



# 1 Geomorphic influences on the contribution of vegetation to soil 2 C accumulation and accretion in *Spartina alterniflora* marshes

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7 **Abstract.** Environmental conditions have a strong influence on rates plant productivity and decomposition. In salt  
8 marshes, hydrology and salinity are important regulators of plant and soil processes, which, in turn, can influence the  
9 rate at which marsh ecosystems accumulate C and adjust to sea-level rise. For this study, we examined the influence  
10 of multivariate environmental conditions on belowground ingrowth (roots + rhizomes), decomposition and biomass  
11 in marshes dominated by *Spartina alterniflora* across two estuaries and a range of geomorphic settings. Secondly, we  
12 examined the influence of belowground plant biomass to soil C density, and C (labile and refractory) accumulation  
13 and accretion rates. Study locations occupied a full range of tidal elevations from below mean low water to above  
14 mean high water. Salinities ranged from 7 – 40, and soil properties also varied across marshes. While many of the  
15 environmental parameters were correlated across marshes, belowground ingrowth of *S. alterniflora* was negatively  
16 influenced by mean low water height, such that root growth increased with more drainage. Belowground decay rate  
17 increased with increasing salinity, but ultimately the percent of mass remaining was similar across marshes, averaging  
18  $59 \pm 1\%$ . Above- and belowground biomass dynamics were estuary-dependent. In the coastal lagoon estuary, less  
19 flooding and a higher sedimentation rate favored above- and belowground biomass, which, in turn, increased soil C  
20 accumulation and accretion rates. Biomass dynamics in the coastal plain estuary, for the most part, were unrelated to  
21 environmental predictor variables, and had little influence on the accumulation of soil C or accretion rate. These  
22 findings indicate that mineral sedimentation is of utmost importance for promoting belowground biomass and soil C  
23 accumulation in sediment-limited systems while in minerogenic systems, belowground biomass may not scale with C  
24 accumulation and accretion, which may be influenced more by smaller submillimetre-sized C particles.

25

## 26 1 Introduction

27 Salt marshes are among the most productive ecosystems on Earth where over half of the annual plant biomass  
28 produced can occur belowground in the form of rhizomes and roots (Valiela et al., 1976; Gallagher and Plumley 1979;  
29 Schubauer and Hopkinson 1984). Belowground biomass of perennial marsh grasses, sedges and rushes is considered  
30 a major contributor to soil organic matter and organic carbon (C) as it accumulates and undergoes relatively slow  
31 decomposition. The preservation of organic matter in marsh soil is promoted by both anaerobic conditions and  
32 refractory C compounds of plant tissues, primarily associated with cell walls (Valiela et al., 1979; Wilson et al., 1986).  
33 However, the same anaerobic conditions that can slow decomposition may constrain the production of roots and  
34 rhizomes with low oxygen and high sulfide concentrations. Hydrology, therefore, is predicted to be of primary  
35 importance influencing root growth and belowground biomass. Root growth of *Spartina alterniflora*, a common low  
36 marsh species along much of the Atlantic and Gulf coasts of the U.S., into new substrate (i.e., ingrowth) has been  
37 shown to be lower in marsh areas with lower redox potential and higher soil moisture (Blum 1993). Interestingly,  
38 these same low redox conditions that limit root ingrowth, can promote high belowground biomass (Gallagher and  
39 Plumley 1979; Dame and Kenny 1986 and references therein). This is hypothesized to be due to greater investment  
40 in belowground production (Hopkinson and Schubauer 1984) and less photosynthate transfer from underground  
41 rhizomes throughout the year, which results in lower aboveground biomass and higher belowground biomass in short-  
42 form interior populations of *S. alterniflora* than tall-form populations growing along creekbank (Gallagher and Kibby



43 1981). While hydrology can play an important role in biomass production, organic matter decay rates have been  
44 shown to be more variable and less related to flooding dynamics (Blum 1993).

45

46 Ultimately, the balance of plant productivity and organic matter preservation contributes to peat formation and soil C  
47 accumulation, which is also highly dependent on mineral sedimentation, both for promoting conditions that enhance  
48 plant productivity relative to decay and contributing directly to the burial and preservation of organic matter and  
49 accretion (DeLaune et al., 1990a; Mendelssohn and Kuhn 2003; Elsey-Quirk et al., 2011; Kirwan and Megonigal  
50 2013; Boyd et al., 2017). Positive relationships between organic matter accumulation, mineral sedimentation, and  
51 accretion are well established with organic matter contributing disproportionately more to soil volume (reviewed in  
52 Turner et al., 2000; Neubauer 2008). However, there have been few empirical studies on the direct contribution of  
53 plant productivity and biomass to soil C and accretion in natural marshes. A greenhouse experiment illustrated that  
54 flooding stimulated surface root growth of a high marsh grass, *Spartina patens*, which was proposed to be a mechanism  
55 by which flooding enhanced organic matter accumulation and accretion (Nyman et al., 2006). In mangrove forests,  
56 the contribution of root production to vertical soil expansion was highly site-specific, with a stronger positive  
57 relationship in peat soils as compared to organic and mineral soil types (Cahoon et al., 2006). These studies suggest  
58 that environmental conditions and soil organic matter content play important roles in the relationship between plant  
59 roots and accretion. In salt marshes, localized environmental conditions such as hydrology, salinity, sediment  
60 availability and soil properties are predicted to play a key role in influencing relationships between biotic processes  
61 and rates of C accumulation and accretion. Determining direct relationships between abiotic factors and vegetation  
62 response across natural systems, however, is challenged by inherent correlations and collinearities. Yet, understanding  
63 relationships across natural systems is extremely important as multiple abiotic conditions will determine the ability of  
64 marshes to accumulate and store C and adjust their elevation relative to sea-level.

65

66 While all marshes were formed in low-energy coastal environments, they occur in a wide range geomorphic settings  
67 ranging from back barrier to deltaic estuaries. Different landscape and coastal processes have influenced their origin  
68 and development (Orson et al., 1985) and environmental factors such as tidal range, sediment supply, salinity, and  
69 nutrient loads may all differ both within and among these estuarine types. It is these interacting geomorphological  
70 characteristics that can affect marsh vulnerability to sea level rise and/or erosion. For example, microtidal marshes in  
71 coastal lagoons are considered vulnerable to submergence with accelerating sea-level rise primarily due to limited  
72 sediment supply and tidal hydrology that may be too weak or infrequent for sufficient sediment transport and  
73 deposition (Reed et al., 2008; Kirwan & Guntenspergen 2010; Ganju et al., 2017). Accretion in these systems depend  
74 primarily on organic matter produced by marsh macrophytes, though our understanding of how geomorphology  
75 influences plant and decay processes and their contribution to biomass structure and longer-term C accumulation and  
76 accretion rates is relatively limited, and largely based on models. Accretion and soil C accumulation can be influenced  
77 by sediment and plant litter deposition, erosion, compaction, as well as root growth and decomposition. Short-term  
78 marsh surface accretion rates ( $\leq 5$  yrs) have been shown to be strongly related to allochthonous sediment inputs rather  
79 than autochthonous plant production (Cahoon et al., 1994; 1996; Saintilan et al., 2013), while C from root biomass



80 may be more important at depth and over time (Saintilan et al., 2013). Given the potential importance of belowground  
81 plant and organic matter dynamics to soil structure in the marsh interior where sedimentation may be lower, and where  
82 conversion to open water due to sea-level rise may be most prevalent (e.g., DeLaune et al., 1994), identifying  
83 environmental constraints on growth and decay and relationships to C accumulation and accretion will be important  
84 for informing marsh management and restoration.

85

86 Though geomorphic influences on the relationship between biotic processes and soil C and accretion are not well  
87 constrained in natural marshes, geomorphic differences in sediment availability has been shown to have a large  
88 influence on organic matter accumulation and accretion (Ibañez et al. 2010). A study of subsiding marshes of the  
89 deltaic region of Louisiana, U.S. illustrated that organic matter accumulation was the dominant factor controlling  
90 accretion, both of which were hypothesized to be constrained by flooding stress and/or low mineral sediment  
91 availability on root production (Nyman et al. 1993). In a previous study, we found geomorphic differences in mineral  
92 sediment accumulation rates influenced higher organic matter accumulation and accretion rates in a coastal plain  
93 estuary as compared to a coastal lagoon (Boyd et al., 2017). A strong relationship between mineral sedimentation and  
94 organic accumulation implies that plant productivity and biomass may be greater in marshes with greater sediment  
95 availability, as sediment deposition creates favorable conditions for plant growth (Mendelssohn and Kuhn 2003).  
96 Further, we found that sediment accumulation rate was positively related to rates of labile C, but not refractory C  
97 accumulation (Unger et al., 2016). Geomorphology, therefore, influenced the relative chemical recalcitrance of soil  
98 C, with greater rates of mineral sedimentation and labile C accumulation in the coastal plain estuary than in the coastal  
99 lagoon (Unger et al., 2016). Potential sources of labile organic C include autochthonously produced plant biomass  
100 and algae and allochthonous C deposited by tidal water. Several important questions arise from these findings  
101 including: do high mineral sediment loads stimulate greater production and biomass of roots and rhizomes and is  
102 belowground biomass (live and dead) a good indicator of C accumulation and accretion rates in marshes? For the  
103 present study, we sought to examine how environmental conditions across marshes influence short-term process rates  
104 of belowground productivity, decay, and longer term biomass stocks, and to relate these biotic processes and properties  
105 to soil C and accretion rates. We used natural gradients in tidal elevation, sedimentation rates, salinity, and soil  
106 properties in interior, short-form *Spartina alterniflora* marshes across two estuaries to test three overarching  
107 hypotheses: (1) environmental parameters are highly correlated across marshes; however, hydrology is the most  
108 important predictor of belowground productivity, decay rates, and above- and belowground biomass; (2) short-term  
109 (< 2 yr) surface accretion rates are influenced by a combination of aboveground vegetation structure, belowground  
110 productivity, decay and mineral sedimentation rate; and (3) longer-term (~50 years) accretion and soil C accumulation  
111 are more strongly related to belowground biomass in organogenic marshes in a coastal lagoon than in more  
112 minerogenic marshes of a coastal plain estuary, where the potential for allochthonous C contributions are greater.

113

## 114 **2 Methods**

### 115 **2.1 Study sites**



116 Six marshes in two estuaries along the Mid-Atlantic coast of the United States, the Delaware Bay and Barnegat Bay,  
117 New Jersey were the focus of this study (Fig. 1). The two estuaries and marshes therein varied in geomorphic setting  
118 and therefore, tidal range, hydrology, salinity, sediment availability, and nutrient concentrations also varied. The  
119 Delaware Estuary is a large coastal plain estuary extending 215 km from the head-of-tides to the bay mouth at the  
120 Atlantic Ocean. Tidal amplitude is approximately 1.5 m at the mouth and increases up-estuary modulated by estuary  
121 and tidal channel geometry. Barnegat Bay is a shallow coastal lagoon extending 62.7 km along the coast of New  
122 Jersey, separated from the Atlantic Ocean by a barrier island apart from two inlets. Barnegat Bay experiences a  
123 relatively small tidal amplitude ranging from 20 to 50 cm depending on location in the bay (Defne and Ganju 2014).  
124 Mean salinity ranges from 18 to 25 with lowest salinities in the northern part of the bay farther from the inlets and  
125 near Toms River (Kennish 2001). Across the two estuaries, marshes ranged from being along a large tidal tributary  
126 with relatively low salinity (Maurice River, MR, in Delaware Bay) to a back-barrier marsh (Island Beach State Park,  
127 IB) in Barnegat Bay, which has been converting from *S. alterniflora* to shallow open water between the parallel  
128 mosquito ditches over approximately the last decade, likely due to a lack of drainage through the ditches (pers obs).  
129 Reedy Creek marsh in northern Barnegat Bay had interior ponds which have been expanding in size over time. These  
130 systems have also been described in Eelsey-Quirk 2016; Unger et al., 2016 and Boyd et al., 2017. Accretion rate in  
131 Barnegat Bay marshes ( $0.28 \pm 0.06$  cm/yr) over the last 50 – 100 years was less than the rate of relative sea-level rise  
132 over a similar time period (0.41 cm/yr; NOAA, Tides and Currents; *in* Boyd et al., 2017). In Delaware Bay salt  
133 marshes accretion rate ( $0.70 \pm 0.26$  cm/yr) exceeded the rate of local relative sea-level rise (0.34 cm/yr, NOAA, Tides  
134 and Currents).

135

## 136 2.2 Experimental design

137 Five plot locations were established in each marsh along a transect of increasing distance from the marsh/estuary  
138 boundary. Transects ranged from 270 to 2970 m with shorter transects in smaller marshes (generally in Barnegat Bay)  
139 and longer transects in marshes along larger tidal channels (in Delaware Bay). This transect-based study design, rather  
140 than replicate plots in close proximity, was employed to capture a range of within-marsh variation, while also  
141 stratifying by short-form *S. alterniflora*. Belowground ingrowth and litterbag decomposition studies were employed  
142 at each of the five locations ( $n = 5$ ). Vegetation structure (i.e., stem density and shoot height and above- and  
143 belowground biomass) was measured at three of the five locations (nearest, middle and farthest from the estuary).  
144 Belowground biomass was determined from 2-cm depth sections from half of a 6-cm diameter soil core. The other  
145 half of the core was used for analysis of soil properties, C (total organic, labile, and refractory) and nitrogen  
146 concentrations, and  $^{137}\text{Cs}$  and  $^{210}\text{Pb}$ -activity (*in* Unger et al., 2016; Boyd et al., 2017). Two of the five locations in  
147 each marsh (nearest and farthest) had continuous water level and salinity recorders installed. Hydrology was  
148 extrapolated to the middle sample plot location using marsh elevation.

## 149 2.3 Environmental parameters

### 150 2.3.1 Hydrology and salinity



151 Two water level/conductivity recorders (In-Situ 5000 vented) were installed in each of the six marshes from August  
152 2012 to October 2013. Probes were placed in each marsh near and far from the estuary approximately 5 m from the  
153 location of two of the five belowground ingrowth and litterbag plots and two of the three standing biomass and soil  
154 core plots. Probes were installed in slotted wells to a depth of 70 cm. Water level and conductivity were recorded  
155 every 15 and 30 minutes, respectively. Three GPS survey points were collected on the marsh surface around each  
156 well and at each plot location using a Leica GS-14.

157

### 158 **2.3.2 Soil properties**

159 Soil cores were collected for testing relationships between belowground biomass and previously reported accretion  
160 (*in* Boyd et al., 2017) and soil C accumulation rates (*in* Unger et al., 2016). PolyCate tubes 15.2 cm in diameter and  
161 110 cm long with a sharpened bottom edge were used to collect soil cores. Cores were taken back to the lab and  
162 sectioned into 2-cm depth sections. Physical and chemical analyses were conducted on half of each the 2 cm sections.  
163 Soil bulk density ( $\text{g/cm}^3$ ), percent organic matter, total organic C, refractory and labile C, total nitrogen, and  
164 radiometric dating were conducted and is reported in Unger et al., 2016 and Boyd et al., 2017. The remaining half of  
165 each 2-cm depth was rinsed and sieved for belowground biomass (see below).

166

### 167 **2.4 Vegetation parameters**

168

#### 169 **2.4.1 Belowground ingrowth**

170 Belowground ingrowth rate ( $\text{g DW m}^{-2} \text{ yr}^{-1}$ ) was measured at five locations in each of the six marshes using rates of  
171 root and rhizome growth into flexible mesh bags filled with a 1:1 mixture of unfertilized top soil and peat moss  
172 (McKee et al., 2007;  $n = 5$ ). Ingrowth bags were constructed of flexible crawfish sack material with a mesh size of 6.3  
173 x 3.2 mm, and, when filled, were 5 cm diameter and 15 cm length. Ingrowth typically underestimates absolute rates  
174 of belowground productivity, but is useful for examining relative responses to varying environmental conditions  
175 (Valiela et al., 1976; Graham and Mendelssohn 2016). Four ingrowth bags were deployed in each of the five plots  
176 and sequentially harvested approximately every four months from April 2013 to October 2014 to calculate  
177 belowground (root + rhizome) ingrowth rate. The four bags were deployed 50 cm apart in each plot and all bags were  
178 installed vertically into 15 cm deep cored holes. Accumulated root and rhizome mass was dried at 60°C to a constant  
179 weight. All of the roots and rhizomes in ingrowth bags were live based on color and structural integrity.

180

#### 181 **2.4.2 Belowground decay**

182 Belowground decomposition of macro-organic matter was estimated using the litterbag technique. Litterbags (20 x  
183 10 cm) made of 1 x 1 mm window screen mesh were filled with 9 g wet weight of macro-organic material comprised  
184 of coarse roots and rhizomes in a live to dead ratio of 1:3. Five replicate samples were dried at 60°C to determine  
185 initial dry weight. Four litterbags were deployed horizontally 10-cm below the surface in each of five plots  
186 approximately 2 m from ingrowth bags in each of the six marshes ( $n = 5$ ). Litterbags in each plot were collected  
187 sequentially over the same ~20 month period of ingrowth study for determination of mass loss over time.



188 Decomposition rates were calculated by fitting mass loss to the single negative exponential model with an asymptote  
189 where a fixed proportion of recalcitrant organic material remains,

$$190 \quad e^{-kt} = \frac{X_t}{X_0} - a$$

191 where  $k$  is the decay constant,  $x_t/x_0$  is the proportion of original mass remaining at time  $t$ ,  $t$  is the time elapsed in  
192 years, and  $a$  is the asymptote (Cotrufo et al., 2009).

193

### 194 **2.5.3 Biomass**

195

196 Aboveground biomass was harvested from three plots within a 0.25 m<sup>2</sup> quadrat where soil cores for radiometric dating,  
197 C analysis and belowground biomass were also collected. In the lab, stems were rinsed of mineral matter, counted,  
198 and measured for height. Belowground biomass from half of each 2 cm soil section was rinsed to remove all mineral  
199 sediment and separated into size classes of coarse and fine organic material. Coarse organic matter, comprised  
200 primarily of stem bases and rhizomes, were further sorted into live and dead based on color and rigidity. A sieve with  
201 a 2 mm mesh size retained coarse material and a sieve with a 1 mm mesh size retained fine organic matter, which  
202 could not be easily separated into live and dead components. All above- and belowground biomass was dried to a  
203 constant weight in a 70°C drying oven. Dry weights were converted to a g m<sup>-2</sup> basis and depth profiles were  
204 constructed.

205

### 206 **2.5 Short-term accretion and organic accumulation rates**

207 Surface accretion and organic matter accumulation rates measured over the study period (Spring 2013 – Fall 2014)  
208 were used to examine relationships with belowground ingrowth and decay rates. Accretion rates measured from the  
209 changes in height above a feldspar marker horizon can be highly temporally and spatially variable, and therefore, we  
210 used a time period that was longer than belowground productivity and decay studies to increase the potential for a  
211 significant linear trend. Three feldspar marker horizons were installed in 50 x 50 cm plots established approximately  
212 5 m from standing biomass core locations in each marsh ( $n = 9$ ). A single plug was collected from each plot quarterly  
213 and accretion was determined by the height of the marsh surface above the white feldspar marker (mm). A subsample  
214 of surface soil was taken to the lab for measurement of wet and dry weight, and loss on ignition (LOI) at 550°C for 4  
215 hours. Annual accretion rate was calculated using the slope of the regression line for each plot and multiplying by  
216 365. Organic accumulation rate was calculated from the product of bulk density of the surface soil (g/cm<sup>3</sup>) determined  
217 by the porosity, percent organic matter from LOI, and accretion rate (cm/yr). Mineral sediment accumulation rate was  
218 also calculated using percent inorganic matter from sediment remaining following LOI.

219

### 220 **2.6 Data analysis**

221 Each environmental and vegetation parameter was checked for normality using the Shapiro-Wilks test. Log  
222 transformations were used for most variables when necessary and appropriate and logit transformations were used for  
223 percent data (e.g., percent soil organic matter, total nitrogen). A square root transformation was necessary to normalize



224 belowground ingrowth data. Matlab was used to calculate hydrologic parameters from the continuous water level time  
225 series (MATLAB 6.1, the Mathworks Inc., Natick, MA). We used a nested analysis of variance to test for differences  
226 among marshes nested within estuaries in belowground ingrowth, decay rate, and vegetation structure (e.g., stem  
227 density, height, rooting depth, biomass). Multivariate correlation analysis was conducted to test for collinearity among  
228 environmental predictor variables. One representative of highly correlated variables was chosen and redundant  
229 variables were removed for future analyses. Correlations within environmental and vegetation data were expected,  
230 and therefore, a multivariate approach were used to analyze the data. Multivariate analysis of variance (MANOVA)  
231 was used to test for differences among marshes nested within estuaries in environmental parameters. If a significant  
232 multivariate treatment affect was found based on the Wilks Lambda test, univariate tests were performed. Univariate  
233 post-hoc tests were conducted using Tukey's HSD test. To examine the relationship between environmental and  
234 vegetation parameters across samples, a stepwise regression was used with forward selection, starting with the full  
235 model and minimum BIC. Belowground ingrowth, decay and biomass components were analyzed in separate stepwise  
236 univariate models. Non-linear modelling was used when relationships were non-linear. Lastly, to test for relationships  
237 between belowground biomass structure and accretion and C (total organic, labile and refractory) accumulation rates  
238 a stepwise regression analysis was conducted. Unless otherwise specified, JMP V.12.1 was used for all statistical  
239 analysis (JMP Version 12.1, SAS Institute Inc.).

### 240 **3 Results**

241 Elevations of marsh study locations ranged from -7 to 87 cm, referenced to the North American Vertical Datum 1988  
242 (NAVD88) and were generally lower in Barnegat Bay than in Delaware Bay (Fig. 2). Relative to the tidal frame,  
243 average elevations ranged from below mean low water (MLW; IB) to above mean high water (MHW; CC), with both  
244 of these marshes in Barnegat Bay. Marsh elevation was more variable in Delaware Bay, but six of the nine locations  
245 fell between mean low and high water. Overall, 65% of marsh areas had elevations within 5 cm of MLW, indicating  
246 that the majority of the root zone was continuously inundated. The lowest MLW of the 18 study areas was 11 cm  
247 below the surface. Tidal amplitudes ranged from 5 to 22 cm (Table 1). Barnegat Bay marshes were flooded for more  
248 time ( $53 \pm 12\%$ ) than Delaware Bay marshes ( $40 \pm 9\%$ ; Estuary:  $p = 0.0341$ ). However, there were also significant  
249 differences among marshes (Marsh[Estuary]:  $F_{4, 11} = 53.15$ ,  $p < 0.0001$ ; Table 1). For example, in Barnegat Bay, time  
250 flooded ranged from an average of 86% in IB to 6% in CC. Similarly, in Delaware Bay, DN was flooded 68% of the  
251 time while DV was flooded only 11% of the time (Table 1).

252

253 Salinities ranged from 7 at MR in Delaware Bay to 40 at CC in Barnegat Bay. Salinity of Barnegat Bay marshes was  
254 an average of 16 psu higher than DB, but there was also a significant difference within Barnegat Bay with RC in the  
255 north having a lower salinity than IB and CC (Marsh[Estuary],  $p = 0.0103$ ; Table 1).

256

#### 257 **3.1 Multivariate correlations among environmental variables**

258 Correlation analysis of environmental factors across estuaries revealed two general groups of correlated variables  
259 related to either hydrology or soil (Table 2). As might be expected, there were strong positive correlations among  
260 hydrologic parameters. MHW was related to the greatest number of other hydrologic variables including % time



261 flooded, mean water level (MWL), MLW, and tidal range. Tidal range was positively related to MHW, but unrelated  
262 to MLW as the average high water largely determined the tidal range experienced in the marsh and low water was less  
263 variable with relatively little drainage in the marsh interior. Similarly, there were significant correlations among soil  
264 parameters, with strong relationships among soil N content, bulk density and long-term mineral sedimentation rate.  
265 Across marshes, bulk density and  $^{137}\text{Cs}$ -based mineral sedimentation rate were positively correlated with each other  
266 and negatively correlated with soil N content and soil organic matter.

267

268 When we conducted a correlation analysis within estuaries, different relationships emerged (correlations not shown).  
269 In Barnegat Bay, hydrologic properties were strongly correlated with soil properties and processes. For example,  
270 MHW was negatively related to mineral sedimentation rate, indicating that lower elevation marshes had less  
271 sedimentation than higher elevation marshes. Here, localized sediment supply rather than flooding time influenced  
272 sedimentation rates and, ultimately, marsh elevation. In Delaware Bay, hydrology and soil parameters were unrelated.  
273 In both estuaries, salinity was negatively related to metrics of flooding (e.g., MHW, # flooding events, % time flooded)  
274 indicating that marshes higher in the tidal frame had higher salinities.

275

276 Based on the results of the correlation analysis, two hydrologic parameters, MHW and MLW, were selected to  
277 represent the suite of variables with which they were related, for which isolating individual relationships with  
278 vegetation parameters would be impossible (Table 2). Salinity was also maintained in the models, although it was  
279 negatively correlated with several hydrologic parameters, but not related to soil properties. Because of the strong  
280 relationship between soil bulk density and long-term mineral sedimentation rate, only sedimentation rate was retained  
281 in subsequent models.

282

### 283 **3.2 Short-term processes**

#### 284 **3.2.1 Belowground ingrowth**

285 Belowground growth of roots and rhizomes into ingrowth bags ranged from 0 – 550 g dw/m<sup>2</sup>/yr. Ingrowth rates were  
286 significantly greater in MR and CC than in IB where 3 of the 5 locations had no root growth, little to no live  
287 aboveground vegetation, and standing water for most of the year (Table 1; Fig. 3). As we hypothesized, of all  
288 environmental factors tested, only MLW influenced ingrowth rates (Fig. 4). This relationship was driven by extremes  
289 of the range where locations with MLW  $\geq 8$  cm below the marsh surface, ingrowth was greater than 200 g/m<sup>2</sup>/yr and  
290 in IB where MLW was over 3 cm above the surface, root growth was zero (Fig. 4).

291

#### 292 **3.2.2 Belowground decay**

293 While the percentage of root and rhizome material remaining at the end of approximately 20 months was similar  
294 among marshes averaging  $59 \pm 1\%$ , the rate of decay was greater in Barnegat Bay marshes than the Delaware Bay  
295 marshes (Fig. 3). We hypothesized that decomposition rate may not be related to measured environmental conditions;  
296 however, we found a positive relationship between decay rate and water table salinity (Fig. 4). Although stepwise  
297 regression indicated that only salinity was significantly related to decay, three hydrologic variables were negatively





298 correlated with salinity. Therefore, it is possible that an increase in decay may also be promoted by a lower tidal range,  
299 lower MHW, and/or fewer flooding events.

300

### 301 **3.2.3 Surface accretion and organic accumulation rates**

302 Short-term surface accretion rate was over two times greater in Delaware Bay marshes ( $0.65 \pm 0.17$  cm/yr) than in  
303 Barnegat marshes ( $0.30 \pm 0.12$  cm/yr), largely driven by high accretion rates in MR and low accretion rates in IB (Fig.  
304 3). Organic accumulation rate was significantly higher in MR and RC than in IB (Marsh[Estuary]:  $F_{4,11} = 5.0$ ,  $p =$   
305  $0.0155$ ) and mineral accumulation rates did not significantly differ among sites or between estuaries over the time  
306 period studied. Surface accretion rate was positively related to both organic and mineral sediment inventories above  
307 the marker horizon, although accretion was much more strongly influenced by mineral sediment than by organic  
308 accumulation (Fig. 5). Neither aboveground vegetation structure (i.e., stem density, height, and biomass) nor  
309 belowground processes (i.e., ingrowth and decay rates) were not related to surface accretion and accumulation rates.  
310 Hydrology was the only environmental variable that influenced accretion and accumulation rates. Rates were  
311 positively related to MHW and negatively related to MLW (Supplemental Table A), indicating that surface accretion  
312 and accumulation rates increased in areas with a higher water above the marsh surface and greater drainage.

313

## 314 **3.3 Vegetation structure**

### 315 **3.3.1 Aboveground**

316 Within marsh variability in *S. alterniflora* stem density was relatively high with coefficients of variation above 30%  
317 for 5 of the 6 marshes and up to 155% (Table 3). Stem density in IB in particular increased with increasing distance  
318 from the Bay ranging from zero stems approximately 67 m from the Bay, 102 stems/m<sup>2</sup> at 150 m distance, and 1372  
319 stems/m<sup>2</sup> at 225 m landward. CC, the highest elevation marsh in Barnegat, had some of the highest stem densities (up  
320 to 4112 stems/m<sup>2</sup>). Shoot height was approximately two times greater in MR than the other marshes with the exception  
321 of RC (Marsh[Estuary]:  $F_{1,4} = 8.15$ ,  $P = 0.0026$ ). Aboveground biomass was significantly related to both shoot height  
322 and stem density as described by the equation:  $AB = -2032 + 521(\log \text{ height}) + 136(\log \text{ density})$  ( $R^2 = 0.65$ ,  $p =$   
323  $0.0030$ ). Aboveground biomass was over six times greater in MR in Delaware Bay than RC and IB in Barnegat Bay  
324 (Marsh[Estuary]:  $F_{1,4} = 8.13$ ,  $P = 0.0021$ ; Table 3).

325

### 326 **3.3.1 Belowground**

327 Aboveground live biomass was not related to any component of belowground biomass, nor total belowground  
328 biomass. Belowground biomass components did not scale with each other either. The 95% rooting depth was greatest  
329 in DN, followed by MR, both of which had greater live root depths than Barnegat Bay marshes (Marsh[Estuary]:  $F_4,$   
330  $t_2 = 10.58$ ,  $p = 0.0007$ ; Table 3; Fig. 6).

331

332 Belowground biomass was examined with both a temporal and spatial perspective. Our temporal examination  
333 involved summing the biomass fractions relative to the <sup>137</sup>Cs peak, which contributes to the variation in accretion rates  
334 among marshes. However, biomass is continually added to the soil column, often to depths below the year 1963 <sup>137</sup>Cs



335 marker, and therefore, a specific depth, 50 cm, was also used, which is typical methodology for quantifying  
336 belowground biomass. Live coarse belowground biomass measured to the  $^{137}\text{Cs}$  peak, which varied by 42 cm among  
337 locations, was highly variable and did not differ significantly among marshes or between estuaries (Table 3). Live  
338 coarse biomass ranged from an average of  $505 \text{ g/m}^2$  in RC to  $2675 \text{ g/m}^2$  in CC where the  $^{137}\text{Cs}$  peaks occurred at an  
339 average of 11 and 16 cm depth, respectively. In addition, the quantity of live biomass in 16 cm at CC was similar to  
340 the amount of live biomass in MR where the  $^{137}\text{Cs}$  peak depth averaged 48 cm. However, much of the live biomass  
341 was confined to the upper 30 cm in general, and therefore the difference in live biomass among marshes down to 50  
342 cm depth was not substantially different from that measured to the respective  $^{137}\text{Cs}$  peaks. Larger differences between  
343 the depth-dependent calculations were found for the dead coarse and fine biomass. For example, marshes of Barnegat  
344 Bay had  $^{137}\text{Cs}$  peaks that were 9 – 17 cm below the surface and the amount of dead coarse and fine biomass increased  
345 by several times when depths to 50 cm were included. In contrast, there was less of an increase in Delaware Bay  
346 marshes, where accretion rates were higher. Dead coarse biomass was also highly variable and did not differ among  
347 marshes using either calculation method. Fine biomass in CC was greater than in RC when measured to the  $^{137}\text{Cs}$   
348 peak and greater than MR when measured to 50 cm depth (Table 3). Total belowground biomass above the  $^{137}\text{Cs}$  peak  
349 was significantly lower in RC than in DN and CC (Marsh[Estuary]:  $F_{4,12} = 5.12$ ,  $p = 0.0121$ ). No significant difference  
350 was found among marshes in total belowground biomass to a 50 cm depth.

351

352 Total live biomass (above-and belowground) was over three times greater in CC ( $3245 \pm 768 \text{ g/m}^2$ ) than in RC ( $833$   
353  $\pm 41 \text{ g/m}^2$ ) with no other differences among marshes (Marsh[Estuary]:  $F_{1,4} = 4.2$ ,  $P = 0.0227$ ). Live root-to-shoot ratio  
354 ranged from 4 to 12 in marshes where live stems were present in all plots (Table 3). Rates of ingrowth and decay  
355 were not related to belowground biomass stocks.

356

### 357 **3.3 Environmental controls on vegetation structure**

358 While the aim of these analyses were to examine cross-system relationships between environmental conditions and  
359 vegetation patterns, it became apparent that the responses of vegetation structure to environmental conditions were  
360 highly estuary-dependent. For example, live above- and belowground biomass were significantly related to long-term  
361 rate of mineral sedimentation in Barnegat Bay only (Fig. 7a). Live aboveground biomass increased linearly with  
362 increasing sedimentation rate and decreased linearly with increasing MHW, which were highly correlated in Barnegat  
363 Bay (Fig. 7b). This indicates that in Barnegat Bay, aboveground biomass responded positively to higher mineral  
364 sedimentation and less flooding, and further that marsh areas experiencing higher MHW are suboptimal within their  
365 elevational growth range. In Delaware Bay, aboveground biomass increased with increasing MHW following a  
366 quadratic relationship (Fig. 7b). Similar to aboveground biomass, live belowground coarse biomass, comprised of  
367 stem bases, rhizomes and large roots, in Barnegat Bay was positively related to sedimentation rate and negatively to  
368 MHW, while there were no significant relationships between live coarse biomass and measured environmental  
369 parameters in Delaware Bay (Fig. 7c,d). Dead belowground coarse biomass was also negatively related to MHW in  
370 Barnegat Bay. Patterns of fine belowground biomass were not explained by environmental predictor variables in  
371 Barnegat Bay; however, in Delaware Bay, fine biomass increased with decreasing mineral sediment accumulation rate



372 and increased with increasing salinity (Fig. 7f). Total belowground biomass was not explained by environmental  
373 parameters in Barnegat Bay, but was negatively related to sedimentation rate in the Delaware Estuary. Fine material  
374 comprised 68 – 80% of the total belowground biomass in Barnegat Bay and 45 – 69% of total belowground biomass  
375 in Delaware Bay. High mineral sediment deposition in MR in Delaware Bay was associated with lower total  
376 belowground biomass, primarily associated with less fine organic material.

377

### 378 **3.4 Relationship between belowground biomass structure and soil C and accretion**

379 Belowground biomass profiles corresponded well with profiles of organic C density, depending on the biomass  
380 component (live coarse, dead coarse, or fine) and whether the C was chemically labile or refractory (Fig. 6). Labile C  
381 density was related to live coarse biomass in 4 of the 6 marshes (Table 4). Labile C density was not related to any  
382 biomass fraction in IB and was related to only fine biomass in MR. Fine biomass was also related to refractory C  
383 density in both MR and DV in Delaware Bay (Table 4). In Barnegat Bay, refractory C was associated with all or most  
384 of the belowground biomass fractions.

385 The pattern of total and live biomass was similar to that of total organic C accumulation in Barnegat Bay, but not in  
386 Delaware Bay (Fig. 8). Carbon accumulation and accretion rates were positively related to belowground biomass in  
387 Barnegat Bay marshes, but not in Delaware Bay (Fig. 9). Live coarse and fine biomass explained 86% of the variation  
388 in OC accumulation in Barnegat Bay and was not significantly related to OC accumulation in DB (Fig. 9). When we  
389 examined which structural components were related to organic C fractions, live coarse biomass was positively related  
390 to labile C accumulation and fine biomass contributed to the accumulation of refractory C (Fig. 9). Biomass was not  
391 related to accretion rate in Delaware Bay, but live and dead coarse biomass explained 78% of the variation in accretion  
392 rate in Barnegat Bay (Fig. 9).

393

## 394 **4.0 Discussion**

395

396 Study locations in both estuaries spanned the tidal frame with *S. alterniflora* above, within, and below the average  
397 tidal range. This relatively wide range of elevations and associated hydrologies along with other environmental  
398 differences were predicted to be biologically significant. Our findings illustrate that within marsh variability in both  
399 environmental conditions and vegetation response can be high such that marshes in very different geomorphological  
400 settings can experience very similar abiotic conditions, and subsequent vegetation properties. Regardless of marsh  
401 location, we found significant relationships between vegetation, decay and environmental factors. Belowground  
402 ingrowth was negatively related to MLW, decay was positively related to salinity, and environmental-biomass  
403 relationships were estuary-dependent. In Barnegat Bay, less flooding and higher sedimentation rates favored above-  
404 and belowground biomass, which, in turn, increased soil C accumulation and accretion rates. Biomass dynamics in  
405 Delaware Bay for the most part, were unrelated to environmental parameters, and had little influence on the  
406 accumulation of soil C or accretion rate.

407



#### 408 4.1 Geomorphic influences

409 Hydrology is predicted to be of primary importance to plant productivity and organic matter accumulation in marshes.  
410 Many experimental and modeling studies suggest that root growth and soil C production is maximized at an optimal  
411 water depth following a parabolic relationship with elevation (Morris et al., 2002; Kirwan and Guntenspergen 2012)  
412 and that the magnitude of organic production depends largely on elevation of the marsh (e.g., Kirwan et al., 2010;  
413 Mariotti & Fagherazzi 2010). While this theory may hold for gradients of inundation where sediment supply is  
414 constant and deposition is controlled by flooding time, at a larger spatial scale, inundation and sediment supply can  
415 vary in non-uniformly (e.g., Butzeck et al. 2015). Belowground responses to flooding have been suggested to be  
416 independent of mineral sediment availability (Kirwan and Guntenspergen 2012). However, this conclusion was based  
417 on a study in a sediment-limited marsh system where only the effect of flooding and associated sediment deposition  
418 was altered. The distinction between flooding and associated sediment deposition and spatial variation in sediment  
419 availability is an important one. Our study illustrated that above- and belowground biomass was positively influenced  
420 by elevation and a high long-term sediment deposition rate in marshes of a coastal lagoon where sediment supply can  
421 be localized and estuarine tidal dynamics can limit the transport and deposition of sediments, and therefore, marshes  
422 are highly dependent on organic matter production for accretion. Here, a high sediment supply promoted a positive  
423 feedback between belowground biomass and elevation. However, at similar rates of mineral sedimentation,  
424 belowground live coarse biomass was over 1000 g/m<sup>2</sup> lower in the coastal plain estuary, potentially associated with  
425 higher soil redox potential and a lower requirement for rhizome photosynthate storage (Gallagher and Kibby 1981).  
426 In marshes of the coastal plain estuary, live belowground biomass was unrelated to measured environmental  
427 parameters, and biomass was not related to rates of soil C accumulation or accretion.

428

429 To examine the relative influence of hydrology and mineral sedimentation on plant productivity, decay and biomass,  
430 it is useful to compare two marshes where the hydrologic conditions in the marsh interior were similar, RC in Barnegat  
431 Bay and DN in Delaware Bay. Tidal range nearest RC and DN averaged approximately 0.3 m and 1.5 m, respectively  
432 (USGS gage 01408167 and 01411435, respectively). In the marsh interior, however, water level statistics between  
433 marshes were quite similar. For example, the average time flooded was approximately 67% at both sites, and MHW,  
434 MLW, and tidal range were all comparable. Although not significantly different, the frequency of flooding was higher  
435 and the duration of flooding was slightly lower in RC than in DN. Salinity also averaged about 7 psu greater in RC,  
436 although not significantly different from that in DN. Given these relative similarities in hydrology, we might predict  
437 similar rates of plant productivity and decay and quantities of biomass. While short-term process rates were similar  
438 between these two marshes, biomass and longer-term processes were more different, and much higher in DN than in  
439 RC. Aboveground biomass averaged two times higher in DN than RC. Belowground live coarse biomass averaged  
440 2456 and 721 g/m<sup>2</sup> in DN and RC, respectively and dead coarse biomass averaged 1063 and 280 g/m<sup>2</sup> in DN and RC,  
441 respectively. Importantly, these two biomass components were most significantly related to long-term accretion rate  
442 in Barnegat Bay, and <sup>137</sup>Cs accretion rates were two and a half times greater in DN than RC (Boyd et al., 2017). Live  
443 rooting depth was also significantly greater in DN (46 cm) as compared to RC (19 cm). Despite similar hydrology in  
444 the marsh interior, mineral sedimentation rates were an order of magnitude larger, and soil bulk density was three



445 times greater in DN than in RC (Boyd et al., 2017; Unger et al., 2016). In Barnegat Bay, differences in mineral  
446 sedimentation explained 62% of the variation in live belowground biomass and RC had among the lowest  
447 sedimentation rate of all the marshes in the study. Geomorphic conditions of high sediment availability and larger  
448 tidal range in the estuary and creeks, which can mobilize and distribute sediments likely work in concert to promote  
449 greater long-term deposition rates in DN than in RC. To further illustrate the importance of mineral sedimentation to  
450 belowground biomass, we can examine CC and DV, two of highest elevation marshes in the two estuaries. DV was  
451 high in elevation closer to Delaware Bay and was lower further inland, resulting in some variability with respect to  
452 hydrology. Overall, many of the hydrologic parameters were comparable between CC and DV. Salinity, however,  
453 was significantly higher at CC than DV, but soil organic matter, bulk density and mineral sedimentation rate were  
454 similar. Belowground ingrowth, and surface accretion rates were also similar, and although decay rates were faster in  
455 CC, potentially related to higher salinity, the percentage of mass remaining in litterbags was similar to DV.  
456 Belowground biomass and biomass profiles were also similar between marshes with the exception of greater fine  
457 organic matter in CC, particularly between 4 and 20 cm depth. With both hydrology and sedimentation rates being  
458 within range of each other, these two marshes in very different geomorphic settings, had comparable biomass and  
459 organic C accumulation rates.

460

#### 461 **4.2 Belowground ingrowth**

462 Belowground ingrowth reflects root growth into new sediment in absence of space-limitation by other roots, rhizomes  
463 and organic matter in natural marsh soils. The experimental increase in resource space inherent to the ingrowth  
464 methodology can result in belowground responses to abiotic conditions that may differ from that of biomass. For  
465 example, nutrient enrichment led to an increase in belowground ingrowth while resulting in a decline in live  
466 belowground biomass (Graham and Mendelssohn 2015). Inundation has been shown to have varying effects on root  
467 ingrowth depending on species (Janousek et al., 2016), but ultimately root productivity declines as inundation time  
468 exceeds the tolerance limit of the species. *Spartina alterniflora* is highly adapted to flooded conditions, possessing  
469 both morphological adaptations such as aerenchyma to facilitate oxygen transport to flooded rhizomes and roots and  
470 physiological adaptations such as anaerobic metabolism (Teal and Kanwisher 1966; Mendelssohn et al., 1981). We  
471 observed that root growth of *S. alterniflora* was highly variable under moderate flooding conditions, potentially more  
472 affected by other abiotic conditions or the density of parental live root structures in close proximity. Because mean  
473 low water was generally above the lowest part of the ingrowth bag, and ingrowth bags were surrounded by water most  
474 of the time, the effect of inundation on root growth was evident at the extremes of MLW, where either average low  
475 water level exposed a significant portion of the ingrowth bag resulting in relatively high root growth or low water  
476 averaged above the surface and the root zone was continuously flooded, where no roots grew. Thus, as others have  
477 found (Blum 1993; Kirwan and Guntenspergen 2012), when new substrate is available, root growth increased with  
478 drainage.

479

#### 480 **4.3 Belowground decay**



481 Environmental effects on belowground organic matter decomposition in marshes have been somewhat inconclusive.  
482 Continuously moist organic substrates (Valiela et al., 1984), high microsite variability in root oxidation (Teal and  
483 Kanwisher 1961) and contact with live roots (Hackney and de la Cruz 1980) create conditions where a seemingly  
484 homogeneous marsh can high variability in decomposition (Hackney 1987). Some studies have shown that decay  
485 rates are not affected when placed in environments with different flooding regimes and redox potentials (Valiela et  
486 al., 1984; Blum 1993), while other studies have shown C dioxide emissions to be greater with a lower water table  
487 depth (Nyman and DeLaune 1991). Depth-dependent decay suggests that decomposition slows in more anaerobic,  
488 potentially cooler, conditions deeper in marsh sediments (Hackney and de la Cruz 1980; Hemminga et al., 1988). In  
489 mesocosms, the relationship between belowground decay and flooding was site-specific where decay increased with  
490 increasing inundation at two of the three study locations (Kirwan et al., 2013). Contrasts in the effects of inundation  
491 have been found between experimental mesocosms and natural marshes, where decomposition of roots and rhizomes  
492 increased with increasing inundation in mesocosms, but in the field decomposition rates were higher in the high as  
493 compared to the low marsh (Janousek et al., 2017). The difference between two outcomes was hypothesized to be  
494 related to other abiotic factors varying along the tidal gradient or differences in nutrient availability and soil organic  
495 matter between mesocosm and marsh. Hemminga et al. (1988) found an increase in the belowground decomposition  
496 of *Spartina anglica* with increased elevation, potentially associated with less inundation time, higher temperatures,  
497 and/or higher salinity. Some have found negative (Hemminga et al., 1991) or no effect (Connolly et al., 2014) of  
498 salinity on marsh plant leaf litter decay at salinities of  $\leq 25$ . We found a significant positive relationship between  
499 belowground decay rate and salinity, which was negatively correlated with tidal range, MHW, and number of flooding  
500 events per year. Ultimately, the more exposure and higher salinity, the greater the rate of decomposition. Salinity in  
501 the present study ranged from an average of 7 to 39. Along a lower gradient in salinity ( $\sim 0 - 15$ ) in *Phragmites*  
502 *australis*-dominated marshes, belowground decay of cotton strip was related more to nutrient availability and specific  
503 constituents in seawater (e.g., boron, calcium, and sulfur) rather than the major seawater cations or salinity as a whole  
504 (Mendelssohn et al., 1999). Lower organic matter preservation along estuary salinity gradients from tidal freshwater  
505 to saline marshes has been suggested to be associated with a positive effect of salt water on decomposition (Craft,  
506 2007). While decay rates were higher in the more saline marshes of Barnegat Bay than Delaware Bay marshes, there  
507 was essentially no difference in the percent remaining at the end of approximately 20 months, which averaged 59%.  
508 The implications are that regardless of environmental conditions, approximately 60% of the plant-derived organic  
509 matter in the soil may be recalcitrant and undergo relatively slow decomposition. This percentage corresponds well  
510 to measurements of lignocellulose, which comprises approximately 79.5% of root and rhizome biomass (Hodson et  
511 al., 1984). The cellulosic portion undergoes higher rates of mineralization than lignin, which comprises approximately  
512 19.3% in roots and rhizomes of short-form *S. alterniflora* (Hodson et al., 1984) resulting in some additional losses  
513 over time.

514

#### 515 **4.4 Biomass**

516 Belowground biomass of *S. alterniflora* can also be quite variable both temporally and spatially. Seasonal changes in  
517 live roots and rhizomes can be due to growth of new tissues, turnover, and/or translocation of non-structural



518 carbohydrates to aboveground tissues (Gallagher 1983). Decay and turnover rates influence changes in the dead  
519 biomass. Thus, biomass-environment relationships can change throughout the year and between years (Reed and  
520 Cahoon 1992). High micro-spatial variability can also confound measurements of seasonal and inter-annual biomass  
521 variations. Spatially, elevation is predicted to be a primary determinant of belowground biomass, as aboveground  
522 biomass responds relatively quickly to changes in inundation. However, it is yet unclear how above- and belowground  
523 biomass scale with each other across complex environmental gradients. Across a gradient of elevation ( $> 10$  cm) in a  
524 marsh on Galveston Island, Texas, *S. alterniflora* aboveground live biomass decreased with increasing elevation, while  
525 root biomass was similar among elevation ranges (Kulawardhana et al., 2015). In a subsiding marsh in Louisiana,  
526 belowground biomass was positively related to marsh surface elevation (Reed and Cahoon 1992). Our data suggest  
527 that above- and belowground biomass do not scale with each other and that belowground live biomass positively  
528 responds to sedimentation when geomorphic conditions limit tidal range and sediment availability. In the coastal plain  
529 estuary, where mineral sediment accumulation rates ranged from less than 500 to over 4000  $\text{g}/\text{m}^2/\text{yr}$ , belowground  
530 biomass did not vary much along this gradient and, for the most part, was not related to measured environmental  
531 explanatory variables.

532

#### 533 **4.5 Relationship between vegetation and soil C and accretion**

534 Positive relationships between *S. alterniflora* belowground productivity and biomass and soil C, C accumulation and  
535 accretion in salt marshes have largely been assumed by high plant production estimates, observations of plant derived  
536 biomass in soil cores and positive correlations between organic matter accumulation and accretion. However, few, if  
537 any, studies have directly tested these relationships across a natural gradient of geomorphology. Over short time  
538 scales ( $\leq 2$  yrs), surface accretion was positively related to mineral sedimentation rate, and to a lesser extent organic  
539 matter accumulation rate. We found no significant relationships between root ingrowth, decay and surface accretion  
540 rate, likely as other factors influenced surface accretion such as sediment deposition and, potentially the accumulation  
541 of surface litter. We found that geomorphology played a large role in influencing the relative importance and  
542 contribution of plant biomass to soil C and marsh accretion rate. Soil C density and biomass profiles illustrated varying  
543 relationships between biomass structural components and labile and refractory C. Two interesting relationships  
544 emerged from the analysis. One is that in the organogenic marshes in Barnegat Bay, the refractory C is supported by  
545 all or most biomass components including live biomass. This was not the case in Delaware Bay marshes, where the  
546 refractory C was supported by either fine or dead coarse biomass. This finding supports the hypothesis that under  
547 constrained growing conditions (e.g., high salinity, high inundation, low tidal range) found in Barnegat Bay marshes,  
548 more energy may be invested into the production of recalcitrant tissues such as lignin, cellulose and hemicellulose. In  
549 Delaware Bay, as we would predict, refractory C was associated with the dead biomass and, in most sites, the broken  
550 down fine biomass. Interestingly, in the marsh with the highest accretion and mineral sediment accumulation rate and  
551 the lowest fine biomass (MR), labile C density was only associated with fine biomass. This may be associated with  
552 greater mineral protection of small labile tissues (as hypothesized in Unger et al., 2016).

553 While relationships between biomass and C densities were relatively strong for all marshes, C accumulation and  
554 accretion rates were more strongly related to biomass in Barnegat Bay marshes than in Delaware Bay marshes. The



555 hypothesis that belowground biomass had a greater influence on soil C accumulation and accretion rates in  
556 organogenic marshes than minerogenic marshes was supported in this study. Based on these data, belowground  
557 biomass (live, dead, fine and/or total) is not necessarily a good predictor of carbon accumulation and accretion rates.  
558 Although previously unknown, it may have been presumed that marshes with higher tidal ranges and higher rates of  
559 mineral sedimentation would have higher stocks of belowground biomass. A lower MLW may promote the growth of  
560 roots and rhizomes to a greater depth, and mineral sediment may create more accommodation space and provide more  
561 mineral nutrients to support growth. However, at high sedimentation rates, such as those observed in marshes of the  
562 Delaware Bay, belowground biomass was largely uncoupled with rates of organic C accumulation, despite significant  
563 correlations between biomass and C (labile and refractory) density. At the low end of mineral sedimentation rates (<  
564 1000 g/m<sup>2</sup>/yr), sediment accumulation, regardless of local hydrologic constraints, was of primary importance in  
565 influencing plant biomass, and C accumulation and accretion rates. Hydrology in the estuary and tidal channels is of  
566 primary importance for mobilizing and distributing sediments onto the marsh surface. Importantly, while studies  
567 suggest the vulnerability of microtidal marshes in coastal lagoons (Reed et al., 2008; Kirwan & Guntenspergen 2010;  
568 Ganju et al., 2017), we illustrate the importance of localized sources of sediments as being the key to their survival  
569 through the positive feedback on live and dead coarse and fine root biomass, and organic matter and C accumulation  
570 rates. Continuous standing water, enlargement of interior ponds, and loss of aboveground vegetation are all signs of  
571 marsh deterioration. At IB, two of the sampling locations had permanent shallow water between ditches, and had lost  
572 the aboveground biomass. Remnants of former vegetation was evident belowground, where significant quantities of  
573 live stem bases, roots and rhizomes were present to below 28 cm depth at least three years after aboveground biomass  
574 was permanently lost. Therefore, belowground biomass is not always a good indicator of marsh health and  
575 vulnerability. In terms of soil C and accretion, our study indicates that biomass can be related to soil C accumulation  
576 and accretion rates, but at the low end of a range in mineral sediment accumulation. At higher sedimentation rates,  
577 fine and total belowground biomass declined significantly. The mechanism of fine organic matter loss or limited input  
578 with greater mineral sedimentation rates is unclear, particularly when these marshes have the highest rates of labile  
579 and total organic C accumulation in our study (Unger et al., 2016). However, the preferential loss of fine organic  
580 matter, which is largely recalcitrant, may have influenced the relatively high labile C content of the soil.

581

#### 582 **4.6 Conclusions**

583 The fate of low-lying salt marshes as sea-level rises depends, in part, on their ability to accumulate organic matter and  
584 to trap sediments. Sediment supply is also a major factor, and may be most important in influencing the biophysical  
585 processes that promote accretion and soil C accumulation. Our study illustrates that while drainage enhances new  
586 root growth into unoccupied substrate, biomass dynamics may be more strongly related to rates of mineral  
587 sedimentation and availability of substrate in *Spartina alterniflora* marshes where sediment availability is limiting  
588 promoting positive feedbacks between biomass, soil C accumulation, and elevation. Soil C and accretion were strongly  
589 related to biomass fractions in the coastal lagoon estuary, where all biomass components were positively related to  
590 refractory C. When sediments are readily available, belowground biomass was not strongly related to important  
591 environmental variables (e.g., hydrology, salinity, sedimentation rate), and was not related to soil C accumulation and





592 accretion rates, which were the highest in our study. In the coastal plain estuary, belowground biomass did not scale  
593 with accretion and accumulation indicating other, smaller-sized organic material, potentially allochthonous, was  
594 contributing to the high rates of C accumulation and accretion in these marshes.  
595



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601

602

603 *Competing interests* The authors declare that they have no conflict of interest.

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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  $\pm$  standard errors (n = 2 for hydrologic parameters and n = 3 for soil and elevation and soil parameters).**

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





**Table 2: Multivariate correlations and associated correlation probabilities for environmental parameters in saline marshes of Delaware Bay and Barnegat Bay, NJ. Only parameters with significant correlations are shown. Properties related to hydrology and soils are highlighted in blue and brown background, respectively.**

Parameter	Marsh elevation	% time flooded	MHW	MWL	MLW	Tidal range	# flooding events/yr	LOG flood duration	Salinity	LOGIT soil N	LOGIT soil organic matter	Soil bulk density	LOG long-term mineral sedimentation rate
Marsh elevation (cm, NAVD88)	<b>1.00</b>												
LOGIT % time flooded	< <b>0.0001</b>	<b>1.00</b>	0.71	0.97	0.94			0.84		-0.85		0.78	0.75
MHW (cm)	0.71	0.0089	<b>1.00</b>	0.83	0.74	0.85		0.0006		0.0004		0.0027	0.0046
MWL (cm)	0.97	0.83	0.83	<b>1.00</b>	0.95	<0.0001							
MLW (cm)	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001			0.74					
Tidal range (cm)	0.94	0.74	0.95	<b>1.00</b>	<b>1.00</b>			0.82					
# flooding events/yr	<0.0001	0.0007	<0.0001	<0.0001	<0.0001			<0.0001					
LOG flood duration (hr)	0.84	0.85	0.81	0.81	0.81								
Salinity	0.0006	<0.0001	<0.0001	<0.0001	<0.0001								
LOGIT soil N (%)													
LOGIT soil organic matter (%)													
Soil bulk density (g/cm <sup>3</sup> )													
LOG mineral sedimentation rate (g/m <sup>2</sup> /yr)													

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

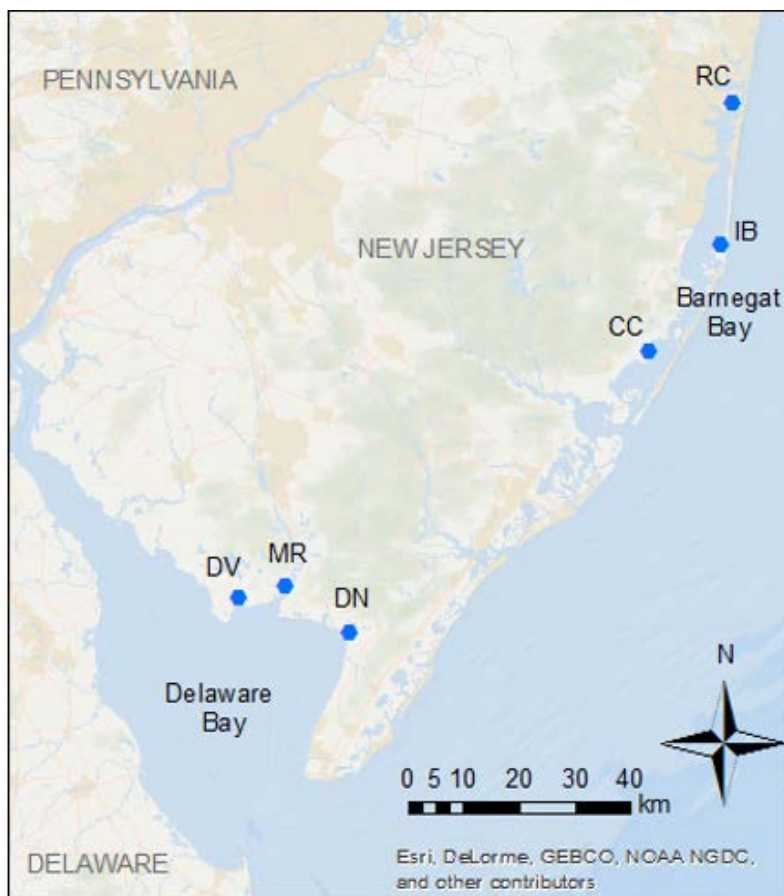
	BB				DB			
	RC	IB	CC	DV	MR	DN		
Stem density (#/m <sup>2</sup> )	509 ± 132	493 ± 440	3276 ± 615	1234 ± 382	612 ± 174	1675 ± 53		
Average height (cm)	17 ± 3 <sup>ab</sup>	14 ± 2 <sup>b</sup>	13 ± 2 <sup>b</sup>	13 ± 1 <sup>b</sup>	26 ± 1 <sup>a</sup>	12 ± 1 <sup>b</sup>		
Aboveground biomass (g/m <sup>2</sup> )								
live	112 ± 41 <sup>b</sup>	93 ± 88 <sup>b</sup>	362 ± 38 <sup>ab</sup>	234 ± 79 <sup>b</sup>	664 ± 90 <sup>a</sup>	353 ± 35 <sup>ab</sup>		
dead	338 ± 129	91 ± 85	317 ± 97	33 ± 8	122 ± 38	100 ± 10		
95% live rooting depth (cm)	19 ± 1 <sup>c</sup>	20 ± 1 <sup>c</sup>	18 ± 1 <sup>c</sup>	23 ± 1 <sup>bc</sup>	30 ± 2 <sup>b</sup>	46 ± 6 <sup>a</sup>		
Belowground biomass (g/m <sup>2</sup> )								
to <sup>137</sup> 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 <sup>b</sup>	3676 ± 186 <sup>ab</sup>	4326 ± 258 <sup>a</sup>	3398 ± 438 <sup>ab</sup>	2484 ± 532 <sup>ab</sup>	3527 ± 448 <sup>ab</sup>		
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 <sup>ab</sup>	8192 ± 2005 <sup>ab</sup>	8999 ± 948 <sup>a</sup>	6599 ± 1654 <sup>ab</sup>	2517 ± 565 <sup>b</sup>	5626 ± 661 <sup>ab</sup>		
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 of belowground biomass to labile and refractory soil C density.**

C density (g/cm <sup>3</sup> )	fraction Marsh	Relationship with belowground biomass (g/m <sup>2</sup> )
labile	RC	Live coarse: adj R <sup>2</sup> = 0.25, P < 0.0001
	IB	ns
	CC	Live coarse: adj R <sup>2</sup> = 0.49, P < 0.0001
	DV	Live coarse: adj R <sup>2</sup> = 0.24, P < 0.0001
	MR	Fine: adj R <sup>2</sup> = 0.60, P = 0.0172
	DN	Live coarse: adj R <sup>2</sup> = 0.23, P < 0.0001
refractory	RC	Live and fine: adj R <sup>2</sup> = 0.60, P < 0.0001
	IB	ALL: adj R <sup>2</sup> = 0.64, P < 0.0001
	CC	ALL: adj R <sup>2</sup> = 0.70, P < 0.0001
	DV	Fine: adj R <sup>2</sup> = 0.17, P = 0.0001
	MR	Fine: adj R <sup>2</sup> = 0.53, P = 0.0306
	DN	Dead coarse: adj R <sup>2</sup> = 0.09, P = 0.0389

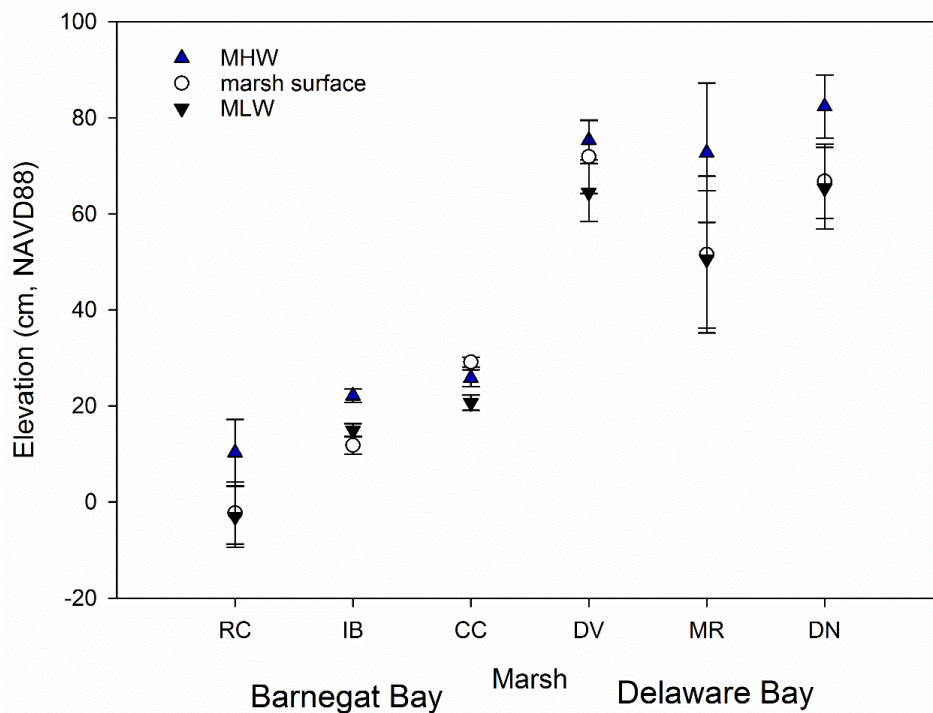
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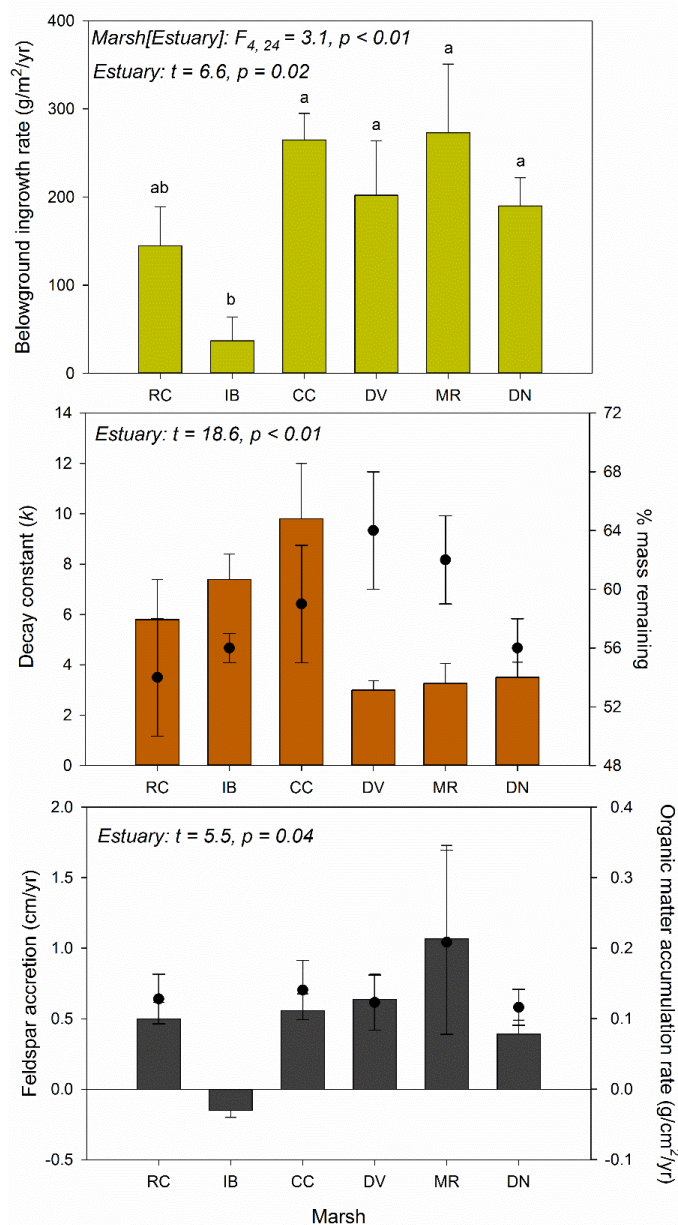
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**Figure 1: Study locations in Barnegat Bay and Delaware Bay along the mid-Atlantic coast, U.S.**



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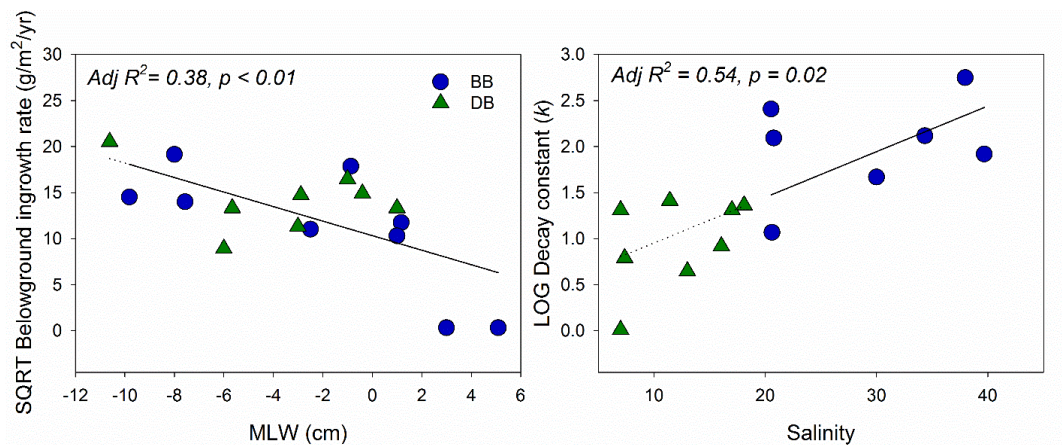
9 **Figure 2.** Mean high and mean low water and marsh surface elevations based upon elevation survey data and  
10 continuous water level recorded 8/12 – 10/13 in six *Spartina alterniflora* marshes in the mid-Atlantic, US (n =  
11 2; 2 water level recorders/marsh).



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 13 **Figure 3: Belowground ingrowth rate, decay constant and percent mass remaining, and short-term surface**  
 14 **accretion and organic matter accumulation rates in salt marshes of two mid-Atlantic estuaries (n = 3, ±**  
 15 **standard error). Decay rates are illustrated by vertical bars while percent mass remaining are dots. Similarly,**  
 16 **accretion rate values are represented by bars and organic accumulation rates by dots. Different letters indicate**  
 17 **significant differences (p < 0.05) with lower case letters corresponding to bar graphs and uppercase letters to**  
 18 **scatter graphs.**

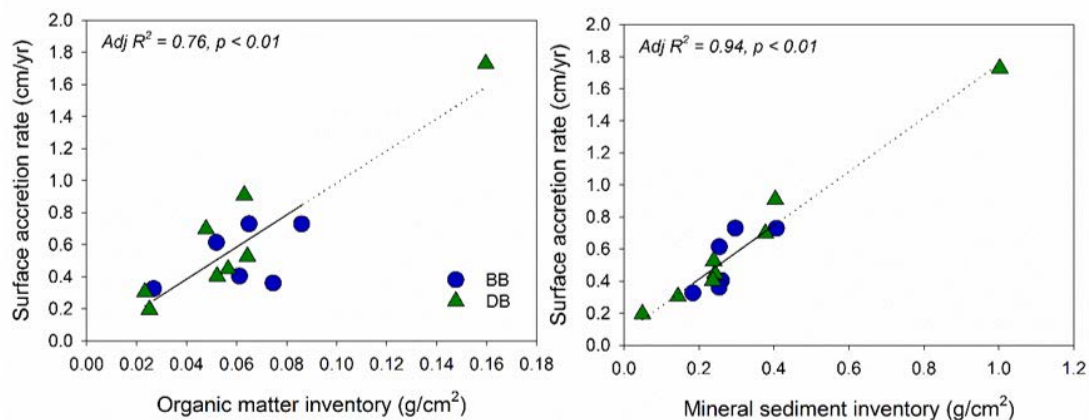


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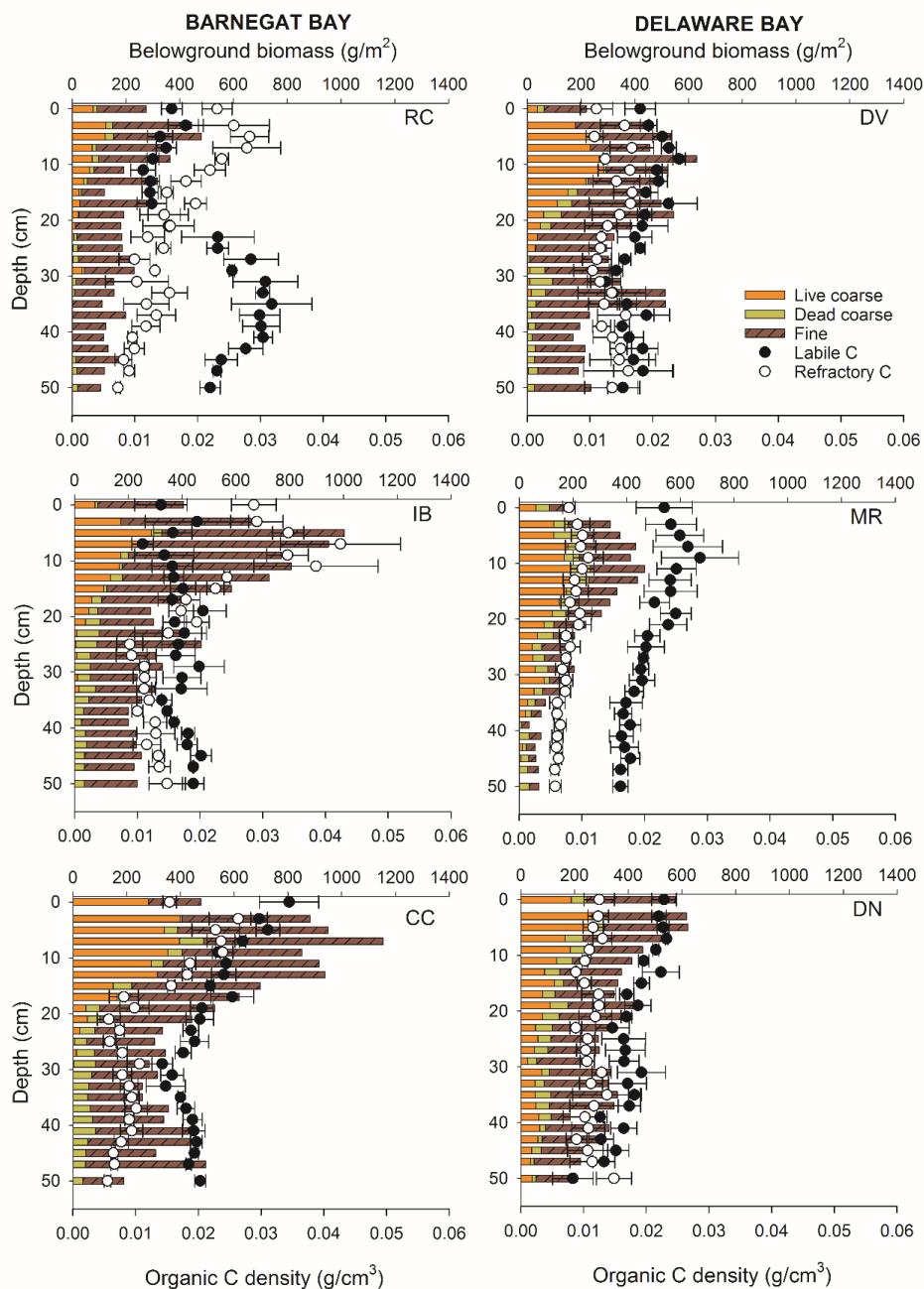
23 **Figure 4: Relationships between belowground ingrowth and mean low water (MLW) relative to the marsh**  
24 **surface (left) and decay constant from litterbags and salinity (right) based on the results of stepwise regression**  
25 **across Barnegat and Delaware bays. Blue dots and green triangles refer to data collected in Barnegat Bay (BB)**  
26 **and Delaware Bay (DB), respectively.**



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**Figure 5: Relationship between surface accretion and organic and mineral accumulation rates above feldspar marker horizons in marshes of two estuaries in the Mid-Atlantic U.S. coast across Barnegat and Delaware bays. Blue dots and green triangles refer to data collected in Barnegat Bay (BB) and Delaware Bay (DB), respectively.**



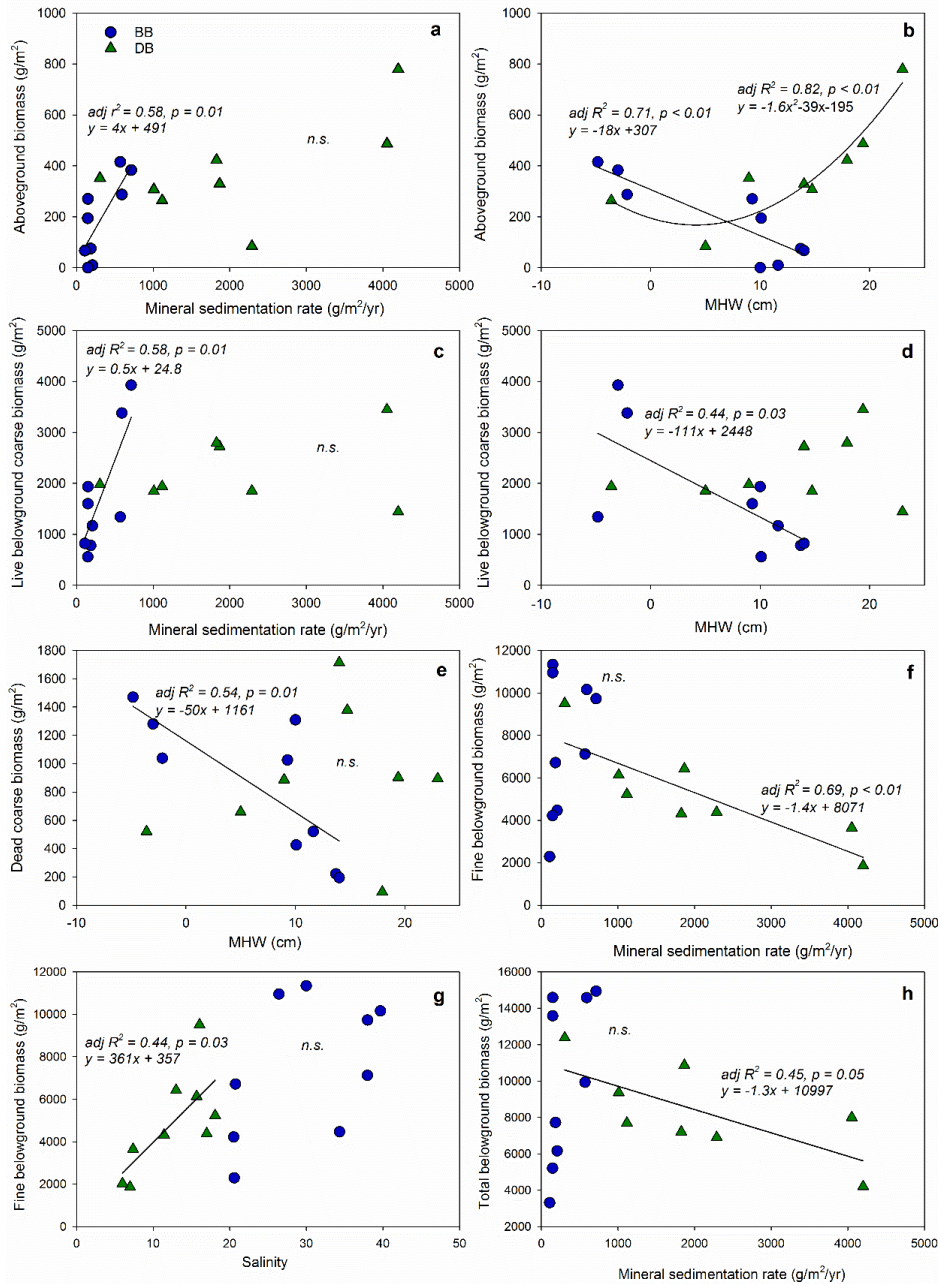


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33 **Figure 6: Belowground biomass and labile and refractory organic C density profiles in marshes of two Mid-**

34 **Atlantic estuaries. Biomass data are means (standard errors not shown). C density data previously reported in**

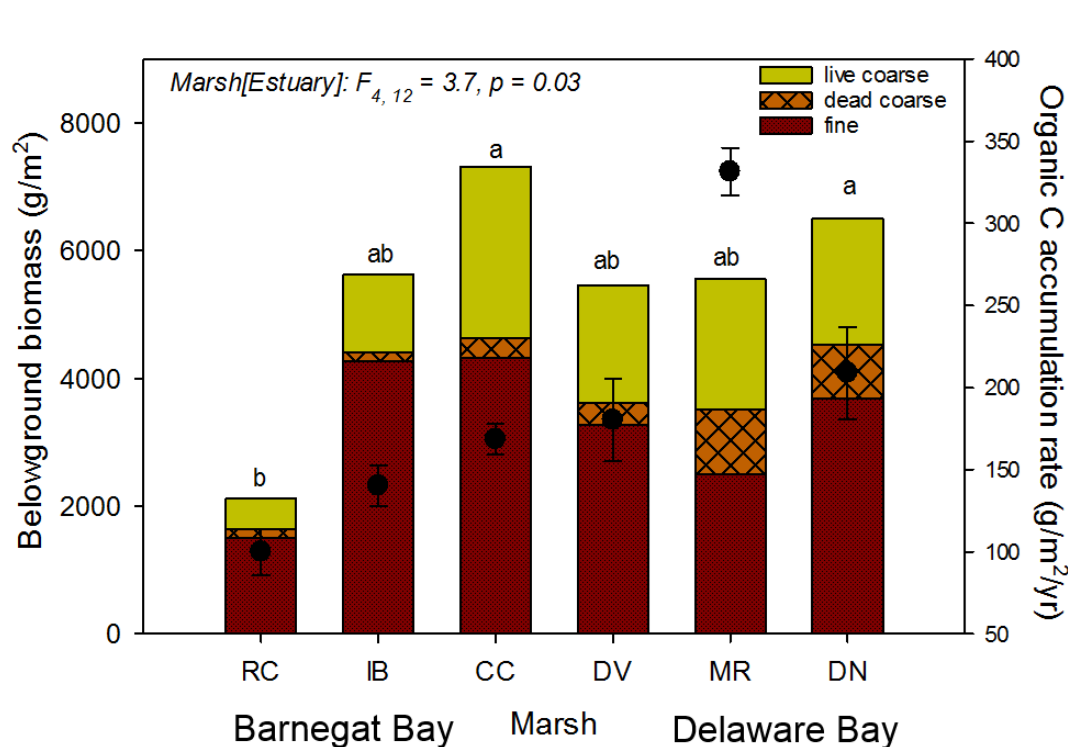
35 **Unger et al., 2016.**



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 37 **Figure 7: Relationships between vegetation structure and environmental parameters. For these analyses,**  
 38 **belowground biomass to 50-cm depth was used. Mineral sedimentation rates were calculated using  $^{137}\text{Cs}$ -**  
 39 **dating, and therefore, are average rates over the last 50 years. Blue dots and green triangles refer to data**  
 40 **collected in Barnegat Bay (BB) and Delaware Bay (DB), respectively, which were analysed separately. Both**  
 41 **significant and non-significant (n.s.) relationships are shown.**

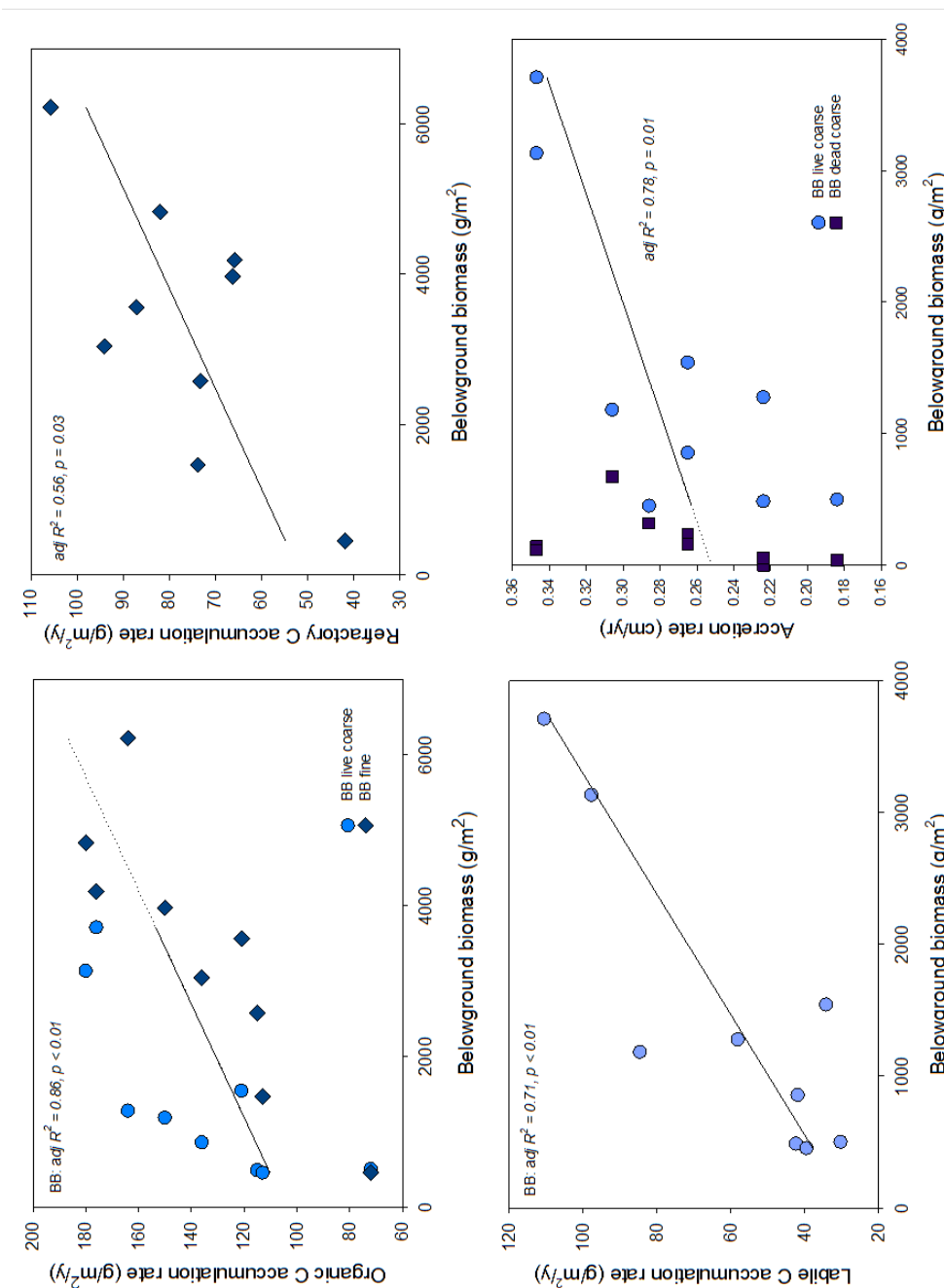


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**Figure 8:** Belowground biomass (scaled on left-axis) and organic C accumulation rate (scaled on right axis; previously reported in Unger et al., 2016) in marshes of two Mid-Atlantic estuaries. Belowground biomass and C accumulation are relative to the <sup>137</sup>Cs peak depth. Statistics for total belowground are shown and letters represent differences ( $p < 0.05$ ). Standard errors are shown in Table 2.



**Figure 9: Relationship between belowground biomass structures 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.**



**Supplemental Table A. Regression model results for the relationship between hydrology variables and surface accretion and accumulation rates in marshes of two mid-Atlantic US estuaries.**

<b>Response variable</b>	<b>Predictor variable</b>	<b>Adjusted R-square</b>	<b>t Ratio</b>	<b>P &gt; F</b>
Surface accretion rate	MHW	0.50	3.20	0.0064
	MLW		-4.26	0.0008
Organic accumulation rate	MHW	0.50	3.30	0.0054
	MLW		-3.69	0.0024
Mineral sediment accumulation rate	MHW	0.43	2.86	0.0126
	MLW		-3.75	0.0022