

Dear Editor,

We appreciate the constructive comments and suggestions from the three reviewers. We have revised the manuscript to address all of the reviewer comments, which has resulted in a much improved paper overall. Below please find the Reviewer Comments in plain text and our responses to each comment in bold text.

REVIEWER # 1

This manuscript covers a lot of topics and presents some interesting data, but it is difficult to follow and could be more effective in highlighting the key findings. Three hypotheses are presented but are poorly linked to data collection and analysis (they seem like after the fact general points rather than truly testable hypotheses). From the manuscript, the hypotheses are: (1) environmental parameters are highly correlated across marshes; however, hydrology is the most important predictor of belowground productivity, decay rates, and above- and belowground biomass; (2) short-term (< 2 yr) surface accretion rates are influenced by a combination of aboveground vegetation structure, belowground productivity, decay and mineral sedimentation rate; and (3) longer-term (~50 years) accretion and soil C accumulation are more strongly related to belowground biomass in organogenic marshes in a coastal lagoon than in more minerogenic marshes of a coastal plain estuary, where the potential for allocthonous C contributions are greater. When I first read these, I wondered how would these be tested? For #1: how can you determine that hydrology is the most important predictor (in part, there are many components of “hydrology”, how do you determine relative importance, and in comparison to what other factors?). For #2: this seems very open ended rather than a testable hypothesis: accretion rates are influenced by a combination of factors? And for #3, the authors come to this conclusion in the discussion, but no mention is made in the analyses of how these comparisons would be made (what is the data/statistical support for this). The manuscript would be much more effective and focused, if clear, testable hypotheses were presented. The data collection and analyses should clearly identify how these hypotheses are to be tested. This would give some structure to the results rather than the wide ranging review of results that currently are difficult to link to specific questions/hypotheses.

We revised the text of the manuscript to improve the overall readability and provide a clear focus for the study. The reviewer is correct, the hypotheses included in the original manuscript were post-hoc and, therefore, poorly constructed. We refocused our manuscript around our a-priori (pre-study) hypotheses, which are directly related to the data analyses and results. The revised hypotheses are outlined in L 102 – 119 of the revised manuscript. Specifically, we hypothesized that rates of *S. alterniflora* belowground productivity were greater in marshes of the coastal plain estuary than in the marshes of the coastal lagoon, where a higher water table, higher salinity, and lower rates of sediment deposition were predicted to limit root and rhizome growth. We predicted that patterns of belowground productivity and turnover would mirror those of longer-term total and labile organic carbon accumulation rates across marshes and estuaries. Our hypothesis would be supported if environmental conditions that promoted C accumulation such as high rates of mineral sedimentation and, potentially, high tidal range and low salinity also promote high belowground biomass production. Further, we examined the role of belowground decay in explaining spatial patterns of C accumulation. We hypothesized that the amount of organic material remaining following 20 months

of belowground decomposition would be greater in marshes with higher C accumulation rates. For this, the conditions that promote high rates of C accumulation may also promote the preservation of C particularly in the upper soil column where much of the decay of labile organic matter occurs (Hackney and de la Cruz 1980; Hackney 1987; Morris and Bowden 1986). Ultimately, the net amount of belowground biomass (C fractions greater than ~1 mm in size) was predicted to be directly and positively related to the density of C in the soil profile and C accumulation rate. Similarly, above- and belowground biomass was predicted to be positively related to soil C accumulation. Finally, because plant productivity and decay processes as well as overall plant structure (e.g., height, stem density, biomass) have been shown to be tightly regulated by abiotic factors, we examined the influence of local environmental conditions (i.e., water level, salinity, soil nutrient status, and sediment deposition rates) on *S. alterniflora* growth, decay and biomass across marshes and estuaries.

There are some arguments that are presented that are difficult to untangle: for example, mineral matter drives productivity. If this is the case, what is the expected “response” that supports this and what “response” would not support this (how would the measured parameters of total biomass, ingrowth, mineral matter accumulation, etc., vary if this is true and what if it is not true – or is the key in the the relationships of different parameters)? As above a clear articulation of expectations (hypotheses) is essential but lacking. Without these, it’s an interesting story but not so clear what is actually being supported from these findings/data. Part of my confusion in interpreting the results is that this is a relatively complex set of experiments with many different factors and response parameters. In terms of factors, there are two locations, with multiple sites within each location – and many factors vary both across locations as well as within locations: tidal range, sediment inputs, salinity, inundation, etc

By revising the hypotheses, the somewhat complex study design and findings are clarified. We have also revised much of the text to provide justification for our hypotheses and context for our findings. The specific argument highlighted above, “mineral matter drives productivity” was removed in the revision of the manuscript.

Plus there are many different response parameters, some closely related, some not (ingrowth, biomass, decomposition, accretion, C accumulation, mineral accumulation, etc . . .). It might be very useful to put together a summary table that links the various components of this research to the hypotheses/research questions of interest (factors, locations/sites, responses, expectations). Or at a minimum, to clearly identify in the methods what these links are: to test the hypothesis #2, we compared xxxx across sites (or across inundation conditions within sites), using xxxx analysis . . .

We revised the text throughout the manuscript to simplify the hypotheses and how they relate to the response variables. For example, the multivariate correlation analyses were removed from the results section and relevant information was summarized in the data analysis section. Table 2 showing the correlation analysis results was moved to a Supplementary Table.

Overall, I found the writing difficult to follow. Many of the paragraphs are very long and cover a mix of topics. I’d suggest focused paragraphs with very clear topic sentences so that the logic of each section is clear and easier to follow than the current paragraphs that ramble over a mix of topics. In addition, there are some grammatical mistakes, dropped

words, etc. that make the manuscript difficult to understand (e.g., l.66: should be wide range OF geomorphic settings) check throughout for grammar (many compound sentences missing commas (l.212-213), etc . . .). Also some sentences are overly complex and difficult to follow (for example, the last sentence of the abstract): “These findings indicate that mineral sedimentation is of utmost importance for promoting belowground biomass and soil C accumulation in sediment-limited systems while in minerogenic systems, belowground biomass may not scale with C accumulation and accretion, which may be influenced more by smaller submillimetre-sized C particles.” (secondarily, I don’t think submillimeter particles are brought up again in the manuscript, so why are they in the abstract?)

The text was revised throughout to improve readability and grammar. Strong topic sentences were added to the beginning of paragraphs and the amount of rambling was minimized. The sentences highlighted by the reviewer above, were ultimately removed from the revised manuscript.

It was not entirely clear what was previously collected background information, and what was new data for this study. For example, you refer to published rates of accretion from Boyd et al. 2017: are the accretion rates here the same data or different?

We added text to both the Introduction (L 78 – L 99) and Methods (L 155 – L 157) to clarify that we used C accumulation rates published in Unger et al. 2016 and Cs-137 based accretion rates published in Boyd et al. 2017 for our examination of how vegetation dynamics relate to soil C dynamics.

The discussion of elevation is not so clear. Be more specific. I’m assuming that it is relative elevation that is critical (where within the tidal frame the marsh surface is found). For example on Figure 4, is this elevation relative MLW (see other point below about MLW)? And are positive elevations above or below MLW? I would put lower elevations on the left side of the x-axis (not sure if this is the case as presented). It also looks like much of this relationship is driven by the two points with zero biomass. How does this affect your interpretation: is it just a threshold relationship or is it really a linear relationship? Also, for figure 5, organic matter inventory: the one outlier seems to be driving this relationship. Does this affect your interpretation?

We have clarified our use of elevation and water level data throughout the methods and results. While we collected elevation data (relative to North American Vertical Datum 1988), what we used in our analyses were water level data, which were calculated relative to the marsh surface. This, as the reviewer indicated, is what is critical for driving plant and soil processes. For Figure 4 (Figure 3 in revised manuscript), we revised the axis to read MLW depth relative to marsh surface (cm). While it appears that the relationship was driven by two points, when those points were removed, the linear relationship remained significant with only a slight reduction in the R-square value. We included this information in the Results section, as well as a sentence on this relationship really being more of a threshold relationship, as the reviewer aptly pointed out.

It’s surprising that you’ve found a strong fit between mineral accumulation and accretion rather than organic matter and accretion. Most others have found differently (e.g., Turner et al. 2000). How can you explain this difference?

This is a good point, which we subsequently worked into the discussion. Actually, Table 2 in Turner et al. 2000 illustrates regional differences in the contribution of mineral sediment to accretion. Along the U.S. Atlantic coastal plain, accretion rates were directly related to *both* mineral sedimentation and organic matter accumulation rates for most marshes (all but 1 study), as well as across all Atlantic coastal marshes combined. Our previous studies have shown a similar trend (Unger et al. 2016; Boyd et al. 2017). Conversely, in U.S. Gulf coast marshes, accretion rates were related to organic matter accumulation rate only. Turner et al. 2000, hypothesized that at high rates of mineral sedimentation, the relationship between accretion and mineral sedimentation becomes variable associated with a threshold of organic production at high rates of mineral sedimentation. I might suggest that these linear averaged accumulation rates, don't account for major declines in mineral sediment over time, and thus with a high historic sediment input and a much lower recent sediment supply to many Gulf Coast marshes, the relationship between accretion and sediment input becomes variable. In addition, accretion rates also respond to changes in relative sea-level and have done so in Gulf Coast marshes mostly by organic matter accumulation. These marshes are experiencing subsidence and deterioration due to the lack of sufficient mineral sediments to support plant growth and biomass. Our study illustrates this point, and suggests that allochthonous C burial and C preservation may also be significant at high rates of sedimentation, provided that marshes have a relatively continuous supply of sediment over time.

For Figure 3: how can the decay rates and the % mass remaining not be indirectly related: How can CC have the highest decay rate, but have more mass remaining than 3 of the other sites? These should be strongly related.

We have included a Supplementary Figure (A) to explain this. Marshes in both estuaries had similar amounts of organic matter remaining, yet Barnegat Bay had a steeper decline in organic matter over time. However, the reviewer's comment highlighted the need for some additional explanation. Litterbags in Barnegat Bay were placed in the marsh slightly later in the year than those in Delaware Bay due to logistical delays following Hurricane Sandy. As a result, asymptotic decay rates were greater in Barnegat Bay, however, this was likely associated with slightly warmer temperatures following deployment as compared to Delaware Bay. We have added this information to the Methods (L 203 – L 206) and removed the decay rate calculation and results, and instead just used % mass remaining following 20 months as the response variable.

Many of the figures present multiple panels, and it is not clear, what is essential to get out of a figure: seems more like a fishing expedition in presenting a wide range of results rather than targeting specific questions/hypotheses.

Each figure in the revised version of the manuscript is directly tied to hypotheses stated in the Introduction, data analyses in the Methods section, and findings in the Results section.

Details: You refer to cores of 6 cm diam. in line 144, but then 15 cm cores in l. 160. Were two different sets of cores taken? This needs to be clarified.

The cores were 15.5 cm in diameter. The size was corrected in the revision.

Be consistent in how you refer to sites: sometimes in the coastal plain site, sometime it's a minerogenic site.

We revised the manuscript for consistency when referring to estuaries and marshes. We refer to coastal plain and coastal lagoon in the Introduction and Discussion. We refer to the specific estuaries (i.e., Delaware Bay and Barnegat Bay) in the Methods and Results sections.

Paragraph starting at l.276 (and paragraph above): this all seems very exploratory, with little focus: you looked at a wide range of variables for patterns, went with MHW and MLW. As above, link the approach to the hypotheses (and move the methods to the methods section and out of the results).

This section was removed in the revision. The correlation analysis was performed so as to select environmental variables that were somewhat independent, not strongly co-varying with others, so as to limit our interpretation. We moved any relevant information to the Data Analysis section.

Also, it was not clear to me how MHW and MLW represent the range of factors (were these absolute elevations of MHW or MLW) – as you can see, I did not follow this section of the ms. very well (it was not clear to me, but maybe it is clear to others). Similarly at l.288: how does “MLW influence ingrowth rates”? MLW is a characteristic of a particular site, but how does it influence growth across a marsh?

This point is now clarified in the revised manuscript. MHW and MLW were average high and low water depths relative to the marsh surface calculated from two years of continuous water level data. Root ingrowth rates were higher in marsh locations where the average low water depth was lower than in areas where the average low water depth was high (i.e., greater root growth with greater drainage during low tide).

Lead with the key issues in presenting the data for each section. For example, for aboveground vegetation structure (paragraph starting at l. 316): clearly stem density is important, but why include the CV here: what is the significance of this? As above, I got lost in the details of the data that were presented, and did not see the key issues from the results.

We highlighted key issues and findings relevant to the hypotheses to the beginning of each result section.

Figure 1: provide some context. Not all readers know where Delaware and New Jersey are.

We added

Other figures: As above, be consistent in mentioning features of sites so people will remember lagoon vs. coastal, minerogenic . . . For example for Figure 3, group sites as you do for Figure 2 (or color bars or use hatching so that the two groups are obvious).

As the reviewer suggested, we have revised figures to be consistent using Barnegat Bay and Delaware Bay for designation of data points.

Figure 3: the dark bars on the bottom panel, make it very difficult to see the symbols for organic matter accumulation rates.

This figure was deleted in the revision of the paper.

Similar to the broader point about figures with multiple panels, some multi-panel figures are not organized intuitively (at least not for this reader). For example, for Figure 7: what is mineral sedimentation the x-axis on the top two LEFT panels and the bottom two RIGHT panels? The wide mix of combinations, makes it very difficult to see patterns and follow the logic of the data presentation.

We revised Figure 7 (Figure 4 in revised manuscript) such that all x-axis mineral sedimentation rates are on the left panel and all x-axis MHW depth are on the left panel, as the reviewer suggested.

References: Some of them are out of order: See Cahoon at l. 618 and again at l. 639. In addition, some journal titles are abbreviated, some are spelled out in full (l.619 &625).

We have edited the references, as suggested by the reviewer.

REVIEWER #2

The authors conducted a study to investigate the impact of environmental conditions across marshes on biomass, belowground production, sediment accretion, organic/mineral accumulation. The scientific questions addressed by the ms fall within the scope of BG. The authors examined different belowground processes, and related them to each other and biogeochemical processes. The study will present some interesting results for the studies of saltmarsh sediment accretion and carbon sequestration after careful revision. General comments This study used many data from paralleled studies, such as Unger et al., (2016) and Boyd et al., 2017. To avoid confusion, you need to clearly show which data come from paralleled studies.

As described above, we have extensively revised this manuscript. We clarified the inclusion of C accumulation rates published in Unger et al. 2016 and Cs-137 based accretion rates published in Boyd et al. 2017 for our examination of how vegetation dynamics relate to soil C dynamics. The text was added to the Introduction (L 78 – L 99) and Methods (L 155 – L 157).

Data analyses need to be checked and refined. Tidal range and mean water level are calculated from mean low water and mean high water, organic/mineral accumulation rate is calculated from sediment accretion rate. You cannot do correlation or regression analysis between the variables and those variables they are calculated from.

We conducted a correlation analysis to examine which variables (mean low water and/or mean high water) was driving variability in tidal range. While statistically, tidal range was calculated from the difference of MHW and MLW, our analysis revealed that spatial variation in tidal range was driven by differences in average high water not average low water. This illustrates how marsh interiors do not drain much at low tide and any difference in tidal range across marshes is due to high tide levels. We maintain that although this is not a main focus of the paper, it is still important.

Surface accretion and accumulation rates were removed in the revision.

The significant difference should be labelled alphabet-sequentially.

I am not exactly sure what this comment is referring to.

Specific comments

Abstract Line 7: add of after rates.

This line of the abstract was changed in the revision.

Line 14: add permil after 7-40.

Some journals show salinity is unitless; I will defer to the Editor for recommendation.

Introduction Line 29-31: you need to add references to support your statement, such as Ouyang et al. (2017).

This specific line was modified in the revised paper to: “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. 1983; Nyman et al. 2006).”

References were added, as the reviewer suggested.

Line 59-61: I suggest you add some references here, such as Haslett et al. (2003).

We appreciate the reference recommendation and added it to the sentence, which is now L 49 – 51 in the revised manuscript.

Line 66: add of after range

This sentence was removed in the revision.

Line 99-100: The allochthonous source of labile C may also include C input from riverine sources where marshes are near rivers or delta. see Craft (2007)

This specific sentence was removed in the revision, however, two sentences in the revised manuscript, L 64 – 67, “Higher tidal range, greater supply of mineral nutrients and sediments, and lower salinities are conditions that are all predicted to enhance both plant productivity and soil C accumulation (Mendelssohn and Kuhn 2003; Craft 2007; Kirwan and Guntespergen 2010).” And L 72 – 74, “In contrast, marshes in geomorphic settings with high rates of mineral sedimentation such as those near river deltas may have greater magnitudes of both allochthonous C deposition and autochthonous plant C inputs (e.g., Craft et al. 2007).” include the Craft et al. 2007 citation. Again, we appreciate the reference recommendation.

2.Methods

Line 162: remove the after each.

The correction was made as the reviewer suggested.

Line 184: what's the diameter of coarse roots and rhizomes used in your study?

We did not measure the diameter of coarse roots and rhizomes.

Line 196-204: from your results, I understand you quantified belowground biomass to both 50cm depth and the maximum of Cs-137 profile. Please clarify this point clearly here.

As the reviewer suggested, we added the methods for calculating belowground biomass to both the ¹³⁷Cs-peak depth and 50-cm depth.

Line 214: Some mineral material may be lost during from high temperatures of LOI analysis. Have you done acid treatment to remove inorganic carbon before LOI analysis?

These data were removed in from the revised manuscript. As the reviewers generally alluded to, there was a lot of data and analysis presented in the original manuscript, and we decided to simplify the scope and just concentrate on longer-term accretion and accumulation rates.

Line 207: Please specify the month of start and end periods. Line 208-10: The justification of longer periods for accretion estimation may also lie in the fact that organic matter accretion lags behind belowground ingrowth as it takes some time for the newly grown roots to decompose.

Yes, the reviewer points out an additional reason for removing these data and comparisons.

Line 225-7: Have you conducted the homogeneity test before ANOVA or MANOVA?

Yes, we used the Levene Test. We added this information to L 235 – 237 of the revised manuscript: “ We tested for homogeneity of variances using the Levene Test on transformed data. The only violation of the equal variance assumption was for the 95% rooting depth, which, following log-transformation, failed the Levene test between estuaries, but not among marshes.”

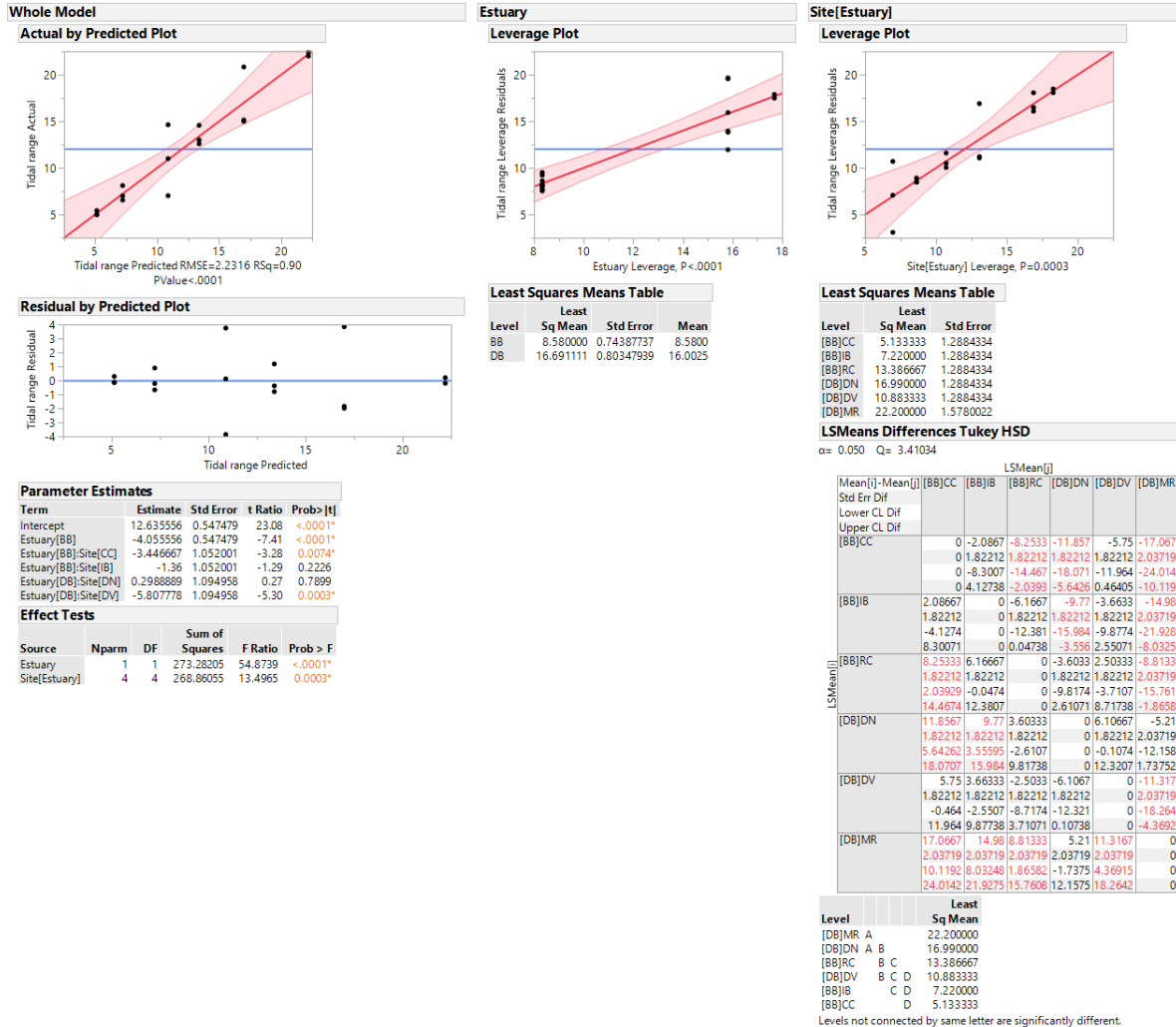
3 Results

Table 1: add the statistical method you used in comparison of the variables.

As the reviewer suggested, we added the statistical test to the legend of Table 1.

Please check the label of 'Mean high water'; you have ab, bc, d, cd, a, ab but it is weird that there is no c. Some other variables also have the same problem, such as 'tidal range' and 'long-term mineral sedimentation rate' . Normally, the labels should be a, ab, b, bc, c.....

We double checked the statistical output, and the letter designations in Table 1 correctly reflect the output of the Post-hoc Tukey Test. I think there is just a lot of overlap in error between sites, which is also a function of the nested design. I have attached some output from our test of tide range differences between marshes nested in estuaries:



You also need to check flooding events and duration of floods. For example, IB has 24 flooding events but 324h (per month or year?) of flooding time while MR has 455 flooding events but 7h of flooding time.

These data are correct. IB has had 24 flooding events and the duration of each flood averaged 324 hrs. By also comparing this with the % time flooded, it is clear that IB is almost continuously flooded so the # of flooding events is low, yet the flood duration is high. MR, on the other hand, is flooded frequently but has an average flood duration of 7 hours for each flooding event.

Table 2: I suggest you remove tidal range and MWL in the correlation analysis, or you keep them and remove MHW and MLW, and modify your results in '3.1'. Tidal range is the difference between MHW and MLW, while MWL is the mean of MHW and MLW. You cannot correlate MHW or MLW with tidal range and MWL just like you will not correlate the area of a circle with the diameter ($A=d^2/4$) since this is common sense.

Results section 3.1 was revised and the correlation analysis was removed from the Results section in the revision. Please see response to the same comment above.

Figure 3: why you do not show organic matter accumulation rate for IB?

Figure 3 was removed in the revision.

Line 294-6: you analyzed decay constant (Figure 3 and 4) rather than decay rates, and need to keep consistency in context.

Decay constant and decay rates were removed in the revision.

Line 309: were related or were not related? The sentence means they are related since you used 'neither' and 'nor'.

This sentence was removed in the revision.

Line 298-9: the last sentence is unnecessary if these variables are excluded in the stepwise regression analysis.

This sentence was removed in the revision.

Figure 5 caption: the dependent variables in your regression analysis should not be organic/mineral accumulation rates, of which the unit is g/(m².yr). The accumulation rates in Table 1 are the correct term. You need to revise '3.2.3' accordingly.

Figure 5 was removed in the revision.

Table 4: why don't you use the data from all the sites to conduct the analysis of labile/refractory C density~belowground biomass?

As the reviewer suggested, we added an analysis using data from all of the sites, as well as site-specific data. Combined this illustrates important biomass-C density relationship across marshes, as well as, how coastal lagoon marshes have a strong refractory C-biomass relationship, but coastal plain estuary marshes do not.

Figure 7: significant outliers are found in the relationship live belowground coarse biomass~MHW.

Indeed, live belowground biomass was much more strongly related to mineral sedimentation rate across marshes, which is also shown in Figure 7 (Figure 4 in revised manuscript). We added a comment about the variability in the relationship between MHW and biomass in the results section, which is reflected in the r-square value (0.44) in Figure 7 (Figure 4 in revised manuscript).

Why do you say mineral sedimentation rates correspond to average rates over the last 50 years? The time dated using Cs-137 relates to nuclear events (e.g.1963). Since sediment accretion rates vary from site to site and even position to position within the same site, the dating time at 50cm depth may not all be 50 years.

This was a misstatement, and was removed in the revision.

Figure 8: a typo in the caption. It should be Table 3 instead of Table 2.

Yes, this was changed as the reviewer suggested and in the revised version, the legend refers correctly to Table 2.

Figure 9: No relationships between belowground biomass and (organic, refractory, labile) C accumulation/accretion are shown for Delaware Bay. Are all the relationships insignificant? Have you considered to examine the relationship between C accumulation rate (as a whole, rather than organic, refractory, labile) and belowground biomass?

Yes, the goal was originally to examine C-biomass relationships across estuaries. Yet, there were no significant relationships across estuaries. The only significant relationships were found in Barnegat Bay. We analyzed relationships for total organic (labile + refractory), labile, and refractory C and all biomass fractions.

Discussion

Line 402: you need to be specific about decay. It is decay constant.

This was changed in the revision, as explained above. The response variable is now percentage of dry mass remaining.

Line 403: add mineral before sedimentation rate.

This sentence was removed in the revision.

Line 404: add coarse before belowground biomass.

This sentence was removed in the revision.

Line 405: replace little with insignificant as you can not consider the insignificant relationship in the linear regression analysis as little influence. Maybe environmental parameters co-vary with other factors, and explain some variance in multiple regression analyses.

This sentence was removed in the revision of the manuscript.

Line 420: I only found you examined the relationship between biomass and MHW. Where do you analyze the influence of elevation on biomass?

We did not analyze the relationship between biomass and elevation. We added text to the revised manuscript to explain why. In the Results section (L259 – L 266) and in the Discussion, we describe how hydrology was uncoupled to elevation across marshes due to factors such as poor drainage through mosquito ditches in IB, which created high water levels throughout the study, despite moderate elevations. Because plant and soil C processes respond more directly to hydrology than elevation relative to a datum, we used hydrologic parameters instead of elevation.

Line 432-3: tidal range is not comparable based on your results. One is labelled bc and the other is ab.

The statistical results indicate that there is not a significant difference in tidal range between RC and DN.

Line 446: the explained variance is 58% rather than 62%.

This sentence was changed in the revision.

Line 454: it is decay constants rather than decay rates which you did not estimate in your results. You need to modify other parts of the ms accordingly.

This was modified in the revision.

Line 484-7: There' are no direct linkage between CO₂ emissions and decay rates although decay contribute to CO₂ emissions, since other sources also contribute to CO₂ emissions such as crab burrows.

As the reviewer suggested, this sentence was removed in the revision.

Line 538-9: the factors relate to surface accretion are organic matter inventory and mineral sediment inventory.

This sentence was removed in the revision.

Line 551: Some sites have fine biomass lower than MR site such as RC.

This sentence was removed in the revision.

Line 553-4: you only show the influence of belowground biomass on specific components of C accumulation rates (organic, refractory, labile), and your discussion here and hereafter should be more specific.

We added some clarification throughout the manuscript that total organic C = labile C + refractory C. Thus, we examined relationships between belowground biomass and labile, refractory and total organic C accumulation rates as a whole.

References Boyd, B., Sommerfield, C.K., and Elsey-Quirk, T.: Hydrogeomorphic influences on salt marsh sediment accumulation 610 and accretion in two estuaries of the U.S. Mid-Atlantic coast. *Mar. Geol.*, 383, 132-145, 2017. Unger, V., Elsey-Quirk, T., Sommerfield, C. and Velinsky, D. J.: Stability of organic C accumulating in *Spartina* 805 alterniflora-dominated marshes of the mid-Atlantic U.S.A. *Estuar. Coastal Shelf Sci.* 182: 179-189, 2016. Ouyang, X., Lee, S. Y., Connolly, R.M. (2017) The role of root decomposition in global mangrove and saltmarsh carbon budgets. *Earth-Science Reviews.* 166: 53-63. Haslett, S. K., Cundy, A. B., Davies, C. F. C., Powell, E. S., & Croudace, I. W. (2003). Salt marsh sedimentation over the past c. 120 years along the

west Cotentin coast of Normandy (France): relationship to sea-level rise and sediment supply. *Journal of coastal research*, 609-620. Craft, Christopher. "Freshwater input structures soil properties, vertical accretion, and nutrient accumulation of Georgia and US tidal marshes." *Limnology and oceanography* 52.3 (2007): 1220-1230.

The format an inclusion of references was corrected in the revision.

REVIEWER #3

This paper is a substantial and interesting addition to the literature and I think that it could be publishable for *Biogeosciences Discussions* pending some revisions. The study reports correlations between geomorphic variation in variables such as tidal elevation, tidal frame, suspended sediment, salinity, etc. with important biotic variables affecting carbon sequestration (above and below ground biomass, root addition, root-shoot ratio, and recalcitrant/labile carbon fraction), and observations of Carbon Accumulation Rate, measured by radiocesium date and previously published by Unger et al. and Boyd et al.. The observations that complex correlations between root production and drainage, and sediment trapping having multiple positive interactions with carbon burial, are compelling conclusions as they point to the complex and dynamic nature of tidal wetland systems more generally. Predicting behavior outside of well-studied plots and sites is a large concern of the community and this paper speaks to many difficulties in those efforts. I think what sets this paper apart from much of the literature is how well monitored all of the sites are. All locations have measured elevation, inundation, and soil properties. This should be commended and in many ways is close to an ideal salt marsh carbon dynamics study design. I have three major critiques of the paper, somewhat overlapping. 1. There is not enough available methods data for the calculation of tidal datums from the water loggers. I found some of the inclusion of comparing NAVD88 elevation, MHW and MLW hard to follow, especially when these were used as proxies for multiple hydrologic properties. I was a bit taken aback at how much variation there were in datums that are located fairly close together. Could this be because of the short 1.5-year time period? 'No data' values deflating MLW datums? Etc? Is there really that much local variation in datums? I would like to see more information before making a judgment there.

Yes, the reviewer is correct, more explanation was needed to discuss the datums. This was similar to a comment made by Reviewer #1. We have clarified our use of elevation and water level data throughout the methods and results. While we collected elevation data (relative to North American Vertical Datum 1988), what we used in our analyses were water level data, which were calculated relative to the marsh surface. We included this information in the Methods and Results section.

2. This leads me to my second critique. A lot of the correlation analysis could be paired down. First because of what I discussed in one, maybe some of these measures are redundant or could be reduced to more directly causal variables.

For example, by converting site elevations (NAVD88) into dimensionless elevation $z = (\text{Elevation} - \text{MTL}) / (\text{MHHW} - \text{MTL})$ [Swanson et al., 2012], or focusing on flooding depth and # of floods a year (maybe converted to volume of water / unit time) since those are probably a clearer functional driver for organic and inorganic sedimentation. Maybe there's a better

metric for drainage, such an average time between inundation events. The number of correlations discussed makes the text especially figure 7 a bit cluttered and hard to decipher on a quick read through (although there are benefits to being thorough). Statistically, the number of correlations presented is problematic. Which leads me to point 3.

Yes, indeed. As the reviewer suggested, we revised the text and removed the multivariate correlation analyses from the results section. Relevant information was summarized in the data analysis section. Table 2 showing the correlation analysis results was moved to a Supplementary Table.

3. There are many correlations presented, but the threshold for significance (0.05) is not adjusted for multiple testing. The more correlations your run, the higher chance of getting false positives. Researchers often address this by using the Bonferroni correction, or some related correction (there are some arguments that the Bonferroni is too restrictive). The fact that many of the regressions presented are barely significant at the 0.05 level and many would no longer be significant after correcting for multiple testing. Maybe a combination of reducing the number of variables tested to a few functionally important variables and adjusting for multiple testing could allow the authors to focus more on the very clearly significant driving geomorphic variables.

The purpose of the correlation analysis was to identify environmental parameters for which other parameters co-varied. Almost all significant relationships had p-values of < 0.01. As a result, we only used a sub-set of environmental parameters in subsequent analyses. Almost all of these had correlations or regressions where the p-values were very low, and only 2 or fewer independent variables influenced response variables. Based on this, we don't feel that a Bonferonni correction is really necessary. However, we rans some exploratory analyses with Bonferonni corrected data, and found similar results to what is presented.

Line comments: 63: This is an excellent point that does not get enough attention in the literature.

Excellent! This sentence is now L57 – 59 in the revised version.

64: Is there any literature you could cite in the hazards literature or other ecosystem-climate change dynamics that discuss complexities in projecting system resilience?

While this is an excellent discussion point, it may be a little outside of the scope of this paper. Particularly, now that we have made changes to improve the clarity and focus.

132: What is the time frame of RSLR? Same as cores, or total length of the gauging period?

The time frame of RSLR was the same as the cores/ We added a few words to clarify. L 148-151 in the revision "Accretion rate in Barnegat Bay marshes (0.28 ± 0.06 cm/yr) over the last 50 – 100 years was less than the rate of relative sea-level rise over approximately the same time period (0.41 cm/yr; NOAA, Tides and Currents; *in* Boyd et al., 2017). In Delaware Bay, salt marsh accretion rate (0.70 ± 0.26 cm/yr) exceeded the rate of local relative sea-level rise over the same time period (0.34 cm/yr, NOAA, Tides and Currents)."

277: If dimensionless elevation may be a better fit than using MHW and MLW. Alternatively inundation time, the number of inundation events or cumulative annual mass of water seem like they would be much better variables to use as there is process-knowledge involved.

The reason why we chose to use MHW and MLW because these variables represent the magnitude of surface flooding at high tide and the magnitude of drainage at low tide. We anticipated that these would be important biologically. However, this was not very well clarified in the original submission, and therefore we added this information explicitly to the data analysis section.

427: Is sediment trapping by biomass part of this positive feedback?

Yes, an excellent point. In the revised manuscript, we highlight the importance of aboveground biomass and its relationship to labile C accumulation rate. While there are several mechanisms that can explain this relationship, sediment and allochthonous labile C trapping is one.

Tab 1 - What is MHW MWL and MLW relative to NAVD88? Station datum?

We added this information to the table and all relevant figures; it is relative to the marsh surface.

Tab 3 - Far left column a bit hard to read. Maybe fix in formatting.

We fixed the formatting of the table, as suggested by the reviewer.

Fig. 1 - How a basemap with better definition. Maybe one that emphasizes the differences between uplands systems and wetlands. I would delete the service layer credits and put it into the figure caption. The map looks low resolution.

We have replaced Figure 1 with a new better resolution map of the study locations.

Citations: Swanson, Kathleen M., et al. "Wetland accretion rate model of ecosystem resilience (WARMER) and its application to habitat sustainability for endangered species in the San Francisco Estuary." *Estuaries and Coasts* 37.2 (2014): 476-492.

Abdi, H. (2007). Bonferroni and Šidák corrections for multiple comparisons. *Encyclopedia of measurement and statistics*, 3, 103-107.

We thank the Reviewer for the citations.

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

Tracy Elsey-Quirk¹, Viktoria Unger²

¹Department of Oceanography and Coastal Sciences, Louisiana State University, Baton Rouge, LA 70803, USA

²University of Rostock, Rostock, 18051, Germany

Correspondence to: Tracy Quirk (tquirk@lsu.edu)

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 plant ingrowth, 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 ingrowth (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/m²/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 (Mendelsohn and Kuhn 2003; Craft 2007; Kirwan and
68 Guntenspergen 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 $\delta^{13}\text{C}$ in soils of mineral-rich and organic marshes showed a depletion of plant-derived $\delta^{13}\text{C}$ signatures
87 in mineral marsh soils and strong signal of local plant $\delta^{13}\text{C}$ in organic marsh soils (Middleburg et al. 1997).
88 Preferential decomposition of labile C, which is enriched, with more negative $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ in mineral-rich marshes (Benner et al. 1991). Another mechanism potentially causing the depletion of
91 $\delta^{13}\text{C}$ 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 *in situ* 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; Mendelsohn 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 $78 \pm 5 \text{ g/m}^2/\text{yr}$ (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 ¹³⁷Cs and
163 ²¹⁰Pb-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 ¹³⁷Cs-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/cm³), 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 ingrowth and turnover**

190 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
191 root and rhizome growth into flexible mesh bags filled with a 1:1 mixture of unfertilized top soil and peat moss
192 (McKee et al., 2007; $n = 5$). Ingrowth bags were constructed of flexible crawfish sack material with a mesh size of 6.3
193 x 3.2 mm, and, when filled, were 5 cm diameter and 15 cm length. Four ingrowth bags were deployed in each of the
194 five plots and sequentially harvested approximately every four months from April 2013 to October 2014 to calculate
195 belowground (root + rhizome) ingrowth rate. The four bags were deployed 50 cm apart in each plot and all bags were
196 installed vertically into 15 cm deep cored holes. Accumulated root and rhizome mass was dried at 60°C to a constant
197 weight. All of the roots and rhizomes in ingrowth bags were live based on color and structural integrity. Belowground
198 turnover was calculated by dividing ingrowth ($\text{g m}^{-2} \text{yr}^{-1}$) by live root and rhizome biomass (g m^{-2} ; Section 2.5.3).
199 Ingrowth typically underestimates absolute rates of belowground productivity, and therefore, both absolute
200 productivity and turnover will be underestimated. However, our goal is to examine relative responses to varying
201 environmental conditions (Valiela et al., 1976; Graham and Mendelsohn 2016).

202

203 **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

217 **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).

290 **3.2. Belowground ingrowth and turnover**

291 Belowground ingrowth, comprised primarily of large roots and rhizomes, ranged from 0 to 550 $\text{g/m}^2/\text{yr}$ 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 $206 \pm 22 \text{ g/m}^2/\text{yr}$ (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., $\text{adj } R^2 = 0.36$, $p = 0.0078$). Belowground turnover ranged from 0.04 to 0.43 yr^{-1} with an average
304 of $0.15 \pm 0.03 \text{ yr}^{-1}$. 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 ($3245 \pm 768 \text{ g/m}^2$) than in RC ($833 \pm 41 \text{ g/m}^2$)
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 ($\text{adj } R^2 < 0.35$) 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 ($\text{adj } R^2 = 0.37$, $p = 0.0058$, 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 total, labile, and refractory C accumulation and accretion. In the coastal plain estuary, only
421 aboveground biomass influenced C accumulation through its positive relationship with labile C accumulation rate.
422 Aboveground biomass was stimulated in the coastal plain estuary by greater flooding, ultimately leading to greater
423 labile and total C accumulation rates. As discussed below, the positive relationship between aboveground biomass
424 and labile C accumulation rate may result from labile tissue production as a function of photosynthetic area and/or
425 increased trapping and deposition of allochthonous labile C such as algal-derived C. Relatively high densities of labile
426 C in the mineral-rich marshes, independent of belowground biomass, indicate potential allochthonous contributions
427 and high preservation of labile C.

428

429 Contrary to our first two hypotheses, belowground ingrowth 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 ingrowth rates with greater ingrowth in areas of greater average
437 low tide depths. This relationship tended to be based on thresholds, where root growth was greater when average
438 mean low water depth was at least 6 cm below the surface. When mean low water averaged above the marsh surface
439 and the marsh surface was flooded for long durations and a higher percentage of the time (e.g., IB), no roots grew.
440 *Spartina alterniflora* is highly adapted to flooded conditions, possessing both morphological adaptations such as
441 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 ingrowth 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 ingrowth and C accumulation being

447 different, the lack of a spatial relationship between root ingrowth and C accumulation rates may also be due to time
448 step differences in short-term (~2 yr) process rates and processes integrated over a longer time period (~50 yr), and
449 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 ingrowth being equal, an increase in live biomass
478 lowers the turnover rate. While turnover explained <35% of the variation in C accumulation rates across estuaries,
479 biomass components (above- and belowground) explained 39 – 86% of the variation in soil C accumulation rates.

480 Rates of soil C accumulation and accretion were strongly related to *S. alterniflora* biomass. Aboveground live biomass
481 was positively related to organic C accumulation rate across estuaries, primarily though the strong relationship with
482 labile C accumulation rate. Mechanisms of aboveground live biomass influencing labile soil C include the direct input

483 of aboveground litter to the soil. For *S. alterniflora* much of the aboveground litter is subject to decay and mechanical
484 breakdown by tidal action (Teal 1962), and therefore, little of the aboveground litter of *S. alterniflora* in these
485 temperate marshes is thought to be incorporated into the marsh soil. The standing live aboveground biomass, however,
486 represents both photosynthetic capacity and growing conditions, which may directly affect the production of labile
487 exudates and new labile tissues belowground. Additionally, aboveground shoots influence surface deposition and
488 accumulation through the direct capture of particles on plant stems and the indirect reduction of flow velocity inducing
489 sediment settling (Stumpf 1983; Leonard and Luther 1995). This has been illustrated for fertilized and unfertilized *S.*
490 *alterniflora* plots, where aboveground biomass was three times greater and surface accretion rate was 2 mm/yr greater
491 in response to fertilization (Morris and Bradley 1999; Morris et al. 2002). The higher accretion rate was accounted for
492 by more efficient trapping of sediments (Mudd et al., 2010). Therefore, both labile live plant tissues and labile organic
493 C associated with sediment may be enhanced with greater aboveground biomass. This finding supports other studies
494 showing positive relationships between aboveground biomass and soil microbial processes, including the
495 decomposition of recalcitrant soil organic matter, which was hypothesized to be due to greater labile C inputs
496 (substrate-induced priming) and/or greater rhizosphere oxygenation (O₂-induced priming; Mueller et al. 2016). Our
497 data suggest that aboveground biomass may increase soil C accumulation directly through the inputs of labile C and
498 positive bio-physical feedbacks for sedimentation, which increases labile C deposition, burial, and preservation.
499 Relationships among aboveground plant biomass, labile and total C accumulation rate, and mineral sedimentation rate
500 indicate positive feedbacks among these processes (Unger et al. 2016; present study).

501
502 Aboveground biomass response to flooding was estuary-dependent. In the coastal plain estuary, aboveground biomass
503 increased with a higher mean high tide level, whereas in the coastal lagoon, aboveground biomass declined with higher
504 mean high water depth. In the coastal lagoon, stem density increased with greater drainage. With all other conditions
505 being equal, plant biomass of *S. alterniflora* has a parabolic relationship with elevation relative to mean sea level
506 (Morris et al. 2002). Above- and below an optimum elevation, biomass declines. Our study of marshes in different
507 geomorphic settings illustrates how environmental conditions in estuaries can illicit differential responses to individual
508 environmental parameters. In the coastal lagoon, a combination of less flooding and greater mineral sedimentation
509 rates promoted greater aboveground (and belowground) biomass. Lower tolerance to flooding in the coastal lagoon
510 marshes as compared to the coastal plain marshes is likely due to greater soil organic matter content, lower redox
511 potential, lower mineral sediment and nutrient availability, and higher sulfide concentrations (Bradley and Morris
512 1990; Reddy and DeLaune 2008). Because aboveground biomass was strongly associated with labile C accumulation
513 in marshes across the two estuaries, flooding dynamics and aboveground plant responses ultimately influenced labile
514 C accumulation.

515
516 Belowground biomass contributes directly to soil organic matter and, in this study, was a good predictor of soil C
517 accumulation rates, but only in the coastal lagoon marshes. This indicates that as geomorphic conditions change such
518 as with an increase in mineral sedimentation rates, belowground biomass can become uncoupled to soil C
519 accumulation and accretion rates. In the coastal lagoon marshes, live roots and rhizomes were concentrated in the top

520 30 cm depths, likely associated with a combination of high water table and high soil organic matter leading to low
521 redox potentials and high sulfide concentrations at depth (DeLaune et al. 1983b; Saunders et al. 2006). In contrast, in
522 the coastal plain estuary, live rooting depths were variable but often extending to 40 – 50 cm depth. Greater neap tide
523 drainage (data not shown), and lower soil organic matter throughout the soil depth profile and higher redox potentials
524 likely account for the lower live rooting depths. Across the coastal lagoon marshes, labile C accumulation rate
525 increased as live belowground biomass increased. Fine biomass had a positive relationship with the rate of refractory
526 C accumulation, and refractory C density was relatively high just below the marsh surface. Both of these live and fine
527 biomass components, therefore, were positively related to the total C accumulation rate. Accretion in these marshes
528 was positively associated with the live and dead coarse biomass, likely due to the high porosity associated with stem
529 bases, rhizomes, macroorganic matter, and surrounding soil. In the coastal plain estuary, C accumulation and accretion
530 rates were not significantly related to belowground biomass. It may have been presumed that marshes with higher
531 tidal ranges and higher rates of mineral sedimentation would have greater stocks of belowground biomass. In these
532 marshes, mineral sediment accumulation rates ranged from less than 500 to over 4000 g/m²/yr, yet belowground
533 biomass did not vary much along this gradient. At similar rates of mineral sedimentation, belowground live coarse
534 biomass was over 1000 g/m² lower in marshes of the coastal plain estuary as compared to the coastal lagoon, despite
535 a greater live rooting depth. This may be associated with higher soil redox potentials and a lower requirement for
536 rhizome photosynthate storage (Gallagher and Kibby 1981) in the coastal plain marshes. High belowground biomass
537 is typically found in marsh areas with lower redox potential (Gallagher and Plumley 1979; Dame and Kenny 1986 and
538 references therein). This is hypothesized to be due to greater investment in belowground production (Hopkinson and
539 Schubauer 1984) and less photosynthate transfer from underground rhizomes throughout the year, which results in
540 lower aboveground biomass and higher belowground biomass in short-form interior populations of *S. alterniflora* than
541 tall-form populations growing along creekbank (Gallagher and Kibby 1981). Differences among estuarine settings
542 and soil organic matter contents may also drive spatial patterns in belowground biomass and allocation. At higher
543 sedimentation rates found in the coastal plain estuary, fine belowground biomass, which was a significant predictor
544 of refractory C accumulation in the coastal lagoon, declined significantly. In the marsh with the highest rates of
545 mineral sedimentation, and labile and total organic C accumulation (MR), the lower quantity of fine biomass may be
546 due to a shorter time period allowed for growth and accumulation. The labile nature of fine biomass here suggests
547 preservation of labile fractions of fine biomass. With relatively low total belowground biomass, burial and small
548 particle (< 1 mm) accumulation support high C accumulation and accretion rates. The mechanism of fine organic
549 matter loss or limited input with greater mineral sedimentation rates is unclear, particularly when these marshes have
550 the highest rates of labile and total organic C accumulation in our study (Unger et al., 2016). In marshes with the
551 highest rates of C accumulation, labile C density, in particular, remained high when biomass stocks were low. High
552 accumulation rates in marshes with low biomass seem to be maintained by a combination of high live root biomass at
553 depth, high allochthonous C deposition, effective preservation of labile C, and high burial rates.

554

555 Our findings also provided insight as to the relative inputs of local plant-derived versus non-plant derived (e.g.,
556 edaphic algae) and allochthonous C to the labile and refractory C pools. We found significant relationships between

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

580
581 Geomorphology played a large role in influencing the relative importance and contribution of plant biomass to soil C
582 and marsh accretion rate. Geomorphic conditions of high sediment availability and larger tidal range, which can
583 mobilize and distribute sediments in the main channel and creeks of the coastal plain estuary work in concert to
584 promote C accumulation and accretion. Estuarine dynamics in the coastal lagoon are characterized by localized
585 sediment supplies and limited tidal energy to resuspend, transport and deposit sediments, and therefore, the marshes
586 are highly dependent on organic matter production for accretion. Within this system, a high sediment supply and high
587 elevation promoted a positive feedback between above- and belowground biomass and elevation. Because of localized
588 sediment supplies (e.g., CC) and other geomorphic differences, there was no correlation between hydrology and
589 longer-term sedimentation rates even over longer time periods (present study, Boyd et al. 2017). Importantly, while
590 studies suggest the vulnerability of microtidal marshes in coastal lagoons (Reed et al., 2008; Kirwan & Guntenspergen
591 2010; Ganju et al., 2017), we illustrate the importance of localized sources of sediments as being the key to their
592 survival through the positive feedback on live and dead coarse and fine root biomass, and organic matter and C
593 accumulation rates. Continuous standing water, enlargement of interior ponds, and loss of aboveground vegetation

594 are all signs of marsh deterioration. At IB, two of the sampling locations had permanent shallow water between ditches
595 and had lost the aboveground biomass. The remnants of former vegetation was evident belowground, where
596 significant quantities of live stem bases, roots and rhizomes were present to below 28 cm depth at least three years
597 after aboveground biomass was permanently lost.

598
599 Our dataset allows for a comparison of dynamics between individual marshes to highlight important geomorphic
600 effects on plant biomass. RC in Barnegat Bay and DN in Delaware Bay experienced comparable hydrology and
601 salinity in the marsh interior (Table 1). Yet, estuarine tidal range averaged approximately 0.3 m and 1.5 m, in RC
602 and DN respectively (USGS gage 01408167 and 01411435, respectively) and longer-term rates of mineral
603 sedimentation were an order of magnitude larger, and soil bulk density was three times greater in DN than in RC
604 (Boyd et al., 2017; Unger et al., 2016). So, despite a similar hydrology in the marsh interior, tidal range in the estuary
605 and creeks and sediment supply were much greater in DN than in RC. Aboveground biomass averaged two times
606 higher in DN than RC. Belowground live coarse biomass averaged 2456 and 721 g/m² in DN and RC, respectively
607 and dead coarse biomass averaged 1063 and 280 g/m² in DN and RC, respectively. Live rooting depth was also
608 significantly greater in DN (46 cm) as compared to RC (19 cm). In contrast, CC and DV, two of highest elevation
609 marshes in the two estuaries. CC was in Barnegat Bay and DV was in Delaware Bay. Overall, many of the hydrologic
610 parameters were comparable. Salinity, however, was significantly higher at CC than DV, but soil organic matter, bulk
611 density and mineral sedimentation rate did not significantly differ. With both hydrology and sedimentation rates being
612 within range of each other, these two marshes in very different geomorphic settings had comparable biomass and
613 organic C accumulation rates. Biomass profiles were also similar between marshes with the exception of greater fine
614 organic matter in CC, particularly between 4 and 20 cm depth.

615

616 **4.6 Conclusions**

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

631
632
633
634
635
636
637
638
639
640
641
642
643

Acknowledgements We would like to thank M. Archer, P. Zelanko, L. Zaoudeh, M. Schafer, M. Mills, M. Brannin, and B. Boyd for help in the field and lab. We would also like to thank all of the Mid-Atlantic Coastal Wetland Assessment partners including D. Kreeger, M. Maxwell-Doyle, D.J. Velinsky, A. Padaletti et al., . This research was largely funded by NJ SeaGrant / NOAA Grant #6210-0011. Surface accretion data were funded by EPA Region 2 Wetland Program Development Grant CD-97225909. We appreciate the thorough and constructive comments from three anonymous reviewers, which helped to improve the manuscript.

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

644 **References**

- 645 Benner, R., Moran, M. A., and Hodson, R. E.: Biogeochemical cycling of lignocellulosic carbon in marine and
646 freshwater ecosystems: relative contributions of procaryotes and eucaryotes. *Limnol. Oceanogr.* 31, 89-100, 1986
647
- 648 Benner, R., Fogel, M. L. and Sprague, E. K.: Diagenesis of belowground biomass of *Spartina alterniflora* in salt-
649 marsh sediments. *Limnol. Oceanogr.* 36, 1358–1374, 1991.
650
- 651 Blum, L. K.: *Spartina alterniflora* root dynamics in a Virginia marsh. *Mar. Ecol. Prog. Ser.*, 102, 169-178, 1993.
652
- 653 Boyd, B., Sommerfield, C. K., and Elsey-Quirk, T.: Hydrogeomorphic influences on salt marsh sediment
654 accumulation and accretion in two estuaries of the U.S. Mid-Atlantic coast. *Mar. Geol.*, 383, 132-145, 2017.
655
- 656 Bradley, P. M. and Morris, J. T.: Influence of oxygen and sulfide concentration on nitrogen uptake kinetics in *Spartina*
657 *alterniflora*. *Ecology* 71, 282-287, 1990.
658
- 659 Chmura, G. L., Anisfeld, S. C., Cahoon, D. R, and Lynch, J. C.: Global carbon sequestration in tidal, saline wetlands.
660 *Global Biogeochem. Cycles* 4, 1-12, 2003.
661
- 662 Connor, R. F., Chmura, G. L., and Beecher, C. B.: Carbon accumulation in Bay of Fundy salt marshes: implications
663 for restoration of reclaimed marshes. *Global Biogeochem. Cycles* 0, 1-12, 2001.
664
- 665 Craft, C. S.: Freshwater input structures soil properties, vertical accretion and nutrient accumulation of Georgia and
666 U.S. tidal marshes. *Limnol. Oceanogr.* 52, 1220-1230, 2007.
667
- 668 Dame, R.F. and Kenny, P.D.: Variability of *Spartina alterniflora* primary production in the euhaline North Inlet
669 estuary. *Mar. Ecol. Prog. Ser.* 32, 71-80, 1986.
670
- 671 Defne, Z., and Ganju, N. K.: Quantifying the residence time and flushing characteristics of a shallow, back-barrier
672 estuary: application of hydrodynamic and particle tracking models. *Estuar. Coasts* DOI 10.1007/s12237-014-9885-3,
673 2014.
674
- 675 DeLaune, R. D., Buresh, R. J., and Patrick, Jr W. H.: Relationship of soil properties to standing crop biomass of
676 *Spartina alterniflora* in a Louisiana salt marsh. *Estuar. Coastal Shelf Sci.* 8, 477-487, 1979.
677
- 678 DeLaune, R. D., Baumann, R. H., and Gosselink, J. G.: Relationships among vertical accretion, coastal submergence,
679 and erosion in a Louisiana Gulf coast salt marsh. *J. Sed. Pet.* 53, 147-157, 1983a.
680
- 681 DeLaune, R. D., Smith, C. J. and Patrick, W. H.: Relationship of marsh elevation, redox potential, and sulfide to
682 *Spartina alterniflora* productivity. *Soil Sci. Soc. Am. J.* 47:930-935, 1983b.
683 doi:10.2136/sssaj1983.03615995004700050018x
684
- 685 DeLaune, R. D., Pezeshki, S. R., Pardue, J. H, Whitcomb, J. H., and Patrick, Jr W. H.: Some influences of sediment
686 addition to a deteriorating salt marsh in the Mississippi River Deltaic Plain: a pilot study. *J. Coastal Res.* 6, 181-188,
687 1990.
688
- 689 DeLaune, R. D., Jugsujinda, A., Peterson, G. W., and Patrick, W. H.: Impact of Mississippi River freshwater
690 reintroduction on enhancing marsh accretionary processes in a Louisiana estuary. *Estuar. Coast. Shelf Sci.* 58:653-
691 662, 2003
692
- 693 Elsey-Quirk, T.: Impact of Hurricane Sandy on salt marshes of New Jersey. *Estuar. Coast, Shelf Sci.* 183, 235-248,
694 2016.
695

696 Gallagher, J. L. and Plumley, F.: Underground biomass profiles and productivity in Atlantic coastal marshes. *Am. J.*
697 *Bot.* 66, 156-161, 1979.
698

699 Gallagher, J.L. and Kibby, H.V.: The Streamside effect in a *Carex lyngbyei* estuarine marsh: the possible role of
700 recoverable underground reserves. *Estuar. Coastal Shelf Sci.* 12, 451-460, 1981.
701

702 Ganju, N. K., Defne, Z., Kirwan, M. L., Fagherazzi, S., D'Alpaos, A., and Carniello, L.: Spatially integrative metrics
703 reveal hidden vulnerability of microtidal salt marshes. *Nature Comm.*, doi: 10.1038/ncomms14156, 2017.
704

705 Graham, S. A. and Mendelssohn, I. A.: Contrasting effects of nutrient enrichment on below-ground biomass in coastal
706 wetlands. *J. Ecol.* 104, 249-260, 2016.
707

708 Gross, M. F., Hardisky, M. A. and Klemas, V.: Inter-annual spatial variability in the response of *Spartina alterniflora*
709 biomass to amount of precipitation. *J. Coast. Res.* 6, 949-960, 1990.
710

711 Hackney, C. T.: Factors affecting accumulation or loss of macroorganic matter in salt marsh sediments. *Ecology* 68,
712 1109–1113, 1987.
713

714 Hackney, C. T. and de la Cruz, A. A.: In situ decomposition of roots and rhizomes of two tidal marsh plants. *Ecology*
715 61, 226-231, 1980.
716

717 Haslett, S. K., Cundy, A. B., Davies, C. F. C., Powell, E. S., and Croudace, I. W.: Salt marsh sedimentation over the
718 past c. 120 years along the West Cotentin coast of Normandy (France): relationship to sea-level rise and sediment
719 supply. *J. Coast. Res.* 19, 609-620, 2003.
720

721 Hopkinson, C. S. and Schubauer, J. P.: Static and dynamic aspects of nitrogen cycling in the salt marsh graminoid,
722 *Spartina alterniflora*. *Ecology* 65, 961-969, 1984.
723

724 Hodson, R. E., Christian, R. R., and Maccubbin, A. E.: Lignocellulose and lignin in the salt marsh grass *Spartina*
725 *alterniflora*: initial concentrations and short-term, post-depositional changes in detrital matter. *Mar. Biol.* 81, 1-7,
726 1984.
727

728 Howes, B. L., Dacey, J. W. H. and Teal, J. M.: Annual carbon mineralization and belowground production of *Spartina*
729 *alterniflora* in a New England salt marsh. *Ecology* 66, 595-605, 1985
730

731 JMP Version 12.1. SAS Institute Inc., Cary, NC, 1989-2017
732

733 Kelleway J. J., Saintilan N., Macreadie P. I. and Ralph P. J. Sedimentary factors are key predictors of carbon storage
734 in SE Australian saltmarshes. *Ecosystems* 19, 865-880, 2016. doi: 10.1007/s10021-016-9972-3
735

736 Kennish, M. J.: Physical description of the Barnegat Bay—Little Egg Harbor estuarine system. *Journal of Coast. Res.*
737 *SI* 32, 13–27, 2001.
738

739 Kirwan, M. L., and Guntenspergen, G. R.: Influence of tidal range on the stability of coastal marshland. *J Geophys*
740 *Res* 115, F02009, 2010. doi: 10.1029/2009JF001400.
741

742 Kirwan, M. L., Langley, J. A., Guntenspergen, G. R., and Megonigal, J. P.: The impact of sea-level rise on organic
743 matter decay rates in Chesapeake Bay brackish tidal marshes. *Biogeosciences* 10, 1869-1976, 2013.
744

745 Kirwan, M. L. and Megonigal, J. P.: Tidal wetland stability in the face of human impacts and sea-level rise. *Nature*
746 504, 53-60, 2013.
747

748 Kirwan, M. L. and Guntenspergen, G. R.: Feedbacks between inundation, root production, and shoot growth in a
749 rapidly submerging brackish marsh, *J. Ecol.* 100, 764-770, 2012.

750 Knops J. M. H., Naeemw S, Reich PB (2007) The impact of elevated CO₂, increased nitrogen availability and
751 biodiversity on plant tissue quality and decomposition. *Global Change Biol.* 13, 1960–1971.

752 Kögel-Knabner, I., Guggenberger, G., Kleber, M., Kandeler, E., Kalbitz, K., Scheu, S., Eusterhues, K. and
753 Leinweber, P. (2008), Organo-mineral associations in temperate soils: Integrating biology, mineralogy, and organic
754 matter chemistry. *Z. Pflanzenernähr. Bodenk.*, 171: 61–82. doi:10.1002/jpln.200700048

755 Leonard, L. A., and Luther, M. E.: Flow hydrodynamics in tidal marsh canopies, *Limnol. Oceanogr.*, 40, 1474–1484,
756 1995
757

758 Macreadie PI, Ollivier QR, Kelleway JJ, et al. Carbon sequestration by Australian tidal marshes. *Scientific Reports*.
759 7, 44071, 2017. doi:10.1038/srep44071.
760

761 McKee, K. L., Cahoon, D. R. and Feller, I. C.: Caribbean mangroves adjust to rising sea level through biotic controls
762 on change in soil elevation. *Global Ecol. Biogeogr.* 16, 545-556, 2007.
763

764 McLeod, E., Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M., Lovelock, C.E., Schlesinger, W.H.,
765 Silliman, B.R., 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal
766 habitats in sequestering CO₂. *Frontiers in the Ecology and the Environment* 9, 552-560.
767

768 Mendelsohn, I. A., McKee, K. L., and Patrick Jr, W. H.: Oxygen deficiency in *Spartina alterniflora* roots: metabolic
769 adaptation to anoxia. *Science* 214, 439-441, 1981.
770

771 Mendelsohn, I. A. and Kuhn, N. L.: Sediment subsidy: effects on soil-plant response in a rapidly submerging coastal
772 salt marsh. *Ecol. Eng.* 21, 115-128, 2003.
773

774 Moran, M. A. and Hodson, R. E.: Contributions of degrading *Spartina alterniflora* lignocellulose to the dissolved
775 organic carbon pool of a salt marsh. *Mar. Ecol. Prog. Ser.*, 62, 161-168, 1990.
776

777 Morris, J. T., and Bowden, W. B.: A Mechanistic, Numerical Model of Sedimentation, Mineralization, and
778 Decomposition for Marsh Sediments I. *Soil Sci. Soc. Am. J.* 50:96-105, 1986.
779 doi:10.2136/sssaj1986.03615995005000010019x
780

781 Morris, J. T., and P. M. Bradley (1999), Effects of nutrient loading on the carbon balance of coastal wetland
782 sediments, *Limnol. Oceanogr.*, 44, 699–702.
783

784 Morris, J.T., Sundareshwar, P.V., Nietch, C.T., Kjerfve, B., and Cahoon, D. R.: Responses of coastal wetlands to
785 rising sea level. *Ecology* 83, 2869-2877, 2002.
786

787 Morris JT, Barber DC, Callaway JC, Chambers R, Hagen SC, Hopkinson CS, Johnson BJ, Megonigal P, Neubauer
788 SC, Troxler T, Wigand C: Contributions of organic and inorganic matter to sediment volume and accretion in tidal
789 wetlands at steady state. *Earth's Future* 4:1–12, 2016
790

791 Mudd SM, D'Alpaos A, Morris JT. 2010. How does vegetation affect sedimentation on tidal marshes? Investigating
792 particle capture and hydrodynamic controls on biologically mediated sedimentation. *Journal of Geophysical Research*
793 115: F03029. DOI:[10.1029/2009JF001566](https://doi.org/10.1029/2009JF001566).
794

795 Mueller, P., Jensen, K., Megonigal, J. P.: Plants mediate soil organic matter decomposition in response to sea level
796 rise. *Global Change Biol.* 22, 404-414, 2016
797

798 Nyman, J. A., Walters, R. J., DeLaune, R. D., and Patrick, Jr., W. H.: Marsh vertical accretion via vegetative growth.
799 *Est. Coast. Shelf Sci.*: 370-380, 2006.
800

801 Ouyang, X., Lee, S.Y., 2014. Updated estimates of carbon accumulation rates in coastal marsh sediments.
802 *Biogeosciences* 11, 5057-5071.

803
804 Reddy, K.R., DeLaune, R.D., 2008. Biogeochemistry of Wetlands: Science and Applications. CRC Press, Boca Raton,
805 Florida.
806
807 Reed, D. J., Bishara, D., Cahoon, D., Donnelly, J., Kearney, M., Kolker, A., Leonard, L., Orson, R. A., Stevenson, J.
808 C.: Site-specific scenarios for wetlands accretion as sea level rises in the mid-Atlantic region. Section 2.1 in:
809 Background Documents Supporting Climate Change Science Program Synthesis and Assessment Product 4.1: Coastal
810 Elevations and Sensitivity to Sea Level Rise [Titus, J.G. and E.M. Strange (eds.)]. EPA 430R07004. U.S.
811 Environmental Protection Agency, Washington, DC, pp. 134-174, 2008.
812 <<http://epa.gov/climatechange/effects/coastal/background.html>>
813
814 Saintilan, N., Rogers, K., Mazumder, D., and Woodroffe, C.: Allochthonous and autochthonous contributions to C
815 accumulation and C store in southeastern Australian coastal wetlands. Est. Coast. Shelf Sci. 128: 84-93, 2013.
816
817 Saunders, C.J., Megonigal, J.P. & Reynolds, J.F. Plant Soil (2006) 280: 305. [https://doi.org/10.1007/s11104-005-](https://doi.org/10.1007/s11104-005-3275-3)
818 [3275-3](https://doi.org/10.1007/s11104-005-3275-3)
819
820 Schubauer, J. P. and Hopkinson, C. S.: Above- and belowground emergent macrophyte production and turnover in a
821 coastal marsh ecosystem, Georgia. Limnol. Oceanogr. 29, 1052 – 1065, 1984.
822
823 Stumpf, R. P.: The process of sedimentation on the surface of a salt-marsh, Estuarine Coastal Shelf Sci., 17, 495–508,
824 1983.
825
826 Teal, J. M.: Energy flow in the salt marsh ecosystem of Georgia. Ecol. 43, 614-624, 1962.
827
828 Teal, J. M. and Kanwisher, J.W.: 1966. Gas transport in the marsh grass, *Spartina alterniflora*. J. Exp. Bot. 17, 355-
829 361, 1966.
830
831 Turner, R. E., Swenson, E. M. and Milan, C. S.: Organic and inorganic contributions to vertical accretion in salt marsh
832 sediments, in Concepts and Controversies in Tidal Marsh Ecology, edited by M. P. Weinstein and D. A. Kreeger, pp.
833 583–595, Kluwer Academic Publishers, Berlin, Germany, 2000.
834
835 Unger, V., Elsey-Quirk, T., Sommerfield, C. and Velinsky, D. J.: Stability of organic C accumulating in *Spartina*
836 *alterniflora*-dominated marshes of the mid-Atlantic U.S.A. Estuar. Coastal Shelf Sci. 182: 179-189, 2016.
837

838
839
840

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). Parameter values across marshes represented 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 \pm 5 ^a	11 \pm 3 ^a	19 \pm 3 ^a	56 \pm 16 ^b	27 \pm 16 ^b	62 \pm 34 ^b
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
Tidal range (cm)	13.4 \pm 0.6 ^{bc}	7.2 \pm 0.5 ^{cd}	5.1 \pm 0.1 ^d	10.9 \pm 2.2 ^{bcd}	22.2 \pm 0.2 ^a	17.0 \pm 1.9 ^{ab}
Mean high water relative to marsh surface (cm)	12.6 \pm 1.2 ^{ab}	10.3 \pm 0.7 ^{bc}	-3.3 \pm 0.8 ^d	3.4 \pm 3.7 ^{cd}	21.2 \pm 1.8 ^a	15.6 \pm 1.2 ^{ab}
Mean water level relative to marsh surface (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 relative to marsh surface (cm)	-0.8 \pm 1.0 ^a	3.1 \pm 1.1 ^a	-8.5 \pm 0.7 ^b	-7.4 \pm 1.6 ^b	-1.0 \pm 2.0 ^a	-1.4 \pm 0.7 ^a
% time flooded	66 \pm 4 ^{ab}	86 \pm 1 ^a	6 \pm 1 ^c	11 \pm 4 ^c	40 \pm 1 ^b	68 \pm 5 ^{ab}
# flooding events/yr	304 \pm 21 ^{ab}	24 \pm 1 ^c	113 \pm 16 ^{bc}	205 \pm 51 ^{bc}	455 \pm 55 ^a	176 \pm 78 ^{bc}
Avg duration of flood (hr)	20 \pm 2 ^b	324 \pm 14 ^a	4 \pm 1 ^b	15 \pm 7 ^b	7 \pm 1 ^b	44 \pm 14 ^b
Salinity	20.6 \pm 0.1 ^{bc}	30.4 \pm 4.0 ^{ab}	38.8 \pm 0.8 ^a	17.1 \pm 1.0 ^c	7.4 \pm 1.0 ^c	13.5 \pm 2.1 ^c
Soil nitrogen (%)	1.6 \pm 0.2 ^a	1.5 \pm 0.1 ^a	0.8 \pm 0.1 ^b	0.7 \pm 0.2 ^b	0.5 \pm 0.1 ^b	0.5 \pm 0.1 ^b
Soil organic matter (%)	39.7 \pm 1.3 ^a	39.4 \pm 0.3 ^a	23.4 \pm 1.4 ^{ab}	32.4 \pm 9.1 ^a	14.1 \pm 0.8 ^b	27.8 \pm 5.5 ^{ab}
Soil bulk density (g/cm ³)	0.14 \pm 0.01 ^c	0.15 \pm 0.02 ^{bc}	0.29 \pm 0.01 ^{abc}	0.34 \pm 0.07 ^{ab}	0.52 \pm 0.04 ^a	0.39 \pm 0.03 ^a
Long-term mineral sedimentation rate (g/m ² /yr)*	147 \pm 22 ^d	168 \pm 19 ^{cd}	626 \pm 45 ^{bc}	1237 \pm 576 ^{ab}	4126 \pm 74 ^a	1568 \pm 279 ^{ab}

841

842
843
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

845

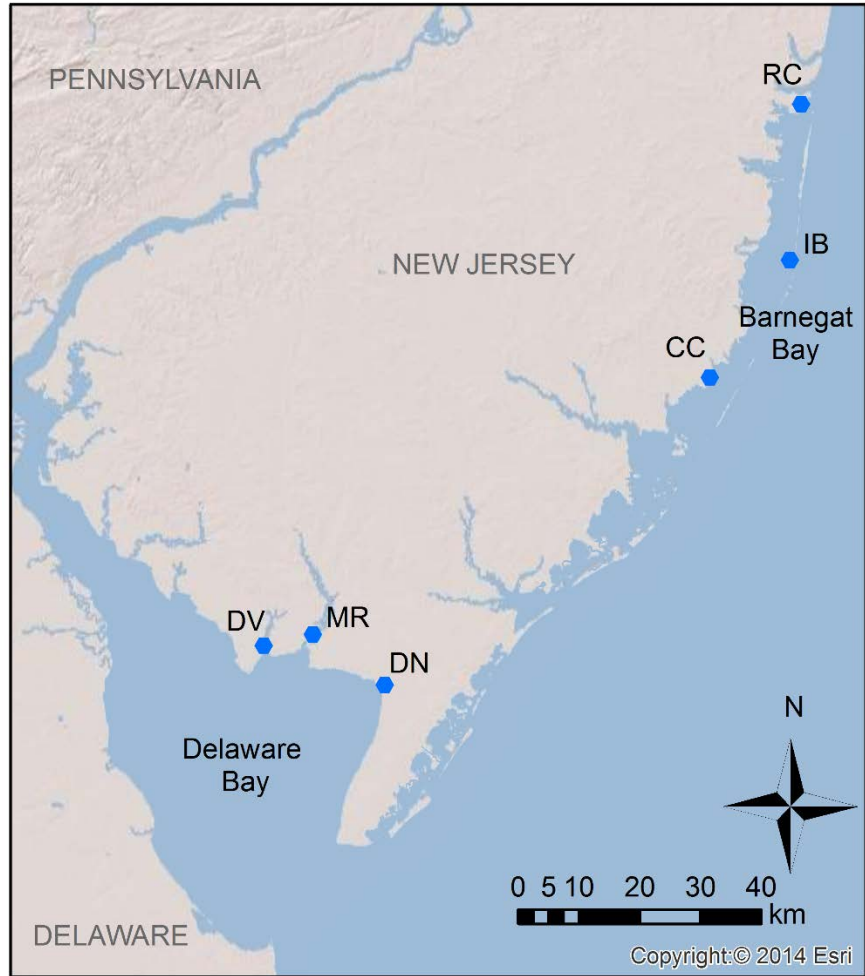
5

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**	<i>n.s.</i>	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	<i>n.s.</i>	ALL: 0.40**	live coarse and fine: 0.68**	live coarse and fine: 0.18*	fine: 0.42**	fine: 0.03*

* $p < 0.05$

** $p < 0.0001$

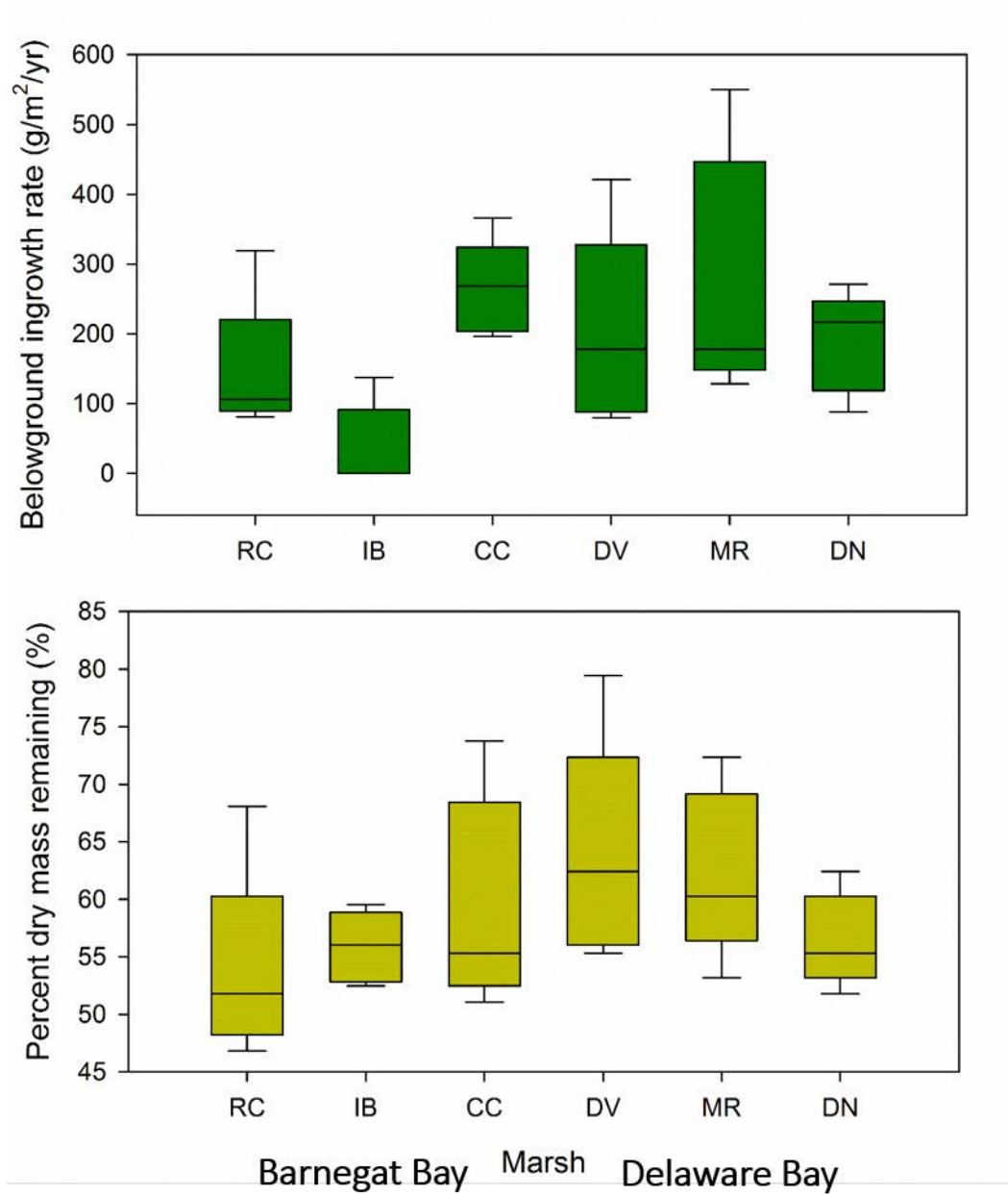


9

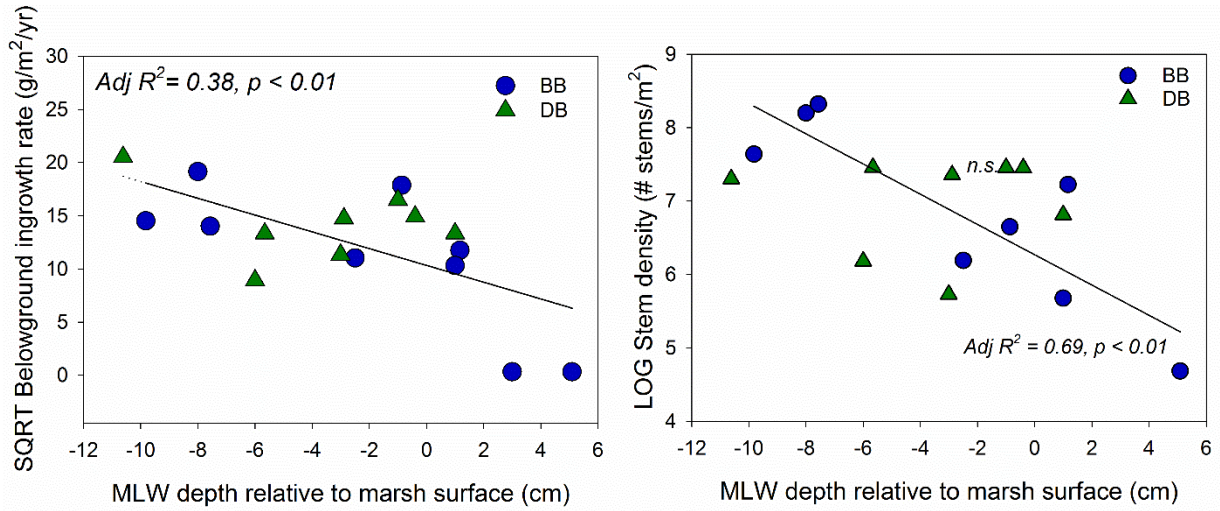
10

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

11
12

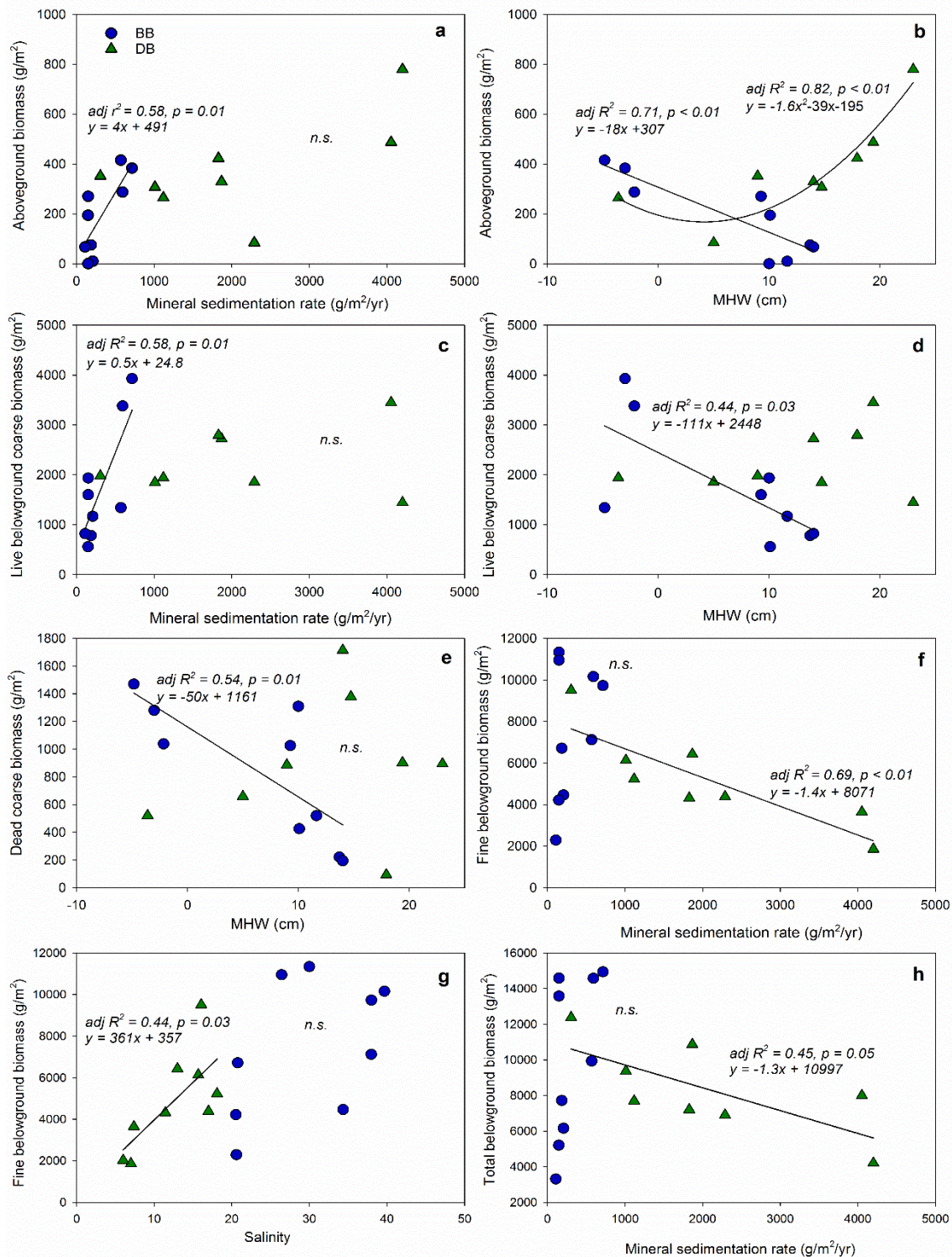


13
14 **Figure 2: Belowground ingrowth rate (upper) and percent mass remaining in belowground litterbags (lower)**
15 **over a 20 month period in salt marshes of two mid-Atlantic estuaries (n = 5, ± standard error).**
16
17

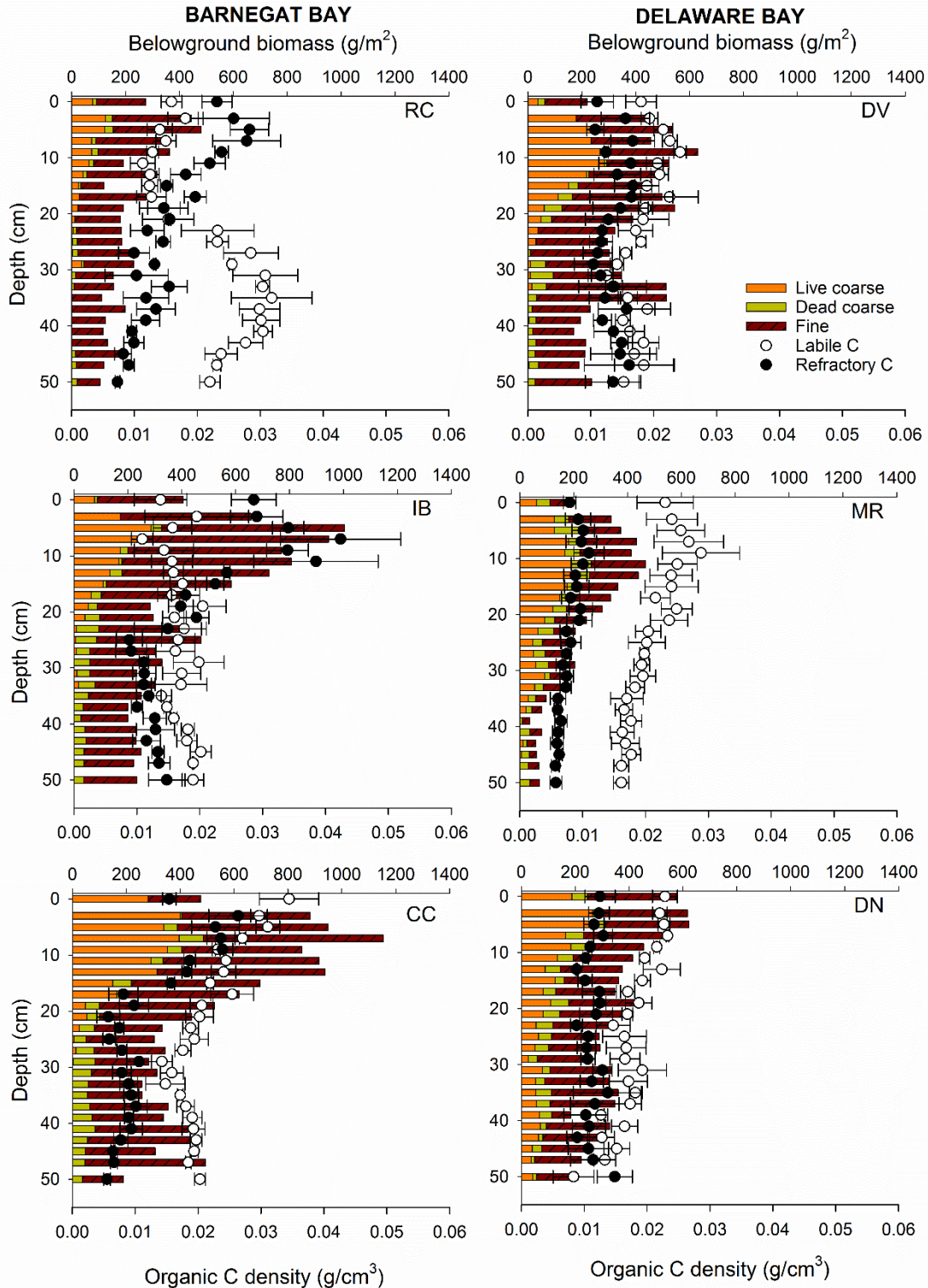


18
19

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.**

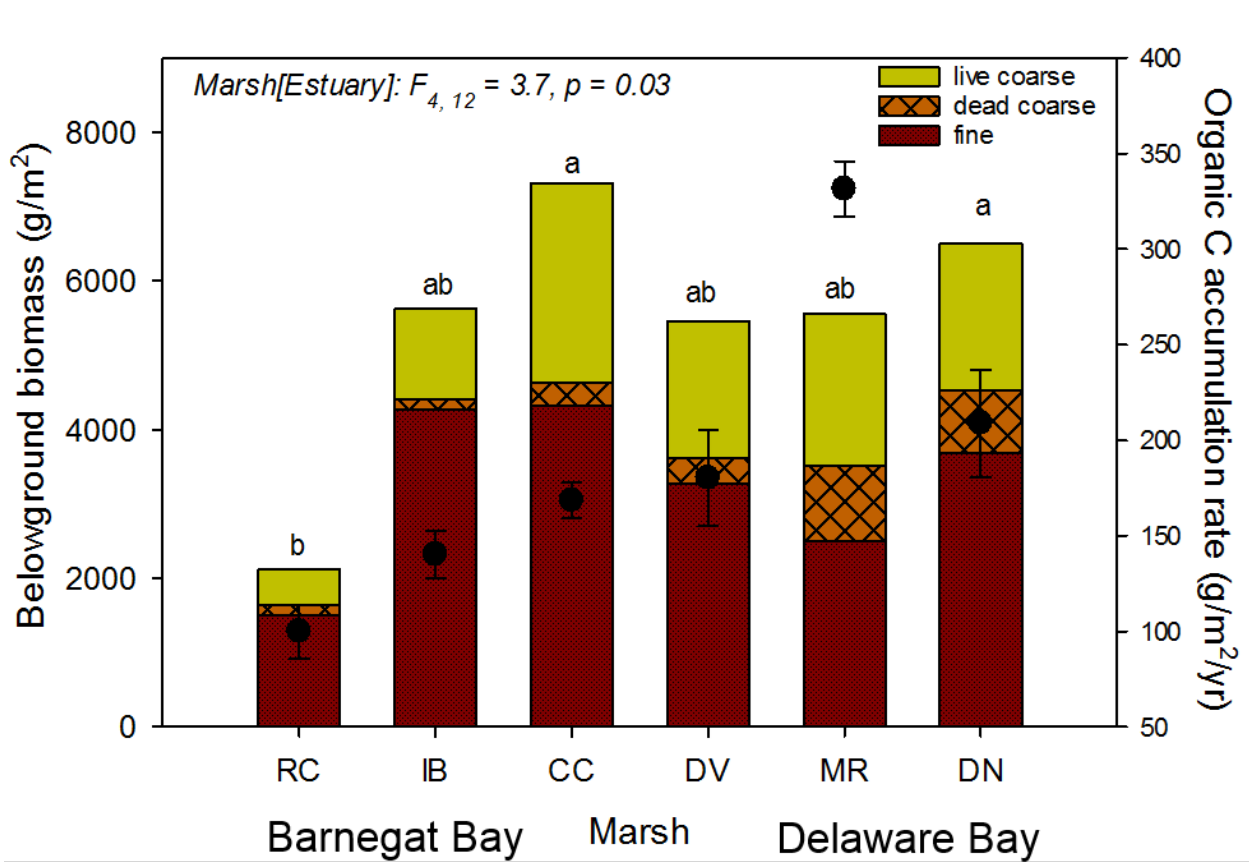


23
 24 **Figure 4: Relationships between vegetation structure and environmental parameters.** For these analyses,
 25 belowground biomass to 50-cm depth was used. Mineral sedimentation rates were calculated using ^{137}Cs -
 26 dating, and therefore, are average rates over the last 50 years (Boyd et al. 2017). Blue dots and green triangles
 27 refer to data collected in Barnegat Bay (BB) and Delaware Bay (DB), respectively, which were analysed
 28 separately. Both significant and non-significant (*n.s.*) relationships are shown.



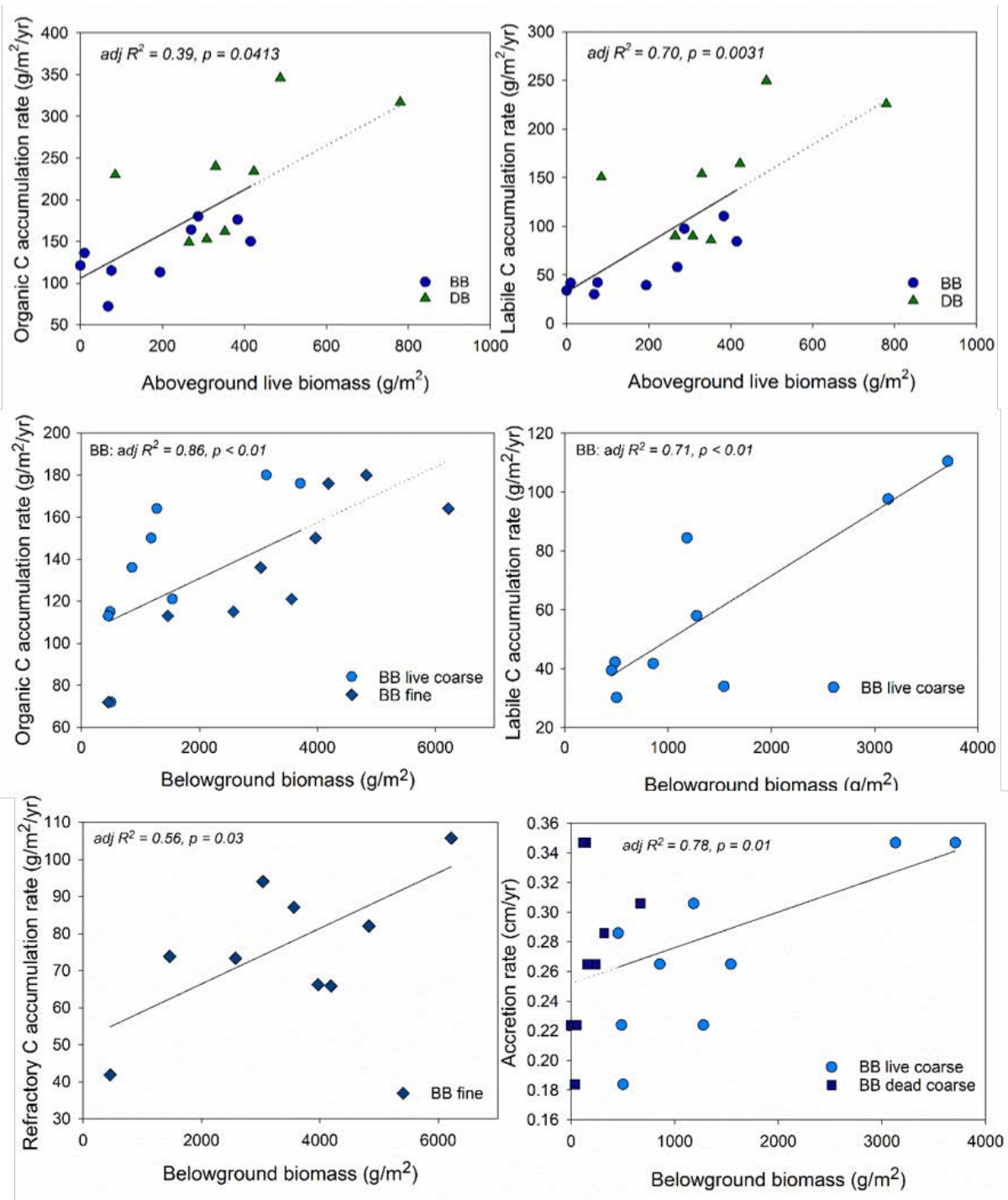
29
 30 **Figure 5: Belowground biomass and labile and refractory organic C density profiles in marshes of two Mid-**
 31 **Atlantic estuaries. Biomass data are means (standard errors not shown). C density data previously reported in**
 32 **Unger et al., 2016.**

33
34
35



36

37 **Figure 6:** Belowground biomass (scaled on left-axis) and organic C accumulation rate (scaled on right axis;
38 previously reported in Unger et al., 2016) in marshes of two Mid-Atlantic estuaries. Belowground biomass and
39 C accumulation are relative to the ¹³⁷Cs peak depth. Statistics for total belowground are shown and letters
40 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.

5

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									-0.85		0.78	0.75
	<0.0001									0.0004		0.0027	0.0046
LOGIT % time flooded		1.00	0.71	0.97	0.94			0.84					
		<0.0001	0.0089	<0.0001	<0.0001			0.0006					
MHW (cm)		0.71	1.00	0.83	0.74	0.85			-0.69				
		0.0089	<0.0001	<0.0001	0.0007	<0.0001			0.0409				
MWL (cm)		0.97	0.83	1.00	0.95			0.74					
		<0.0001	<0.0001	<0.0001	<0.0001			0.0007					
MLW (cm)		0.94	0.74	0.95	1.00			0.82					
		<0.0001	0.0007	<0.0001	<0.0001			<0.0001					
Tidal range (cm)			0.85			1.00	0.81		-0.87				
			<0.0001			<0.0001	<0.0001		0.0023				
# flooding events/yr						0.81	1.00		-0.68				
						<0.0001	<0.0001		0.0428				
LOG flood duration (hr)		0.84		0.74	0.82			1.00					
		0.0006		0.0007	<0.0001			<0.0001					
Salinity			-0.69			-0.87	-0.68		1.00				
			0.0409			0.0023	0.0428		<0.0001				
LOGIT soil N (%)	-0.85									1.00	0.74	-0.93	-0.96
	0.0004									<0.0001	0.0054	<0.0001	<0.0001
LOGIT soil organic matter (%)										0.74	1.00	-0.78	-0.84
										0.0054	<0.0001	0.0025	0.0005
Soil bulk density (g/cm ³)	0.78									-0.93	-0.78	1.00	0.94
	0.0027									<0.0001	0.0025	<0.0001	<0.0001
LOG mineral sedimentation rate (g/m ² /yr)	0.75									-0.96	-0.84	0.94	1.00
	0.0046									<0.0001	0.0005	<0.0001	<0.0001

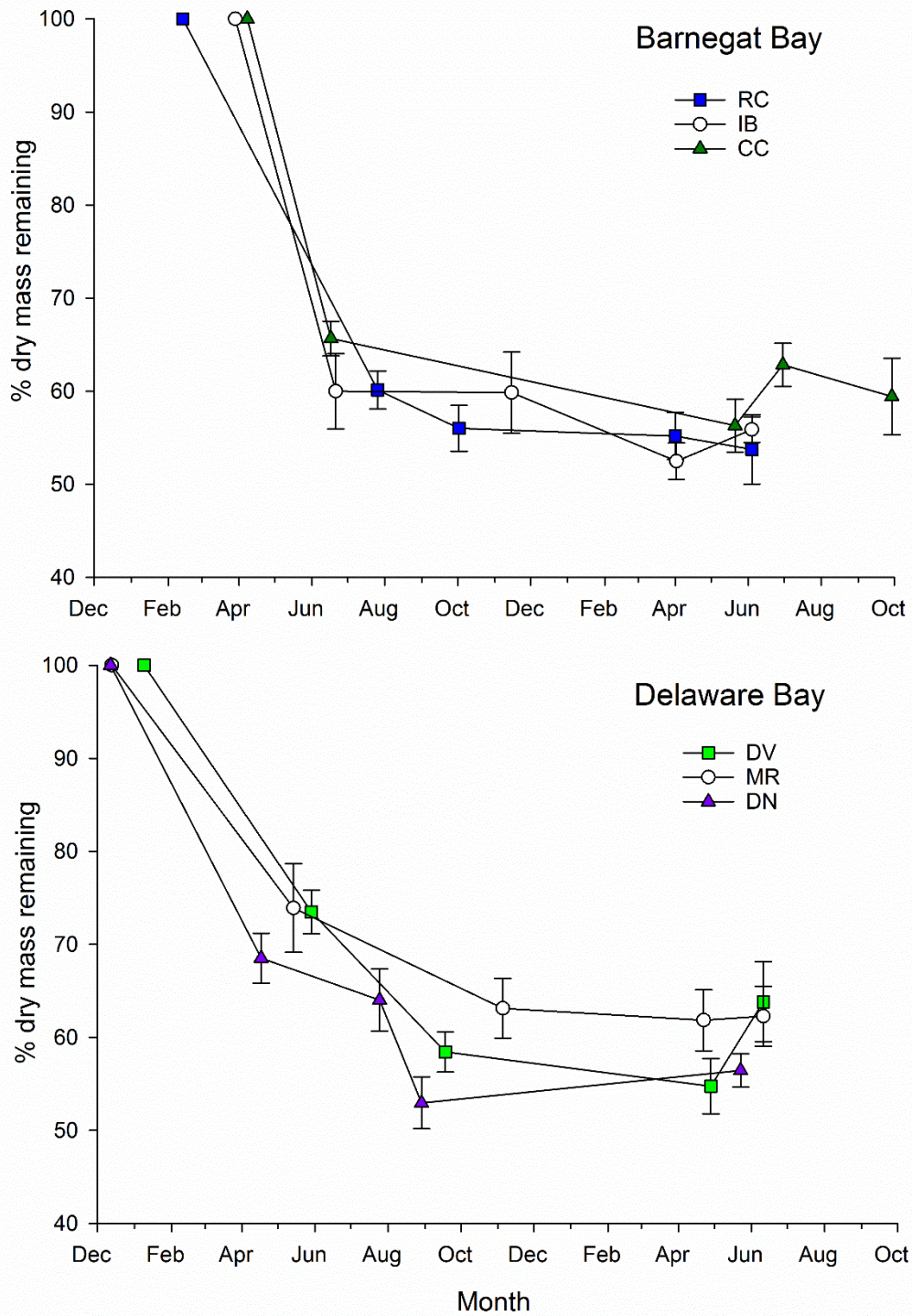


Figure A1. Mass loss from litterbags over time in three salt marshes in Barnegat Bay and three salt marshes in Delaware Bay from 2013 – 2014 (n = 5, ± standard error).

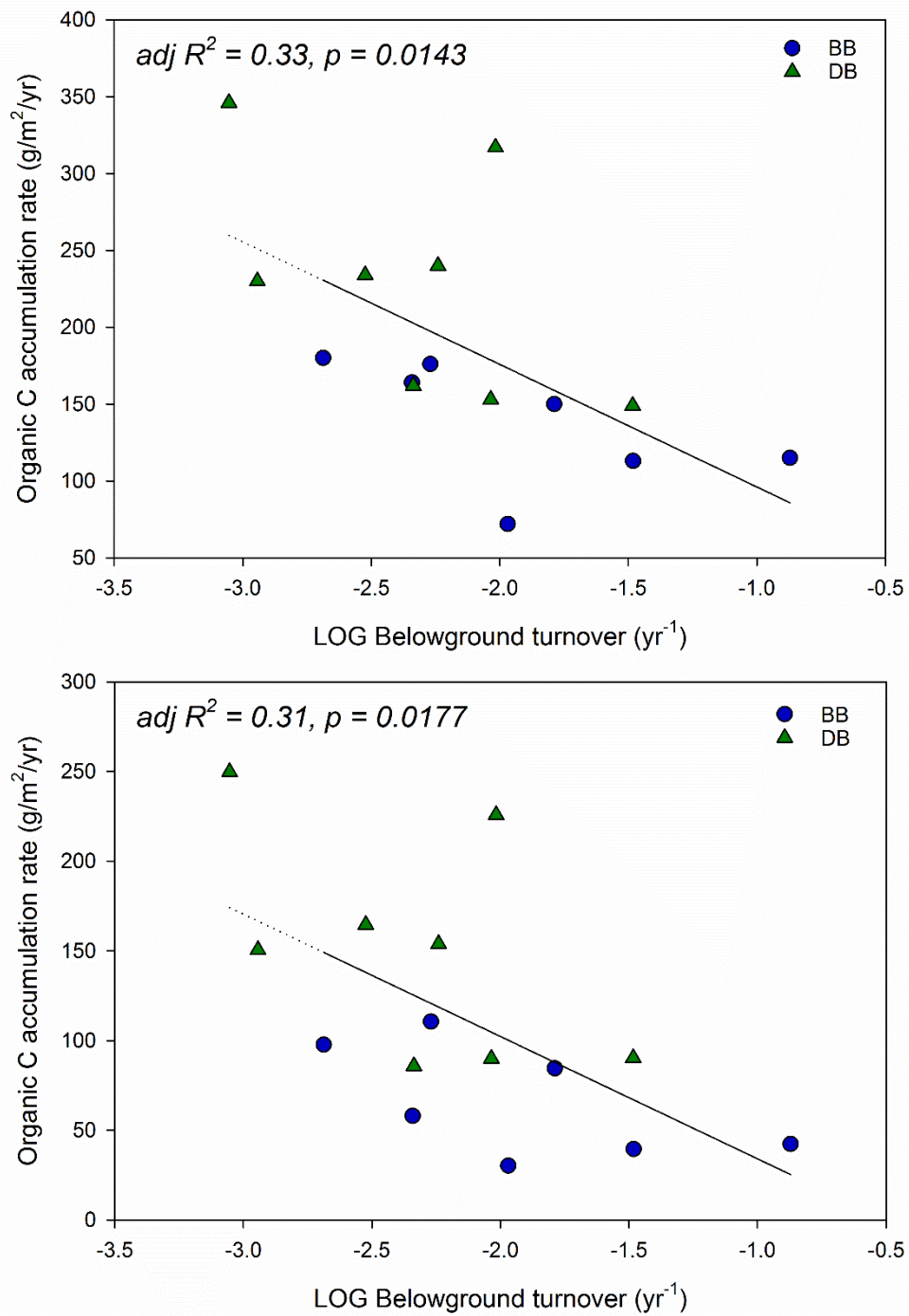


Figure A2. Relationship between belowground turnover and total organic and labile C accumulation rate for *Spartina alterniflora*-dominated marshes.