomass that contributed directly to accretion above the ^{137}Cs peak depth. However, live biomass is continually added to the soil column, and is often at depths well below the year 1963 ^{137}Cs marker, and therefore, biomass was also summed to a specific depth, 50 cm, which is typical methodology for quantifying belowground biomass.

2.5 Data analysis

Each environmental and vegetation parameter was checked for normality using the Shapiro-Wilks test. Log transformations were used for most variables when necessary and appropriate and logit transformations were used for percent data (e.g., percent soil organic matter, total nitrogen). A square root transformation was necessary to normalize belowground ingrowth data. We tested for homogeneity of variances using the Levene Test on transformed data. The only violation of the equal variance assumption was for the 95% rooting depth, which, following log-transformation, failed the Levene test between estuaries, but not among marshes. We used a nested analysis of variance to test for differences among marshes nested within estuaries in belowground ingrowth, decay rate, and vegetation structure (e.g., stem density, height, rooting depth, and biomass). To test for relationships between belowground biomass structure and accretion and C (total organic, labile and refractory) accumulation rates a stepwise regression analysis was conducted. For analysis of relationships between belowground biomass and ^{137}Cs-based accumulation and accretion rates, biomass summed above the ^{137}Cs peak depth was used. Matlab was used to calculate hydrologic parameters including mean low water (MLW), mean high water (MHW), and frequency and percentage of time flooded from the continuous water level time series (MATLAB 6.1, the Mathworks Inc., Natick, MA). Multivariate correlation analysis was conducted to test for collinearity among environmental predictor variables. One representative of highly correlated variables was chosen and redundant variables were removed for future analyses. Based on the results of the correlation analysis, two hydrologic parameters, MHW and MLW depths relative to the marsh surface, were selected to represent the suite of variables with which they were related, for which isolating individual relationships with vegetation parameters would be impossible (Supplementary Table A). We chose to use MHW and MLW over other variables such as % time flooded because these variables represent the magnitude of surface flooding at high tide and the magnitude of drainage at low tide, respectively, both of which we predicted to be biologically important. Salinity was also maintained in the models, although it was negatively correlated with several hydrologic parameters, but not related to soil properties. Because of the strong relationship between soil bulk density and long-term mineral sedimentation rate, only sedimentation rate was retained in subsequent models. Correlations within environmental and vegetation data were expected, and therefore, a multivariate approach were used to analyze the data. Multivariate analysis of variance (MANOVA) was used to test for differences among marshes nested within estuaries in environmental parameters. If a significant multivariate treatment effect was found based on the Wilks Lambda test, univariate tests were performed. Univariate post-hoc tests were conducted using Tukey’s HSD test. To examine the relationship between environmental and vegetation parameters across samples, a stepwise regression was used with forward selection, starting with the full model and minimum BIC. Belowground ingrowth, decay and biomass components were analysed in separate stepwise univariate models. Non-linear modelling was used when relationships were non-linear. Unless otherwise specified, JMP V.12.1 was used for all statistical analysis (JMP Version 12.1, SAS Institute Inc.).

3 Results

3.1 Local environmental conditions

Despite the stratification of our study plots in marsh interiors dominated by short-form *S. alterniflora*, environmental conditions varied across marshes and estuaries. Elevations ranged from -7 to 87 cm, (NAVD88; Table 1). Tidal amplitudes ranged from 5 to 22 cm (Table 1). Relative to the tidal frame, marsh surfaces ranged from below MLW (IB) to above MHW (CC). Generally, marshes in Barnegat Bay experienced a lower tidal range, but were flooded for a greater percentage of the year than Delaware Bay marshes (53 ± 12 and 40 ± 9%, respectively; Estuary: $p = 0.0341$). Among the marshes in Barnegat Bay, CC was the highest in elevation, sitting on average 3 cm above MHW. CC was flooded less often (6% of the time), with higher water table salinities, and higher long-term rates of mineral sedimentation than RC (Table 1). IB was moderate in elevation but flooded 86% of the time with long durations of individual flood events, due to poor drainage through mosquito ditches. RC was the lowest elevation marsh, and although not flooded as much as IB, was flooded 66% of the time. In Delaware Bay, DV was sitting high in the tidal frame and, therefore, was flooded less often than the other marshes (MR and DN; Marsh[Estuary]: $F_{4, 11} = 53.15$, $p < 0.0001$). Overall, 65% of marsh areas had MLW depths within 5 cm of the marsh surface, indicating that the majority of the root zone was continuously inundated. The lowest MLW depth of the 18 study areas was 11 cm below the surface in a relatively high elevation area of DV in Delaware Bay.

Salinities ranged from 7 psu at MR in Delaware Bay to 40 psu at CC in Barnegat Bay. Salinity of Barnegat Bay marshes was an average of 16 psu higher than Delaware Bay marshes, but there was also a significant difference within Barnegat Bay with RC in the north having a lower salinity than IB and CC (Marsh[Estuary], $p = 0.0103$; Table 1). In Delaware Bay, salinity was variable across marshes as were soil properties, although MR had a higher soil bulk density and less variable high rates of mineral sedimentation (Table 1). Soil nitrogen concentrations were greater in RC and IB in Barnegat Bay than all other marshes (Table 1). Total soil N concentrations were positively correlated with soil organic matter and strongly negatively correlated with bulk density (Supplemental Table A).

3.2. Belowground growth and turnover

Belowground ingrowth, comprised primarily of large roots and rhizomes, ranged from 0 to 550 g/m^2/yr across plots. There were two plots in IB where no root ingrowth occurred, where previously vegetated areas had converted to ponded mudflat. Regardless of the inclusion of these zero data points, ingrowth rates did not differ among marshes (Fig. 2) and averaged 206 ± 22 g/m^2/yr (excluding zeros). Significant differences in belowground ingrowth were not found among marshes because within marsh differences in environmental conditions influenced large variability. Across all sampling plots, belowground ingrowth was negatively related to MLW depth, indicating that root and rhizome growth was positively influenced by low tide drainage (Fig. 3). However, under moderate inundation, root growth was highly variable. Because MLW was generally above the lowest part of the ingrowth bag, and therefore, ingrowth bags were inundated most of the time, the effect of hydrology on root growth was evident at the extremes of

MLW, where either average low water level exposed a significant portion of the ingrowth bag resulting in relatively high root growth or low water averaged above the surface and the root zone was continuously flooded, where no roots grew. However, even with the zero root growth data points removed, a positive relationship between drainage and root growth remained (i.e., adj $R^2 = 0.36$, $p = 0.0078$). Belowground turnover ranged from 0.04 to 0.43 yr^{-1} with an average of 0.15 ± 0.03 yr^{-1}. Turnover rates did not vary among marshes and were not influenced by measured environmental parameters.

3.3. Belowground decay

Live and dead biomass in a ratio of 1:3 placed in litterbags 10 cm below the marsh surface tended to decline rapidly following deployment. Litterbags placed in Barnegat Bay a few months later in the spring than those in Delaware Bay may have led to a more rapid initial decline in mass (Supplemental Figure A). However, regardless of the initial decay slopes, the percentage of root and rhizome material remaining at the end of approximately 20 months was similar among marshes averaging 59 ± 1% (Fig. 2). The percent mass remaining was not significantly related to any of the environmental factors tested (i.e., water level, salinity, soil nutrient concentration, sedimentation rate), as it did not vary much among plots.

3.4 Vegetation structure

3.4.1 Aboveground

Spartina alterniflora stem density ranged from 0 to 4112 stems/m^2 across plots and did not differ significantly among marshes (Table 3). In Barnegat Bay, there was a strong negative relationship between stem density and mean low water depth, such that stem density increased with more drainage (Fig. 3). Stem density in Delaware Bay marshes was not related to any environmental predictor variable.

Shoot height was approximately two times greater in MR in Delaware Bay than the other marshes with the exception of RC (Marsh [Estuary]: $F_{1, 4} = 8.15$, $p = 0.0026$). Aboveground biomass was over six times greater in MR than RC and IB in Barnegat Bay (Marsh [Estuary]: $F_{1, 4} = 8.13$, $p = 0.0021$; Table 3). In Barnegat Bay, live aboveground biomass increased linearly with increasing mineral sedimentation rate and decreased linearly with increasing MHW. This indicates that aboveground biomass responded positively to higher mineral sedimentation and less flooding. In Delaware Bay, aboveground biomass increased with increasing MHW following a quadratic relationship (Fig. 7b). Therefore, geomorphic differences between the two estuaries led to differences in vegetation response to hydrology with aboveground biomass stimulated by higher MHW in Delaware Bay and reduced in Barnegat Bay.

3.4.2 Belowground

Aboveground live biomass was not related to live, dead, fine, or total belowground biomass. Rates of belowground ingrowth and decay were also not statistically related to belowground biomass stocks. The total amount of live biomass (above- and belowground) was over three times greater in CC (3245 ± 768 g/m^2) than in RC (833 ± 41 g/m^2) with no other differences among marshes (Marsh[Estuary]: $F_{1,4} = 4.2$, $P = 0.0227$).

Belowground biomass was variable within marshes. When calculated to a 50 cm depth, there was no difference among marshes or between estuaries in total, live coarse, or dead coarse biomass (Table 3). However, the depth of live biomass differed among marshes. The 95% rooting depth was greatest in DN, followed by MR, both of which had greater live root depths than Barnegat Bay marshes (Marsh [Estuary]: $F_{4, 12} = 10.58$, $p = 0.0007$; Table 3; Fig. 6). There was greater fine biomass in CC in Barnegat Bay than in MR in Delaware Bay (Table 3).

Biomass was also summed to ^{137}Cs-peak depths, which varied by 42 cm across plots. Depth of the ^{137}Cs peak ranged from 9 to 17 cm in Barnegat Bay marshes and 17 to 51 cm in Delaware Bay marshes (Boyd et al. 2017). There was similar or less biomass in Delaware Bay marshes to a greater depth than in Barnegat Bay marshes (Fig. 6). For example, the quantity of live biomass to a 16 cm depth at CC was similar to the amount to a 48 cm depth in MR. Total belowground biomass (live coarse, dead coarse and fine) above the ^{137}Cs peak, was significantly greater in DN and CC than in RC (Marsh [Estuary]: $F_{4, 12} = 5.12$, $p = 0.0121$), partly due to the shallower depth of the ^{137}Cs peak in RC. However, live coarse biomass ranged from an average of 505 g/m^2 in RC to 2675 g/m^2 in CC where ^{137}Cs peaks occurred at depths averaging 11 and 16 cm, respectively. Fine biomass was also greater in CC than in RC (Table 3).

Belowground biomass stocks were related to several measured environmental parameters. And while the aim of these analyses was to examine cross-system relationships between environmental conditions and vegetation patterns, it became apparent that the relationships were highly estuary-dependent. In Barnegat Bay, live belowground coarse biomass was positively related to sedimentation rate and negatively to MHW (Fig. 4c, d). Dead belowground coarse biomass was also negatively related to MHW in Barnegat Bay (Fig. 4f). This indicates that while mineral sedimentation stimulated live root and rhizome biomass, an increase in high tide over the marsh surface was associated with a decline in both live and dead coarse biomass. In Delaware Bay, live and dead coarse biomass was variable across the range of environmental conditions. However, both fine and total biomass declined with increasing rates of mineral sedimentation. Fine biomass comprised 45 – 69% of total belowground biomass in Delaware Bay marshes, and the decline in fine biomass resulted in a decline in the total biomass. Fine biomass also increased with an increase in salinity in Delaware Bay.

3.5 Relationship between vegetation and soil C and accretion

3.5.1. Soil C density profiles

Belowground biomass profiles corresponded well with profiles of organic C density, depending on the biomass component (live coarse, dead coarse, or fine), depth, and whether the C was chemically labile or refractory (Fig. 6). Across marshes, total C density profiles were positively correlated with dead coarse and fine biomass (adj $r^2 = 0.25$, $p < 0.0001$). Labile C density was weakly related to biomass stocks (live and dead coarse: adj $r^2 = 0.05$, $p < 0.0001$), while all (live, dead, and fine) biomass stocks explained 28% of the variation in downcore refractory C densities (adj $r^2 = 0.28$, $p < 0.0001$). Live coarse biomass was the only significant predictor of labile C density in four of the six marshes (Table 4). In IB, no belowground biomass component was related to labile C density and in MR, labile C density was related to fine biomass (Table 4). In RC, labile C density was negatively related to live biomass, indicating that as live root biomass increased, labile C declined (Fig. 6). This is due to changes in the relationship between live biomass and labile C with depth. From the soil profiles, it is clear that labile C density mirrors live coarse biomass dynamics to the depth limit of the live root zone. Below the live rooting depth, labile C density tends to increase (RC, IB, and CC), likely associated with an increase in preservation of labile C, compaction and increased soil bulk density.

Refractory C density increased in-step with belowground biomass toward the surface in Barnegat Bay marshes, but is relatively uniform with depth regardless of biomass changes in Delaware Bay marshes (Fig. 6). Nevertheless, refractory C density in the Delaware Bay marshes was positively related to the amount of dead biomass (Table 4). In the Barnegat Bay, refractory C density was related to both live and dead biomass (Table 4). This suggests that the labile/refractory nature of the biomass produced may differ among the marshes and estuaries. While interesting relationships emerged for labile and refractory C densities and biomass components, some of the relationships were masked when examining total (labile + refractory) soil organic C densities, which were variably related to biomass components. Three marshes, IB, CC, and MR, had relatively strong soil C density-belowground biomass relationships while other marshes had weak or non-detectable relationships (RC, DV, and DN).

3.5.1. C accumulation and accretion rates

We found no relationship between rates of belowground ingrowth and longer-term labile and total C accumulation rates. Belowground turnover was weakly (adj $R^2 < 0.35$) negatively related to total organic and labile C accumulation, largely due to the positive relationship between live belowground biomass and labile C accumulation rates (Supplemental Figure B; see below). Percent mass remaining in belowground litterbags was, likewise, unrelated to C accumulation rates. However, across the two estuaries, there was a positive relationship between aboveground biomass and longer-term total organic and labile C accumulation (Fig. 7). Aboveground live biomass also explained 37% of the variation in ^{137}Cs-based accretion rates (adj $R^2 = 0.37$, $p = 0.0058$, data not shown), which was largely related to the effect of aboveground biomass on labile C accumulation rate. Aboveground live biomass explained 70% of the variation in labile C accumulation (Fig. 7).

Relationships between belowground biomass and C accumulation and accretion rates were estuary dependant. Total and live belowground biomass corresponded to the pattern of total organic C accumulation across marshes in Barnegat Bay, but not Delaware Bay (Fig. 8). When compared statistically, C accumulation and accretion rates were positively related to cumulative belowground biomass above the ^{137}Cs peak depth only for Barnegat Bay marshes (Fig. 9). Live coarse and fine biomass explained 86% of the variation in total C accumulation in Barnegat Bay marshes (Fig. 9). Live coarse biomass was positively related to labile C accumulation and fine biomass was positively related to refractory C accumulation rate (Fig. 9). Accretion rate did not scale with the amount of belowground biomass in Delaware Bay, but live and dead coarse biomass explained 78% of the variation in accretion rate in Barnegat Bay (Fig. 9).

4.0 Discussion

Our study illustrated significant relationships between plant biomass and soil C densities and C accumulation and accretion rates in *S. alterniflora* marshes. Geomorphic setting within and between estuaries played a large role in influencing these relationships. Marshes in the coastal lagoon had C accumulation and accretion rates that were positively related to both above- and belowground biomass. Aboveground biomass was positively related to labile C accumulation while belowground biomass was positively related to both labile and refractory C accumulation rates. Here, above- and belowground biomass was stimulated by less flooding and greater mineral sedimentation, which, in turn, increased rates of labile, refractory, and total C accumulation and accretion. In the coastal plain estuary, there was no relationship between belowground biomass and C accumulation or accretion rates. However, total and labile organic C accumulation rates were related to aboveground biomass, which was stimulated by greater flooding. As discussed below, the positive relationship between aboveground biomass and labile C accumulation rate across both estuaries may result from labile tissue production as a function of photosynthetic area and/or increased trapping and deposition of allochthonous labile C such as algal-derived C. Relatively high densities of labile C in the mineral-rich marshes, independent of belowground biomass, indicate potential allochthonous contributions and high preservation of labile C.

Contrary to our first two hypotheses, belowground growth and decay did not differ among marshes and were not related to longer-term rates of C accumulation. These predictions were based on the premise that the environmental conditions that lead to high rates of insitu production and greater C preservation, in turn, contribute to longer-term autochthonous C accumulation. In a previous study, C accumulation rates across these marshes were found to be strongly related to rates of mineral sedimentation (Unger et al. 2016). Root growth, however, was not related to longer-term rates of mineral sedimentation, nor related bulk densities, despite the potential for positive responses to higher soil bulk density and associated mineral nutrients (DeLaune et al. 1979). Subsurface hydrology seemed to be the dominant factor influencing root and rhizome growth rates with greater productivity in areas of greater average low tide depths. This relationship tended to be based on thresholds, where root growth was greater when average mean low water depth was at least 6 cm below the surface. When mean low water averaged above the marsh surface and the marsh surface was flooded for long durations and a higher percentage of the time (e.g., IB), no roots grew. *Spartina alterniflora* is highly adapted to flooded conditions, possessing both morphological adaptations such as aerenchyma to facilitate oxygen transport to flooded rhizomes and roots and physiological adaptations such as anaerobic metabolism (Teal and Kanwisher 1966; Mendelssohn et al., 1981). We observed that root growth of *S. alterniflora* was highly variable under moderate flooding conditions, potentially more affected by other abiotic conditions and/or the density of parental live root structures in close proximity. Others have also found that root productivity increases with less flooding, lower soil moisture and higher redox potentials (Blum 1993; Kirwan and Guntenspergen 2012). In addition to the main environmental drivers of root growth and C accumulation being different, the lack of a spatial relationship between root productivity and C accumulation rates may also be due to time step differences in short-term (~2 yr) process rates and processes integrated over a longer time period (~50 yr), and the potential for allochthonous C deposition across marshes.

Belowground decay did not vary much across a wide range of environmental conditions, and was not related to longer-term C accumulation rate. By using a composite of biomass collected across study sites for our decomposition study, we were able to examine the effect of abiotic factors on belowground decay. Our results indicated that the range of environmental conditions across marshes did not differentially affect belowground decay. This could be because the range of conditions in the subsurface soil in the marsh interior were not great enough to illicit a strong effect. With respect to hydrology, however, several studies have shown that decay rates are variable in or insensitive to different flooding regimes and redox potentials (Valiela et al., 1984; Blum 1993; Kirwan et al., 2013). The loss of organic matter reaching similar asymptotes of dry mass across our study sites suggests that the amount of recalcitrant tissue was more influential than environmental differences. While both labile polysaccharides and refractory lignin can be leached during initial decay (Benner et al. 1986; Moran and Hodson 1990), enrichment of recalcitrant tissues in the latter stages of decay slows decomposition, particularly under anaerobic conditions. We used a composite mix of live and dead large organic material in a ratio of 1:3, which experienced rapid initial decomposition, likely the decay of labile live and recently dead tissues, followed by an asymptotic decline in loss of organic matter to an average of 59% dry mass remaining. This percentage corresponds well with the 55% of roots and rhizomes remaining following 18 months in a Sapelo Island, GA salt marsh (Benner et al., 1991). Lignocellulose content in root and rhizome biomass of short-form *S. alterniflora* is approximately 79.5% (Hodson et al., 1984). Though relatively slow to decay under anaerobic conditions, the cellulosic portion undergoes higher rates of mineralization than lignin, which comprises approximately 19.3% in roots and rhizomes (Hodson et al., 1984). Lignin components can continue to be lost under anaerobic conditions (Benner et al. 1991); however, the decay of recalcitrant soil organic matter can also be relatively insensitive to flooding and subtle changes in redox potentials (Mueller et al. 2016). In the present study, we used a composite of root and rhizome samples collected across our study sites, and therefore, site differences in lability of biomass was not tested in this study, which may have implications for spatial variability in soil C storage.

Belowground turnover rates of *S. alterniflora* were within the range found in other studies (0.17 – 0.71 yr^{-1}; Schubauer and Hopkinson 1984), despite much lower productivity rates inherent to the ingrowth technique in the present study. We found a significant but variable negative relationship between belowground turnover and total organic and labile C accumulation rates. This finding was largely due to the positive relationship between live coarse biomass and labile C accumulation rate. With rates of root productivity being equal, an increase in live biomass lowers the turnover rate. While turnover explained <35% of the variation in C accumulation rates across estuaries, biomass components (above- and belowground) explained 39 – 86% of the variation in soil C accumulation rates.

Rates of soil C accumulation and accretion were strongly related to *S. alterniflora* biomass. Aboveground live biomass was positively related to organic C accumulation rate across estuaries, primarily though the strong relationship with labile C accumulation rate. Mechanisms of aboveground live biomass influencing labile soil C include the direct input of aboveground litter to the soil. For *S. alterniflora* much of the aboveground litter is subject to decay and mechanical breakdown by tidal action (Teal 1962), and therefore, little of the aboveground litter of *S. alterniflora* in these temperate marshes is thought to be incorporated into the marsh soil. The standing live aboveground biomass, however, represents both photosynthetic capacity and growing conditions, which may directly affect the production of labile exudates and new labile tissues belowground. Additionally, aboveground shoots influence surface deposition and accumulation through the direct capture of particles on plant stems and the indirect reduction of flow velocity inducing sediment settling (Stumpf 1983; Leonard and Luther 1995). This has been illustrated for fertilized and unfertilized *S. alterniflora* plots, where aboveground biomass was three times greater and surface accretion rate was 2 mm/yr greater in response to fertilization (Morris and Bradley 1999; Morris et al. 2002). The higher accretion rate was accounted for by more efficient trapping of sediments (Mudd et al., 2010). Therefore, both labile live plant tissues and labile organic C associated with sediment may be enhanced with greater aboveground biomass. This finding supports other studies showing positive relationships between aboveground biomass and soil microbial processes, including the decomposition of recalcitrant soil organic matter, which was hypothesized to be due to greater labile C inputs (substrate-induced priming) and/or greater rhizosphere oxygenation (O_2-induced priming; Mueller et al. 2016). Our data suggest that aboveground biomass may increase soil C accumulation directly through the inputs of labile C and positive bio-physical feedbacks for sedimentation, which increases labile C deposition, burial, and preservation. Relationships among aboveground plant biomass, labile and total C accumulation rate, and mineral sedimentation rate indicate positive feedbacks among these processes (Unger et al. 2016; present study).

While aboveground biomass was positively related to organic and labile C accumulation rate across estuaries, aboveground biomass response to flooding was estuary-dependent. In the coastal plain estuary, aboveground biomass increased with a higher mean high tide level, whereas in the coastal lagoon, aboveground biomass declined with higher mean high water depth. In the coastal lagoon, stem density increased with greater drainage. With all other conditions being equal, plant biomass of *S. alterniflora* has a parabolic relationship with elevation relative to mean sea level (Morris et al. 2002). Above- and below an optimum elevation, biomass declines. Our study of marshes in different geomorphic settings illustrates how environmental conditions in estuaries can illicit differential responses to individual environmental parameters. In the coastal lagoon, a combination of less flooding and greater mineral sedimentation rates promoted greater aboveground (and belowground) biomass. Lower tolerance to flooding in the coastal lagoon marshes as compared to the coastal plain marshes is likely due to greater soil organic matter content, lower redox potential, lower mineral sediment and nutrient availability, and higher sulfide concentrations (Bradley and Morris 1990; Reddy and DeLaune 2008). Differential flooding effects on aboveground biomass driven broadly by estuary geomorphology can partially explain spatial variation in labile and total organic C accumulation rate across estuaries, which was linearly and positively related to aboveground biomass.

Belowground biomass contributes directly to soil organic matter and, in this study, was a good predictor of soil C accumulation rates, but only in the coastal lagoon marshes. This indicates that as geomorphic conditions change such as with an increase in mineral sedimentation rates, belowground biomass can become uncoupled to soil C accumulation and accretion rates. In the coastal lagoon marshes, live roots and rhizomes were concentrated in the top 30 cm depths, likely associated with a combination of high water table and high soil organic matter leading to low redox potentials and high sulfide concentrations at depth (DeLaune et al. 1983b; Saunders et al. 2006). In contrast, in the coastal plain estuary, live rooting depths were variable but often extending to 40 – 50 cm depth. Greater neap tide drainage (data not shown), lower soil organic matter content throughout the soil depth profile, and higher redox potentials likely accounted for the lower live rooting depths. Across the coastal lagoon marshes, labile C accumulation rate increased as live belowground biomass increased. Fine biomass had a positive relationship with the rate of refractory C accumulation, and refractory C density was relatively high just below the marsh surface. Both of these live and fine biomass components, therefore, were positively related to the total C accumulation rate. Accretion in these marshes was positively associated with the live and dead coarse biomass, likely due to the high porosity associated with stem bases, rhizomes, macroorganic matter, and surrounding soil. In the coastal plain estuary, C accumulation and accretion rates were not significantly related to belowground biomass. It may have been presumed that marshes with higher tidal ranges and higher rates of mineral sedimentation would have greater stocks of belowground biomass. In these marshes, mineral sediment accumulation rates ranged from less than 500 to over 4000 g/m^2/yr, yet belowground biomass did not vary much along this gradient. At similar rates of mineral sedimentation, belowground live coarse biomass was over 1000 g/m^2 lower in marshes of the coastal plain estuary as compared to the coastal lagoon, despite a greater live rooting depth. This may be associated with higher soil redox potentials and a lower requirement for rhizome photosynthate storage (Gallagher and Kibby 1981) in the coastal plain marshes. High belowground biomass is typically found in marsh areas with lower redox potential (Gallagher and Plumley 1979; Dame and Kenny 1986 and references therein). This is hypothesized to be due to greater investment in belowground production (Hopkinson and Schubauer 1984) and less photosynthate transfer from underground rhizomes throughout the year, which results in lower aboveground biomass and higher belowground biomass in short-form interior populations of *S. alterniflora* than tall-form populations growing along creekbank (Gallagher and Kibby 1981). Differences among estuarine settings and soil organic matter contents may also drive spatial patterns in belowground biomass and allocation. At higher sedimentation rates found in the coastal plain estuary, fine belowground biomass, which was a significant predictor of refractory C accumulation in the coastal lagoon, declined significantly. In the marsh with the highest rates of mineral sedimentation, and labile and total organic C accumulation (MR), the lower quantity of fine biomass may be due to a shorter time period allowed for growth and accumulation. The labile nature of fine biomass here suggests preservation of labile fractions of fine biomass. With relatively low total belowground biomass, burial and small particle (< 1 mm) accumulation support high C accumulation and accretion rates. The mechanism of fine organic matter loss or limited input with greater mineral sedimentation rates is unclear, particularly when these marshes have the highest rates of labile and total organic C accumulation in our study (Unger et al., 2016). In marshes with the highest rates of C accumulation, labile C density, in particular, remained high when biomass stocks were low. High accumulation rates in marshes with low biomass seem to be maintained by a combination of high live root biomass at depth, high allochthonous C deposition, effective preservation of labile C, and high burial rates.

Our findings also provided insight as to the relative inputs of local plant-derived versus non-plant derived (e.g., edaphic algae) and allochthonous C to the labile and refractory C pools. We found significant relationships between belowground biomass stocks and soil C density. The significance and strength of these relationships depended on geomorphic setting, anatomical part, and the labile or refractory nature of the soil C. Comparisons of biomass and C density profiles to profiles of mineral sediment volume (Unger et al. 2016), yields several important insights on how plants and sediments interact to influence soil C. Labile C density was related to live belowground biomass in most marshes. Below the live root zone and in marshes with high sedimentation rates, labile C preservation was high. In marshes where mineral sedimentation was high, labile soil C became more important, regardless of the belowground biomass pools. Labile C density was weakly related to biomass stocks, and despite, significant relationships between live root biomass and labile C accumulation in the root zone above the ^{137}Cs peak depth in Barnegat Bay, labile C density was often higher at deeper depths with lower biomass. This suggests that labile C density, while significantly related to live root biomass at the surface is being physio-chemically preserved at depth regardless of the source. Associations with iron oxide minerals seem to be particularly important for long-term organic C preservation (Kögel-Knabner et al. 2008). Refractory soil C density was more strongly related to belowground biomass across all marshes, indicating, as expected, that plant biomass is the primary contributor to refractory soil C. In the highly organic marshes of the coastal lagoon, biomass played a strong role in increasing refractory C in the upper soil column with both live and dead biomass related to refractory C density. Soil profiles indicated that in marshes with a concentration of biomass just below the surface and where mineral sedimentation was low, refractory C dominated the soil C pool. The relationship between live and dead biomass and refractory C in the coastal lagoon marshes, suggests that the tissue quality may be more refractory than in marshes of the coastal plain estuary, where only dead biomass was associated with refractory soil C density. This finding supports the hypothesis that under constrained growing conditions (e.g., high salinity, high inundation, low tidal range), more energy may be invested into the production of recalcitrant tissues such as lignin, cellulose and hemicellulose (Knops et al. 2007). This is also supported by marshes with higher live and total biomass (e.g., DN vs IB) yet much lower refractory C densities. In the coastal plain estuary, refractory C was associated with dead biomass and, in most sites, the broken down fine biomass.

Geomorphology played a large role in influencing the relative importance and contribution of plant biomass to soil C and marsh accretion rate. Geomorphic conditions of high sediment availability and larger tidal range, which can mobilize and distribute sediments in the main channel and creeks of the coastal plain estuary work in concert to promote C accumulation and accretion. Estuarine dynamics in the coastal lagoon are characterized by localized sediment supplies and limited tidal energy to resuspend, transport and deposit sediments, and therefore, the marshes are highly dependent on organic matter production for accretion. Within this system, a high sediment supply and high elevation promoted a positive feedback between above- and belowground biomass and elevation. Because of localized sediment supplies (e.g., CC) and other geomorphic differences, there was no correlation between hydrology and longer-term sedimentation rates even over longer time periods (present study, Boyd et al. 2017). Importantly, while studies suggest the vulnerability of microtidal marshes in coastal lagoons (Reed et al., 2008; Kirwan & Guntenspergen 2010; Ganju et al., 2017), we illustrate the importance of localized sources of sediments as being the key to their survival through the positive feedback on live and dead coarse and fine root biomass, and organic matter and C accumulation rates. Continuous standing water, enlargement of interior ponds, and loss of aboveground vegetation are all signs of marsh deterioration. At IB, two of the sampling locations had permanent shallow water between ditches and had lost the aboveground biomass. The remnants of former vegetation was evident belowground, where significant quantities of live stem bases, roots and rhizomes were present to below 28 cm depth at least three years after aboveground biomass was permanently lost. Comparison of dynamics between individual marshes can also highlight important geomorphic effects on plant biomass. RC in Barnegat Bay and DN in Delaware Bay experienced comparable hydrology and salinity in the marsh interior (Table 1). Yet, estuarine tidal range averaged approximately 0.3 m and 1.5 m, in RC and DN respectively (USGS gage 01408167 and 01411435, respectively) and longer-term rates of mineral sedimentation were an order of magnitude larger, and soil bulk density was three times greater in DN than in RC (Boyd et al., 2017; Unger et al., 2016). So, despite a similar hydrology in the marsh interior, tidal range in the estuary and creeks and sediment supply were much greater in DN than in RC. Aboveground biomass averaged two times higher in DN than RC. Belowground live coarse biomass averaged 2456 and 721 g/m^2 in DN and RC, respectively and dead coarse biomass averaged 1063 and 280 g/m^2 in DN and RC, respectively. Live rooting depth was also significantly greater in DN (46 cm) as compared to RC (19 cm). In contrast, CC in Barnegat Bay and DV in Delaware Bay, two of highest elevation marshes in the two estuaries experienced comparable hydrology. Salinity was significantly higher at CC than DV, but soil organic matter, bulk density and mineral sedimentation rate did not significantly differ. With both hydrology and sedimentation rates being within range of each other, these two marshes in very different geomorphic settings had similar plant biomass and organic C accumulation rates. Biomass profiles were also similar between marshes with the exception of greater fine organic matter in CC, particularly between 4 and 20 cm depth.

4.6 Conclusions

The fate of low-lying salt marshes as sea-level rises depends, in part, on their ability to accumulate organic matter and to trap sediments. Sediment supply is also a major factor and may be most important in influencing the biophysical processes that promote accretion and soil C accumulation. Our study illustrates that above- and belowground biomass dynamics in sediment-limited *S. alterniflora* marshes are strongly related to rates of mineral sedimentation, which promotes positive feedbacks between biomass, soil C accumulation, and elevation. Soil C accumulation and accretion rates were strongly related to biomass fractions in the coastal lagoon estuary, where all biomass components were positively related to refractory C. In marshes where sediments were more readily available, total belowground biomass and fine biomass declined with increasing rate of mineral sedimentation and lower salinity. In the coastal plain estuary, aboveground biomass was a significant predictor of labile C accumulation rate while belowground biomass did not scale with C accumulation and accretion. Overall, our study shows that marshes in geomorphic settings with limited sediment supply and delivery, have lower rates of organic C accumulation and accretion, which are related to and limited by plant biomass. Plant biomass can be further stimulated by additional sediment input. In geomorphic settings where sediment supply and deposition rates are high, a strong positive relationship between aboveground biomass and labile C accumulation can promote high total C accumulation and accretion rates.

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Table 1: Environmental conditions of interior *Spartina alterniflora*-dominated marshes in two estuaries of the Mid-Atlantic, USA. Values are means ± standard errors (n = 2 for hydrologic parameters and n = 3 for soil and elevation and soil parameters). Parameter values across marshes represented by different letters are significantly different based on nested analysis of variance ($p < 0.05$).

	Barnegat Bay			Delaware Bay		
Environmental parameter	**RC**	**IB**	**CC**	**DV**	**MR**	**DN**
Distance to tidal channel (m)	13 ± 5^{a}	11 ± 3^{a}	19 ± 3^{a}	56 ± 16^{b}	27 ± 16^{b}	62 ± 34^{b}
Marsh elevation (cm, NAVD88)	-2.3 ± 6.4	11.8 ± 1.9	29.1 ± 1.0	71.9 ± 7.7	51.5 ± 16.3	66.8 ± 7.7
Tidal range (cm)	13.4 ± 0.6^{bc}	7.2 ± 0.5^{cd}	5.1 ± 0.1^{d}	10.9 ± 2.2^{bcd}	22.2 ± 0.2^{a}	17.0 ± 1.9^{ab}
Mean high water relative to marsh surface (cm)	12.6 ± 1.2^{ab}	10.3 ± 0.7^{bc}	-3.3 ± 0.8^{d}	3.4 ± 3.7^{cd}	21.2 ± 1.8^{a}	15.6 ± 1.2^{ab}
Mean water level relative to marsh surface (cm)	3.5 ± 0.7	5.5 ± 1.0	-6.5 ± 0.7	-4.9 ± 1.9	2.7 ± 0.3	2.8 ± 0.5
Mean low water relative to marsh surface (cm)	-0.8 ± 1.0^{a}	3.1 ± 1.1^{a}	-8.5 ± 0.7^{b}	-7.4 ± 1.6^{b}	-1.0 ± 2.0^{a}	-1.4 ± 0.7^{a}
% time flooded	66 ± 4^{ab}	86 ± 1^{a}	6 ± 1^{c}	11 ± 4^{c}	40 ± 1^{b}	68 ± 5^{ab}
# flooding events/yr	304 ± 21^{ab}	24 ± 1^{c}	113 ± 16^{bc}	205 ± 51^{bc}	455 ± 55^{a}	176 ± 78^{bc}
Avg duration of flood (hr)	20 ± 2^{b}	324 ± 14^{a}	4 ± 1^{b}	15 ± 7^{b}	7 ± 1^{b}	44 ± 14^{b}
Salinity	20.6 ± 0.1^{bc}	30.4 ± 4.0^{ab}	38.8 ± 0.8^{a}	17.1 ± 1.0^{c}	7.4 ± 1.0^{c}	13.5 ± 2.1^{c}
Soil nitrogen (%)	1.6 ± 0.2^{a}	1.5 ± 0.1^{a}	0.8 ± 0.1^{b}	0.7 ± 0.2^{b}	0.5 ± 0.1^{b}	0.5 ± 0.1^{b}
Soil organic matter (%)	39.7 ± 1.3^{a}	39.4 ± 0.3^{a}	23.4 ± 1.4^{ab}	32.4 ± 9.1^{a}	14.1 ± 0.8^{b}	27.8 ± 5.5^{ab}
Soil bulk density (g/cm3)	0.14 ± 0.01^{c}	0.15 ± 0.02^{bc}	0.29 ± 0.01^{abc}	0.34 ± 0.07^{ab}	0.52 ± 0.04^{a}	0.39 ± 0.03^{a}
Long-term mineral sedimentation rate (g/m2/yr)*	147 ± 22^{d}	168 ± 19^{cd}	626 ± 45^{bc}	1237 ± 576^{ab}	4126 ± 74^{a}	1568 ± 279^{ab}

Table 3: Vegetation structure in *Spartina alterniflora* salt marshes in two Mid-Atlantic estuaries (n = 3, ± standard error).

	BB			DB		
	RC	IB	CC	DV	MR	DN
Stem density (#/m^2)	509 ± 132	493 ± 440	3276 ± 615	1234 ± 382	612 ± 174	1675 ± 53
Average height (cm)	17 ± 3^{ab}	14 ± 2^{b}	13 ± 2^{b}	13 ± 1^{b}	26 ± 1^{a}	12 ± 1^{b}
Aboveground biomass (g/m^2)						
live	112 ± 41^{b}	93 ± 88^{b}	362 ± 38^{ab}	234 ± 79^{b}	664 ± 90^{a}	353 ± 35^{ab}
dead	338 ± 129	91 ± 85	317 ± 97	33 ± 8	122 ± 38	100 ± 10
95% live rooting depth (cm)	19 ± 1^{c}	20 ± 1^{c}	18 ± 1^{c}	23 ± 1^{bc}	30 ± 2^{b}	46 ± 6^{a}
Belowground biomass (g/m^2)						
to ^{137}Cs-peak						
live coarse	505 ± 21	1225 ± 200	2675 ± 764	1842 ± 7	2055 ± 700	1973 ± 201
dead coarse	138 ± 91	131 ± 69	310 ± 180	341 ± 191	985 ± 124	708 ± 469
fine	1498 ± 612^{b}	3676 ± 186^{ab}	4326 ± 258^{a}	3398 ± 438^{ab}	2484 ± 532^{ab}	3527 ± 448^{ab}
to 50 cm depth						
live coarse	721 ± 81	1568 ± 222	2839 ± 758	1931 ± 34	2055 ± 700	2456 ± 305
dead coarse	280 ± 73	952 ± 231	1262 ± 125	690 ± 106	1010 ± 111	1063 ± 494
fine	4406 ± 1280^{ab}	8192 ± 2005^{ab}	8999 ± 948^{a}	6599 ± 1654^{ab}	2517 ± 565^{b}	5626 ± 661^{ab}
Live BG:AB ratio	8 ± 3	62 ± 56	8 ± 3	12 ± 5	4 ± 2	7 ± 1

Table 4: Results of regression analysis of the relationship between belowground biomass and labile, refractory, and total soil organic C density in marshes of a coastal lagoon (Barnegat Bay) and a coastal plain estuary (Delaware Bay). Shown are adjusted r-square values.

	Barnegat Bay			Delaware Bay		
C density fraction	RC	IB	CC	DV	MR	DN
labile	live coarse: 0.39**	*n.s.*	live coarse: 0.54**	live coarse: 0.26*	fine: 0.42**	live coarse: 0.23**
refractory	live coarse and fine: 0.55**	live and dead coarse: 0.66**	live and dead coarse: 0.63**	fine: 0.17*	dead coarse and fine: 0.46**	dead coarse: 0.17*
total	*n.s.*	ALL: 0.40**	live coarse and fine: 0.68**	live coarse and fine: 0.18*	fine: 0.42**	fine: 0.03*

*$p < 0.05$
**$p < 0.0001$

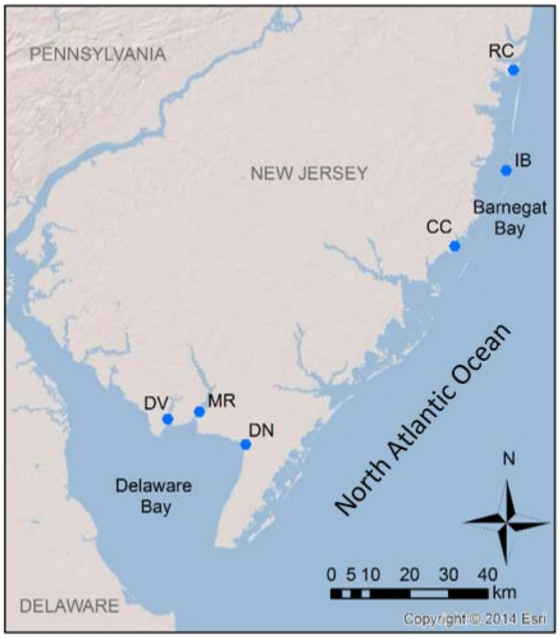

Figure 1: Study locations in Barnegat Bay and Delaware Bay along the mid-Atlantic coast, U.S.

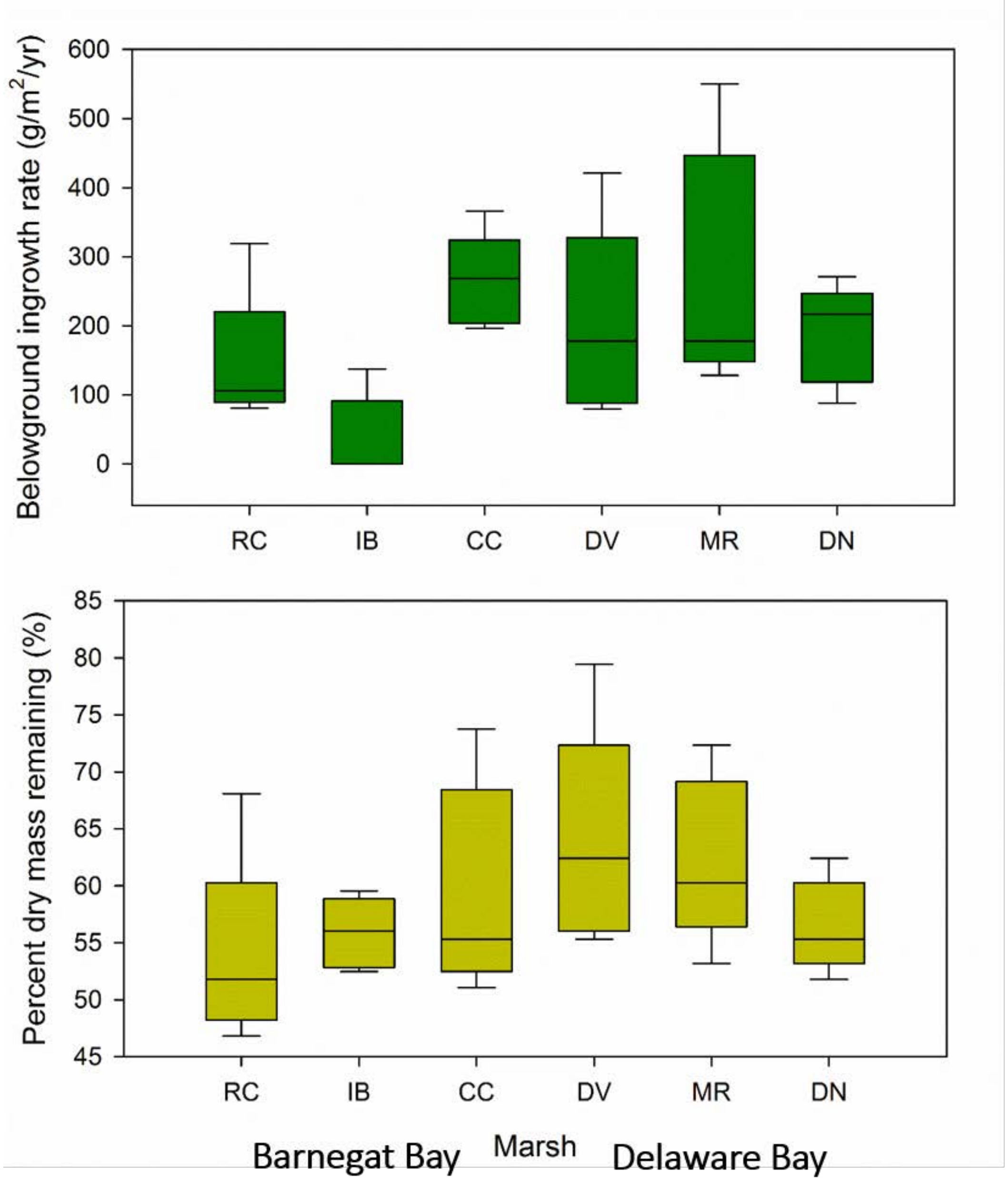

Figure 2: Belowground ingrowth rate (upper) and percent mass remaining in belowground litterbags (lower) over a 20 month period in salt marshes of two mid-Atlantic estuaries (n = 5, ± standard error).

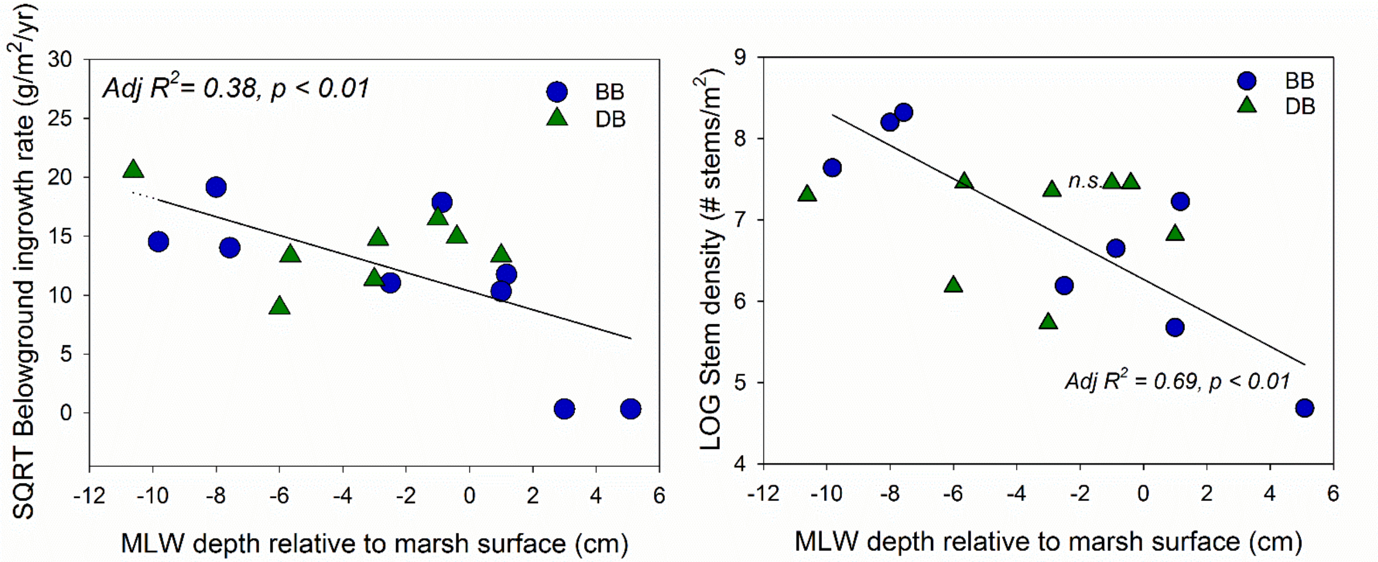

Figure 3: Relationships between belowground ingrowth and mean low water (MLW) relative to the marsh surface (left) and stem density and MLW (right). Blue dots and green triangles refer to data collected in Barnegat Bay (BB) and Delaware Bay (DB), respectively.

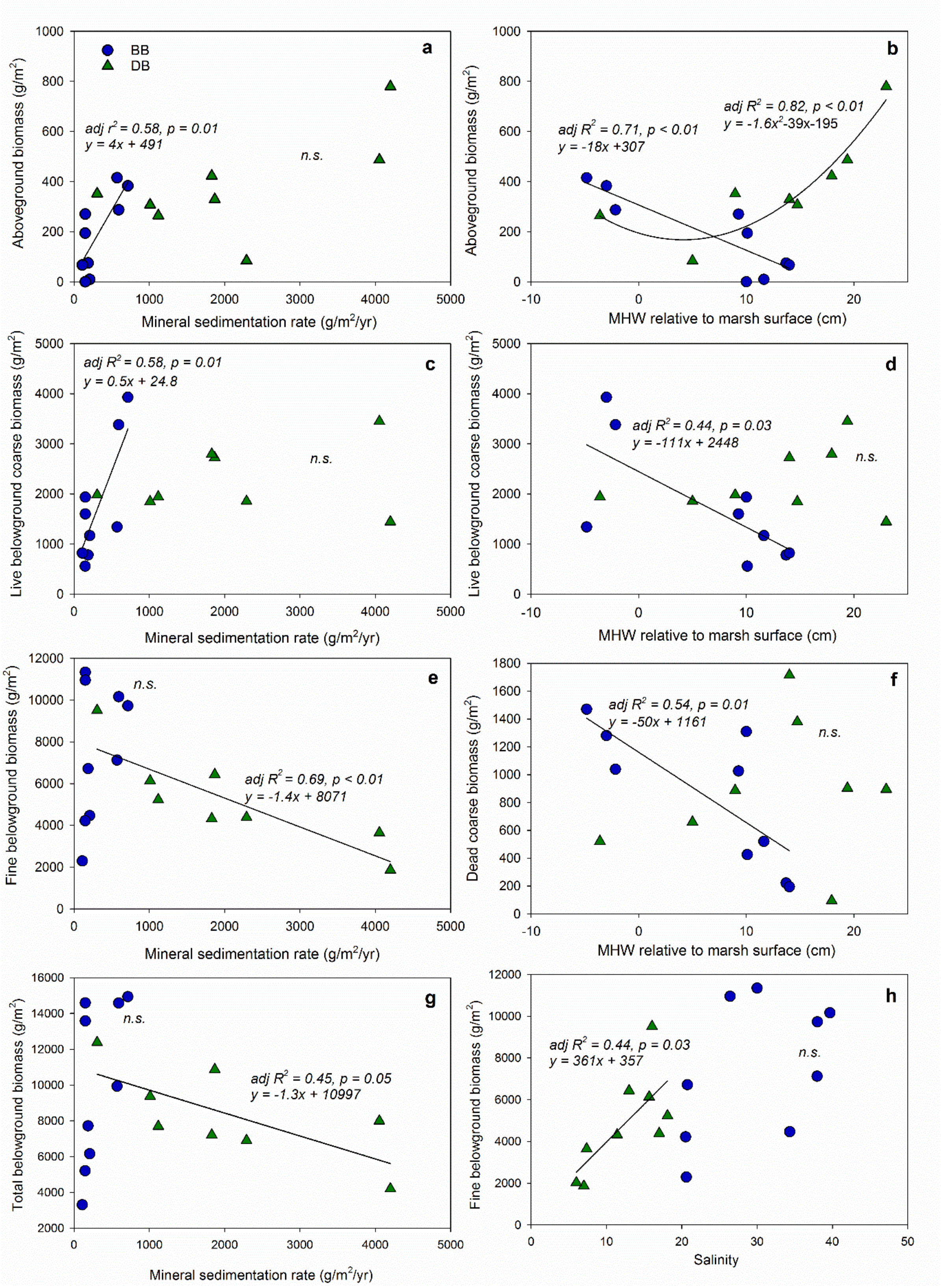

Figure 4: Relationships between vegetation structure and environmental parameters. For these analyses, belowground biomass to 50-cm depth was used. Mineral sedimentation rates were calculated using ^{137}Cs-dating, and therefore, are average rates over the last 50 years (Boyd et al. 2017). Blue dots and green triangles refer to data collected in Barnegat Bay (BB) and Delaware Bay (DB), respectively, which were analysed separately. Both significant and non-significant (n.s.) relationships are shown.

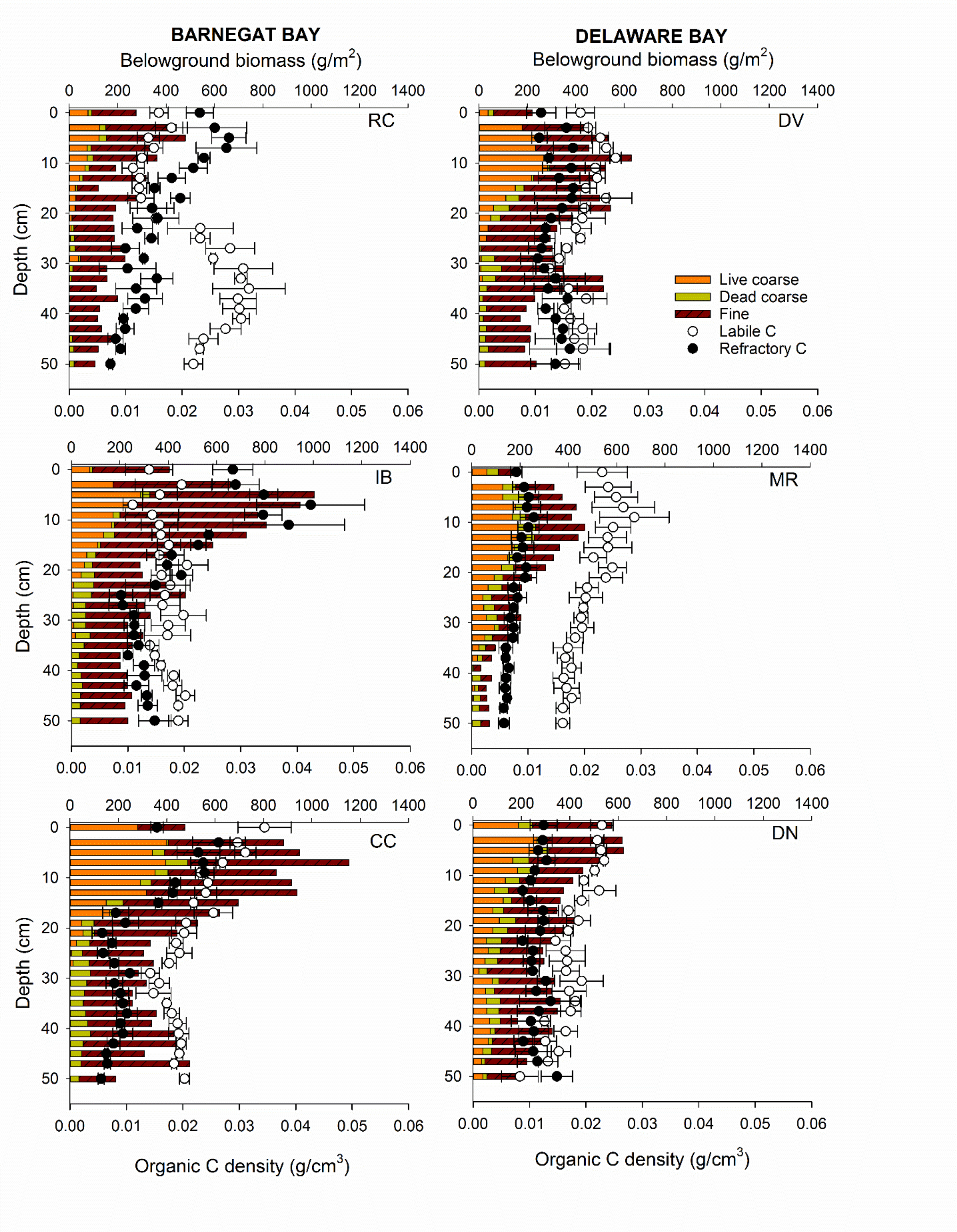

Figure 5: Belowground biomass and labile and refractory organic C density profiles in marshes of two Mid-Atlantic estuaries. Biomass data are means (standard errors not shown). C density data previously reported

in Unger et al., 2016.

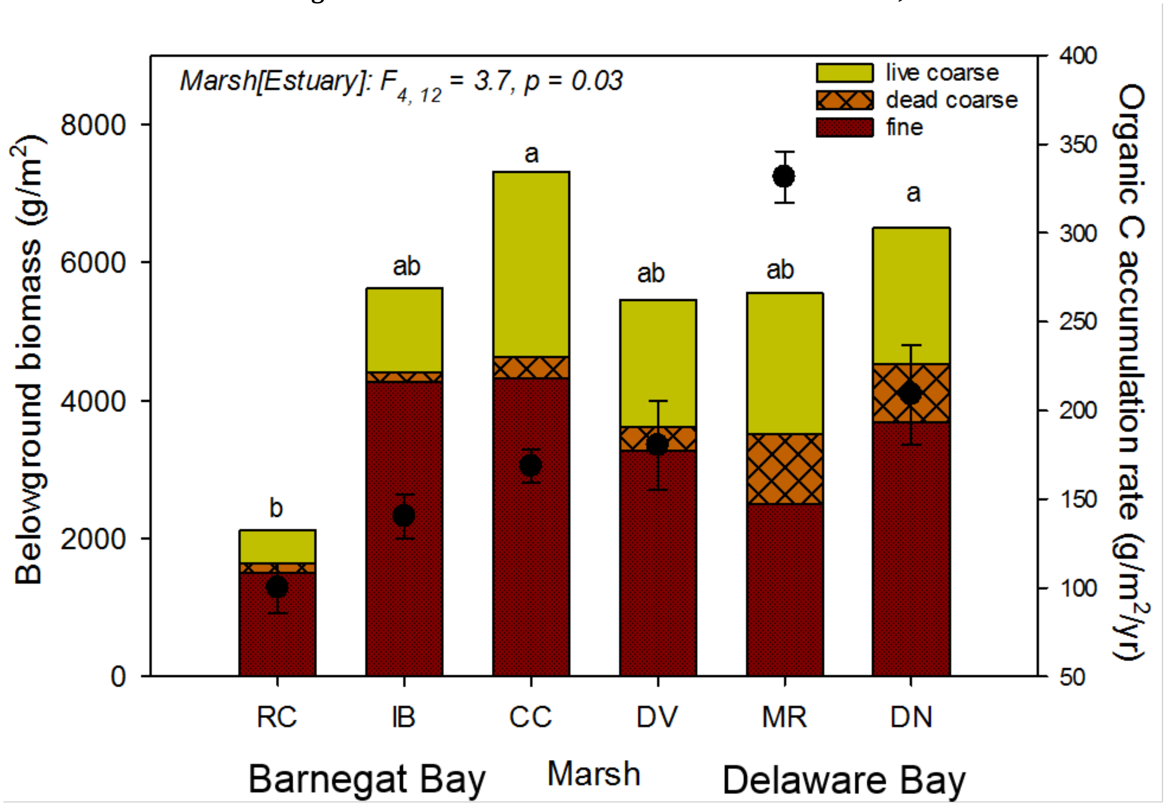

Figure 6: Belowground biomass (scaled on left-axis) and organic C accumulation rate (scaled on right axis; previously reported in Unger et al., 2016) in marshes of two Mid-Atlantic estuaries. Belowground biomass and C accumulation are relative to the ^{137}Cs peak depth. Statistics for total belowground are shown and letters represent differences ($p < 0.05$). Standard errors are shown in Table 2.

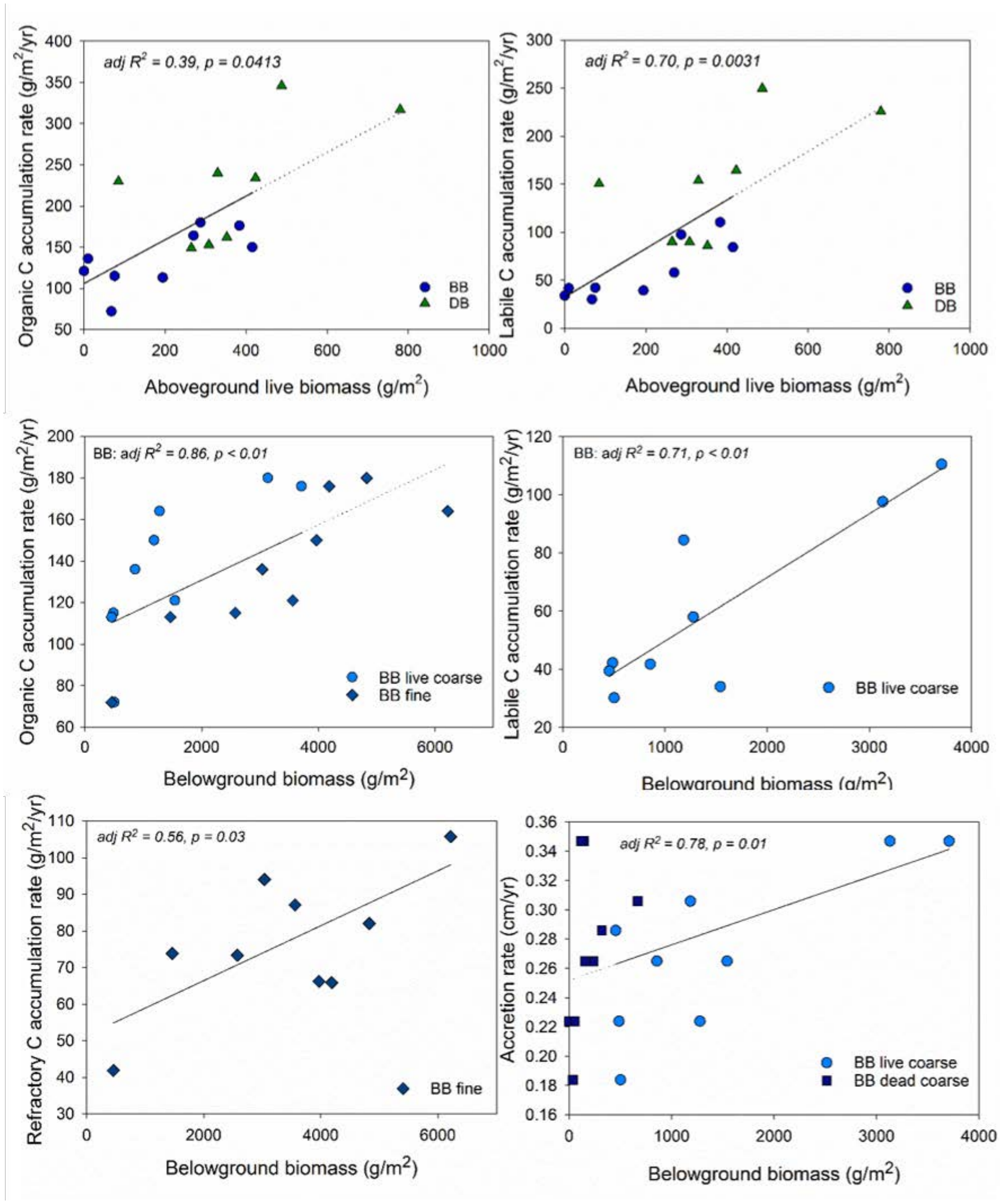

Figure 7: Relationship between *Spartina alterniflora* biomass and organic C (total, labile and refractory) accumulation and accretion rate in marshes of Barnegat Bay (BB) and Delaware Bay (DB). Only significant ($p < 0.05$) relationships are shown.