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, above- and belowground biomass were directly and positively related to rates of total, labile and refractory C accumulation. 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, only aboveground biomass was positively related to C accumulation, through the positive relationship with labile C accumulation rate. 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*

44 marshes, which naturally occur along the Atlantic and Gulf coasts of the U.S., roots and rhizomes of marsh plants are

45 estimated to comprise up to 90% of organic input (Howes et al. 1985). Accretion rates above the local organic

46 production, must be due to allochthonous sources of C and sediment (Morris et al. 2016). Yet, it is unclear whether

47 local plant organic matter input is constant across geomorphic settings that experience a range of environmental

48 conditions and sedimentation rates. Local environmental conditions such as hydrology, salinity, sediment availability,

49 and soil properties are predicted to play a key role in influencing relationships between biotic processes and rates of

50 C accumulation and accretion (Haslett et al. 2003). Despite knowledge of bio-physical feedbacks governing C

51 accumulation and accretion, and the recent emphasis on the efficiency of salt marshes in sequestering C, fine-scale

52 controls of marsh C accumulation are still poorly understood (Connor et al. 2001, Chmura et al. 2003, Mcleod et al.

53 2011). These fine-scale controls may account for a large portion of the spatial variability in C accumulation rates in

54 marshes (e.g., Mcleod et al. 2011; Ouyang and Lee 2014). Of the numerous studies that have separately quantified

55 plant productivity or biomass and soil carbon accumulation rates, few have examined relationships between plant

56 growth, decay, and biomass in concert with soil C accumulation and accretion. In addition, understanding these

57 relationships across natural systems is extremely important as multiple abiotic conditions will determine the ability of

58 marshes to accumulate and store C and adjust their elevation relative to sea-level.

59

60 While *insitu* plant biomass production may be a major C source, non-plant derived (e.g., edaphic algae) and

61 allochthonous C deposition also contributes to carbon accumulation in marsh soil. Some have suggested that

62 allochthonous C may be a more important component of surface sediments, while the accumulation of plant-derived

63 C from root productivity becomes more important at depth (Santilan et al. 2013). The relative magnitude of

64 allochthonous versus autochthonous carbon inputs may also differ within and among marshes depending on rates of

65 deposition (mineral and organic) and environmental conditions that regulate *insitu* productivity and decay. Higher

66 tidal range, greater supply of mineral nutrients and sediments, and lower salinities are conditions that are all predicted

67 to enhance both plant productivity and soil C accumulation (Mendelssohn and Kuhn 2003; Craft 2007; Kirwan and

68 Guntespergen 2010). Across geomorphic settings of estuaries, from deltas to coastal lagoons, physical and abiotic

69 factors often co-vary with potential consequences for C sequestration and even vulnerability to relative sea-level rise.

70 Microtidal marshes in coastal lagoons, for example, are considered particularly vulnerable to relative sea-level rise

71 due to limited sediment supply, weak and limited tidal movement for sufficient sediment transport and surface

72 deposition leading to a reliance on *insitu* organic matter production for accretion (Reed et al., 2008; Kirwan &

73 Guntenspergen 2010; Ganju et al., 2017). In contrast, marshes in geomorphic settings with high rates of mineral

74 sedimentation such as those near river deltas may have greater magnitudes of both allochthonous C deposition and

75 autochthonous plant C inputs (e.g., Craft et al. 2007). In tidal marshes of Australia, for example, soil C stocks in

76 fluvial environments containing finer-grained sediments were approximately double the C stocks in marshes of marine

77 sandy estuaries (Macreadie et al. 2017). Higher contributions of allochthonous C and greater preservation of plant-

78 derived C likely influenced greater soil C accumulation in fluvial versus marine geomorphic settings (Saintilan et al.

79 2013; Kelleway et al. 2016). Similarly, in marshes of a coastal plain estuary, soil C accumulation and accretion were

80 greater than in marshes of a coastal lagoon (Unger et al. 2016). In these systems, C accumulation rate was strongly

81 and positively related to the rate of mineral sedimentation. The strong positive relationship between mineral

82 sedimentation and C accumulation rates implied that mineral sediment availability influenced greater plant-derived C

83 inputs, greater allochthonous C inputs, and/or greater C preservation.

84

85 Stable C isotopic signatures have shed some light on the relative importance of different C sources in marsh soil. A

86 comparison of $\delta^{13}C$ in soils of mineral-rich and organic marshes showed a depletion of plant-derived $\delta^{13}C$ signatures

87 in mineral marsh soils and strong signal of local plant $\delta^{13}C$ in organic marsh soils (Middleburg et al. 1997).

88 Preferential decomposition of labile C, which is enriched, with more negative $\delta^{13}C$ values, relative to *Spartina* tissue

89 and preservation of refractory lignin, which is depleted relative to *Spartina* tissue, may partially explain the overall

90 shift in $\delta^{13}C$ in mineral-rich marshes (Benner et al. 1991). Another mechanism potentially causing the depletion of

91 $\delta^{13}C$ signatures relative to local plant tissue is a greater allochthonous C input consisting of organic matter sorbed onto

92 mineral particles, estuarine phytoplankton, microphytobenthos and non-local macrophytes (Middleburg et al. 1997).

93 Though labile soil C may be derived from algal sources, it is also possible that the environmental conditions in mineral-

94 rich marshes stimulate *insitu* plant productivity and inputs of labile plant C. Mineral sedimentation, for example,

95 tends to be positively related to C accumulation (Chmura et al. 2003; Unger et al. 2016) and also creates favourable

96 conditions for plant growth (DeLaune et al. 1990; Mendelssohn and Kuhn 2003). Specifically, mineral sediment input

97 can increase marsh elevation, supply a physical substrate for root growth, supply inorganic nutrients, raise the redox

98 potential, and promote the precipitation of sulfide with iron and manganese to form non-toxic compounds (DeLaune

99 et al. 2003). Regardless of the source, labile organic C can be more abundant in marshes with higher rates of mineral

100 sediment deposition, and ultimately drive total C accumulation rates (Unger et al. 2016).

101

102 The goal of this study was to examine the relationship between autochthonous plant-derived C inputs and longer-term

103 labile, refractory, and total organic C accumulation rates in short-form *Spartina alterniflora* marshes. In a previous

104 study, we found rates of C accumulation to be significantly greater in marshes of a coastal plain estuary, Delaware

105 Bay, USA than marshes of an adjacent coastal lagoon, Barnegat Bay (Unger et al. 2016). Total organic C accumulation

106 rates were positively associated with rates of mineral sedimentation and labile C accumulation. Refractory C

107 accumulation was similar across marshes averaging 78 ± 5 g/m^2/yr (Unger et al. 2016). The sources of the C fractions

108 were unknown. For this study, we tested the hypothesis that rates of *S. alterniflora* belowground productivity were

109 greater in marshes of the coastal plain estuary than in the marshes of the coastal lagoon, where a higher water table,

110 higher salinity, and lower rates of sediment deposition were predicted to limit root and rhizome growth. We predicted

111 that patterns of belowground productivity and turnover would mirror those of longer-term total and labile organic

112 carbon accumulation rates across marshes and estuaries. Our hypothesis would be supported if environmental

113 conditions that promoted C accumulation such as high rates of mineral sedimentation and, potentially, high tidal range

114 and low salinity also promote high belowground biomass production. Further, we examined the role of belowground

115 decay in explaining spatial patterns of C accumulation. We hypothesized that the amount of organic material remaining

116 following 20 months of belowground decomposition would be greater in marshes with higher C accumulation rates.

117 For this, the conditions that promote high rates of C accumulation may also promote the preservation of C particularly

118   in the upper soil column where much of the decay of labile organic matter occurs (Hackney and de la Cruz 1980;

119   Hackney 1987; Morris and Bowden 1986). Ultimately, the net amount of belowground biomass (C fractions greater

120   than ~1 mm in size) was predicted to be directly and positively related to the density of C in the soil profile and C

121   accumulation rate. Similarly, above-and belowground biomass was predicted to be positively related to soil C

122   accumulation. Finally, because plant productivity and decay processes as well as overall plant structure (e.g., height,

123   stem density, biomass) have been shown to be tightly regulated by abiotic factors, we examined the influence of local

124   environmental conditions (i.e., water level, salinity, soil nutrient status, and sediment deposition rates) on *S.*

125   *alterniflora* growth, decay and biomass across marshes and estuaries.

126

127   **2 Methods**

128   **2.1 Study sites**

129   Six marshes in two estuaries along the Mid-Atlantic coast of the United States, Barnegat Bay and Delaware Bay, New

130   Jersey were the focus of this study (Fig. 1). The two estuaries and marshes therein varied in geomorphic setting and

131   therefore, tidal range, hydrology, salinity, sediment availability, and nutrient concentrations also varied. The Delaware

132   Bay is a large coastal plain estuary extending 215 km from the head-of-tides to the bay mouth at the Atlantic Ocean.

133   Tidal amplitude is approximately 1.5 m at the mouth and increases up-estuary modulated by estuary and tidal channel

134   geometry. Barnegat Bay is a shallow coastal lagoon extending 62.7 km along the coast of New Jersey, separated from

135   the Atlantic Ocean by a barrier island apart from two inlets. Barnegat Bay experiences a relatively small tidal

136   amplitude ranging from 20 to 50 cm depending on location in the bay (Defne and Ganju 2014). Mean salinity ranges

137   from 18 to 25 with lowest salinities in the northern part of the bay farther from the inlets and also near Toms River

138   (Kennish 2001). Across the two estuaries, marshes ranged from being along a large tidal tributary with relatively low

139   salinity (Maurice River, MR, in Delaware Bay) to a back-barrier marsh (Island Beach State Park, IB) in Barnegat Bay,

140   which has been converting from *S. alterniflora* to shallow open water between the parallel mosquito ditches over

141   approximately the last decade, likely due to a lack of drainage through the ditches (pers obs). All six marshes had

142   some level of mosquito ditching. Reedy Creek (RC) marsh in northern Barnegat Bay had interior ponds which have

143   been expanding in size over time. Of the six marshes in the study, MR had the highest freshwater input and the highest

144   longer-term mineral sediment, total organic C and labile C accumulation and accretion rates (Unger et al. 2016). RC

145   and IB in Barnegat Bay, had the lowest rates of accumulation and accretion, while Channel Creek (CC) to the south

146   had larger mineral sediment input and was intermediate in accumulation and accretion rates to RC and IB and those

147   in Delaware Bay (Unger et al. 2016). Accretion rate in Barnegat Bay marshes (0.28 ± 0.06 cm/yr) over the last 50 –

148   100 years was less than the rate of relative sea-level rise over approximately the same time period (0.41 cm/yr; NOAA,

149   Tides and Currents; *in* Boyd et al., 2017). In Delaware Bay, salt marsh accretion rate (0.70 ± 0.26 cm/yr) exceeded

150   the rate of local relative sea-level rise over the same time period (0.34 cm/yr, NOAA, Tides and Currents). Study

151   locations have also been described in Elsey-Quirk 2016; Unger et al., 2016 and Boyd et al., 2017.

152

153   **2.2 Experimental design**

154 In each of the six marshes, five plots were established along a transect of increasing distance from the marsh/estuary
155 boundary. Transects ranged from 270 to 2970 m with shorter transects in smaller marshes (generally in Barnegat Bay)
156 and longer transects in marshes along larger tidal channels (in Delaware Bay). This transect-based study design, rather
157 than replicate plots in close proximity, was employed to capture a range of within-marsh variation, while also
158 stratifying by short-form *S. alterniflora*. Belowground ingrowth and litterbag decomposition studies were employed
159 at each of the five plots (n = 5). Vegetation structure (i.e., stem density and shoot height and above- and belowground
160 biomass) was measured at three of the five plots (nearest, middle and farthest from the estuary). Belowground biomass
161 was determined from 2-cm depth sections from half of a 15.2-cm diameter soil core. The other half of the core was
162 used for analysis of soil properties, C (total organic, labile, and refractory) and nitrogen concentrations, and ^{137}Cs and
163 ^{210}Pb-activity (*reported in* Unger et al., 2016; Boyd et al., 2017). Organic C (labile, refractory and total) accumulation
164 rates, with which we examined relationships with plant processes and properties (present study) were previously
165 published in Unger et al. 2016. C accumulation rates were calculated using ^{137}Cs-based accretion rates published in
166 Boyd et al. 2017.

167 **2.3 Environmental conditions**

168 **2.3.1 Marsh elevation, hydrology and salinity**
169 Elevations of the plots were collected using a Leica GS-14 (NJ NAD83, Geoid 12A). A minimum of three GPS survey
170 points were collected on the marsh surface at each plot. Two water level/conductivity recorders (In-Situ 5000 vented)
171 were installed in each of the six marshes from August 2012 to October 2013. Probes were placed in each marsh near
172 and far from the estuary approximately 5 m from the location of two of the five belowground ingrowth and litterbag
173 plots and two of the three standing biomass and soil core plots. Probes were installed in slotted wells to a depth of 70
174 cm. Water level and conductivity were recorded every 15 and 30 minutes, respectively. Elevation of the marsh surface
175 around each well was also collected. Water levels were referenced to the marsh surface, while elevations were
176 referenced to the North American Vertical Datum 1988 (NAVD88).

177

178 **2.3.2 Soil properties**
179 Soil cores were collected for testing relationships between belowground biomass and previously reported soil C
180 accumulation (*in* Unger et al., 2016) and accretion rates (*in* Boyd et al., 2017). PolyCate tubes 15.2 cm in diameter
181 and 110 cm long with a sharpened bottom edge were used to collect soil cores. Cores were taken back to the lab and
182 sectioned into 2-cm depth sections. Physical and chemical analyses were conducted on half of each 2 cm section. Soil
183 bulk density (g/cm^3), percent organic matter, total organic C, refractory and labile C, total nitrogen, and radiometric
184 analyses were conducted and is reported in Unger et al., 2016 and Boyd et al., 2017. The remaining half of each 2-
185 cm depth was rinsed and sieved for belowground biomass (see below).

186

187 **2.4 Vegetation parameters**

188

189 **2.4.1 Belowground growth and turnover**

190   Belowground growth rate (g DW m^{-2} yr^{-1}) was measured at five locations in each of the six marshes using rates of root

191   and rhizome growth into flexible mesh bags filled with a 1:1 mixture of unfertilized top soil and peat moss (i.e.,

192   ingrowth technique; McKee et al., 2007; n = 5). Ingrowth bags were constructed of flexible crawfish sack material

193   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

194   deployed in each of the five plots and sequentially harvested approximately every four months from April 2013 to

195   October 2014 to calculate belowground (root + rhizome) ingrowth rate. The four bags were deployed 50 cm apart in

196   each plot and all bags were installed vertically into 15 cm deep cored holes. Accumulated root and rhizome mass was

197   dried at 60°C to a constant weight. All of the roots and rhizomes in ingrowth bags were live based on color and

198   structural integrity. Belowground turnover was calculated by dividing ingrowth (g m^{-2} yr^{-1}) by live root and rhizome

199   biomass (g m^{-2}; Section 2.5.3). Ingrowth typically underestimates absolute rates of belowground productivity, and

200   therefore, both absolute productivity and turnover will be underestimated. However, our goal is to examine relative

201   responses to varying environmental conditions (Valiela et al., 1976; Graham and Mendelssohn 2016).

202

2.4.2 Belowground decay

204   Belowground decomposition of macro-organic matter was estimated using the litterbag technique. Litterbags (20 x

205   10 cm) made of 1 x 1 mm window screen mesh were filled with 9 g wet weight of macro-organic material comprised

206   of coarse roots and rhizomes in a live to dead ratio of 1:3. Organic material was subsampled from all soil cores (Section

207   2.5.3) and combined as a composite sample. Five replicate 9 g wet weight samples were dried at 60°C to estimate

208   initial dry weight. Four litterbags were deployed horizontally 10-cm below the surface in each of five plots

209   approximately 2 m from ingrowth bags in each of the six marshes (n = 5). Litterbags were placed in Delaware Bay

210   marshes on 12 December (DN), 13 December (MR), and 9 January (DV). Litterbags were deployed later in BB

211   marshes (13 February (RC), 29 March (IB), and 8 April (CC)) because of the difficulty of accessing these sites in the

212   months following Hurricane Sandy, which made landfall within 115 km of the marsh study sites on 29 October 2012.

213   Once deployed, litterbags were collected sequentially over the same ~20 month period of ingrowth study for

214   determination of mass loss over time. Percent of the original dry mass remaining at the end of the study period was

215   determined.

216

2.5.3 Biomass

218   Aboveground biomass was harvested from three plots within a 0.25 m^2 quadrat where soil cores for radiometric dating,

219   C analysis and belowground biomass were also collected. In the lab, stems were rinsed of mineral matter, counted,

220   and measured for height. Belowground biomass from half of each 2 cm soil section was rinsed to remove all mineral

221   sediment and separated into size classes of coarse and fine organic material. Coarse organic matter, comprised

222   primarily of stem bases and rhizomes, were further sorted into live and dead categories based on color and rigidity. A

223   sieve with a 2 mm mesh size retained coarse material and a sieve with a 1 mm mesh size retained fine organic matter,

224   which could not be easily separated into live and dead components. All above- and belowground biomass was dried

225   to a constant weight in a 70°C drying oven. Dry weights were converted to a g m^{-2} basis and depth profiles were

226   constructed. For analysis, belowground biomass in each core was summed to two depths in the soil profile. One was

227   to each respective ^{137}Cs peak, accounting for biomass that contributed directly to accretion above the ^{137}Cs peak depth.

228   However, live biomass is continually added to the soil column, and is often at depths well below the year 1963 ^{137}Cs

229   marker, and therefore, biomass was also summed to a specific depth, 50 cm, which is typical methodology for

230   quantifying belowground biomass.

231

232   **2.6 Data analysis**

233   Each environmental and vegetation parameter was checked for normality using the Shapiro-Wilks test. Log

234   transformations were used for most variables when necessary and appropriate and logit transformations were used for

235   percent data (e.g., percent soil organic matter, total nitrogen). A square root transformation was necessary to normalize

236   belowground ingrowth data. We tested for homogeneity of variances using the Levene Test on transformed data. The

237   only violation of the equal variance assumption was for the 95% rooting depth, which, following log-transformation,

238   failed the Levene test between estuaries, but not among marshes. We used a nested analysis of variance to test for

239   differences among marshes nested within estuaries in belowground ingrowth, decay rate, and vegetation structure

240   (e.g., stem density, height, rooting depth, and biomass). To test for relationships between belowground biomass

241   structure and accretion and C (total organic, labile and refractory) accumulation rates a stepwise regression analysis

242   was conducted. For analysis of relationships between belowground biomass and ^{137}Cs-based accumulation and

243   accretion rates, biomass summed above the ^{137}Cs peak depth was used. Matlab was used to calculate hydrologic

244   parameters including mean low water (MLW), mean high water (MHW), and frequency and percentage of time

245   flooded from the continuous water level time series (MATLAB 6.1, the Mathworks Inc., Natick, MA). Multivariate

246   correlation analysis was conducted to test for collinearity among environmental predictor variables. One

247   representative of highly correlated variables was chosen and redundant variables were removed for future analyses.

248   Based on the results of the correlation analysis, two hydrologic parameters, MHW and MLW depths relative to the

249   marsh surface, were selected to represent the suite of variables with which they were related, for which isolating

250   individual relationships with vegetation parameters would be impossible (Supplementary Table A). We chose to use

251   MHW and MLW over other variable such as % time flooded because these variables represent the magnitude of

252   surface flooding at high tide and the magnitude of drainage at low tide, respectively, both of which we predicted to be

253   biologically important. Salinity was also maintained in the models, although it was negatively correlated with several

254   hydrologic parameters, but not related to soil properties. Because of the strong relationship between soil bulk density

255   and long-term mineral sedimentation rate, only sedimentation rate was retained in subsequent models. Correlations

256   within environmental and vegetation data were expected, and therefore, a multivariate approach were used to analyze

257   the data. Multivariate analysis of variance (MANOVA) was used to test for differences among marshes nested within

258   estuaries in environmental parameters. If a significant multivariate treatment effect was found based on the Wilks

259   Lambda test, univariate tests were performed. Univariate post-hoc tests were conducted using Tukey's HSD test. To

260   examine the relationship between environmental and vegetation parameters across samples, a stepwise regression was

261   used with forward selection, starting with the full model and minimum BIC. Belowground ingrowth, decay and

262   biomass components were analysed in separate stepwise univariate models. Non-linear modelling was used when

263 relationships were non-linear. Unless otherwise specified, JMP V.12.1 was used for all statistical analysis (JMP

264 Version 12.1, SAS Institute Inc.).

265 **3 Results**

266 **3.1 Local environmental conditions**

267 Despite the stratification of our study plots in marsh interiors dominated by short-form *S. alterniflora*, environmental

268 conditions varied across marshes and estuaries. Elevations ranged from -7 to 87 cm, (NAVD88; Table 1). Tidal

269 amplitudes ranged from 5 to 22 cm (Table 1). Relative to the tidal frame, marsh surfaces ranged from below MLW

270 (IB) to above MHW (CC). Generally, marshes in Barnegat Bay experienced a lower tidal range, but were flooded for

271 a greater percentage of the year than Delaware Bay marshes (53 ± 12 and $40 \pm 9\%$, respectively; Estuary: $p = 0.0341$).

272 Among the marshes in Barnegat Bay, CC was the highest in elevation, sitting on average 3 cm above MHW. CC was

273 flooded less often (6% of the time), with higher water table salinities, and higher long-term rates of mineral

274 sedimentation than RC (Table 1). IB was moderate in elevation but flooded 86% of the time with long durations of

275 individual flood events, due to poor drainage through mosquito ditches. RC was the lowest elevation marsh, and

276 although not flooded as much as IB, was flooded 66% of the time. In Delaware Bay, DV was sitting high in the tidal

277 frame and, therefore, was flooded less often than the other marshes (MR and DN; Marsh[Estuary]: $F_{4, 11} = 53.15$, $p <$

278 0.0001). Overall, 65% of marsh areas had MLW depths within 5 cm of the marsh surface, indicating that the majority

279 of the root zone was continuously inundated. The lowest MLW depth of the 18 study areas was 11 cm below the

280 surface in a relatively high elevation area of DV in Delaware Bay.

281

282 Salinities ranged from 7 psu at MR in Delaware Bay to 40 psu at CC in Barnegat Bay. Salinity of Barnegat Bay

283 marshes was an average of 16 psu higher than Delaware Bay marshes, but there was also a significant difference

284 within Barnegat Bay with RC in the north having a lower salinity than IB and CC (Marsh[Estuary], $p = 0.0103$; Table

285 1). In Delaware Bay, salinity was variable across marshes as were soil properties, although MR had a higher soil bulk

286 density and less variable high rates of mineral sedimentation (Table 1). Soil nitrogen concentrations were greater in

287 RC and IB in Barnegat Bay than all other marshes (Table 1). Total soil N concentrations were positively correlated

288 with soil organic matter and strongly negatively correlated with bulk density (Supplemental Table A).

289

290 **3.2. Belowground growth and turnover**

291 Belowground ingrowth, comprised primarily of large roots and rhizomes, ranged from 0 to 550 g/m^2/yr across plots.

292 There were two plots in IB where no root ingrowth occurred, where previously vegetated areas had converted to

293 ponded mudflat. Regardless of the inclusion of these zero data points, ingrowth rates did not differ among marshes

294 (Fig. 2) and averaged 206 ± 22 g/m^2/yr (excluding zeros). Significant differences in belowground ingrowth were not

295 found among marshes because within marsh differences in environmental conditions influenced large variability.

296 Across all sampling plots, belowground ingrowth was negatively related to MLW depth, indicating that root and

297 rhizome growth was positively influenced by drainage (Fig. 3). However, under moderate inundation, root growth

298 was highly variable. Because MLW was generally above the lowest part of the ingrowth bag, and therefore, ingrowth

299 bags were inundated most of the time, the effect of hydrology on root growth was evident at the extremes of MLW,

300   where either average low water level exposed a significant portion of the ingrowth bag resulting in relatively high root

301   growth or low water averaged above the surface and the root zone was continuously flooded, where no roots grew.

302   However, even with the zero root growth data points removed, a positive relationship between drainage and root

303   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

304   of 0.15 ± 0.03 yr^{-1}. Turnover rates did not vary among marshes and were not influenced by measured environmental

305   parameters.

306

307   **3.3. Belowground decay**

308   Live and dead biomass in a ratio of 1:3 placed in litterbags 10 cm below the marsh surface tended to decline rapidly

309   following deployment. Litterbags were placed in Barnegat Bay a few months later in the spring than those in Delaware

310   Bay and may have led to a more rapid initial decline in mass (Supplemental Figure A). However, regardless of the

311   initial decay slopes, the percentage of root and rhizome material remaining at the end of approximately 20 months

312   was similar among marshes averaging $59 \pm 1\%$ (Fig. 2). The percent mass remaining was not significantly related to

313   any of the environmental factors tested (i.e., water level, salinity, soil nutrient concentration, sedimentation rate), as it

314   did not vary much among plots.

315

316   **3.4 Vegetation structure**

317   **3.4.1 Aboveground**

318   *Spartina alterniflora* stem density ranged from 0 to 4112 stems/m^2 across plots and did not differ significantly among

319   marshes (Table 3). In Barnegat Bay, there was a strong negative relationship between stem density and mean low

320   water depth, such that stem density increased with more drainage (Fig. 3). Stem density in Delaware Bay marshes

321   was not related to any environmental predictor variable.

322

323   Shoot height was approximately two times greater in MR in Delaware Bay than the other marshes with the exception

324   of RC (Marsh [Estuary]: $F_{1, 4} = 8.15$, p = 0.0026). Aboveground biomass was over six times greater in MR than RC

325   and IB in Barnegat Bay (Marsh [Estuary]: $F_{1, 4} = 8.13$, p = 0.0021; Table 3). In Barnegat Bay, live aboveground

326   biomass increased linearly with increasing mineral sedimentation rate and decreased linearly with increasing MHW.

327   This indicates that aboveground biomass responded positively to higher mineral sedimentation and less flooding. In

328   Delaware Bay, aboveground biomass increased with increasing MHW following a quadratic relationship (Fig. 7b).

329   Therefore, geomorphic differences between the two estuaries led to differences in vegetation response with

330   aboveground biomass stimulated by higher MHW in Delaware Bay, while aboveground biomass responded negatively

331   to increasing MHW depth in Barnegat Bay.

332

333   **3.4.2 Belowground**

334   Aboveground live biomass was not related to live, dead, fine, or total belowground biomass. Rates of belowground

335   ingrowth and decay were also not statistically related to belowground biomass stocks. The total amount of live

336   biomass (above- and belowground) was over three times greater in CC (3245 ± 768 g/m^2) than in RC (833 ± 41 g/m^2)

337   with no other differences among marshes (Marsh[Estuary]: $F_{1,4} = 4.2$, $P = 0.0227$).

338

339   Belowground biomass was variable within marshes. When calculated to a 50 cm depth, there was no difference among

340   marshes or between estuaries in total, live coarse, or dead coarse biomass (Table 3). However, the depth of live

341   biomass differed among marshes. The 95% rooting depth was greatest in DN, followed by MR, both of which had

342   greater live root depths than Barnegat Bay marshes (Marsh [Estuary]: $F_{4,\ 12} = 10.58$, $p = 0.0007$; Table 3; Fig. 6).

343   There was greater fine biomass in CC in Barnegat Bay than in MR in Delaware Bay (Table 3).

344

345   Biomass was also summed to ^{137}Cs-peak depths, which varied by 42 cm across plots. Depth of the ^{137}Cs peak ranged

346   from 9 to 17 cm in Barnegat Bay marshes and 17 to 51 cm in Delaware Bay marshes (Boyd et al. 2017). There was

347   similar or less biomass in Delaware Bay marshes to a greater depth than in Barnegat Bay marshes (Fig. 6). For

348   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

349   belowground biomass (live coarse, dead coarse and fine) above the ^{137}Cs peak, was significantly greater in DN and

350   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.

351   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

352   occurred at depths averaging 11 and 16 cm, respectively. Fine biomass was also greater in CC than in RC (Table 3).

353

354   Belowground biomass stocks were related to several measured environmental parameters. And while the aim of these

355   analyses was to examine cross-system relationships between environmental conditions and vegetation patterns, it

356   became apparent that the relationships were highly estuary-dependent. In Barnegat Bay, live belowground coarse

357   biomass was positively related to sedimentation rate and negatively to MHW (Fig. 4c, d). Dead belowground coarse

358   biomass was also negatively related to MHW in Barnegat Bay (Fig. 4f). This indicates that while mineral

359   sedimentation stimulated live root and rhizome biomass, an increase in high tide over the marsh surface was associated

360   with a decline in both live and dead coarse biomass. In Delaware Bay, live and dead coarse biomass was variable

361   across the range of environmental conditions. However, both fine and total biomass declined with increasing rates of

362   mineral sedimentation. Fine biomass comprised 45 – 69% of total belowground biomass in Delaware Bay marshes,

363   and the decline in fine biomass resulted in a decline in the total biomass. Fine biomass also declined with a decline

364   in salinity in Delaware Bay.

365

366   **3.5 Relationship between vegetation and soil C and accretion**

367   3.5.1. Soil C density profiles

368   Belowground biomass profiles corresponded well with profiles of organic C density, depending on the biomass

369   component (live coarse, dead coarse, or fine), depth, and whether the C was chemically labile or refractory (Fig. 6).

370   Across marshes, total C density profiles were positively correlated with dead coarse and fine biomass (adj r^2 = 0.25,

371   p < 0.0001). Labile C density was weakly related to biomass stocks (live and dead coarse: adj r^2 = 0.05, p < 0.0001),

372   while all (live, dead, and fine) biomass stocks explained 28% of the variation in downcore refractory C densities (adj

373 $r^2 = 0.28$, p < 0.0001). Live coarse biomass was the only significant predictor of labile C density in four of the six

374 marshes (Table 4). In IB, no belowground biomass component was related to labile C density and in MR, labile C

375 density was related to fine biomass (Table 4). In RC, labile C density was negatively related to live biomass, indicating

376 that as live root biomass increased, labile C declined (Fig. 6). This is due to changes in the relationship between live

377 biomass and labile C with depth. From the soil profiles, it is clear that labile C density mirrors live coarse biomass

378 dynamics to the depth limit of the live root zone. Below the live rooting depth, labile C density tends to increase (RC,

379 IB, and CC), likely associated with an increase in preservation of labile C and compaction and increased soil bulk

380 density.

381

382 Refractory C density increased in-step with belowground biomass toward the surface in Barnegat Bay marshes, but is

383 relatively uniform with depth regardless of biomass changes in Delaware Bay marshes (Fig. 6). Nevertheless,

384 refractory C density in the Delaware Bay marshes was positively related to the amount of dead biomass (Table 4). In

385 the Barnegat Bay, refractory C density was related to both live and dead biomass (Table 4). This suggests that the

386 labile/refractory nature of the biomass produced may differ among the marshes and estuaries. While interesting

387 relationships emerged for labile and refractory C densities and biomass components, some of the relationships were

388 masked when examining total (labile + refractory) soil organic C densities, which were variably related to biomass

389 components. Three marshes, IB, CC, and MR, had relatively strong soil C density-belowground biomass relationships

390 while other marshes had weak or non-detectable relationships (RC, DV, and DN).

391

392 3.5.1. C accumulation and accretion rates

393 We found no relationship between rates of belowground ingrowth and longer-term labile and total C accumulation

394 rates. Belowground turnover was weakly (adj $R^2 < 0.35$) negatively related to total organic and labile C accumulation,

395 largely due to the positive relationship between live belowground biomass and labile C accumulation rates

396 (Supplemental Figure B; see below). Percent mass remaining in belowground litterbags was, likewise, unrelated to C

397 accumulation rates. However, across the two estuaries, there was a positive relationship between aboveground

398 biomass and longer-term total organic and labile C accumulation (Fig. 7). Aboveground live biomass also explained

399 37% of the variation in ^{137}Cs-based accretion rates (adj $R^2 = 0.37$, p = 0.0058, data not shown), which was largely

400 related to the effect of aboveground biomass on labile C accumulation rate. Aboveground live biomass explained

401 70% of the variation in labile C accumulation (Fig. 7).

402

403 Relationships between belowground biomass and C accumulation and accretion rates were estuary dependant. Total

404 and live belowground biomass corresponded to the pattern of total organic C accumulation across marshes in Barnegat

405 Bay, but not Delaware Bay (Fig. 8). When compared statistically, C accumulation and accretion rates were positively

406 related to cumulative belowground biomass above the ^{137}Cs peak depth only for Barnegat Bay marshes (Fig. 9). Live

407 coarse and fine biomass explained 86% of the variation in total C accumulation in Barnegat Bay marshes (Fig. 9).

408 Live coarse biomass was positively related to labile C accumulation and fine biomass was positively related to

409 refractory C accumulation rate (Fig. 9). Accretion rate did not scale with the amount of belowground biomass in

410   Delaware Bay, but live and dead coarse biomass explained 78% of the variation in accretion rate in Barnegat Bay
411   (Fig. 9).

412

413   **4.0 Discussion**

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

428

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

447   different, the lack of a spatial relationship between root productivity and C accumulation rates may also be due to

448   time step differences in short-term (~2 yr) process rates and processes integrated over a longer time period (~50 yr),

449   and the potential for allochthonous C deposition across marshes.

450   Belowground decay did not vary much across a wide range of environmental conditions, and was not related to longer-

451   term C accumulation rate. By using a composite of biomass collected across study sites for our decomposition study,

452   we were able to examine the effect of abiotic factors on belowground decay. Our results indicated that the range of

453   environmental conditions across marshes did not differentially affect belowground decay. This could be because the

454   range of conditions in the subsurface soil in the marsh interior were not great enough to illicit a strong effect. With

455   respect to hydrology, however, several studies have shown that decay rates are variable in or insensitive to different

456   flooding regimes and redox potentials (Valiela et al., 1984; Blum 1993; Kirwan et al., 2013). The loss of organic

457   matter reaching similar asymptotes of dry mass across our study sites suggests that the amount of recalcitrant tissue

458   was more influential than environmental differences. While both labile polysaccharides and refractory lignin can be

459   leached during initial decay (Benner et al. 1986; Moran and Hodson 1990), enrichment of recalcitrant tissues in the

460   latter stages of decay slows decomposition, particularly under anaerobic conditions. We used a composite mix of live

461   and dead large organic material in a ratio of 1:3, which experienced rapid initial decomposition, likely the decay of

462   labile live and recently dead tissues, followed by an asymptotic decline in loss of organic matter to an average of 59%

463   dry mass remaining. This percentage corresponds well with the 55% of roots and rhizomes remaining following 18

464   months in a Sapelo Island, GA salt marsh (Benner et al., 1991). Lignocellulose content in root and rhizome biomass

465   of short-form *S. alterniflora* is approximately 79.5% (Hodson et al., 1984). Though relatively slow to decay under

466   anaerobic conditions, the cellulosic portion undergoes higher rates of mineralization than lignin, which comprises

467   approximately 19.3% in roots and rhizomes (Hodson et al., 1984). Lignin components can continue to be lost under

468   anaerobic conditions (Benner et al. 1991); however, the decay of recalcitrant soil organic matter can also be relatively

469   insensitive to flooding and subtle changes in redox potentials (Mueller et al. 2016). In the present study, we used a

470   composite of root and rhizome samples collected across our study sites, and therefore, site differences in lability of

471   biomass was not tested in this study, which may have implications for spatial variability in soil C storage.

472

473   Belowground turnover rates of *S. alterniflora* were within the range found in other studies ($0.17 - 0.71$ yr^{-1};

474   Schubauer and Hopkinson 1984), despite much lower productivity rates inherent to the ingrowth technique in the

475   present study. We found a significant but variable negative relationship between belowground turnover and total

476   organic and labile C accumulation rates. This finding was largely due to the positive relationship between live

477   coarse biomass and labile C accumulation rate. With rates of root productivity being equal, an increase in live

478   biomass lowers the turnover rate. While turnover explained <35% of the variation in C accumulation rates across

479   estuaries, biomass components (above- and belowground) explained $39 - 86\%$ of the variation in soil C

480   accumulation rates.

481   Rates of soil C accumulation and accretion were strongly related to *S. alterniflora* biomass. Aboveground live biomass

482   was positively related to organic C accumulation rate across estuaries, primarily though the strong relationship with

483   labile C accumulation rate. Mechanisms of aboveground live biomass influencing labile soil C include the direct input

484   of aboveground litter to the soil. For *S. alterniflora* much of the aboveground litter is subject to decay and mechanical

485   breakdown by tidal action (Teal 1962), and therefore, little of the aboveground litter of *S. alterniflora* in these

486   temperate marshes is thought to be incorporated into the marsh soil. The standing live aboveground biomass, however,

487   represents both photosynthetic capacity and growing conditions, which may directly affect the production of labile

488   exudates and new labile tissues belowground. Additionally, aboveground shoots influence surface deposition and

489   accumulation through the direct capture of particles on plant stems and the indirect reduction of flow velocity inducing

490   sediment settling (Stumpf 1983; Leonard and Luther 1995). This has been illustrated for fertilized and unfertilized *S.*

491   *alterniflora* plots, where aboveground biomass was three times greater and surface accretion rate was 2 mm/yr greater

492   in response to fertilization (Morris and Bradley 1999; Morris et al. 2002). The higher accretion rate was accounted for

493   by more efficient trapping of sediments (Mudd et al., 2010). Therefore, both labile live plant tissues and labile organic

494   C associated with sediment may be enhanced with greater aboveground biomass. This finding supports other studies

495   showing positive relationships between aboveground biomass and soil microbial processes, including the

496   decomposition of recalcitrant soil organic matter, which was hypothesized to be due to greater labile C inputs

497   (substrate-induced priming) and/or greater rhizosphere oxygenation (O_2-induced priming; Mueller et al. 2016). Our

498   data suggest that aboveground biomass may increase soil C accumulation directly through the inputs of labile C and

499   positive bio-physical feedbacks for sedimentation, which increases labile C deposition, burial, and preservation.

500   Relationships among aboveground plant biomass, labile and total C accumulation rate, and mineral sedimentation rate

501   indicate positive feedbacks among these processes (Unger et al. 2016; present study).

502

503   While aboveground biomass was positively related to organic and labile C accumulation rate across estuaries,

504   aboveground biomass response to flooding was estuary-dependent. In the coastal plain estuary, aboveground biomass

505   increased with a higher mean high tide level, whereas in the coastal lagoon, aboveground biomass declined with higher

506   mean high water depth. In the coastal lagoon, stem density increased with greater drainage. With all other conditions

507   being equal, plant biomass of *S. alterniflora* has a parabolic relationship with elevation relative to mean sea level

508   (Morris et al. 2002). Above- and below an optimum elevation, biomass declines. Our study of marshes in different

509   geomorphic settings illustrates how environmental conditions in estuaries can illicit differential responses to individual

510   environmental parameters. In the coastal lagoon, a combination of less flooding and greater mineral sedimentation

511   rates promoted greater aboveground (and belowground) biomass. Lower tolerance to flooding in the coastal lagoon

512   marshes as compared to the coastal plain marshes is likely due to greater soil organic matter content, lower redox

513   potential, lower mineral sediment and nutrient availability, and higher sulfide concentrations (Bradley and Morris

514   1990; Reddy and DeLaune 2008). Differential flooding effects on aboveground biomass driven broadly by estuary

515   geomorphology can partially explain spatial variation in labile and total organic C accumulation rate across estuaries,

516   which was linearly and positively related to aboveground biomass.

517

518   Belowground biomass contributes directly to soil organic matter and, in this study, was a good predictor of soil C

519   accumulation rates, but only in the coastal lagoon marshes. This indicates that as geomorphic conditions change such

520   as with an increase in mineral sedimentation rates, belowground biomass can become uncoupled to soil C

521   accumulation and accretion rates. In the coastal lagoon marshes, live roots and rhizomes were concentrated in the top

522   30 cm depths, likely associated with a combination of high water table and high soil organic matter leading to low

523   redox potentials and high sulfide concentrations at depth (DeLaune et al. 1983b; Saunders et al. 2006). In contrast, in

524   the coastal plain estuary, live rooting depths were variable but often extending to 40 – 50 cm depth. Greater neap tide

525   drainage (data not shown), lower soil organic matter content throughout the soil depth profile, and higher redox

526   potentials likely accounted for the lower live rooting depths. Across the coastal lagoon marshes, labile C accumulation

527   rate increased as live belowground biomass increased. Fine biomass had a positive relationship with the rate of

528   refractory C accumulation, and refractory C density was relatively high just below the marsh surface. Both of these

529   live and fine biomass components, therefore, were positively related to the total C accumulation rate. Accretion in

530   these marshes was positively associated with the live and dead coarse biomass, likely due to the high porosity

531   associated with stem bases, rhizomes, macroorganic matter, and surrounding soil. In the coastal plain estuary, C

532   accumulation and accretion rates were not significantly related to belowground biomass. It may have been presumed

533   that marshes with higher tidal ranges and higher rates of mineral sedimentation would have greater stocks of

534   belowground biomass. In these marshes, mineral sediment accumulation rates ranged from less than 500 to over 4000

535     $g/m^2/yr$, yet belowground biomass did not vary much along this gradient. At similar rates of mineral sedimentation,

536   belowground live coarse biomass was over 1000 g/m^2 lower in marshes of the coastal plain estuary as compared to

537   the coastal lagoon, despite a greater live rooting depth. This may be associated with higher soil redox potentials and a

538   lower requirement for rhizome photosynthate storage (Gallagher and Kibby 1981) in the coastal plain marshes. High

539   belowground biomass is typically found in marsh areas with lower redox potential (Gallagher and Plumley 1979;

540   Dame and Kenny 1986 and references therein). This is hypothesized to be due to greater investment in belowground

541   production (Hopkinson and Schubauer 1984) and less photosynthate transfer from underground rhizomes throughout

542   the year, which results in lower aboveground biomass and higher belowground biomass in short-form interior

543   populations of *S. alterniflora* than tall-form populations growing along creekbank (Gallagher and Kibby 1981).

544   Differences among estuarine settings and soil organic matter contents may also drive spatial patterns in belowground

545   biomass and allocation. At higher sedimentation rates found in the coastal plain estuary, fine belowground biomass,

546   which was a significant predictor of refractory C accumulation in the coastal lagoon, declined significantly. In the

547   marsh with the highest rates of mineral sedimentation, and labile and total organic C accumulation (MR), the lower

548   quantity of fine biomass may be due to a shorter time period allowed for growth and accumulation. The labile nature

549   of fine biomass here suggests preservation of labile fractions of fine biomass. With relatively low total belowground

550   biomass, burial and small particle (< 1 mm) accumulation support high C accumulation and accretion rates. The

551   mechanism of fine organic matter loss or limited input with greater mineral sedimentation rates is unclear, particularly

552   when these marshes have the highest rates of labile and total organic C accumulation in our study (Unger et al., 2016).

553   In marshes with the highest rates of C accumulation, labile C density, in particular, remained high when biomass

554   stocks were low. High accumulation rates in marshes with low biomass seem to be maintained by a combination of

555   high live root biomass at depth, high allochthonous C deposition, effective preservation of labile C, and high burial

556   rates.

557

558 Our findings also provided insight as to the relative inputs of local plant-derived versus non-plant derived (e.g.,

559 edaphic algae) and allochthonous C to the labile and refractory C pools. We found significant relationships between

560 belowground biomass stocks and soil C density. The significance and strength of these relationships depended on

561 geomorphic setting, anatomical part, and the labile or refractory nature of the soil C. Comparisons of biomass and C

562 density profiles to profiles of mineral sediment volume (Unger et al. 2016), yields several important insights on how

563 plants and sediments interact to influence soil C. Labile C density was related to live belowground biomass in most

564 marshes. Below the live root zone and in marshes with high sedimentation rates, labile C preservation was high. In

565 marshes where mineral sedimentation was high, labile soil C became more important, regardless of the belowground

566 biomass pools. Labile C density was weakly related to biomass stocks, and despite, significant relationships between

567 live root biomass and labile C accumulation in the root zone above the ^{137}Cs peak depth in Barnegat Bay, labile C

568 density was often higher at deeper depths with lower biomass. This suggests that labile C density, while significantly

569 related to live root biomass at the surface is being physio-chemically preserved at depth regardless of the source.

570 Associations with iron oxide minerals seem to be particularly important for long-term organic C preservation (Kögel-

571 Knabner et al. 2008). Refractory soil C density was more strongly related to belowground biomass across all marshes,

572 indicating, as expected, that plant biomass is the primary contributor to refractory soil C. In the highly organic marshes

573 of the coastal lagoon, biomass played a strong role in increasing refractory C in the upper soil column with both live

574 and dead biomass related to refractory C density. Soil profiles indicated that in marshes with a concentration of

575 biomass just below the surface and where mineral sedimentation was low, refractory C dominated the soil C pool. The

576 relationship between live and dead biomass and refractory C in the coastal lagoon marshes, suggests that the tissue

577 quality may be more refractory than in marshes of the coastal plain estuary, where only dead biomass was associated

578 with refractory soil C density. This finding supports the hypothesis that under constrained growing conditions (e.g.,

579 high salinity, high inundation, low tidal range), more energy may be invested into the production of recalcitrant tissues

580 such as lignin, cellulose and hemicellulose (Knops et al. 2007). This is also supported by marshes with higher live

581 and total biomass (e.g., DN vs IB) yet much lower refractory C densities. In the coastal plain estuary, refractory C was

582 associated with dead biomass and, in most sites, the broken down fine biomass.

583

584 Geomorphology played a large role in influencing the relative importance and contribution of plant biomass to soil C

585 and marsh accretion rate. Geomorphic conditions of high sediment availability and larger tidal range, which can

586 mobilize and distribute sediments in the main channel and creeks of the coastal plain estuary work in concert to

587 promote C accumulation and accretion. Estuarine dynamics in the coastal lagoon are characterized by localized

588 sediment supplies and limited tidal energy to resuspend, transport and deposit sediments, and therefore, the marshes

589 are highly dependent on organic matter production for accretion. Within this system, a high sediment supply and high

590 elevation promoted a positive feedback between above- and belowground biomass and elevation. Because of localized

591 sediment supplies (e.g., CC) and other geomorphic differences, there was no correlation between hydrology and

592 longer-term sedimentation rates even over longer time periods (present study, Boyd et al. 2017). Importantly, while

593 studies suggest the vulnerability of microtidal marshes in coastal lagoons (Reed et al., 2008; Kirwan & Guntenspergen

594   2010; Ganju et al., 2017), we illustrate the importance of localized sources of sediments as being the key to their
595   survival through the positive feedback on live and dead coarse and fine root biomass, and organic matter and C
596   accumulation rates. Continuous standing water, enlargement of interior ponds, and loss of aboveground vegetation
597   are all signs of marsh deterioration. At IB, two of the sampling locations had permanent shallow water between ditches
598   and had lost the aboveground biomass. The remnants of former vegetation was evident belowground, where
599   significant quantities of live stem bases, roots and rhizomes were present to below 28 cm depth at least three years
600   after aboveground biomass was permanently lost.

601

602   Our dataset allows for a comparison of dynamics between individual marshes to highlight important geomorphic
603   effects on plant biomass. RC in Barnegat Bay and DN in Delaware Bay experienced comparable hydrology and
604   salinity in the marsh interior (Table 1).   Yet, estuarine tidal range averaged approximately 0.3 m and 1.5 m, in RC
605   and DN respectively (USGS gage 01408167 and 01411435, respectively) and longer-term rates of mineral
606   sedimentation were an order of magnitude larger, and soil bulk density was three times greater in DN than in RC
607   (Boyd et al., 2017; Unger et al., 2016). So, despite a similar hydrology in the marsh interior, tidal range in the estuary
608   and creeks and sediment supply were much greater in DN than in RC. Aboveground biomass averaged two times
609   higher in DN than RC. Belowground live coarse biomass averaged 2456 and 721 g/m^2 in DN and RC, respectively
610   and dead coarse biomass averaged 1063 and 280 g/m^2 in DN and RC, respectively. Live rooting depth was also
611   significantly greater in DN (46 cm) as compared to RC (19 cm). In contrast, CC and DV, two of highest elevation
612   marshes in the two estuaries. CC was in Barnegat Bay and DV was in Delaware Bay. Overall, many of the hydrologic
613   parameters were comparable. Salinity, however, was significantly higher at CC than DV, but soil organic matter, bulk
614   density and mineral sedimentation rate did not significantly differ. With both hydrology and sedimentation rates being
615   within range of each other, these two marshes in very different geomorphic settings had comparable biomass and
616   organic C accumulation rates. Biomass profiles were also similar between marshes with the exception of greater fine
617   organic matter in CC, particularly between 4 and 20 cm depth.

618

619   **4.6 Conclusions**
620   The fate of low-lying salt marshes as sea-level rises depends, in part, on their ability to accumulate organic matter and
621   to trap sediments. Sediment supply is also a major factor and may be most important in influencing the biophysical
622   processes that promote accretion and soil C accumulation. Our study illustrates that above- and belowground biomass
623   dynamics in sediment-limited *S. alterniflora* marshes are strongly related to rates of mineral sedimentation, which
624   promotes positive feedbacks between biomass, soil C accumulation, and elevation. Soil C accumulation and accretion
625   rates were strongly related to biomass fractions in the coastal lagoon estuary, where all biomass components were
626   positively related to refractory C. In marshes where sediments were more readily available, total belowground
627   biomass and fine biomass declined with increasing rate of mineral sedimentation and lower salinity. In the coastal
628   plain estuary, aboveground biomass was a significant predictor of labile C accumulation rate while belowground
629   biomass did not scale with C accumulation and accretion. Overall, our study shows that marshes in geomorphic
630   settings with limited sediment supply and delivery, have lower rates of organic C accumulation and accretion, which

631   are related to and limited by plant biomass. Plant biomass can be further stimulated by additional sediment input. In

632   geomorphic settings where sediment supply and deposition rates are high, a strong positive relationship between

633   aboveground biomass and labile C accumulation can promote high total C accumulation and accretion rates.

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637

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644

645

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

Environmental parameter	Barnegat Bay			Delaware Bay		
	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}

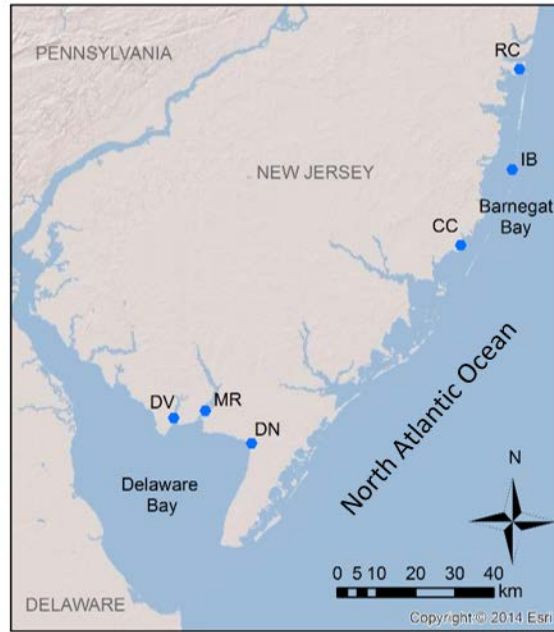
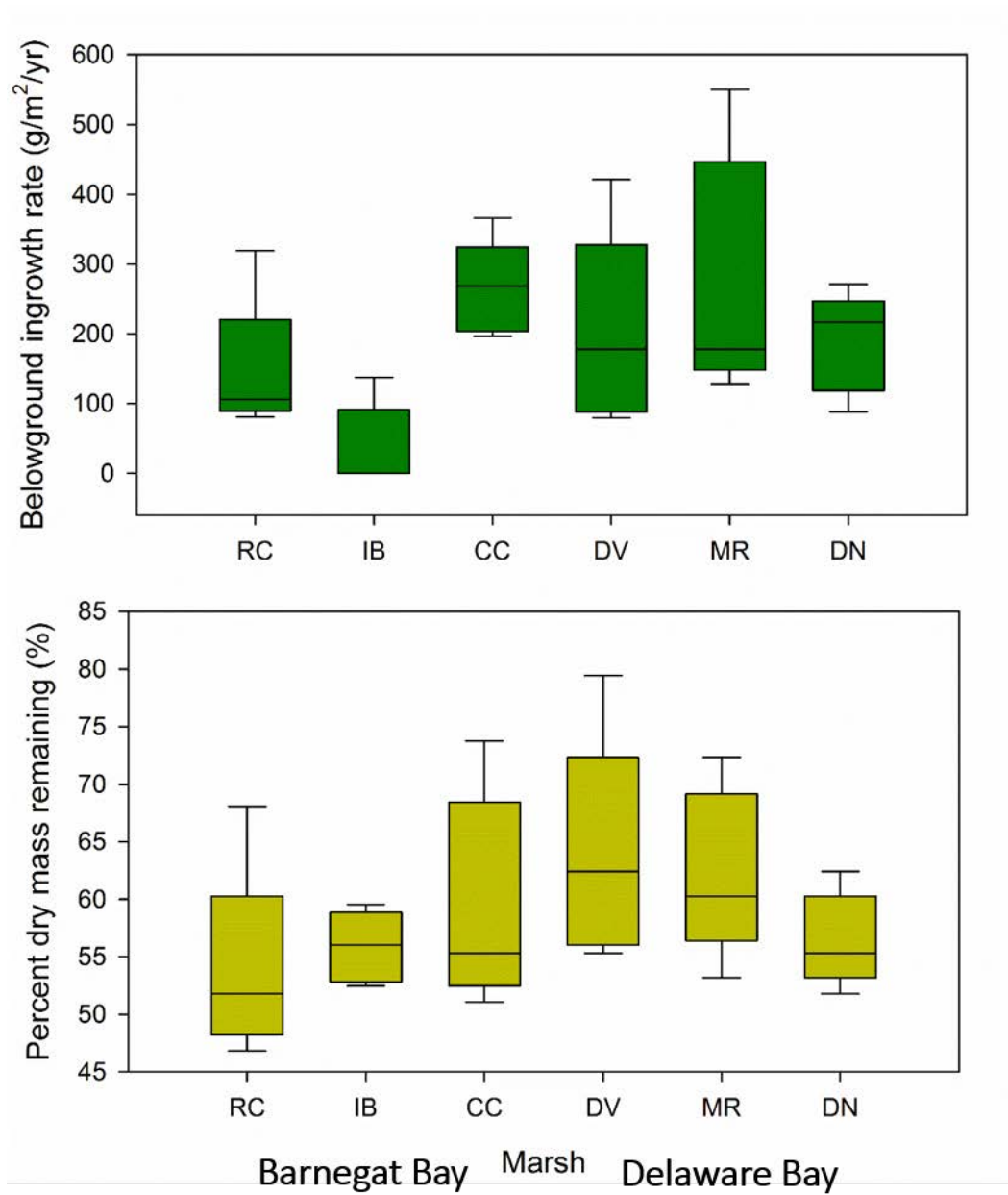
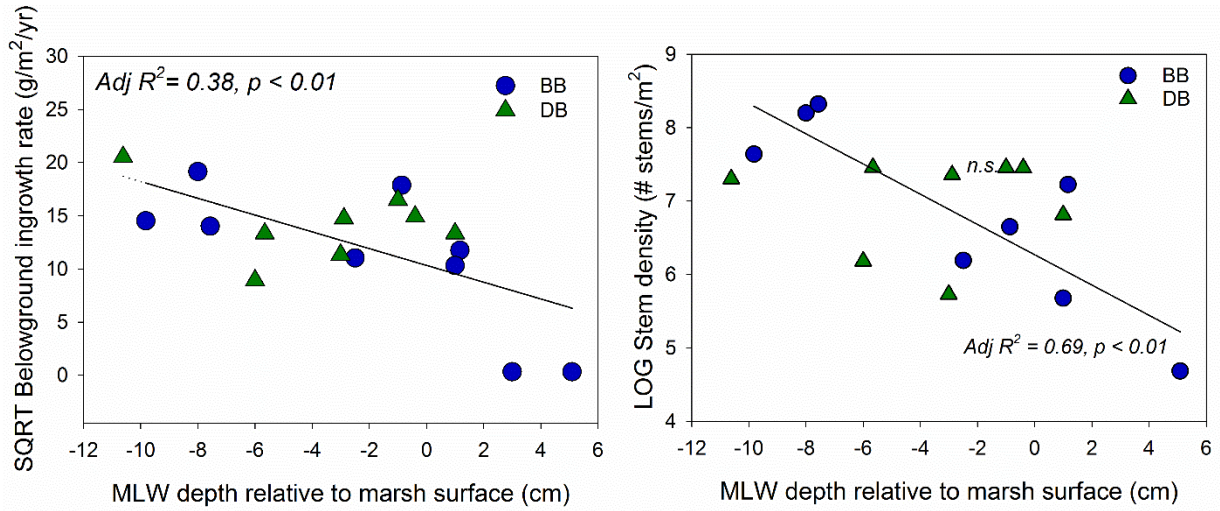
844

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.

C density fraction	Barnegat Bay			Delaware Bay		
	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

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

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

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

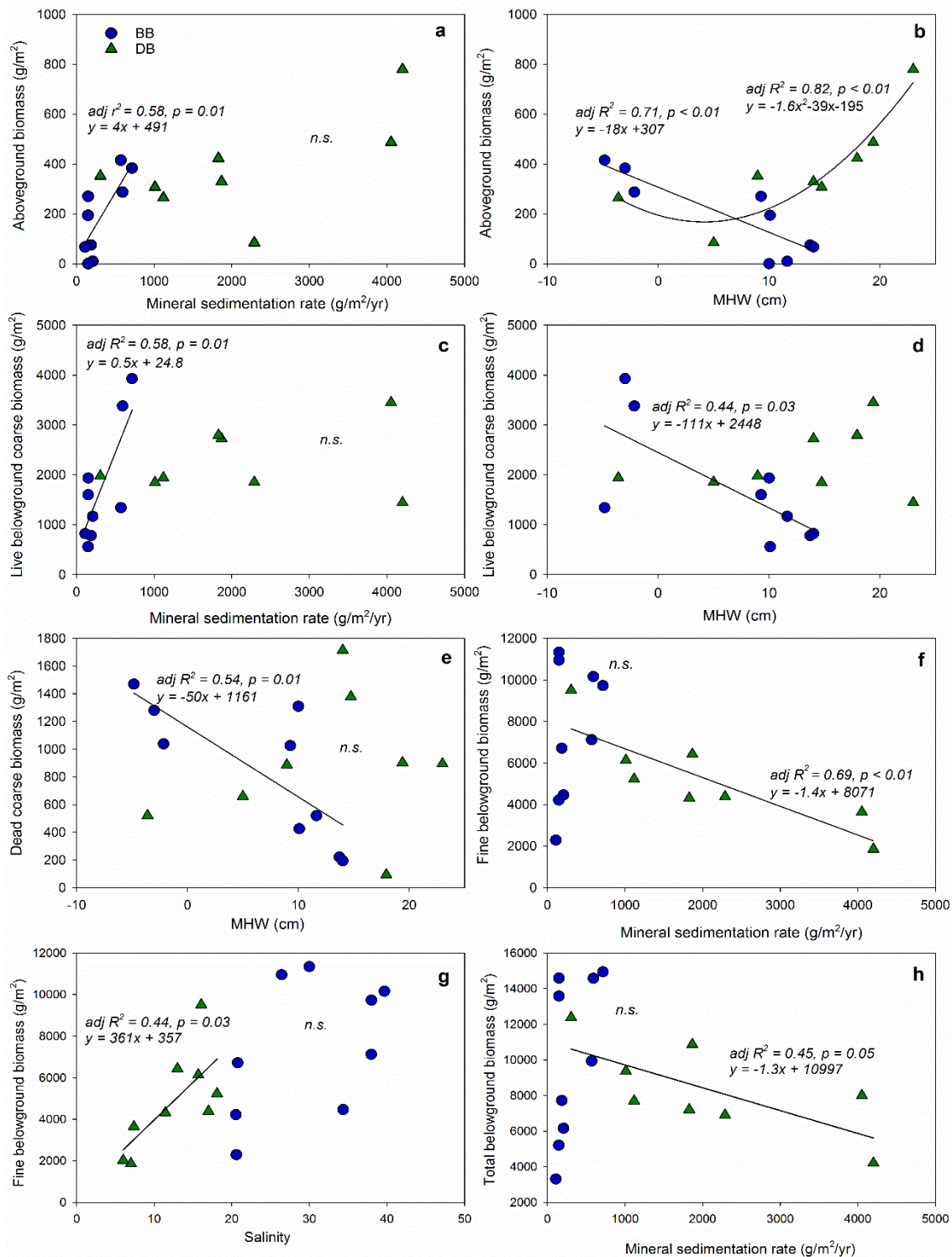



Figure 4: Relationships between vegetation structure and environmental parameters. For these analyses, belowground biomass to 50-cm depth was used. Mineral sedimentation rates were calculated using ^{137}Cs-dating, and therefore, are average rates over the last 50 years (Boyd et al. 2017). Blue dots 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.

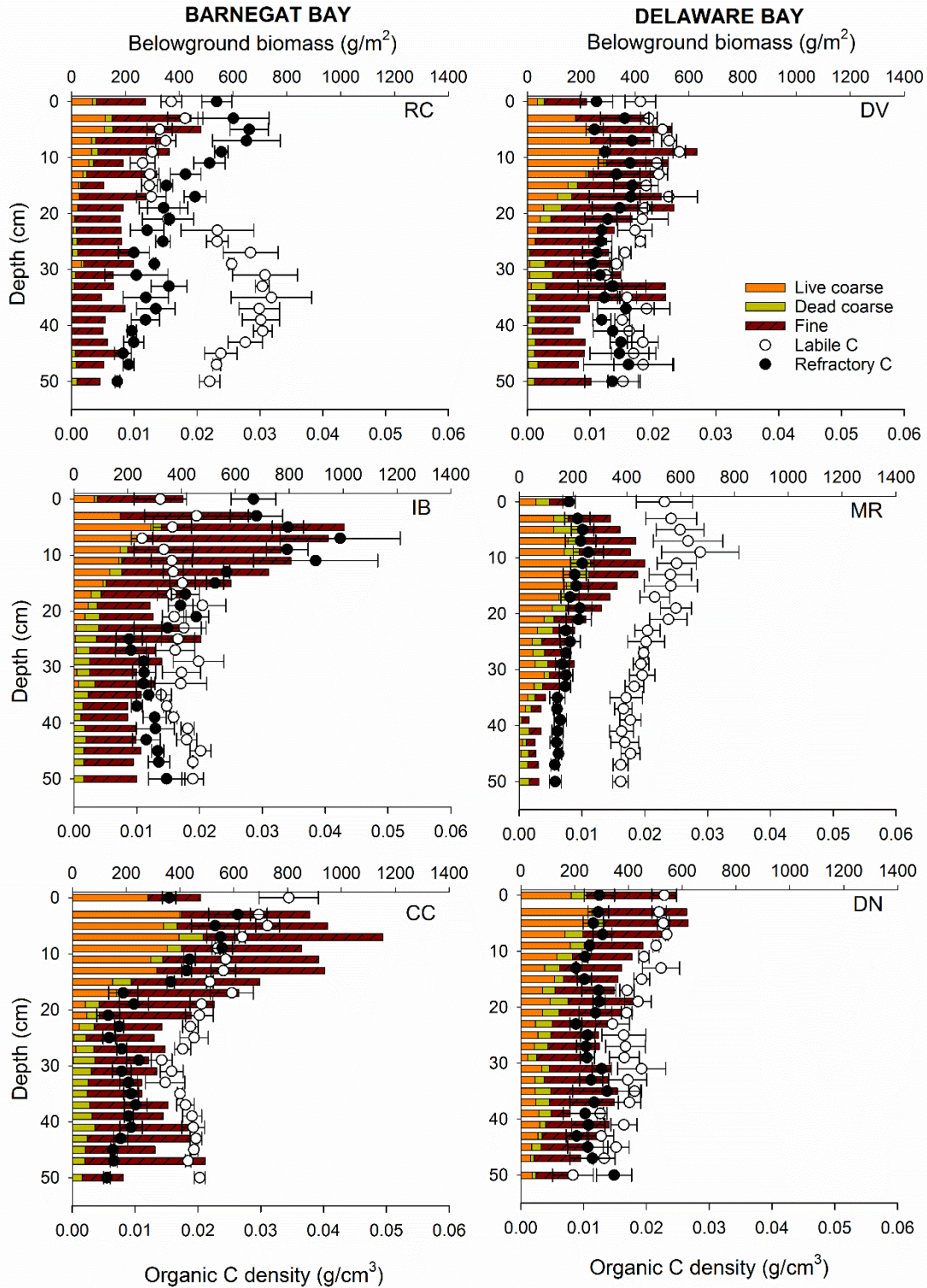



Figure 5: Belowground biomass and labile and refractory organic C density profiles in marshes of two Mid-Atlantic estuaries. Biomass data are means (standard errors not shown). C density data previously reported in Unger et al., 2016.

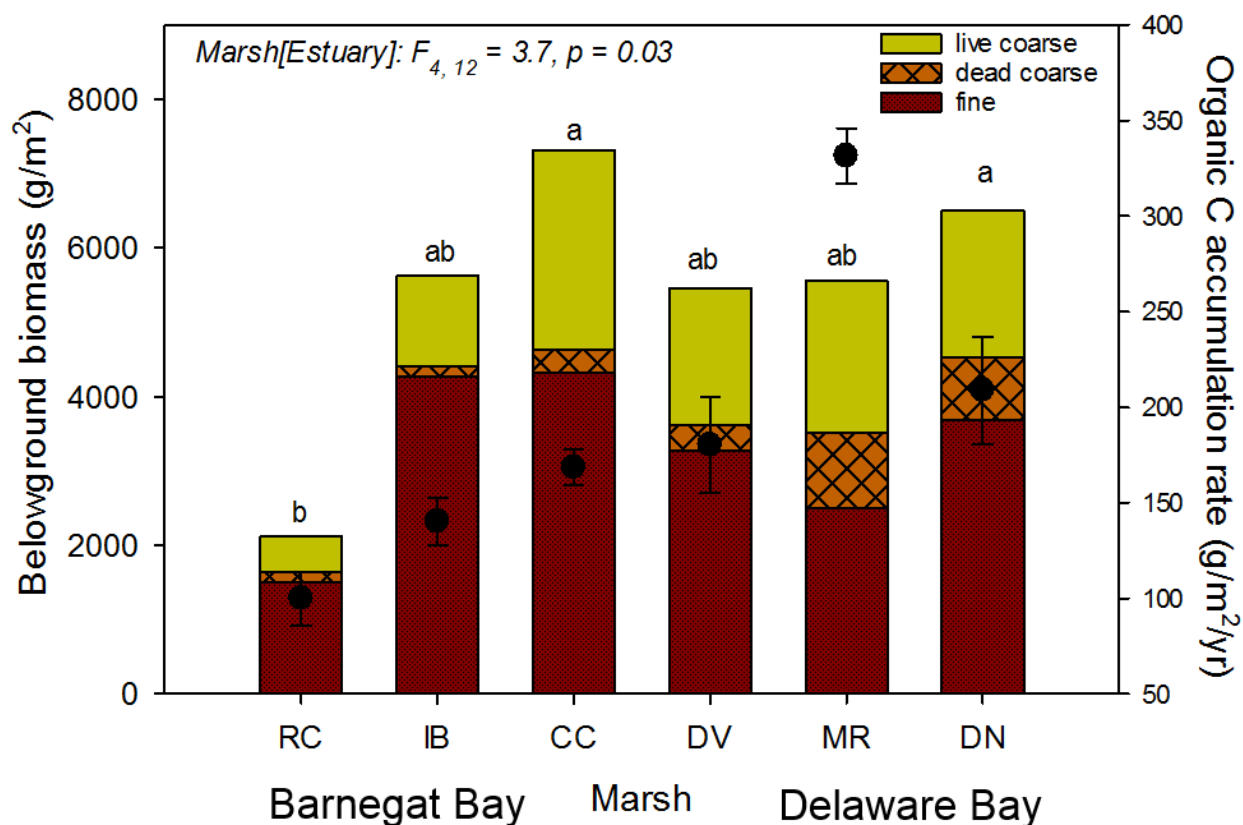



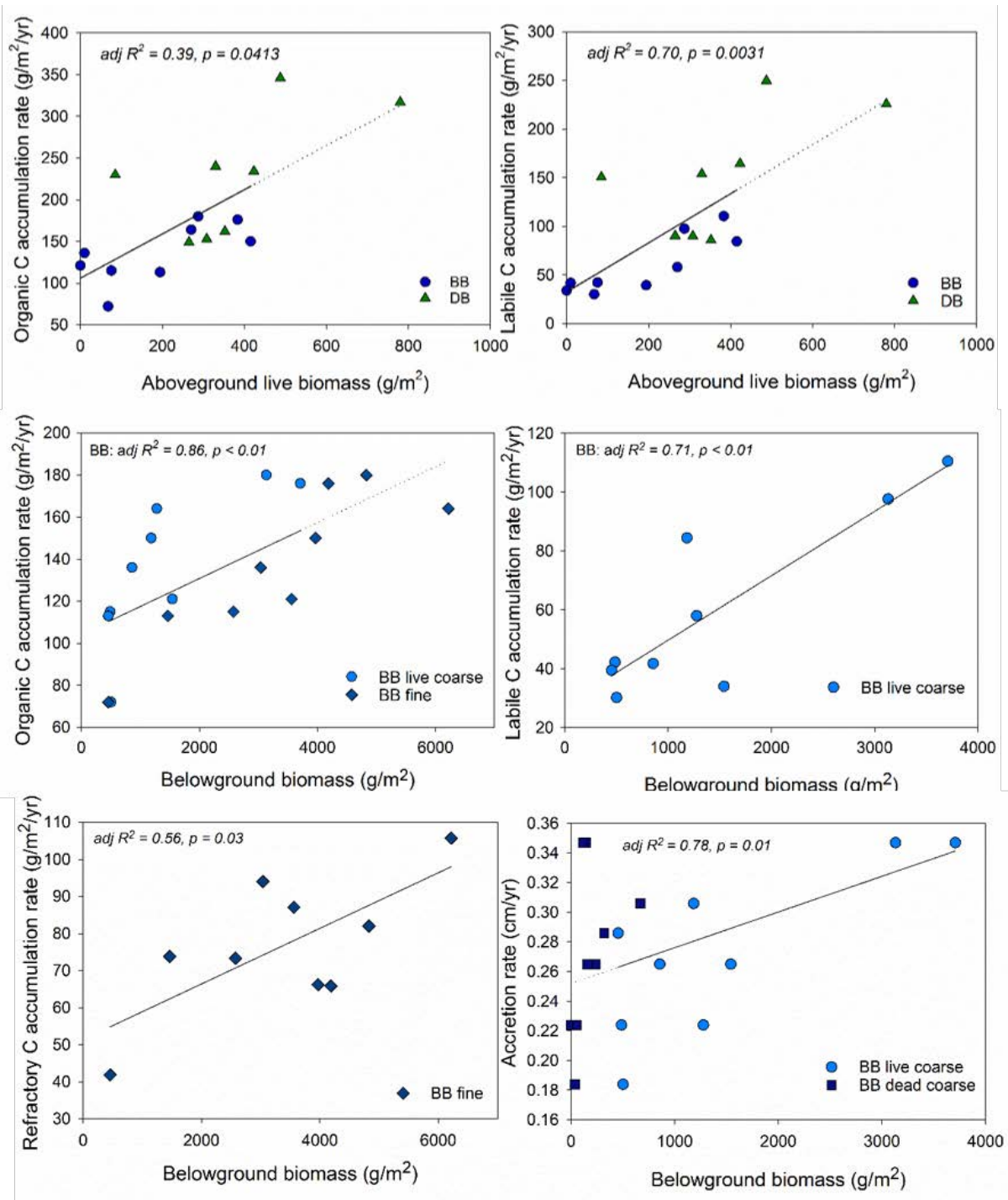
Figure 6: Belowground biomass (scaled on left-axis) and organic C accumulation rate (scaled on right axis; previously reported in Unger et al., 2016) in marshes of two Mid-Atlantic estuaries. Belowground biomass and C accumulation are relative to the ^{137}Cs peak depth. Statistics for total belowground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

5   **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.**

Table A1: 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 have a 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)	**1.00** **<0.0001**									-0.85 0.0004	0.78 0.0027		0.75 0.0046
LOGIT % time flooded		**1.00** **<0.0001**	0.71 0.0089	0.97 <0.0001	0.94 <0.0001			0.84 0.0006					
MHW (cm)		0.71 0.0089	**1.00** **<0.0001**	0.83 <0.0001	0.74 0.0007	0.85 <0.0001			-0.69 0.0409				
MWL (cm)		0.97 <0.0001	0.83 <0.0001	**1.00** **<0.0001**	0.95 <0.0001			0.74 0.0007					
MLW (cm)		0.94 <0.0001	0.74 0.0007	0.95 <0.0001	**1.00** **<0.0001**			0.82 <0.0001					
Tidal range (cm)			0.85 <0.0001			**1.00** **<0.0001**	0.81 <0.0001		-0.87 0.0023				
# flooding events/yr						0.81 <0.0001	**1.00** **<0.0001**		-0.68 0.0428				
LOG flood duration (hr)		0.84 0.0006		0.74 0.0007	0.82 <0.0001			**1.00** **<0.0001**					
Salinity			-0.69 0.0409			-0.87 0.0023	-0.68 0.0428		**1.00** **<0.0001**				
LOGIT soil N (%)	-0.85 0.0004									**1.00** **<0.0001**	0.74 0.0054	-0.93 <0.0001	-0.96 <0.0001
LOGIT soil organic matter (%)										0.74 0.0054	**1.00** **<0.0001**	-0.78 0.0025	-0.84 0.0005
Soil bulk density (g/cm³)	0.78 0.0027									-0.93 <0.0001	-0.78 0.0025	**1.00** **<0.0001**	0.94 <0.0001
LOG mineral sedimentation rate (g/m²/yr)	0.75 0.0046									-0.96 <0.0001	-0.84 0.0005	0.94 <0.0001	**1.00** **<0.0001**

Figure A1. Mass loss from litterbags over time in three salt marshes in Barnegat Bay and three salt marshes in Delaware Bay from 2013 – 2014 (n = 5, ± standard error).

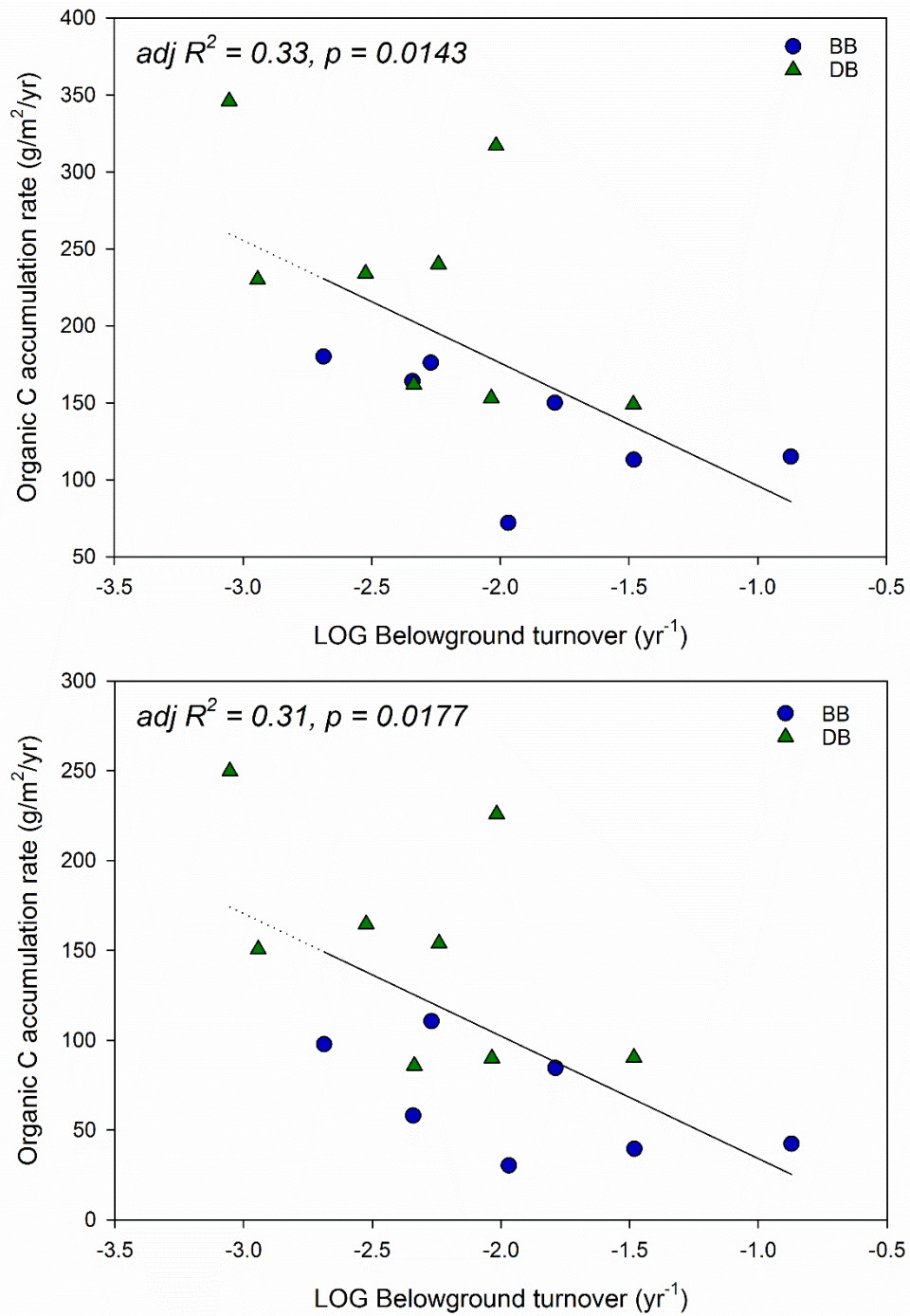



Figure A2. Relationship between belowground turnover and total organic and labile C accumulation rate for *Spartina alterniflora*-dominated marshes.